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Outer Continental Shelf Environmental Assessment Program

Final Reports of Principal Investigators

Volume 25

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OUTER CONTINENTAL SHELF
ENVIRONMENTAL ASSESSMENT PROGRAM

FINAL REPORTS OF PRINCIPAL INVESTIGATORS

VOLUME 25

OCTOBER 1984

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Outer Continental Shelf Environmental Assessment Program

Final Reports of Principal Investigators

VOLUME 25 OCTOBER 1984

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ICE EDGE ECOSYSTEM STUDY:
PRIMARY PRODUCTIVITY, NUTRIENT CYCLING, AND ORGANIC MATTER TRANSFER

by

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Final Report
Outer Continental Shelf Environmental Assessment Program
Research Unit 427

March 1979

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Although authorship of this final report is the responsibility of the principal investigators, credit must be given to the dedicated and excellent contributions by our collaborators, technical personnel and graduate student assistants. Dr. J. Niebauer assisted with the analysis and synthesis of many of the oceanographic observations, particularly those dealing with the physical oceanography. He wrote a significant portion of Chapter IV. Ms. Linda Schandelmeier was responsible for all phytoplankton enumeration and taxonomy as well as the cluster analysis work. She should be credited with primary authorship of Chapter II. Dr. Charles Geist served as statistical consultant and was responsible for the cluster analysis and analysis of variance models run for the studies of zooplankton and micronekton.

Much of the responsibility for supervising the physical and primary productivity-phytoplankton work on all the cruises was handled by Mr. David Brickell, who also contributed to the synthesis of information. However, in the final stages of the project, Mr. Tom Chapman handled all the final analyses and data organization and synthesis. Mr. Carl Tobin participated in cruises, and carried out the helicopter fieldwork from Nome in 1976 as well as the laboratory analyses resulting from this. Major credit for nutrient analyses goes to Ms. Cindy Mildbrand, Ms. Margaret Billington and Mr. Keith Mueller. Ms. Patricia Wager and Mr. Albert Adams were responsible for the zooplankton taxonomy. Mr. Ken Coyle supervised and participated in much of the fieldwork as well as identifying micronekton in the laboratory. Mr. Lee Niemark and Ms. Liz Clarke assisted aboard ship and at remote field stations while completing theses related to some of the specific aspects of the overall study. Without the very able assistance of these associates the work could not have been completed.

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CHAPTER I

INTRODUCTION, OBJECTIVES AND STRATEGY

This report is the final synthesis of work carried out over a four year period, from 1975 to 1978, of which the first three years were primarily field efforts, and the final year was spent in analysis, synthesis and interpretation. The study focused on the role of the ice edge ecosystem in the southeast Bering Sea, emphasizing the planktonic components, in an attempt to determine the potential impact of commercial petroleum exploration and development in the St. George's Basin area. The rationale for emphasizing the ice edge rests in the observation that biologically this is an extremely productive zone which serves as a focal point for the congregation of large numbers of marine birds and mammals. It represents a critical habitat in this subpolar region. Furthermore, the ice edge is associated with an intense phytoplankton bloom each spring, and this accounts for a significant proportion of the total annual primary production in the southeast Bering Sea shelf. This high productivity at the lower trophic levels must in turn influence the survival of higher order consumers living on or in the ice, as well as in the water column or on the seabed below the ice. We know that the process of organic matter transfer is an exceedingly complex one, and dependent not only upon the kinds and amounts of plant cells present at any time, but also on the kinds and numbers of pelagic grazers available to utilize these cells. This trophic level interaction is further modified annually by differing weather patterns and periodic shifts in hydrography which alter the timing and sequence of important seasonal events and the relative position of the southern edge of the ice. We have reason to suppose that the coupling of the spring phytoplankton bloom at the ice edge to the grazing community may be "loose" at least over the central shelf, and that the bloom may develop in the absence of a strong grazing component in the system. This, when added to the high nutrient conditions, the sudden availability of light due to ice break-up and the relative stability of a shallow layer of surface water, triggers a bloom of extreme intensity. It is the nature of this production, its components and the relationship of the zooplankton communities on the shelf and the factors controlling their distribution that form the basis for the conclusions to be presented here. Since this report is written in several discrete sections, introductory material relevant to each section will be incorporated there. Therefore, no overall background on the current status of Bering Sea information is included here. The same applies to any method description - most of this has been presented earlier, and details will not generally be repeated in this synthesis report. Where essential, comments will be included in the chapters to follow.

Objectives

1. Assess the significance of the ice-edge region in the productivity of the potential lease areas by studying the dynamics and mechanisms regulating the phytoplankton populations.
2. Determine the temporal and spatial density distributions and environmental requirements of the principal species of zooplankton, micronekton and ichthyoplankton associated with the ice edge region.
3. Determine the transfer of organic matter between the phytoplankton and the grazing community and the factors controlling this transfer.
4. To analyze and interpret the information obtained in fulfilling Objectives 1, 2 and 3 in light of physical oceanographic and climatological considerations.
5. To identify sensitive ecological parameters and areas in the St. George's Basin area to serve as an information input for decision making. A conceptual model will be used to aid in this.

All oceanographic sampling was conducted from the NOAA ships *Discoverer*, *Miller Freeman* and *Surveyor* for a total of nine cruises from May 1975 until June 1977. Specific dates were:

1. *Discoverer*, Leg I - May 15 - May 30, 1975
2. *Discoverer*, Leg II - June 2 - June 9, 1975
3. *Discoverer*, Leg I - August 9 - August 28, 1975
4. *Miller Freeman*, Leg II - November 10 - November 26, 1975
5. *Surveyor*, Leg I - March 14 - April 2, 1976
6. *Surveyor*, Leg II - April 12 - April 30, 1976
7. *Surveyor*, Leg II - March 12 - April 7, 1977
8. *Surveyor*, Leg III - April 13 - May 2, 1977
9. *Discoverer*, Leg IV - May 20 - June 11, 1977

In addition, a UHIH helicopter flight was conducted from Nome during the first week of April, 1977.

CHAPTER II

A QUANTITATIVE STUDY OF THE PHYTOPLANKTON FROM THE EASTERN BERING SEA

INTRODUCTION

A large part of the Bering Sea is influenced by ice. The continental shelf area (about 45 percent of the total Bering Sea) is generally ice covered, November through May each year. During March and April ice cover reaches its maximum extent, covering nearly 75 percent of the Bering Sea area (McRoy and Goering, 1974). Previous investigators have shown that spring productivity near the ice edge is higher than that in the surrounding waters. It has been suggested that water column stratification resulting from low salinity ice melt water permits a bloom to develop in the surface layer at the ice edge (Marshall, 1957; McRoy and Goering, 1974). Konishi and Saito (1974) found that a stagnant frontal zone was always present at the southern edge of the ice. Alexander and Cooney (1978), and other workers have postulated that the ice adds stability to the water column and allows phytoplankton populations to increase rapidly.

The high phytoplankton biomass along the southeast shelf break and in the eastern Bering Sea supports large populations of birds and mammals. The productivity of the phytoplankton is highly seasonal and therefore understanding the timing of the bloom and the dynamics of species succession is important to understanding the productivity of the entire ecosystem. In addition, the phytoplankton associated with the ice edge appear to be biologically unique.

We used numerical analysis techniques to analysis phytoplankton species composition in the Bering Sea with particular emphasis on the ice edge ecosystem. These techniques have been used by botanists with some success in recent years. Williams and Lambert (1959), McConnaughey (1964), Ducker, Williams and Lance (1965), Pritchard and Anderson (1971), Thorrington-Smith

(1971), Reid *et al.* (1978) and others have used various techniques of multivariate analysis in studies of plant communities.

PREVIOUS INVESTIGATIONS

There have been numerous studies of the phytoplankton in the Bering Sea or in adjacent waters. Phytoplankton studies in the Bering Sea are summarized in Table II-1. Until recently most investigators collected qualitative data, sampling by vertical net hauls extending to the surface from below the thermocline or the euphotic zone, or by collecting surface water and filtering the samples through fine silk bolting cloth (Allen, 1927, 1929; Cupp, 1937; Motoda and Kawarada, 1955; Karohji, 1959, 1972). Other techniques have included centrifuging or simply settling of the samples (Phifer, 1934; Marumo, 1954; Kawarada, 1957; Ohwada and Kon, 1963).

Allen (1927, 1929, 1930); Cupp (1937, 1943); and Phifer (1934) studied phytoplankton populations in the coastal waters of the Bering Sea near the Aleutian Islands and in the Gulf of Alaska. Their studies dealt primarily with the seasonal distribution and occurrence of phytoplankton. Cupp (1937) delineated the pattern of diatom succession at Scotch Cape (southern point of Unimak Island, Aleutian Islands). *Biddulphia aurita* appeared early and reached its maximum abundance usually in April. Then various species of *Thalassiosira,* particularly *Thalassiosira nordenskioldii*, and *Chaetoceros socialis* occurred in maximum numbers during April and May. In some years *Chaetoceros debilis* reached its maximum densities in April and May but usually it followed *Thalassiosira nordenskioldii* and became dominant in June or July. *Leptocylindrus danicus* became important in July and *Asterionella japonica* in September, October or early November.

TABLE II-1

PREVIOUS INVESTIGATIONS IN THE BERING SEA, SELECTED STUDIES

Investigators	Area	Dominant Species	Date	Method	Cells/liter
Allen (1927)	Unimak Island	*Chaetoceros debilis, C. scolopendra, Thalasiosira nordenskioldii*	May 1923	Surface water filtered through silk bolting cloth	
Allen (1929)	Unimak Island	*Chaetoceros debilis, Skeletonema costatum*	April 1924 August 1924		
Aikawa (1932)	Bering Sea	*Chaetoceros atlanticus, C. criphilum, Corethron hystrix, Rhizosolenia alata, R. hebetata f. semispina, R. hebetata f. hiemalis, Thalassiothrix longissima*	July, August 1928		
Phifer (1934)	Bering Sea, Bering Strait	*Denticula seminae, Stephanopyxis nipponica*	July 26, Aug. 1934	centrifugation and settling	
Cupp (1937)	Scotch Cap, southern pt. of Unimak Island	*Biddulphia aurita, Thalassiosira* spp. especially *T. nordenskioldii, Chaetoceros socialis, C. debilis Leptocylindrus danicus, Asterionella japonica*	April Ap-May or June-July July, Sept. or early Nov.		
Motoda and Kawarada (1955)	Aleutian waters	*Chaetoceros* spp. *Corethron hystrix, Denticula* sp. *Nitzschia seriata, Rhizosolenia hebetata f. semispina*			1X10^5 to 1X10^7cells/m^3
Marumo (1956)	S. of Kamchatka Peninsula	*Chataceros convolutus, C. debilis, Corethron hystrix, Denticula* sp., *Nitzschia seriata*		centrifugation and settling	
Kawarada (1957)	Bering Sea	*Chaetoceros convolutus, C. compressus, C. debilis, C. radicans, C. constrictus, Nitzschia closterium, N. delicatissima, N. longissima, N. seriata, Rhizosolenia hebetata f. semispina*		centrifugation and settling	10^3 to 10^4min 10^6 max cells/liter
Kawarada and	Bering Sea	*Thalassiosira*, some *Chaetoceros, Chaetoceros* spp. *Corethron hystrix, Coscinodiscus oculus-iridis, Denticula* sp. *Thalassiosira decipiens*	April, May	centrifugation and settling	
Karohji (1959)	Northern Bering Eastern Bering	*Chaetoceros* (subgenus Hyalochaete), *Nitzschia seriata Chaetoceros* (subgenus Phaeoceros), *Chaetoceros concavicornis, Coscinodiscus* sp. *Rhizosolenia hebetata f. semispina, C. atlanticus*		underway plankton recorder with silk bolting cloth net	
Ohwada and Kon	Bering Sea	*Chaetoceros atlanticus, C. concavicornis, C. convolutus, C. compressus, C. constrictus, C. debilis, C. decipiens, Corethron hystrix, Denticula* sp., *Fragilaria islandica, Rhizosolenia alata, R. hebetata f. hiemalis, R. hebetata f. semispina, Nitzschia seriata, N. closterium*		concentrating surface water	$10^4$to 10^7cells/liter

TABLE II-1

CONTINUED

Investigators	Area	Dominant Species	Date	Method	Cells/liter
Smirnova (1959)	Okhotsk Sea	Flora similar to the Bering Sea			
Zenkevitch	Northern Bering Sea	*Chaetoceros* (subgenus Hyalochaete), predominantly *Chaetoceros furcellatus*		sedimented plankton samples	
Karohji (1972)	Bering Sea	*Denticula seminae, Thalassiothrix longissima, Chaetoceros atlanticus, C. convolutus, Coscinodiscus curvatulus, C. oculus-iridis, Nitzschia seriata, Rhizosolenia hebetata f. hiemalis*	June, July	net	Alaska Coastal area: $6800X10^3$ cells/m^3
Motoda and Minoda (1974)	off shore waters Bering Sea	*Chaetoceros convolutus, C. convavicornis, C. debilis, C. compressus, C. radicans, C. didymus, C. seiracanthus, C. furcellatus, C. constrictus, Rhizosolenia hebetata f. hiemalis, Denticula seminae, Nitzschia seriata, N, delicatissima, N. longissima, Fragilaria* spp., *Thalassiothrix longissima*	Early mid-summer	surface water and vertical net hauls	$1X10^5$ to $1X10^9$ cells/m^3
Taniguchi *et al.* (1976)	Eastern Bering Sea	*Thalassiosira hyalina, T. nordenskioldii, Fragilaria, Navicula*	May	water samples at discrete depths	

In a review Karohji (1972) lists the major Japanese investigations up till that time. The following is a summary of their findings: Motoda and Kawarada (1955) surveyed diatom communities in Aleutian waters and found the leading species to be *Chaetoceros* spp., *Corethron hystrix (= C. criophilum)*, *Denticula* sp., *Nitzschia seriata* and *Rhizosolenia hebetata f. semispina.* Marumo (1956) found that plankton diatoms were thinly populated in the Bering Sea in 1956 except in the waters south of the Kamchatka Peninsula. The most numerous species were *Chaetoceros convolutus, C. debilis, Corethron hystrix (= C. criophilum). Denticula* sp. and *Nitzschia seriata.* Kawarada and Ohwada (1957) discussed seasonal variation in phytoplankton populations. They found members of the genus *Thalassiosira* to be most important in the Bering Sea in April. Some *Chaetoceros* spp. were also found. In May *Chaetoceros* spp.*, Corothron criophilum, Coscinodiscus oculus-iridis, Denticula* sp., and *Thalassiosira decipiens* were important. Karohji has studied the phytoplankton populations in the Bering Sea extensively (1958, 1959, 1972). He noted that areas with rich populations were generally dominated by neritic forms: *Nitzchia seriata, Chaetoceros* (Hyalochaeta), and *Coscinodiscus* in western Aleutian waters and *Chaetoceros* (Hyalochaete) and *Thalassiosira* in the area north of Unimak Island (Karohji, 1972). *Fragilariopsis oceanica* was dominant near the Kurile Islands (now *Nitzschia grunowii*, Hasle, 1972) and areas where phytoplankton abundance was low were dominated by oceanic forms: *Thalassiosira longissima, Denticula seminae, Coscinodiscus* spp, *Chaetoceros* (Phaeoceros) and dinoflagellates in the Bering Sea, and *Chaetoceros* (Phaeoceros), *Denticula seminae, Nitzschia seriata, Rhizosolenia hebetata f. semispina* and *Rhizosolenia alata* in the western and northern Subarctic regions (E. of the Kurile Islands and S. of the Aleutian Islands) Karohji, 1972.

Guillard and Kilham (1977) noted that previous workers: (Karohji, 1972; Smirnova, 1960; Zenkevitch, 1963) found the phytoplankton of the Bering Sea to be very similar to the flora of the North Pacific waters. The following species were found to be abundant by Zenkevitch (1963) or Kawarada (1960): *Chaetoceros concavicornis, C. debilis, C. convolutus, C. furcellatus, C. constrictus, C. atlanticus, C. borealis, Thalassiosira nordenskioldii, T. gravida, Thalassiothrix longissima, Coscinodiscus marginatus, Leptocylindrus danicus, Bacteriosira fragilis, Detonula confervacea, Denticula seminae,* (ex *D. marina), Nitzschia grunowii* (ex *Fragilaria oceanica), Nitzschia closterium* (now *Cylindrotheca closterium*), *Rhizosolenia fragilissima.*

Karohji (1972) recognizes six regions across the Subarctic Pacific from east of the Kurile Islands to south of the Alaska Peninsula. These regions were characterized by distinctive hydrographic features, overall phytoplankton abundance and relative abundances of species. The species he found to be important are noted earlier in this paper and are similar to those listed by Kawarada (1960) and Zenkevitch (1963).

Japanese workers often used phytoplankton as indicators of water masses. Kawarada (1957) predicted the flow of Alaskan coastal water from phytoplankton data and suggested from the distribution of oceanic-boreal diatom species that oceanic cold waters lie in three regions in the Bering Sea: near the Alaskan coast, in the central portion of the Bering Sea, and near the southern Kamchatka Peninsula. Ohwada and Kon (1963) divided the area into seven regions based on the distribution of the dominant species of microplankton. They postulated a southward outflow of water from the central Bering Sea passing over the Aleutian Ridge.

Taniguchi *et al.* (1976) investigated vertical distribution of phytoplankton in the early warming season in the eastern Bering Sea and adjacent areas. He obtained water samples at discrete depths. The surface areas under the influence of newly melted sea ice in the shelf water region in May had dense populations of *Thalassiosira hyalina*, and *T. nordenskioldii*, and relatively large populations of *Fragilaria* (now *Nitzschia*, see Hasle, 1972) and *Navicula*. He also found that the thickness of the euphotic zone in the shelf region in the summer is about 30 m and suggested that the light intensity might be too low for phytoplankton to grow within the bottom water (below the 40-50 m depth). He stated that phytoplankton collected from the bottom water are not of the population grown *in situ* but a part of surface populations which had sunk into the bottom water before a sharp thermocline had been established.

Horner (1976) briefly discusses sea ice algal communities in the Bering Sea. McRoy and Goering's data (1974) is the only available information from this area. They found a dense community of microalgae on the underside of the ice from late winter through breakup. Horner (1976), poses two unanswered questions: what are the origins of the sea ice algal cells, and what is their fate when they leave the ice. In the Arctic, at least, she says few pennate diatoms are present in the water column in the autumn when the ice forms and that living ice diatoms are not usually recovered from the water column when the ice community disintegrates in the spring. She also says it is possible that the ice algae are rapidly dispersed in the water column and are not collected by normal sampling means.

This study is the only one to apply numerical analysis techniques to phytoplankton data from the Bering Sea. We collected phytoplankton samples from discrete depths in the water column and present data from three field seasons (1975-1977). Taniguchi *et al.* (1976), the only other investigators to sample discrete depths, collected phytoplankton in the eastern Bering Sea at only 15 stations and in one field season (1972). In addition, we have studied the ice edge ecosystem in detail.

MATERIALS AND METHODS

Collection and Preservation

Samples were collected during the following cruises:

1.	*Discoverer* 808 (leg one)	May 15-May 30, 1975
2.	*Discoverer* 808 (leg two)	June 2-June 19, 1975
3.	*Discoverer* 810	August 9-August 28, 1975
4.	*Miller Freeman* 815	November 10-November 26, 1975
5.	*Surveyor* 1	March 14-April 2, 1976
6.	*Surveyor* 2	April 12-April 30, 1976
7.	*Surveyor* 5	March 16-April 4, 1977
8.	*Surveyor* 6	April 14-May 1, 1977
9.	*Discoverer* 4	May 20-June 9, 1977

We analyzed 445 samples from 109 stations. All sampling was done with a CTD/Rosette Niskin sampler. Water for the phytoplankton standing stock determinations was collected from Niskin bottles from various depths, placed in screw cap jars and preserved with a modified acetic acid Lugol's solution (Rodhe, Vollenweider and Nauwerck, 1958). Lugol's solution was used because preservation with solutions containing formaldehyde damages naked flagellates (Hasle, 1959) which we expected to find in large numbers at least under winter and early spring conditions in the Bering Sea. Lugol's solution, however, does not sediment blue-green algae properly and calcareous flagellates (coccolithophorids) may be destroyed due to its low pH (Hobro and Willen, 1977). Coccolithophorid species *Pontosphaera* sp., *Emiliania huxleyi* and *Calciopappus caudatus* were found to be important in Alaskan waters. *Pontosphaera*, an oceanic species, has been reported from the Bering Basin by Taniguchi *et al.* (1976). *Emiliania huxleyi* and *Caliciopappus caudatus* were found to be important in the shallow water between 50 and 45 N by Okada and Honjo (1973), who used an electron microscope to count and identify the coccolithophorids described in their paper.

Another member of the phytoplankton community not often seen in cell counts was *Halosphaera* sp. cf. *viridis*. This member of the Prasinophyceae was observed in examination of live material aboard ship in 1977 and 1978 and was seen in some of the sedimented samples. The spheres of the nonmotile *Halosphaera* tend to float to the surface and may be missed if only the sedimented plankton is examined (Round, 1973; p. 109).

Nonquantitative surface phytoplankton samples for taxonomic studies were occasionally obtained by hanging a ½ m mesh net over the side of the ship for about ten minutes while the ship was stationary.

Standing Stock Determinations

Standing stock determinations were made by doing cell counts under a Zeiss Phase Contrast Microscope using a modified Utermohl Inverted Microscope technique (Utermohl, 1931, 1958). Phytoplankton were identified and counted using Zeiss 5 ml settling chambers at 500 X magnification. Each preserved sample was agitated thoroughly, poured into a settling chamber and left to settle overnight. Organisms were identified to the species level whenever possible using an inverted microscope. Periodically some of the diatoms were cleared for taxonomic work. Specimens were sent to Dr. Greta A. Fryxell (Texas A & M University) for taxonomic clarification of *Thalassiosira* species (see section on taxonomic problems).

Numerical Analysis

We used cluster analysis techniques to identify station groups and species assemblages in the Bering Sea. These techniques were used because of their capacity for data summary, for their ability to recognize general trends in the data, and to reduce the subjective element in the assessments. Because we had obtained a large data set, we used a numerical approach to discriminate between strong and weak relationships in the data.

Cluster analysis techniques can be divided into three basic steps:

1. Calculation of a measure of similarity or dissimilarity between entities to be classified.
2. Sorting through a matrix of similarity coefficients to arrange the entities in a hierarchy or dendrogram.
3. Recognition of classes within the hierarchy.

Data reduction was carried out prior to calculation of the similarity coefficients. Phytoplankton taxa, which could not be identified at least to genera, were eliminated from the data set unless they were generally found to occur together under certain environmental conditions. For example, large numbers of microflagellates were indicative of winter phytoplankton populations.

We used the Czekanowski coefficient[1] to calculate the similarity matrices used for cluster analysis routines:

Czekanowski

$$Cs_{1,\ 2} = \frac{2W}{A + B}$$ where

A = the sum of the measures of attributes of entity 1

B = the sum of the measures of attributes entity 2

W = the sum of the lesser measures of attributes shared by entities 1 and 2

C_s = percent similarity

This coefficient has been used effectively in marine benthic studies by Field (1971), Stephenson *et al.* (1972), Feder *et al.* (1976) and others. This coefficient emphasizes the effect of dominant species on the classification and therefore is often used with some form of transformation. Since we had sampled discrete depths each individual sample depth was treated as an individual station in the analysis (each depth at a station could join any group). We could then view the water column vertically and horizontally in terms of phytoplankton distribution. The Czekanowski coefficient was used in (1) normal cluster analyses (with stations as the entities to be classified and species as their attributes) to produce matrices of interstation similarities and (2) inverse cluster analyses (with species as entities and stations as attributes) to form species-species similarity matrices. Normal and inverse cluster analyses were run

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[1] The Czekanowski coefficient is synonymous with the Motyka (Mueller-Dumbois and Ellenberg, 1974) and Bray-Curtis (Clifford and Stephanson, 1975).

on untransformed and natural logarithm transformed data (cells/liter). The natural logarithm transformation, $Y = ln(X+1)$ where Y = the transformed datum and X = cells/liter, reduces the relative influence that the larger values in a set of data have on the similarity determination. Dendrograms were constructed from similarity matrices using a group-average agglomerate hierarchical cluster analysis (Lance and Williams, 1966).

As an aid in the interpretation of the dendrograms formed by cluster analyses a two-way coincidence tables comparing the station groups formed by inverse analysis were constructed (Stephenson *et al.*, 1972). In this table the original species X stations data matrix was rearranged (based on the results of both normal and inverse analysis) so that the stations or species with the higher similarities are adjacent to each other. The two-way coincidence table can then be divided into cells whose elements are the abundance of each of the species in a species group in each of the stations in a station group. The two-way table, by rearranging the original data matrix so that the most similar stations (in terms of the flora) and the most similar species (in terms of their distributions) are adjacent, enables the investigators to identify blocks of species (species groups) which characterize the various station groups. The distribution of species groups can also be identified. The two-way tables produced in these studies were too large to be reproduced in this report. A small two-way table from Stephensen and Williams (1971) is presented (Table II-2) as an example.

TABLE II-2

TWO-WAY COINCIDENCE TABLE FROM STEPHENSON AND WILLIAMS, 1971

SITE-GROUP/SPECIES-GROUP COINCIDENCE TABLE USING "PROXIMITY VALUES"

Site Groups

Species Groups		1								2					3						4					5							
		55	56	57	58	59	60	61	62	25	26	27	30	37	48	49	50	52	53	54	1	2	3	12	13	4	5	6	7	8	9	10	11
I	1	1	1	1				1	1	6	4				6	3	2	1	1	1	6	6	6	3	3	6	5	4	5	5	5	3	1
	2									2	1										5	5	5	9	9	3	2	4	3	3	4	4	3
II	8									51	52	52	52	52																			
III	3																									1		1		1	1	1	1
	13							1	1																								
	14																																
	20											2																					
IV	15	1													1	2	2	1	2	1													
V	5	6	8	8	15	16	15	10	10																								
	6	1	2	2	4	4	4	3	3																								
	11	2	2	2	2	2	2																										
VI	4									1		2	2	2	1	1		1															
	10												1	1										1	1								
	12									1	1	1	1	1				1						1	1	1		1		1	1	1	2
	16									1																							
	17									1	2		2	2																			
	18									1			1	1																			
	19									1	1	1	1	1										1	1							1	1
VII	7																				1	1	1	1	1	4	3	3	3	4	4	3	2
VIII	9																									1	1	2	1	2	1	1	1

Species Groups		6A		6B			7			8			9																		
		47	51	29	35	36	23	24	28	14	15	16	17	18	19	20	21	22	31	32	33	34	38	39	40	41	42	43	44	45	46
I	1	11	10	5	5	2	20	18	16	5	14	26	43	43	44	42	23	42	48	46	37	26	33	45	48	32	36	36	36	35	50
	2	1	1	1	1		8	6	6	17	21	30	23	23	21	15	14	15	15	4	3	4	7	3	6		3	3	3	4	4
II	8			2		2	1	2	2									1				1									
III	3						2	2	2				1	1	1	1	1	3	1	3	3	4	1	4	4	3	3	3	3	3	4
	13						1	1	1	1			2	2	2	2	2	3	2			1									
	14												1	1	1	1	1		1	2	2	2			2	2					
	20				1															1	2	1		1	1	2					1
IV	15																														
V	5																		1	1	1		1			1					
	6																														
	11												1	1	1	1	1	1	1	1	1			1	1	1					1
VI	4	2	2	1	2			1	1										1	1	1		2	1	2		1	1	1	2	2
	10			1	1	1				1	1																				
	12	1	1	1		1		1	1		1	1																			
	16	1	1	1	1		1	1	1																					1	1
	17			2		2		1	1																						
	18			2	2	1	1	1	1																						
	19			1		1		1	1	1	1																				
VII	7									1	1																				
VIII	9																1		1	1				1							

RESULTS

Discoverer Cruise 808 (1975)

Four major station groups were delineated at the 37 percent similarity level by a cluster analysis of data collected in the summer of 1975 (Figures II-1 and II-2). Station Group 1 consisted of a large group of stations at or near the ice edge. Station Group 2 was made up of the 20, 30 and 40 m depths of a transect of stations near the ice edge (Figure II-2) and of the 0 and 10 m depths of Station 54 (just north of the Pribilof Islands). Station Group 3 composed of stations located at the shelf break near Unimak Pass contains species which are common in the north Pacific waters. Station Group 4 was composed of stations located near the shelf break just below the Pribilof Islands.

Although the data are not conclusive, it appears that phytoplankton were less abundant in lower depths of the water column away from the immediate ice edge (Table II-3). Station Groups 1 and 2 have similar species assemblages, but the abundance of these species differ by an order of magnitude. In addition, cf. *Detonula* sp., *Chaetoceros laciniosus*, *Chaetoceros* sp., cf. *wighami* and two *Thalassiosira* species occur in Station Group 1 but not in Station Group 2. The diatom cf. *Detonula* sp. was very abundant at all depths at the ice edge but not found on the transect away from the ice in the lower part of the water column. *Nitzschia* spp. (section *Fragilariopsis*) and microflagellates which were abundant at every station and in every sample depth in Station Group 1 also occurred in Station Group 2, but in lower abundance. *Navicula vanhoffeni*, *Thalassiosira nordenskioldii* and *Thalassiosira* sp. cf. *hyalina*, *Chaetoceros socialis* and *Peridinium* spp. also occurred in both station groups, but they did not occur as frequently in Station Group 1 as in Station Group 2.

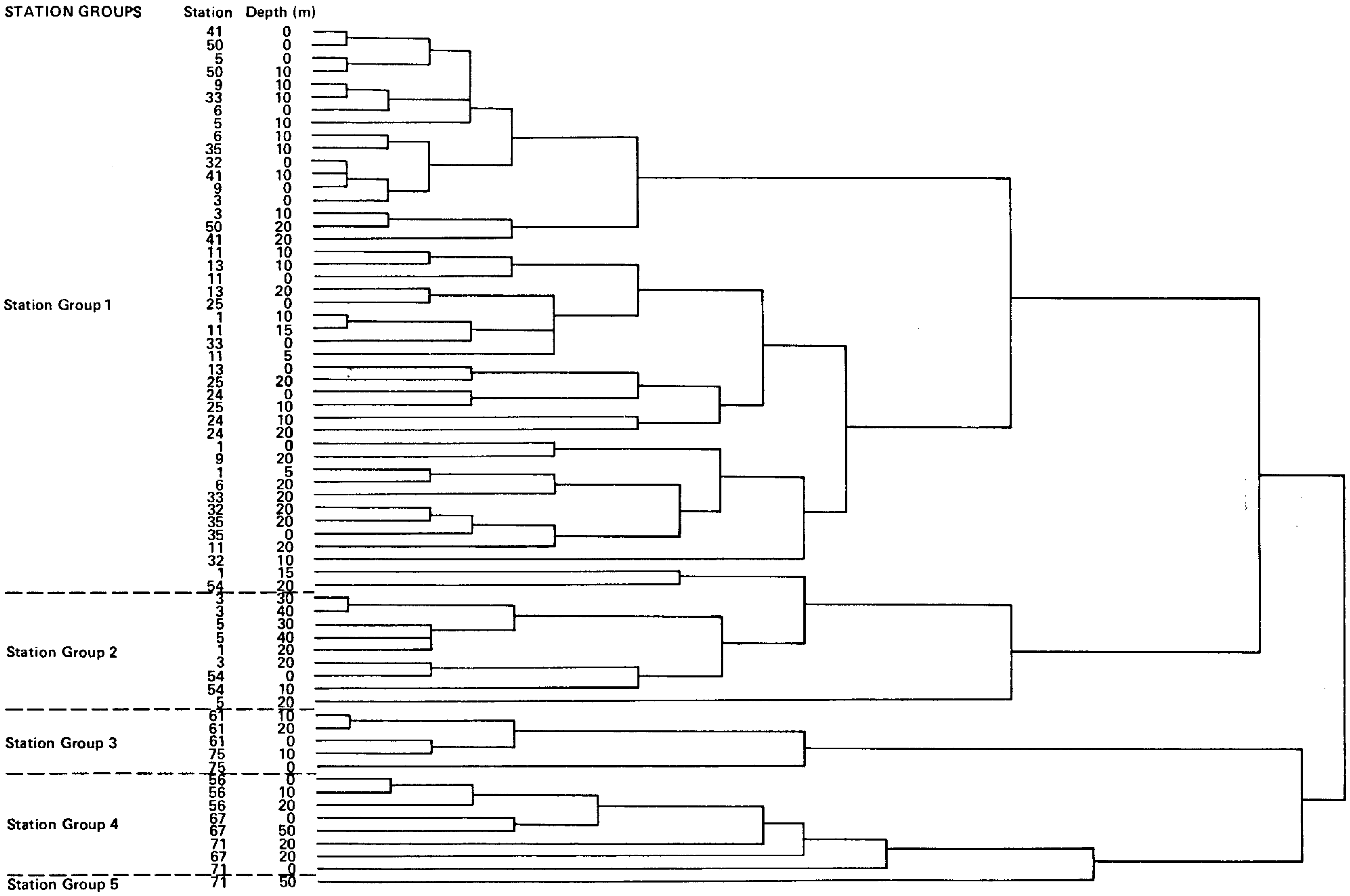


Figure II-1. Dendrogram of the station groups formed by cluster analysis using the Czekanowski similarity coefficient with untransformed data. *Discoverer* Cruise 808, May-June 1975.

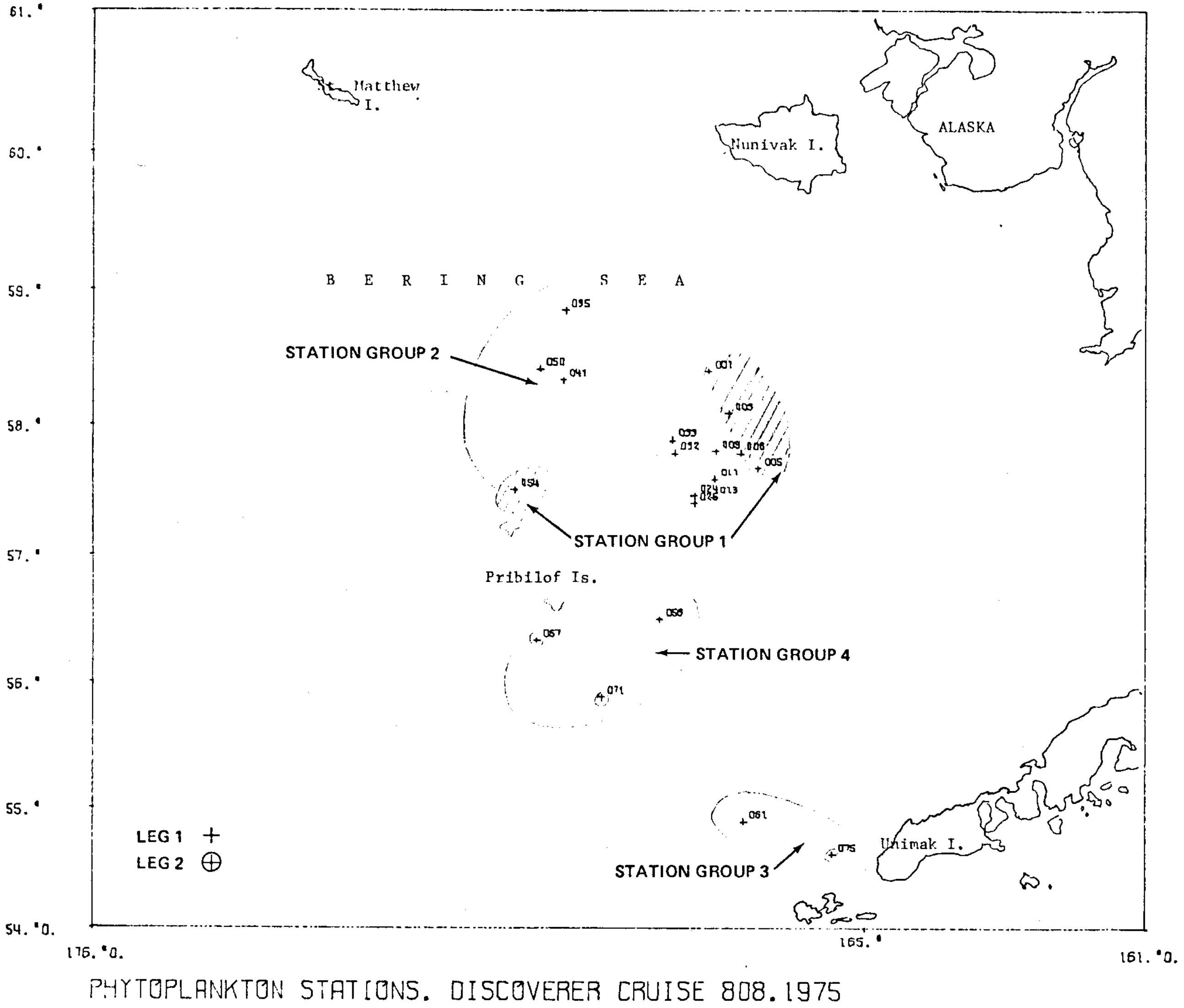


Figure II-2. Major station groups formed by cluster analysis using the Czekanowski similarity coefficient with untransformed data, *Discoverer* Cruise 808.

TABLE II-3

MAJOR STATION GROUPS FORMED BY CLUSTER ANALYSIS USING THE CZEKANOWSKI SIMILARITY COEFFICIENT WITH UNTRANSFORMED DATA, *DISCOVERER* CRUISE 808, MAY-JUNE 1975

Numbers correspond to cells/liter x 10^5; x indicates the sample is a member of the Station Group indicated

STATION GROUP 1

Station	Depth (m)								Location	Date Collected	Notes
	0	5	10	15	20	30	40	50			
1	x 6.08	x 13.5	x 17.1	x 3.36	group 2				58.4000 167.2333	18 May 1975	N. of ice edge
3	x 43.29		x 30.91		group 2	group 2	group 2		58.0833 166.9500	19 May 1975	transect to ice
5	x 58.52		x 68.35		group 2	group 2	group 2		57.6667 166.5333	19 May 1975	transect to ice
6	x 65.95		x 35.90		x 11.55				57.7833 166.7833	19 May 1975	transect to ice
9	x 50.91		x 64.22		x 7.07				57.8000 067.1333	20 May 1975	ice edge
11	x 45.76	x 27.97	x 40.96	x 33.41	x 18.34				57.5833 167.1500	20 May 1975	ice edge
13	x 22.62		x 35.74		x 23.33				57.4500 167.1617	21 May 1975	ice edge
24	x 25.79		x 18.59		x 17.78				57.4583 167.4467	22 May 1975	ice edge
25	x 19.84		x 29.15		x 17.72				57.3983 167.4483	22 May 1975	ice edge
32	x 46.69		x 17.06		x 7.52				57.7833 167.7167	23 May 1975	ice edge
33	x 19.90		x 59.78		x 14.30				57.8833 167.7500	23 May 1975	ice edge
35	x 11.04		x 39.78		x 6.53				58.8500 169.2833	24 May 1975	
41	x 42.27		x 39.23		x 25.66				58.3333 169.3167	25 May 1975	
50	x 34.56		x 46.81		x 25.06				58.4150 169.6383	26 May 1975	
54	group 2		group 2		x 4.19				57.5000 170.0000	27 May 1975	North of Pribilof Is.

TABLE II-3

CONTINUED

STATION GROUP 2

	Depth (m)										
Station	0	5	10	15	20	30	40	50	Location	Date Collected	Notes
1	group 1	group 1	group 1	group 1	x 1.65				58.4000 167.2333	18 May 1975	N. of ice edge
3	group 1		group 1		x 2.32	x 2.59	x 2.77		58.0833 166.9500	19 May 1975	transect to ice edge
5	group 1		group 1		x 4.8	x 3.33	x 2.8		57.6667 166.5333	19 May 1975	transect to ice edge
54	x 1.8		x 1.62	group 1					57.5000 170.0000	27 May 1975	North of Pribilof Is.

STATION GROUP 3

	Depth (m)										
Station	0	5	10	15	20	30	40	50	Location	Date Collected	Notes
61	x 57.25		x 44.67		x 45.02				54.5500 166.7333	28 May 1975	near Unimak Pass
75	x 109.02		x 50.24						54.6167 165.4750	7 June 1975	near Unimak Pass

STATION GROUP 4

	Depth (m)										
Station	0	5	10	15	20	30	40	50	Location	Date Collected	Notes
56	x 13.38		x 12.69		x 11.82				56.5000 167.9333	27 May 1975	shelf break
67	x 20.70				x 12.99			x 18.59	56.3333 169.6833	4 June 1975 4 June 1975	shelf break
71	x 24.51				x 21.57			group 5	55.8833 168.7667	5 June 1975	shelf break

Station Group 3 which showed the influence of the Aleutian Pass water, was unique because it contained large quantities of *Nitzschia* spp. (*Pseudo-nitzschia* group). *Thalassiosira nordenskioldii* was also important. Other species, which occurred in Station Group 3, were *Chaetoceros* spp., *Nitzschia* (section *Fragilariopsis*) and *Thalassiosira*.

Station Group 4, located in the shelf break area just below the Pribilof Islands, was the only station group containing the diatom *Rhizosolenia* spp. In addition, this group contained *Corethron criophilum, Chaetoceros convolutus, C. decipiens, C. septentrionalis, C. furcellatus,* and *Nitzschia* spp. (section *Fragilariopsis*); all cold water species.

Surveyor Cruise 1 and 2 (1976)

In 1976 there were two cruises to the ice edge (*Surveyor* 1, March 14-April 2 and *Surveyor* 2, April 12-April 30; station locations are plotted in Figure II-3). *Surveyor* Cruise 1 arrived at the ice edge prior to the initiation of the spring bloom and data collected during this cruise indicated the presence of a typical winter population of phytoplankton near the ice edge. The spring bloom had begun when the *Surveyor* Cruise 2 had reached the ice edge.

Analysis of data collected during these two cruises delineated four major station groups at the 33 percent similarity level; Station Groups 1, 3, 9, and 10 (Table II-4). The first two groups (Station Groups 1 and Station Group 3) contained all of the *Surveyor* Cruise 1 stations (Table II-4). This grouping occurred because the bloom had not begun during the *Surveyor* Cruise 1 and therefore similar (winter) phytoplankton populations were present at all of the phytoplankton stations occupied. Station Group 1 was

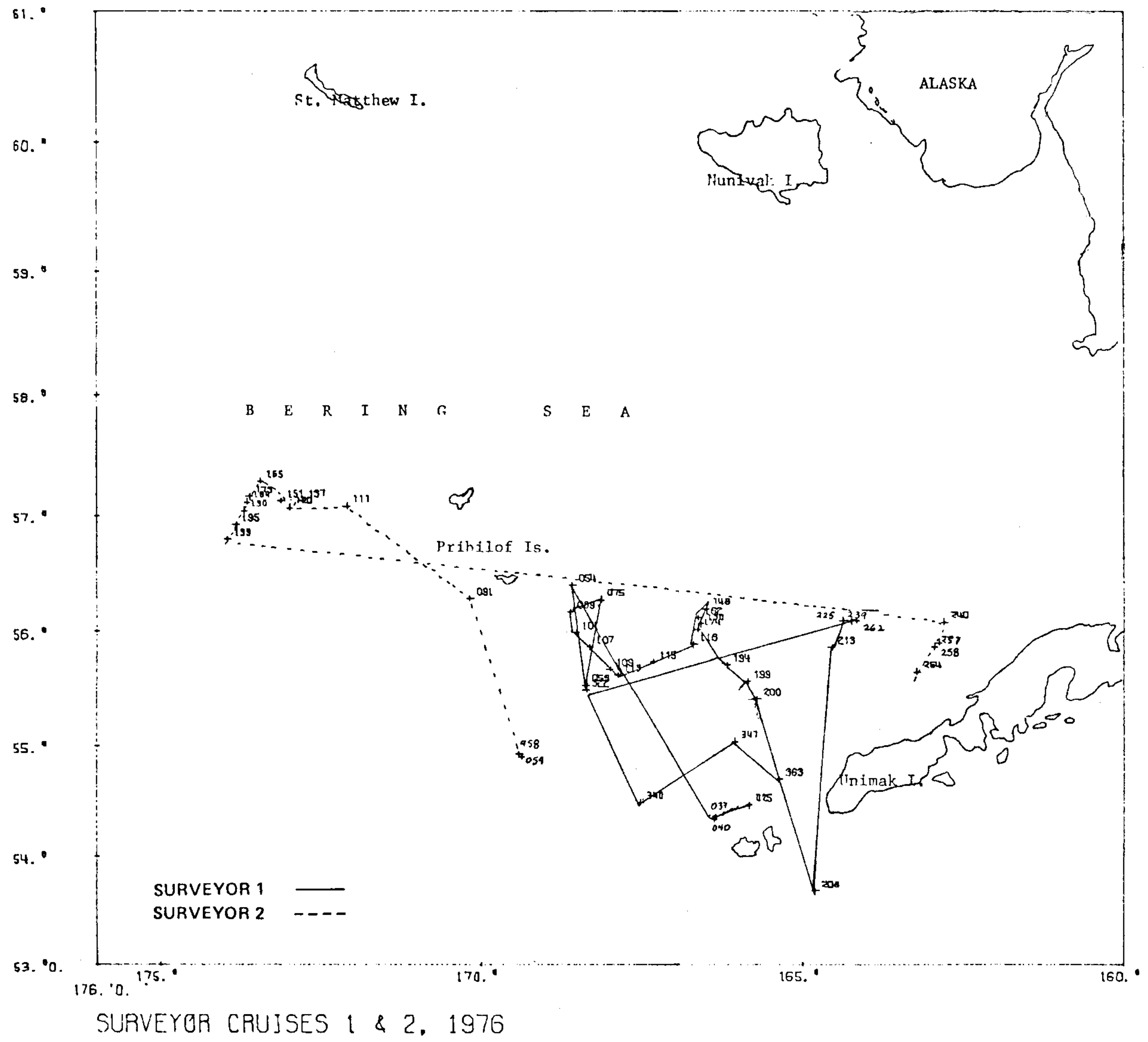


Figure II-3. Major cruise tracks and stations occupied by the *Surveyor* (Cruise 1 and 2) in the Bering Sea, 1976.

TABLE II-4

MAJOR STATION GROUPS FORMED BY CLUSTER ANALYSIS USING THE CZEKANOWSKI SIMILARITY COEFFICIENT WITH UNTRANSFORMED DATA, *SURVEYOR* CRUISES 1 & 2, MARCH-APRIL 1976

Numbers correspond to cells/liter x 10^5; x indicates the sample is a member of the Station Group indicated

STATION GROUP 1

	Depth (m)												
Station	0	10	20	30	40	50	60	75	90	100	Location	Date Collected	Notes
25	x .356		x .408								54.4617 165.83	17 March 1976	N. of Unimak Pass
101	x .160		x .152								55.9867 168.5333	21 March 1976	ice
130	group 6	x .212									56.0617 166.5867	21 March 1976	ice influence
148	x .796	x 1.06	x 4.88	x .472							56.2000 166.5033	22 March 1976	ice
162	group 3	group 3	x .536	x .556							56.1200 166.6233	21 March 1976	ice
174	x .500			x .708							56.0217 166.6450	23 March 1976	ice
200		x .284	group 5								55.4033 165.7050	24 March 1976	ice
208	group 3	x .272									53.6767 164.8033	24 March 1976 24 March 1976	ice edge
322	group 2	x .268									55.4867 168.3717	29 March 1976	ice
363	group 8	x .300	x .352								54.6917 165.3600	1 April 1976	no ice
59	3	x .840	x .380			group 5					54.8950 169.3717	15 April 1976	no ice
91	x 1.24	x .840		x 1.17						x .036	56.2833 170.1733	16 April 1976	no ice
120		group 10	group 10	group 10	group 10	group 9	group 3	group 3	x .268	group 3	57.0633 172.9933	18 April 1976	ice
190	group 9	group 9	group 9	group 9	group 9	x .420		group 3			57.0350 173.7033	22 April 1976	ice influence
264	x 1.63		group 8								55.6450 163.2167	26 April 1976	

TABLE II-4

CONTINUED

STATION GROUP 3

	Depth (m)												
Station	0	10	20	30	40	50	60	75	90	100	Location	Date Collected	Notes
107	x .872										55.6667 168.0000	21 March 1976	10 miles from ice
113	x .780										55.6167 167.8783	21 March 1976	30 miles from ice
162	x 1.0	x 1.12									56.1200 166.6233	March 1976	ice
194		x .416									55.7050 166.1833	24 March 1976	ice edge
208	x .824	group 1									53.6767 164.8033	24 March 1976	ice edge
59	x .856	group 1	group 1								54.8950 169.3717	25 April 1976	no ice
111	group 10	group 10	group 10		group 10	group 9		x .132			57.0733 172.1000	17 April 1976	ice
120							x .320	x .152	x .268	x .172	57.0633 172.9933	18 April 1976	ice
137						x .200	x .728	group 6			57.1183 172.7883	19 April 1976	ice
190	group 9	group 9	group 9	group 9	group 9	group 9		x .136			57.0350 173.7033	22 April 1976	ice influence
240	group 10	group 9	group 10	x .404		x .520		x .856			56.0833 162.8033	24 April 1976	ice
257		group 8	group 8	x .372							55.9033 162.8900	25 April 1976	ice edge

therefore designated "Pre-bloom Group 1". The major species in Pre-bloom Group 1 were microflagellates and members of the diatom genera *Nitzschia, Thalassiosira* and *Cylindrotheca*. Densities ranged from 3.6 X 10^3 - 1.6 X 10^5 cells/liter with microflagellates making up about 68 percent of all individuals in Station Group 1. We also labelled Station Group 3 as a "Pre-bloom Group" since it contained five *Surveyor* 1 stations and the phytoplankton community was typical of pre-bloom conditions (Table II-4). The remaining stations in this groups were from *Surveyor* Cruise 2 (with the exception of Station 50, 0 m) but included samples only from the deeper layers of the water column: 60 m or below (Table II-4). Again, as in 1975, it appears that at least early in the season phytoplankton were not as abundant in the lower layers of the water column; the number of phytoplankton species present was still low and essentially the same species were found in Station Group 3 as in Station Group 1. The major difference between these groups was an increase in the abundance of several phytoplankton species in Station Group 3 as opposed to Station Group 1. Microflagellates comprised 41 percent of the phytoplankton population in Station Group 3 and 68 percent in Station Group 1. The diatoms *Nitzschia* spp. (section *Fragilariopsis*) and *Chaetoceros* spp. were largely responsible for this change. The other two major station groups, Station Groups 9 and 10, were composed of stations from *Surveyor* Cruise 2. Station Group 9 was composed mostly of non-ice stations; it contained only three stations located near the ice edge (Figure II-3; Table II-4). Some of the non-ice stations included in Group 9 were located near the ice edge however, and the phytoplankton community would be expected to be influenced by the presence of ice. The following diatom species were abundant in Station

Group 9: *Nitzschia* spp. (section *Fragilariopsis*), *Thalassiosira* sp. cf. *gravida, T. nordenskioldii* sp. cf. *hyalina, Chaetoceros* spp., and *Cylindrotheca closterium. Chaetoceros socialis* was also important.

Station Group 10 was composed entirely of ice edge stations. The stations in this group contained diatoms of the genera *Nitzschia* spp. (section *Fragilariopsis*) and *Thalassiosira.* The family Thalassiosiraceae was well represented, including *Thalassiosira nordenskioldii,* T. sp. cf. *gravida,* T. sp. cf. *rotula*, T. sp. cf. *aestivalis*, T. *polychorda*, T. sp. cf. *hyalina, Porosira glacialis* and other unidentified *Thalassiosira* (see section on taxonomic problems). *Chaetoceros debilis* was also important in this group. Other diatoms occurring frequently in Station Group 10 were *Bacteriosira fragilis, Chaetoceros* sp. cf. *wighami*, *Navicula vanhoffeni, Navicula pelagica, Navicula* spp. and *Detonula* sp.

Surveyor Cruise 5 and 6, *Discoverer* Cruise 4 (1977)

During 1977 there were three OCSEAP Cruises in the Bering Sea. (*Surveyor* Cruise 5, *Surveyor* Cruise 6 and *Discoverer* Cruise 4 (Figure II-4). A winter phytoplankton community was present in the Bering Sea in March in 1977 (*Surveyor* Cruise 5 and 6, 1977). Major components of the March population were microflagellates, dinoflagellates and members of the diatom genera *Chaetoceros* and *Thalassiosira* (Figure II-5). Phytoplankton abundance was usually low (2 X 10^4 cells/liter) but, occasionally increased to 2 X 10^5 cells/liter. By the time of the 1977 *Discoverer* Cruise in late May, phytoplankton abundance had increased (Table II-5) and more species were present than in the winter community.

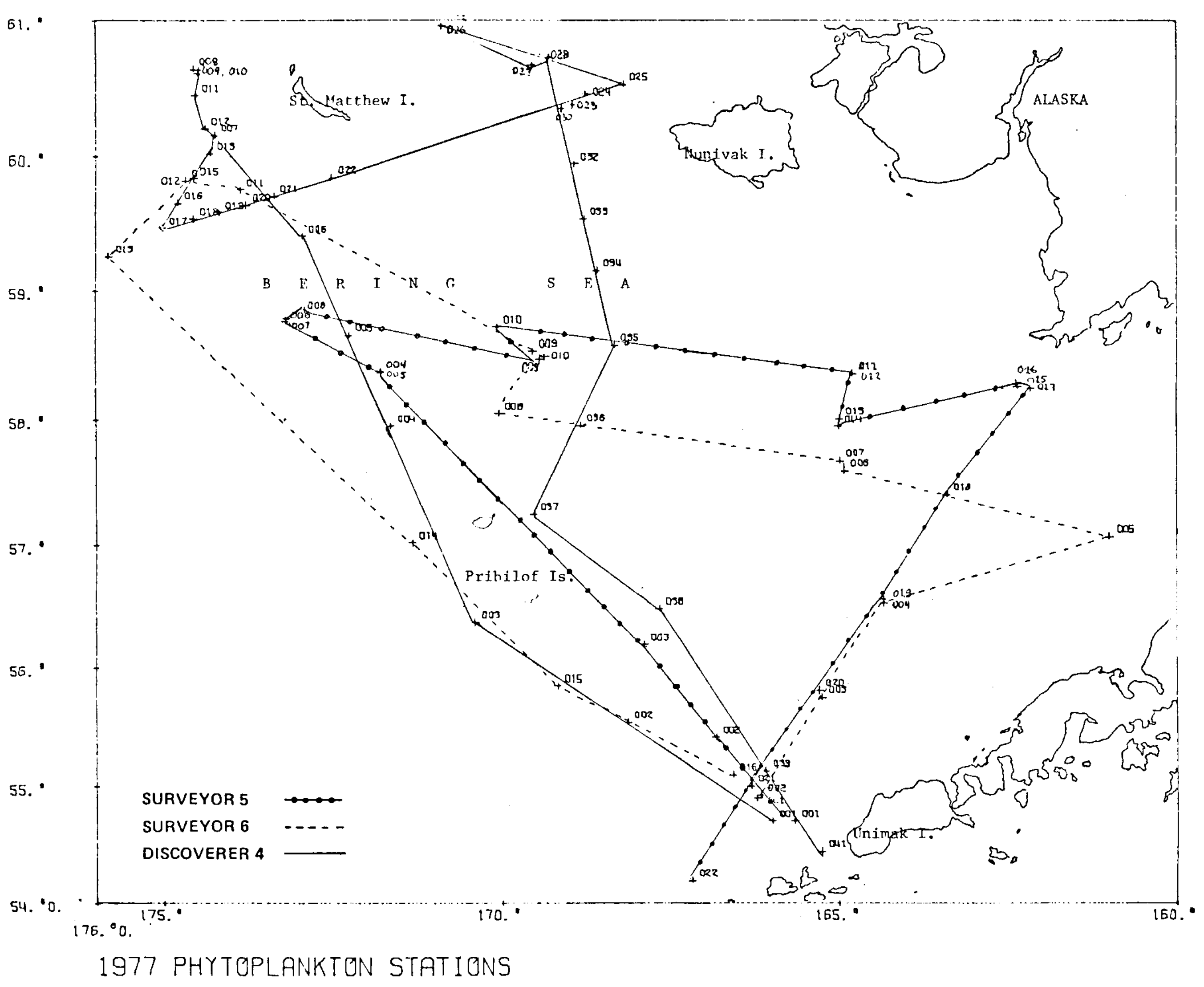


Figure II-4. Major cruise tracks and stations occupied by the *Surveyor* Cruise 5 and 6 and the *Discoverer* Cruise 4 in the Bering Sea, 1977.

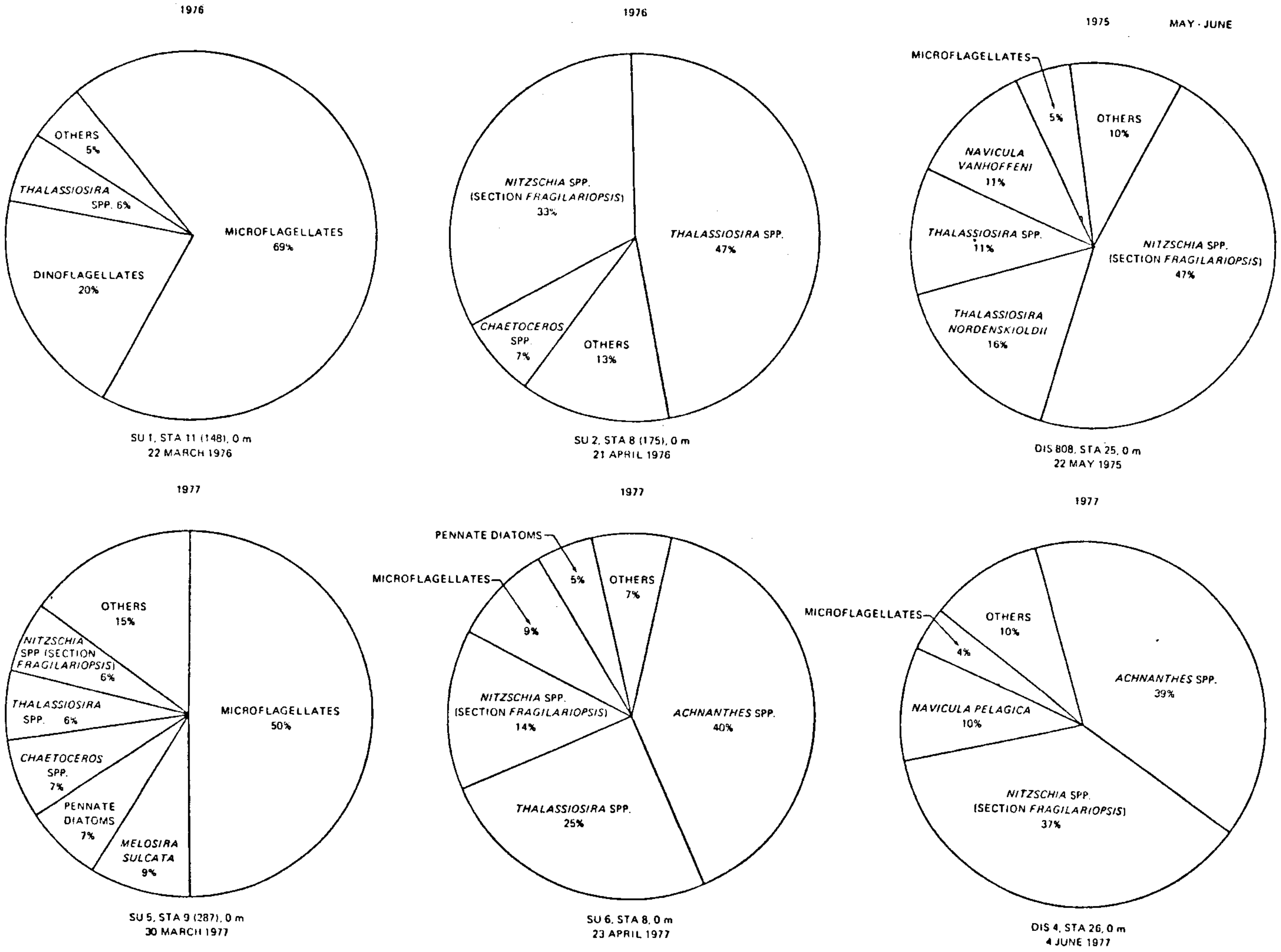


Figure II-5. Percentage composition of the phytoplankton at Bering Sea ice stations over different months, in 3 successive years. (On depth).

TABLE II-5

MAJOR STATION GROUPS FORMED BY CLUSTER ANALYSIS USING THE CZEKANOWSKI SIMILARITY COEFFICIENT WITH NATURAL LOGARITHM TRANSFORMED DATA, *DISCOVERER* CRUISE 4, MAY-JUNE 1977

Numbers correspond to cells/liter x 10^5; x indicates the sample is a member of the Station Group indicated

STATION GROUP 1

	Depth (m)							
Station	0	10	20	30	50	Location	Date Collected	Notes
6	x 16.91	x 13.66	x 8.56	x 13.90	x 13.60	54.4100 172.9367	24 May 1977	ice influence
8	x 7.76	x 10.46	x 6.99	x 1.60		60.6467 174.4150	25 May 1977 25 May 1977	ice ice
11	x 14.42	x 76.64	x 26.70	x 7.97	x 8.26	60.4567 174.5817	27 May 1977	just outside ice
17	x 3.36	x 3.99	x 9.42	x 8.06	x 11.09	59.4733 173.0083	28 May 1977	on transect no ice
20	group 3	x 5.62	x 7.22	x 12.08	x 6.69	59.6428 173.7683	28 May 1977	on transect no ice
22	group 6	group 5	x 6.10	x 3.78	x 5.83	59.8500 172.4933	28 May 1977	on transect no ice
23	x 21.55	x 11.20	x 11.09	x 8.45	x 3.87	60.3867 168.9933	30 May 1977	ice station
25	x 4.74	x 12.14	x 11.31			60.5333 168.1833	1 June 1977	near ice
26	x 19.09	group 4	group 5	group 8	group 8	60.9583 170.8633	4 June 1977	ice station
27	x 13.05	group 2				60.6750 169.5383	5 June 1977	ice station

STATION GROUP 2

	Depth (m)							
Station	0	10	20	30	50	Location	Date Collected	Notes
1	x 9.63	x 11.39	x 7.26	group 7	group 7	54.7083 165.9917	22 May 1977	transect, no ice
2	x 10.50	x 8.98	x 4.36	x 4.09	group 7	55.54 168.1367	23 May 1977	transect, no ice
3	x 9.80	x 18.58		x 3.70		56.3667 170.3850	23 May 1977	transect, no ice
4	x 12.68	x 15.30				57.9467 171.6350	23 May 1977	transect, no ice
27	group 1	x .920				60.6750 169.5383	5 June 1977	ice station

Cluster analysis of the 1977 data delineated two major station groups at the 55 percent similarity level, an ice edge group (Station Group 1) and a shelf break group (Station Group 2; Figure II-6). Station Group 1 consisted of stations located either in the ice pack or adjacent to the ice pack. The ice stations were characterized by a high phytoplankton standing stock (10^6 cells/liter; Table II-5) and they appeared to contain a distinctive assemblage of species: *Nitzschia* spp. (section *Fragilariopsis*), *Achnanthes*, *Navicula* spp. or other chain forming diatoms were dominant. *Thalassiosira* spp. and *Chaetoceros* spp. were present also, but in lower numbers (Figure II-5; Figure II-7).

Station Group 2 (shelf break stations) was characterized by large numbers of *Chaetoceros* spp. and *Thalassiosira nordenskioldii*. *Rhiozosolenia alata*, *Eucampia zoodiacus*, and *Thalassiosira* spp. were also common in the shelf break stations (Figure II-8). *Nitzschia* spp. (Section *Fragilariopsis*) was present but it was not as abundant in Station Group 2 as at the ice edge. Figure II-9 shows the major cluster location for this cruise.

DISCUSSION

Taxonomic Problems

Craspedophyceae (collared flagellates) were reported in the 1975 data, but recent studies by Leadbeater and Manton (1974) suggest that these organisms belong to the animal kingdom. They regard the taxonomic treatment of the group as colorless members of the class Chrysophyceae (Bourrelly, 1968) or as a subclass of the Chromophyta (Christensen, 1962, 1966) as misguided, since the classification depends on small numbers of incompletely known pigmented flagellates. They feel the Craspedophyceae should

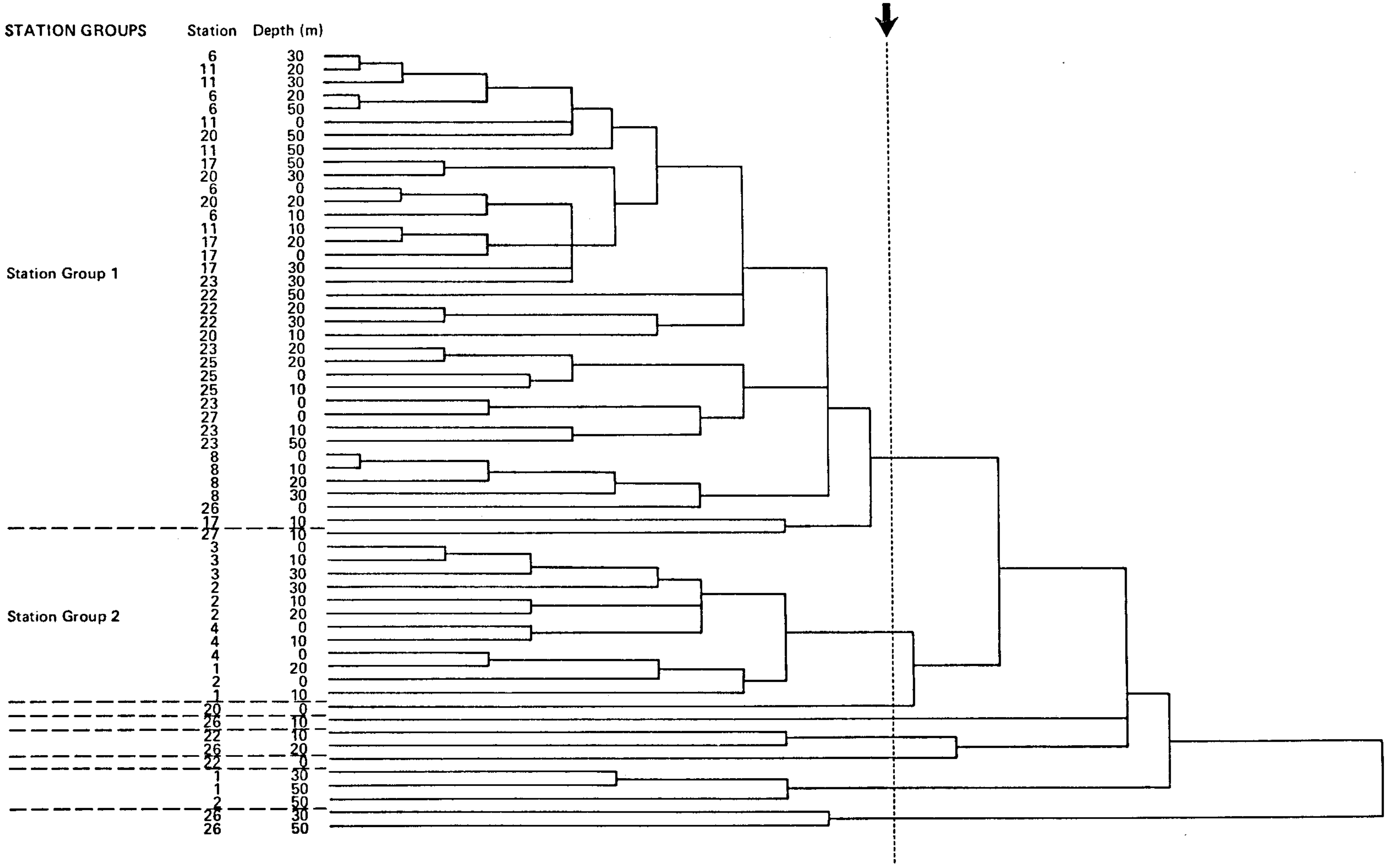
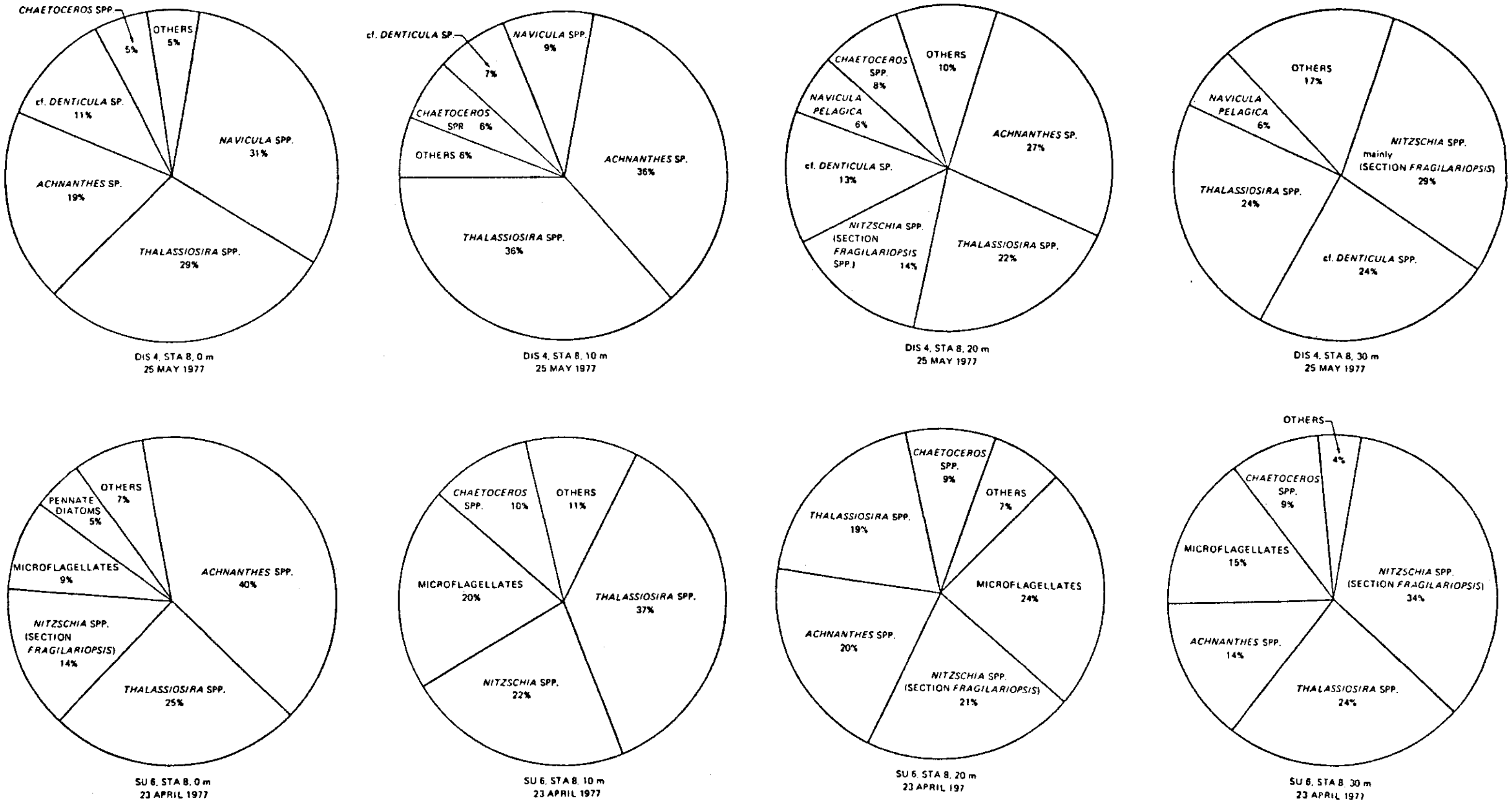


Figure II-6. Dendrogram of station groups formed by cluster analysis using the Czekanowski similarity coefficient with natural logarithm transformed data. *Discoverer* Cruise 4, May-June 1977.



DIS 4, STA 8, 0 m
25 MAY 1977

DIS 4, STA 8, 10 m
25 MAY 1977

DIS 4, STA 8, 20 m
25 MAY 1977

DIS 4, STA 8, 30 m
25 MAY 1977

SU 6, STA 8, 0 m
23 APRIL 1977

SU 6, STA 8, 10 m
23 APRIL 1977

SU 6, STA 8, 20 m
23 APRIL 197

SU 6, STA 8, 30 m
23 APRIL 1977

Figure II-7. Percentage composition of the phytoplankton at selected ice stations in the Bering Sea, *Discoverer* Cruise 4, May 1977, *Surveyor* Cruise 6, April 1977. Vertical distribution through the water column.

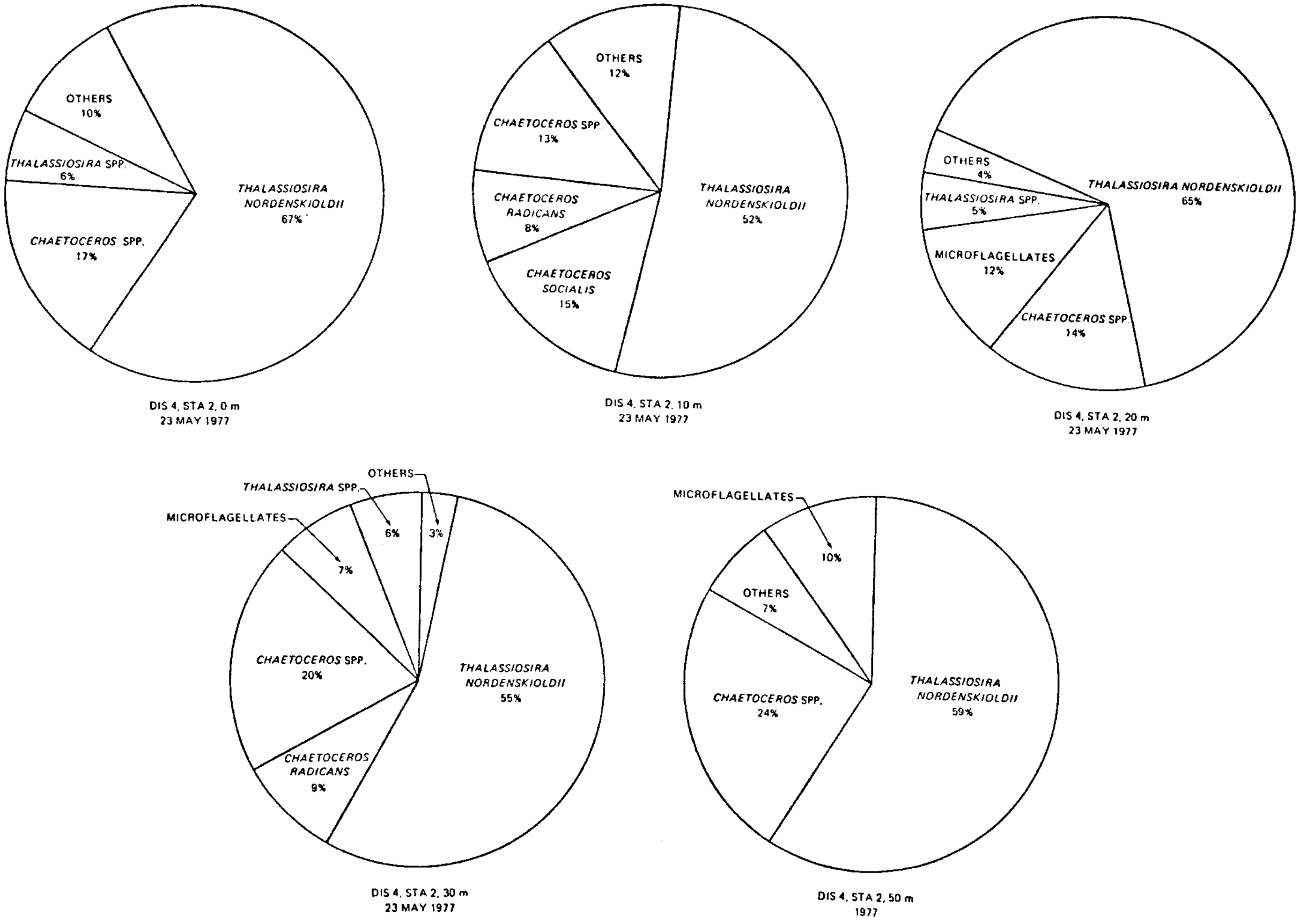
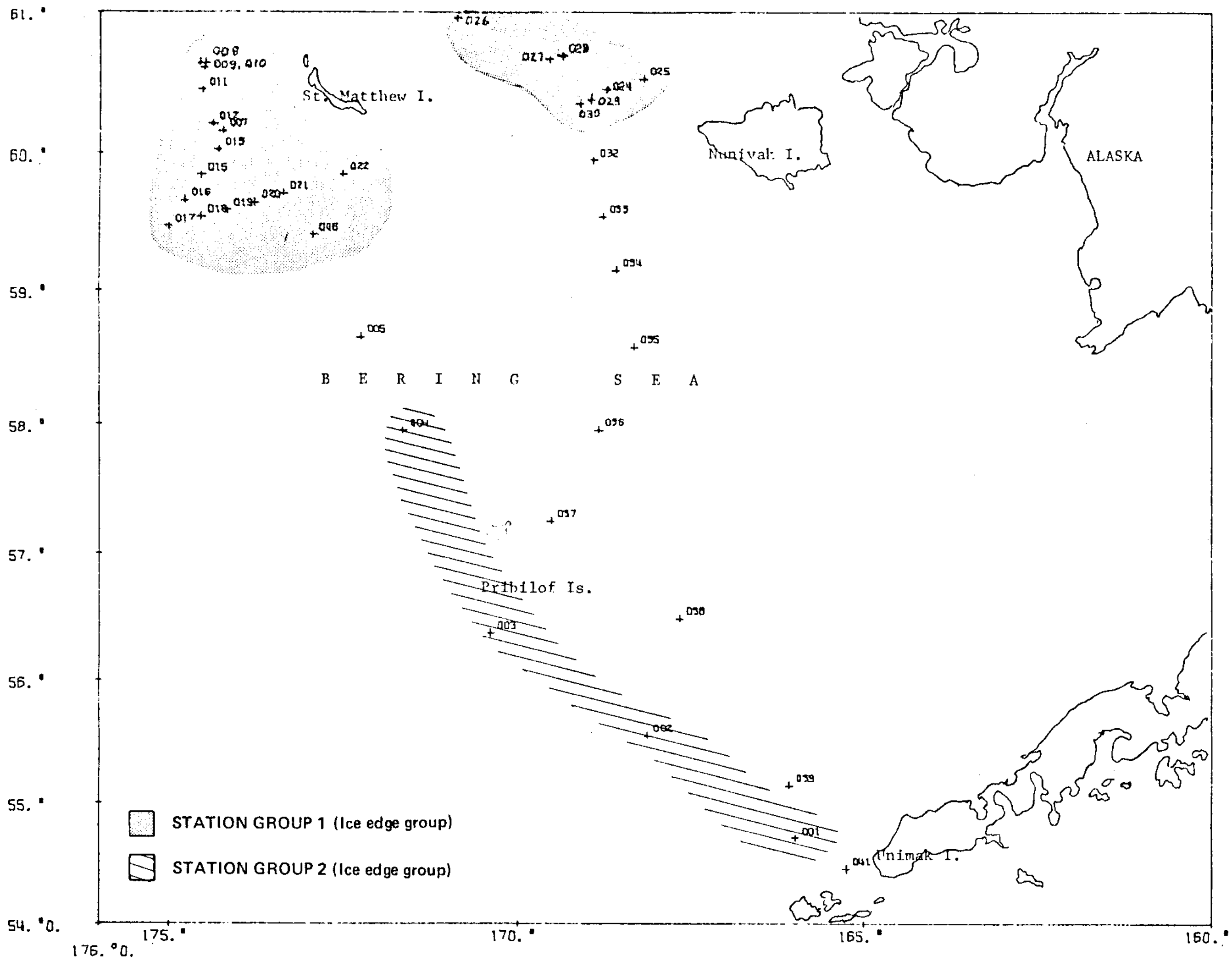


Figure II-8. Percentage composition of the phytoplankton at shelf break Station 2, in the Bering Sea, *Discoverer* Cruise 4, May 1977. Vertical distribution through the water column.



DISCOVERER CRUISE 04, 1977

Figure II-9. Major station groups formed by cluster analysis using the Czekanowski coefficient with transformed data.

be deleted from the plant kingdom. For this reason they have not been included in the 1976 or 1977 data.

The genus *Fragilariopsis* has been synonymized under *Nitzschia* spp. In 1975 this group was reported as *Fragilariopsis* but Hasle (1972) stated that she felt the descriptive peculiarities of *Fragilariopsis* were not sufficient to warrant the rank of genus so it is retained as a section of the genus *Nitzschia* with *Pseudonitzschia* as its closest ally.

Melosira moniliformis reported in 1975 is a misidentification. The following years data lists this diatom as cf. *Detonula* spp. but the identification is still uncertain.

The diatom *Denticula seminae* has been lumped with *Nitzschia* spp. in some of the data. This species may be an important component of the Bering Sea phytoplankton in some areas of the Bering Sea. Similarily *Achnanthes* spp. were lumped with *Nitzschia* in the 1975 data.

Members of the family Thalassiosiraceae have always been difficult to identify to species in settling chamber. Dr. Greta A. Fryxell examined member of this family and stated "any attempt to identify cells in girdle view from a water mount is difficult at best and often impossible" (Fryxell, personal communication). She listed these species from the Bering Sea: (preliminary list) *Thalassiosira* sp. cf. *exentrica*, T. sp. cf. *plicata*, T. sp. cf. *hyalina* T. sp. cf. *lineata* T. sp. cf. *ambigua* T. sp. cf. *antarctica*, T. sp. cf. *bioculata*, *T. angusta-lineata*, *T. nordenskioldii* T. spp., *Porosira glacialis*, *Coscinodiscus oculus-iridis* and *C. curvatulus*.

The dinoflagellate genus *Peridinium* is now listed as *Protoperidinium* see Parke and Dixon (1976), Wall and Dale (1968), Wall (1970), Loeblich III (1970), and Balech (1973 a. b. 1974) for details.

Cluster Analysis

Numerical analysis makes the evaluation of large data sets feasible, and its use has greatly reduced the subjective element in the analysis of species distributions (Thorrington-Smith, 1971; Iuimey-Cook, 1969). However, numerical techniques have not completely eliminated subjectivity. Among the subjective decisions required during the development of the cluster analysis routines used in this study were the selection of (1) a method of data standardization of transformation (if any is desired); (2) a similarity coefficient; and (3) a clustering strategy or method of ordination. A subjective judgement delimiting the groups formed by the analysis must also be made by examining a dendrogram. Rather than make an *a priori* selection of any single method of analysis we decided to use a range of analytical strategies. The effectiveness of each analysis was then evaluated by using two-way coincidence tables and examining the extent to which the groupings that were formed by cluster analysis reflected environmental (physical, chemical, biological) conditions. The use of the Czekanowski coefficient with *ln* transformed abundance data (cells/liter) to form similarity matrices and a hierarchical agglomerative cluster analysis using the group average sorting strategy produced groupings which distinguished pre-bloom and bloom communities and demonstrated the effect of sea ice on phytoplankton populations.

Cluster analysis techniques consistently delineated two major station groups in the area surveyed by the OCSEAP phytoplankton program during all three years of data collection (an ice edge group and a shelf break group). The ice edge group consisted of stations located in the ice or in areas under the influence of the ice and the shelf break group was made up of stations along the shelf break. Occasionally other major groups were delineated by the analyses. An analysis of data collected during 1975 delineated a station group composed of stations near the Aleutian Islands in the region of Unimak Pass (Station Group 3; Table II-3). This group did not occur in the 1975 or 1977 analysis. Samples from the same area collected in 1976 were classified in "Pre-bloom Group 5" (Table II-4), and in 1977, stations from this area were grouped with the shelf break stations (Table II-5).

Our data show that in the winter and early spring preceding the major phytoplankton bloom microflagellates comprise the major portion of the phytoplankton population in the Bering Sea. Dinoflagellates, and diatoms of the genera *Thalassiosira* and *Chaetoceros* are nearly always present, and usually *Cylindrotheca closterium* and *Nitzschia* spp. occur in low densities in the winter. Many other species are found in the winter phytoplankton community in low numbers.

As the bloom begins (usually in April) the total cell density often does not increase markedly although the composition of the flora changes (Figure II-8). Diatoms of the genera *Chaetoceros, Thalassiosira* and *Nitzschia* become abundant replacing the previously dominant microflagellates. As the bloom progresses, cell densities increase.

Cell densities range between 10^4 and 10^7 cells/liter during the bloom. Usually during the peak of the bloom one or two species of diatoms dominate the population (Figures II-5, II-8). Analysis of samples collected from ice stations indicates that the same species are not always important temporarily and spatially; however, the same basic species assemblages are present.

Ice edge stations characteristically contain large numbers of chain forming diatoms, particularily those that form flat ribbon shaped colonies (Figures II-5, II-7). The most important species of diatoms at the ice edge numerically are *Thalassiosira* spp. *Nitzschia* spp. (section *Fragilariopsis*), *Achnanthes* spp. *Navicula pelagica, Navicula vanhoffeni, Chaetoceros* spp. and cf. *Detonula* sp. Other species which are not as abundant, but which seem to prefer the ice edge environment include *Nitzchia frigida, Bacteriosira fragilis, Porosira glacialis, Gyrosigma* or *Pleurosigma* sp.

The shelf break stations were dominated by *Chaetoceros debilis* (1975), *C. socialis, C. compressus, C. radicans* and *Thalassiosira nordenskioldii* in 1977 (Figures II-7, II-10). In 1975 *Phaeocystis* was dominant at some shelf break stations.

It is not clear from our data whether there are several discrete phytoplankton communities with different species assemblages or if there is a complicated species succession in which dominant species succeed one another rapidly. Other workers (Lillick, 1940, Lund, 1966) have demonstrated that fairly rapid succession can occur in phytoplankton populations. Because succession of planktonic diatoms involves a large number of interrelated biotic and abiotic factors, there are few comprehensive studies dealing with it (Guillard and Kilham, 1977). An understanding of phytoplankton succession can not be obtained from studies focusing attention only on community properties such as primary productivity, chlorophyll *a* content, and not on biological properties of the organisms which actually make up the community (Smayda, 1973). All planktonic diatoms have environmental requirements which differ from one another, and the patterns of seasonal succession are a product of those differences

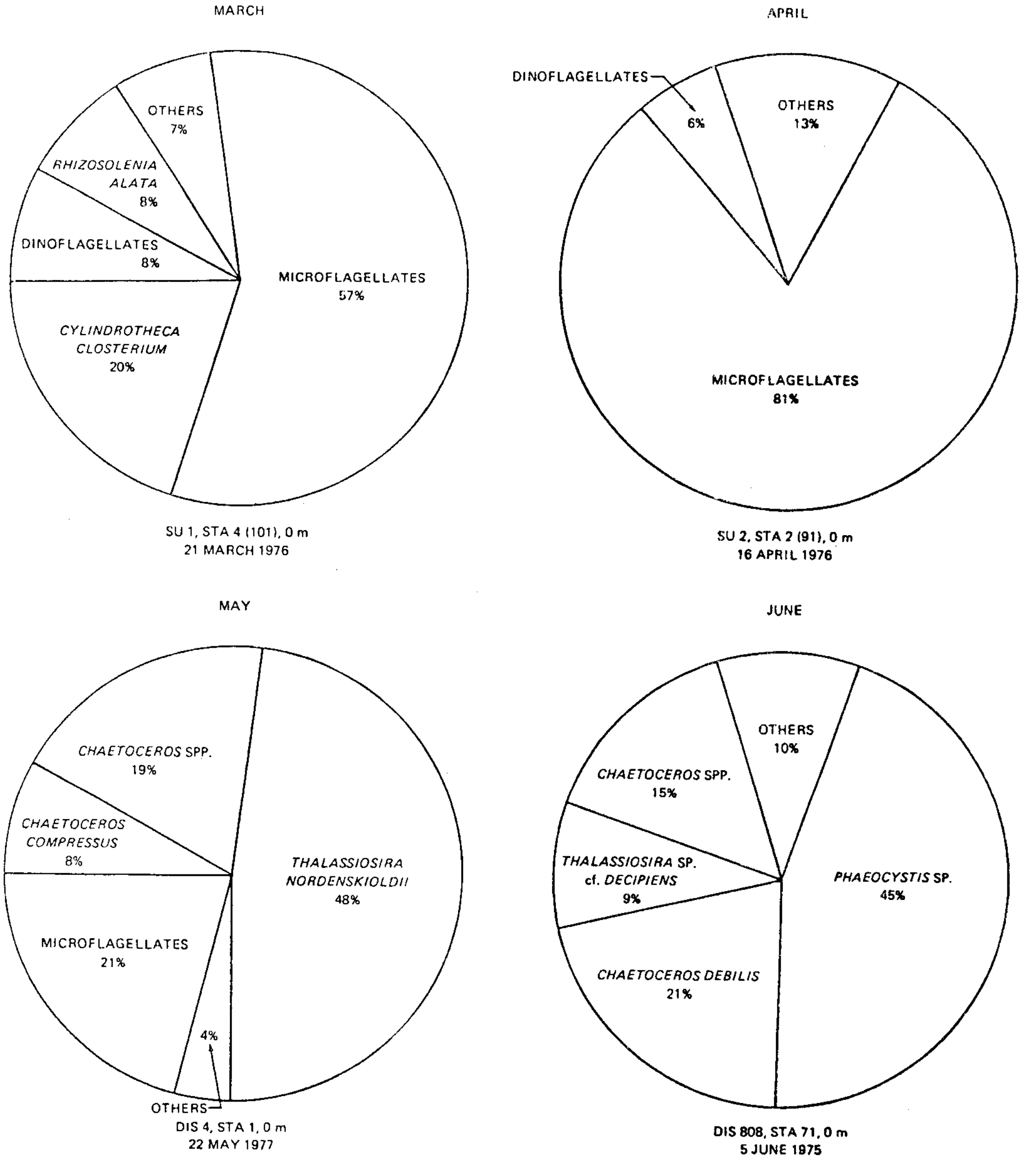


Figure II-10. Percentage composition of the phytoplankton at shelf break stations in the Bering Sea in different months. (On depth).

(Guillard and Kilham, 1977; Braarud, 1962). Braarud (1962) lists many characteristics which may differ from species to species. Our method of data analysis enables us to show general trends of species succession in the Bering Sea and provides information that the community properties approach to phytoplankton ecology can not provide.

The spring phytoplankton bloom apparently begins near the ice edge, in the upper portion of the water column (0-30 m). As the season progresses mixing occurs and the phytoplankton become distributed throughout a greater portion of the water column. As the ice edge moves north, surface waters warm and the cold water from the ice edge with its phytoplankton populations sinks below the warmer surface waters (Alexander and Cooney, 1978). Our data supports the contention of Taniguchi *et al.* (1976) that these phytoplankton cells are probably not metabolically active for any length of time after sinking. Examination of phytoplankton from these lower layers (40 m and below) show fragmented and unhealthy looking cells (Schandelmeier, unpublished data). The occurrence of large numbers of these cells in deeper water may also reflect a lack of coupling between the grazing population and the ice edge bloom resulting in the direct input of phytoplankton carbon to the benthos.

Our data suggest that some of the phytoplankton living in the slush ice may contribute species to the water column, at least early in the phytoplankton bloom. We compared species found in nonquantitative ice core samples and the species found in the water column at the same location (Tables II-6 and II-7). Many species occurred in both places. At Station 9 (*Surveyor* Cruise 5, 30 March 1977) *Melosira sulcata* was a common diatom found in both the slush ice and in the water column (Table II-6).

TABLE II-6

COMPARISON OF SLUSH ICE ALGAE AND PHYTOPLANKTON IDENTIFIED FROM *SURVEYOR* CRUISE 5, STATION 9, 30 MARCH 1977

x indicates the taxon was found in that environment

Taxon	Slush ice	Water column
Actinoptychus undulatus	x	
Amphiprora sp.	x	
Biddulphia aurita	x	x
Chaetoceros radicans		x
Chaetoceros spp.	x	x
Coscinodiscus radiatus	x	
Cylindrotheca closterium	x	x
Gyrosigma or *Pleurosigma* spp.	x	x
Melosira sulcata	x	x
Navicula spp.	x	x
Nitzschia spp. (section Fragilariopsis)	x	x
Pleurosigma sp.	x	
Porosira glacialis	x	
Rhizosolenia hebetata		x
Thalassionema nitzschioides	x	x
Thalassiosira polychorda		x
Thalassiosira sp.	x	x
unidentified pennates	x	x
Peridinium spp.		x
dinoflagellates		x
Halosphaera		x
unidentified cells		x
microflagellates		x

TABLE II-7

COMPARISON OF ICE ALGAE AND PHYTOPLANKTON IDENTIFIED FROM *DISCOVERER* CRUISE 4, STATION 6, 24 MAY 1977

x indicates the taxon was found in that environment

Taxon	Ice	Water Column
Achnanthes sp.	x	x
Amphiprora sp.		x
Asterionella japonica		x
A. kariana	x	x
Bacteriosira fragilis		x
Biddulphia aurita	x	x
Chaetoceros sp. cf. *cinctus*		x
C. compressus		x
C. convolutus		x
C. debilis		x
C. decipiens		x
C. laciniosus		x
C. radicans		x
C. socialis		x
Chaetoceros sp.	x	x
Coscinodiscus sp.	x	x
Cylindrotheca closterium		x
Cylindrotheca sp.		x
cf. *Denticula* sp.		x
cf. *Detonula* sp.		x
Ditylum brightwellii	x	
Eucampia zoodiacus		x
Gyrosigma or *Pleurosigma* sp.	xx	x
Melosira sulcata	x	
Navicula pelagica		x
N. vanhoffeni		x
Navicula sp.		x
Nitzschia frigida	x	x
N. seriata	x	x
Nitzschia sp. (section *Fragilariopsis*)	xx	x
Porosira glacialis		x
Stephanopyxis nipponica		x
cf. *Tabellaria* sp.		x
Thelassionema nitzschiodes	x	x
Thalassiosira gravida		x
T. nordenskioldii		x
T. polychorda		x
T. rotula		x
Thalassiosira sp.	xx	x
Thalassiothrix frauenfeldii		x
unidentified pennate diatoms	x	x
Peridinium sp.		
flagellates	xx	x

However, our data do not indicate that this diatom is a conspicuous member of all ice edge communities. There is some evidence to suggest that in the early spring the ice flora could provide a significant inoculum to the water column, but later in the bloom the contribution of ice flora is not as important. Comparison of the species of diatoms found at Station 6, (*Discoverer* Cruise 4, June 1977) indicates that there is a more diverse population in the water column than in the ice (Table 11-6). However, some of the same diatoms are present in both environments. Although it is true that some of the ice diatoms are motile littoral species and are not well suited for a pelagic or neritic existence, we have also found centric diatoms and chain forming pennate diatoms in the slush ice samples and in some ice core samples. These organisms are common components of the water column phytoplankton communities.

SUMMARY

We used cluster analysis techniques to analyse phytoplankton species composition from 109 stations in the Bering Sea with particular emphasis on the ice edge ecosystem. Data was collected during three field seasons as part of the Outer Continental Shelf Assessment Program (OCSEAP). Numerical analysis techniques allowed us to discriminate between strong and weak relationships in a large data set. We found two major groups to be present in the Bering Sea (ice edge group and a shelf break group). We were also able to make some general comments about species succession at the ice edge and at other locations in the Bering Sea. Evidence is presented which suggests the ice flora may act as an inoculant early in the spring bloom. We concur with Taniguchi *et al.* (1976) that the phytoplankton cells

found in the bottom water (below 40 m and at the ice edge) are part of the preceding surface populations which have sunk before sharp thermocline was established and that they are probably not metabolically active. This occurrence may also reflect a lack of coupling between the grazing population, and the ice edge bloom resulting in a direct carbon input to benthos.

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APPENDIX

PHYTOPLANKTON SPECIES FROM THE BERING SEA

Chrysophyta

Bacillariophyceae (diatoms)

- *Achnanthes* sp.
- *Actinocyclus roperii* (de Breb.) Grun. ex. Van Heurck
- *Actinoptychus splendens* (Shad.) Ralfs ex. Pritch.
- *A. undulatus* (Bail.) Ralfs
- *Amphiprora* sp.
- *Asterionella glacialis* Cast. (ex. *A. japonica* Cleve and Moller)
- *A. kariana* Grun.
- *Bacteriosira fragilis* Gran
- *Bellerochea malleus* (Brightw.) Van Heurck
- *Biddulphia aurita* (Lyng.) Breb. & God.
- *B.* sp. cf. *longicuris* Grev.
- *Chaetoceros affinis* Laud.
- *C. atlanticus* C.
- *C. borealis* Bail.
- *C. cinctus* Gran
- *C. compressus* Laud.
- *C. concavicornis* Mang.
- *C. convolutus* Castr.
- *C.* sp. cf. *curvisetus* Cl.
- *C. danicus* Cl.
- *C. debilis* Cl.
- *C. decipiens* Cl.
- *C. furcellatus* Bail.
- *C.* sp. cf. *fragilis* Meun.
- *C.* sp. cf. *holsaticus* Schutt
- *C. laciniosus* Schutt
- *C. lorenzianus* Grun.
- *C. radicans* Schutt
- *C. seiracanthus* Gran
- *C. septentrionalis* Oestrup
- *C. similis* Cl.
- *C. socialis* Cl.
- *C. subsecundus* (Grun.) Husted
- *C.* sp. cf. *wighami* Brighw.
- *Chaetoceros* spp.
- *Cocconeis* sp.
- *Corethron criophilum* Castr. (ex. *C. hystrix* Hensen)
- *Coscinodiscus centralis* Ehr.
- *C. concinnus* Ehr.
- *C. curvatulus* Grun.
- *C. excentricus* Ehr.
- *C. lineatus* Ehr.
- *C. marginatus* Ehr.

APPENDIX

CONTINUED

C. oculus-iridis Ehr.
C. radiatus Ehr.
Coscinodiscus sp.
Cylindrotheca closterium (Ehr.) Reiman & Lewin (ex. *Nitzschia closterium*)
Cylindrotheca sp. cf. *gracilis* (de Breb.) Grun.
Cylindrotheca sp.
Dactyliosolen mediterraneus H. Per.
Denticula seminae Simonsen et. Kanaya (ex. D. *marina*)
Denticula sp.
cf. *Detonula confervacea* (Cleve) Gran
cf. *Detonula* sp.
Ditylum brightwellii (West) Grun.
Eucampia zoodiacus Ehr.
Gyrosigma or *Pleurosigma* sp. I
Gyrosigma or *Pleurosigma* sp. II
Gyrosigma or *Pleurosigma* sp. III
Gyrosigma sp. cf. *tenuissimum* (W. Sm.) Cleve
cf. *Hemiaulus* sp.
cf. *Hyalodiscus* sp.
Leptocylindrus danicus Cl.
Licmophora sp.
Melosira sulcata (Ehr.) Kutz.
Melosira sp. cf. *hyperborea* (Grun.) Van Hewrck
Melosira sp.
Navicula pelagica (Cleve) (ex. *Stauropsis pelagica* (Cleve) Meum.)
N. vanhoffeni Gran (ex. *Stauropsis vanhoffeni* (Gran) Meun.)
N. transitans Cleve
Navicula spp.
Nitzschia frigida Grun.
Nitzschia sp. cf. *longissima* (Breb.) Ralfs
N. seriata Cl.
Nitzschia sp. cf. *subpacifica* Hasle
Nitzschia sp. cf. *paradoxa* (Gmel.) Grun.
Pleurosigma sp.
Porosira glacialis (Gran) Jorg. (ex. *Podosira glacialis*, Cl., *Lauderia glacialis*)
Rhizosolenia alata Brightw.
R. delicatula Cl.
R. fragilissima Berg.
R. hebetata f. semispina (Hen.) Gran
R. hebetata f. hiemalis (Gran
R. setigera Brightw.
R. stolterfothii H. Per.
R. styliformis Brightw.
cf. *Rhabbonema* sp. Kuetzing

cf. *Schroderella delicatula* (H. Per.) Pav.
Skeletonema costatum (Grev.) Cl.
Stephanopyxis nipponica Gran & Yendo
Synedra sp.
Tabellaria sp.
Thalassionema nitzschioides Grun.
Thalassiosira aestivalis Gran & Angst
T. angusta-lineata (Grun.) G. Fryx et. Hasle 1977 (= T. Polychorda)
T. sp. cf. *ambigua*
T. sp. cf. *antarctica* Comber
T. sp. cf. *bioculata* (Grun.) Ostenf.
T. sp. cf. *decipiens* (Grun.) Jorgensen
T. sp. cf. *excentrica* (Ehrenb.) Cl.
T. gravida Cl.
T. hyalina (Grun.) Gran
T. lineata
T. nordenskioldii Cl.
T. sp. cf. *plicata*
T. rotula Mean.
T. sp. cf. *subtilis* (Ostenf.) Gran
T. spp.
Thalassiothrix sp. cf. *frauenfeldii* Grun.
Thalassiothrix sp.
Tropidoneis sp. cf. *lepidoptera* (Greg.) Cl.
Unidentified centric diatoms
unidentified pennate diatoms

Chrysophyceae
Dictyocha fibula Ehr.
Ebria tripartita (Schum.) Lemm.

Dinophyta

Ceratium fusus (Ehbg.) Clap. Lachm.
C. lineatum (Ehr.) Cleve
C. tripos (O.F. Muller) Nitzsch.
Dinophysis norvegica Clap. et. Lachm.
cf. *Gymnodinium* sp.
cf. *Oxytoxum* sp.
Protoperidinium minisculum (Pavil.) (ex. *Peridinium minisculum* Pavil.)
P. pallidum (Ostenf.) Balech (ex. *P. pallidum* Ostenf.)
P. depressum (Bail.) Balech (ex. *P. depressum* Bail.)
Protoperidinium spp.

Prasinophyta

Prasinophyceae

Halosphaera sp.

APPENDIX

CONTINUED

- Haptophyta
  - Haptophyceae
  - Coccolithaceae
  - Phaeocystaceae
    - *Phaeocystis* sp. cf. *pouchetti* (Hariot) Lagerheim
- Cyanophyta
  - Unidentified bluegreens
- Euglenophyta
  - Unidentified euglenoids
- Uncertain taxonomic status
  - microflagellates

CHAPTER III

ZOOPLANKTON AND MICRONEKTON DISTRIBUTIONS IN THE SOUTHEAST BERING SEA WITH SPECIAL REFERENCE TO THE ICE-EDGE ZONE

INTRODUCTION

This chapter presents a synthesis of the many detailed observations obtained during the late spring, summer, and fall of 1975, and the early springs of 1976 and 1977 in the open water and near-ice zone of the southeastern Bering Sea. Outer Bristol Bay and the St. George Basin areas were both considered potential sites for offshore petroleum development and as such warranted careful examinations of community composition and descriptions of animal plankton and micronekton seasonality. Since most species found in these waters (excluding of course sea birds and marine mammals) pass through an early planktonic life history stage, an understanding of the ecology of this complex assemblage was thought to be of great importance in assessing the possible effects of offshore industrial development.

The major objective of this study was to characterize the species composition and standing stock of the pelagic fauna of the southeastern Bering Sea in the approximate size range 0.3-50 mm using collections obtained by standard oceanographic means. A field design was conceived, which generated measures of variability associated with sampling a single location, with samples taken from relatively large spatial regimes, with samples acquired at various times of the year, and with samples collected at different depths and times of day.

Cooney (1976) reviewed the literature pertaining to zooplankton and micronekton in the Bering Sea. The bulk of this information was available as reports and papers of the faculty of fisheries of Hokkaido University, and the Fisheries Agency of Japan from studies dating back to 1953. Most investigations were carried out during the late spring, and summer periods of the year, which cover the biologically productive times, but contain little or no information pertaining to levels of overwintering stocks or relationships to the seasonal ice pack. Work funded by NOAA specifically to study ichthyoplankton of the eastern Bering Sea (K. Waldron and F. Favorite) is adding valuable information, particularly during the early spring season when the reproductive processes of many finfish species occurs in this region. A large, multi-disciplinary ecosystem study, PROBES (Processes and Resources of the Bering Sea Shelf) is currently in its third field season examining the relationships between numerous oceanographic variables and the overall productivity of the outer shelf region south of the Pribilof Islands. The walleye pollock, *Theragra chalcogramma*, is serving as an ecosystem tracer for this project since in its life history the species integrates many processes occurring both in the pelagic realm and near the sea bed.

Notions presented by Motoda and Minoda (1974) concerning regional aspects of animal plankton communities as reflective of broad hydrographic regimes are probably quite representative of the large scale features of the Bering Sea and northern Pacific Ocean for the ice free periods of the year, but continuity with season is lacking. The literature is very sparse regarding the possible effects of seasonal ice on resident populations at lower trophic levels, particularly during the late fall and winter. The field work funded for this study and the subsequent sysnthesis of the information collected is a contribution to the overall understanding of animal plankton ecology in this northern Sea. Our observation in November and March/April provide insight into the biological problems of overwintering and recruitment which are characteristic of seasonally fluctuaring high latitude populations.

STUDY AREA AND CRUISES

This report describes results from four cruises which visited the southeast Bering Sea in May-June 1975, in August 1975, in November 1975, and in March-April 1976:

1. NOAA Ship *Discoverer*, cruise 808; 1975
2. NOAA Ship *Discoverer*, cruise 810; 1975
3. NOAA Ship *Miller Freeman*, cruise 815; 1975
4. NOAA Ship *Surveyor*, cruise SU 1 and 2; 1976
5. NOAA Ship *Surveyor*, cruises SU 5 and SU 6; 1977

The area of study included the open ocean, outer shelf, central shelf, and northern coastal regimes of the southeastern Bering Sea as depicted in Figure III-1.

METHODS AND SOURCES OF DATA

The achievement of a predictive understanding of the occurrence and seasonal abundance of natural populations of animal plankton and micronekton is only vaguely possible after the major components of the variance structure of a system have been described at some arbitrary level of precision. In high-latitude marine ecosystems, a very strong seasonal source of variation is always present and usually modified locally by hydrographic processes unique to a region. Overlying this strong seasonal signal are additional sources of variability which include both non-random diel displacements and ontogenetic migrations, and smaller-scale random patchiness associated with weather influences or internal advective processes. Since by definition plankters are weak swimmers, their overall distributions most often mirror the dynamics of physical fields of motion modified by temperature and salinity gradients which place biological constraints (i.e. upper and lower tolerance limits) on survival. It is within this complex association of variables that collections are obtained which in themselves are used to describe the framework of the system's structure. Because of the dynamic nature of the pelagic regime, both biologically and physically, a strict interpretation of time and space patterns is limited to a statistical evaluation of observations in which the precision of the methodology is usually very "sample size" dependent. Quantitative plankton investigations are notorious for the amount of work involved in the field, in sample processing, and in interpretation of results. This project was no exception.

The field program was designed to test hypotheses and to estimate levels of variability using the statistical procedures of Analysis of Variance. This technique objectively evaluates the additive effects of major factors and their interactions relative to a background of variability associated with a combination of natural patchiness and error introduced by equipment and analytical technique. The procedure is widely used in plankton field research and affords a methodology whereby limited resources are most efficiently allocated within complex temporal and spatial sampling programs. We also examined the data using R-mode cluster analyses.

Following results form the analysis of data collected in the northern Gulf of Alaska (Cooney, 1975), the research area in the southeast Bering Sea was divided into several discrete regimes by depth, these were periodically visited for sampling with nets and trawls of appropriate dimension to representatively collect the numerically dominant zooplankton and micronekton species. The ice-edge zone was considered a separate province.

For purposes of analysis, an original plan of eight regimes and multiple cruises per year was revised by pooling to four subareas and four cruises within the period May 1975-April 1976 (Fig. III-1). An attempt was made to obtain 10 observations per regime each cruise since previous analyses of within-area variance predicted that differences in population abundance of about one-half order of magnitude (i.e. factor of 5.0) or more could be discerned with this level of effort. The resulting matrix became unbalanced with missing observations due to ice conditions encountered during the early spring of 1976.

A fixed split plot model of Analysis of Variance was used to examine the main effect of cruise and regime, and their interaction on distributions of numerically dominant species or composites. As mentioned, four regimes were identified: 1) open ocean (depths greater than 200 m); 2) outer shelf (depth between 100 and 200 m); 3) central shelf (depths between 50 and 100 m); and 4) northern coast (depths shallower than 50 m). Because the seasonal ice pack prevented sampling the northern coastal area during the spring of 1976, the analysis was performed on two configurations of the data: 1) four cruises and three spatial regimes (omitting the northern coastal area in 1976); and 2) three cruises and four regimes (omitting the entire spring block 1976). This same ANOVA model was employed to test for the significance of locations, depths in the water column, and times of day for samples collected in the ice-edge zone during the spring of 1977.

Counts of organisms per unit area of sea suface or per unit volume were transformed to base ten logarithms, an acceptable technique that tends

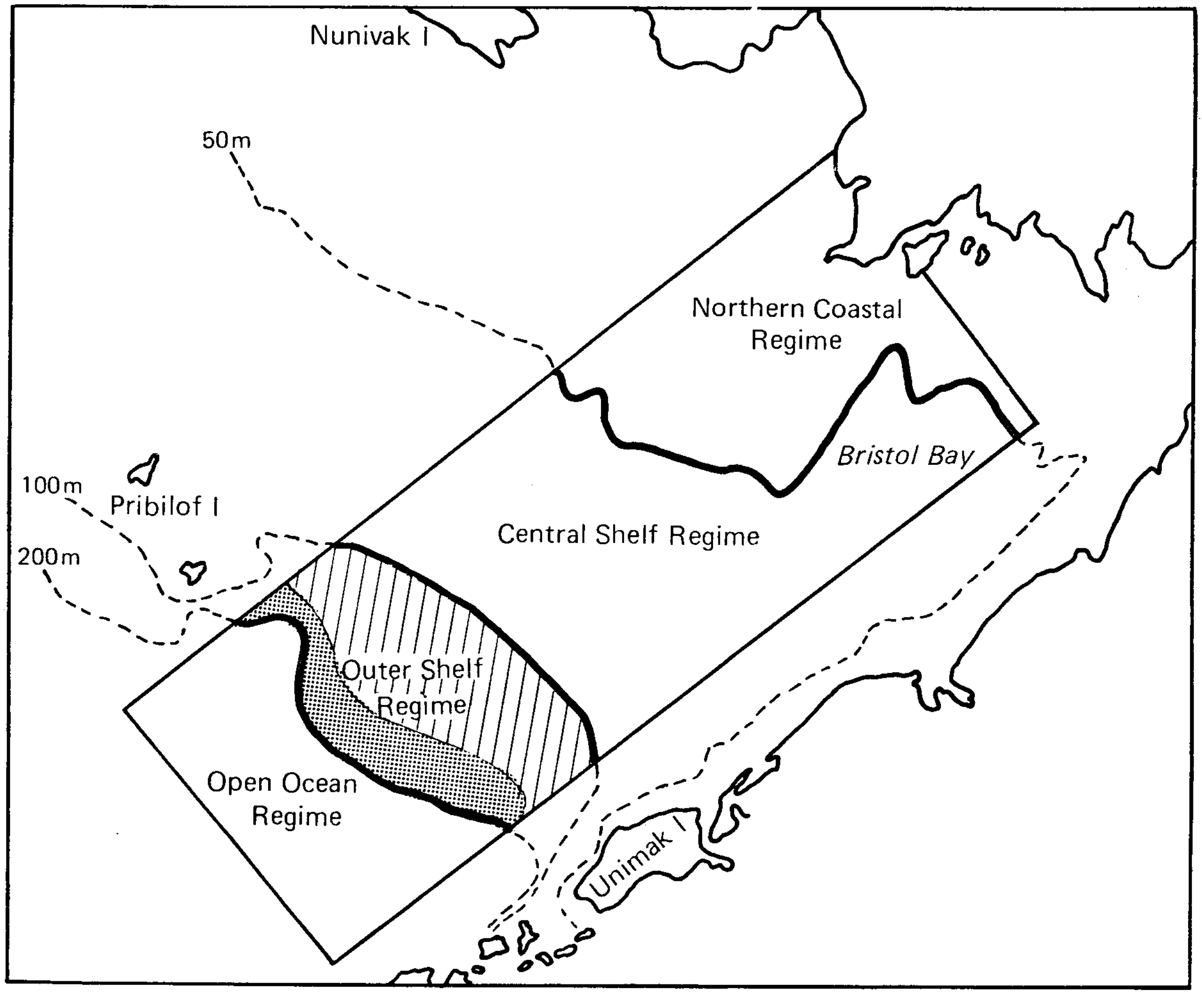


Figure III-1. Bathymetric regimes used as sampling areas in the southeast Bering Sea.

to normalize the variance and adjust data sets in which the main effects are suspected of being proportional rather than additive. All analyses were conducted on transformed data.

Field collections were obtained using a 1-m net (0.333-mm Nitex) fished vertically from the seabed or from 200 m to the surface, if deeper, at each oceanographic station. During the 1977 ice-edge cruises, closing vertical tows were obtained with a modified Juday net closed by messenger from the surface. The relative simplicity and reproducibility of this operation were factors considered in selecting the methodology. The major advantages of the vertically integrated collection include knowing the depth increment sampled from simple wire metering, avoiding difficulties in positioning a net to fish horizontally layered populations which may migrate dielly in the water column, and the small volume of catch to be processed and preserved. The disadvantages are with the small actual volumes filtered ($\sim 80^3$ in 100 tow) and the relatively slow retrival speed of the net ($\sim$1m/sec). The amount of water filtered, 160 m^3 per tow from 200 m to the surface, was adequate for the common species but exceedingly marginal or completely inapropriate to sample the rarer members of the plankton community such as fish eggs and larvae. Since this study proposed to deal quantitatively with the numerically dominant or otherwise obvious organims, the disadvantages were considered of second-order importance.

The 1-m vertical net towing was augmented with occasional samples obtained from a small mid-water trawl (1-m NIO version of the Tucker trawl; 1/8-inch knotless nylon). The trawl was lowered with the vessel underway (2-3 m/sec), fished to depth as determined by wire length monitored with a mechanical time-depth recorder, and then retrieved. Volumes filtered were measured with a flowmeter hung in the mouth of the trawl.

All samples were preserved in 10% buffered seawater and returned to the University of Alaska Marine Sorting Center for processing. Identification and enumeration of taxa was performed on sub-samples obtained using a Stempel pipet; between 100 and 300 animals were routinely counted per sub-sample. In addition, a fraction of most samples was dried to constant weight and reported for each station using the method of Lovegrove (1966).

RESULTS

The findings reported here represent a synthesis of data collected specifically to examine the time-space distribution patterns of zooplankton and micronekton occurring in the open water and edge-zone of the southeastern Bering Sea, May 1975-May 1977. A synopsis of results obtained for the Bering Sea in general is given to provide context for the ice-edge findings.

Southeast Bering Sea Shelf and Open Ocean

During the course of the investigation, 167 species and 6 composite taxa were sorted from 1-m net samples. Of these, only 21 species were designated numerically common at most locations and seasons (Table III-1). Likewise, 161 species and 4 composite taxa are reported for 2-m NIO trawl samples taken at the same time and at many of the same locations. Only 18 of these species were consistantly numerically common (Table III-2). Although these two gear types sampled different size classes and consequently taxa due to mesh size selectivity, 9 species of the common groups were shared.

TABLE III-1

ZOOPLANKTON AND MICRONEKTON SAMPLED WITH A 1-M NET IN THE SOUTHEASTERN BERING SEA; MAY 1975-APRIL 1976

Taxa	Common	Rare
Cnidaria		
Hydrozoa		
Aequorea forskalea		X
Perigonimus yoldia-arcticae		X
P. multicirratus		X
P. breviconis		X
Calycopsis nematophora		X
Bougainvillia superciliaris		X
Corymorpha flammea		X
Tubularia prolifer		X
Coryne tubulosa		X
C. principes	X	
Obelia longissima		X
Ptychogena lactea		X
Eirene indicans		X
Aglanthe digitale	X	
Aegina rosea		X
Dimophyes arctica		X
Scyphozoa		
Periphylla hyacinthina		X
Chrysaora helova		X
Ctenophora		
Beroe spp.		X
Annelida		
Polychaeta		
Hesperone complanata		X
Eteone longa		X
Lopadorrhynchus sp.		X
Pelagobia longicirrata		X
Typhloscolex muelleri	X	
Tomopteris septentrionalis		X
Laonice cirrata		X
Glycera capitata		X
Lumbrinereis sp.		X
Scoloplos armiger		X
Pelagobia longicirrata		X
Capitella capitata		X
Maldane sarsi		X
Terebellides stroemii		X

TABLE III-1

CONTINUED

Taxa	Common	Rare
Mollusca		
Gastropoda		
Euclio sp.		X
Limacina helicina	X	
Clione limacina	X	
Gonatus fabricii		X
Crustacea		
Cladocera		
Podon sp.		X
Evadne sp.		X
Ostracoda		
Conchoecia alata minor		X
Conchoecia borealis var. *antipoda*		X
C. borealis var. *maxima*		X
C. curta		X
C. pseudoalata		X
C. pseudodiscophora		X
C. skogsbergi		X
Copepoda		
Harpacticoida		
Microsetella rosea		X
Bradya sp.		X
Ectinosome sp.		X
Tisbe sp.		X
Calanoida		
Calanus cristatus	X	
C. glacialis		X
C. marshallae	X	
C. plumchrus	X	
Eucalanus bungii bungii	X	
Microcalanus spp.		X
Pseudocalanus spp.	X	
Aetideus pacificus		X
A. sp.		X
Bradyidius saanichi		X
Chiridius gracilis		X
Gaetanus intermedius		X
Gaidius variabilis		X
Euchaeta elongata		X
Haloptilus pseudooxycephalus		X
Xanthocalanus kurilensis		X
X. sp.		X

TABLE III-1

CONTINUED

Taxa	Common	Rare
Calanoid (cont'd)		
Racovitzanus antarcticus		X
Spinocalanus sp.		X
Scolecithricella minor		X
S. ovata		X
Eurytemora herdmani		X
E. pacifica		X
Metridia lucens	X	
M. okhotensis		X
Pleuromamma scutullata		X
Centropages abdominalis		X
Lucicutia sp.		X
Heterorhabdus compactus		X
H. sp.		X
Candacia columbiae		X
Acartia longiremis	X	
A. tumida		X
Lucicutia ovaliformis		X
Cyclopoida		
Oithona similis	X	
O. spinirostris		X
Onceae borealis		X
Nebaliacea		
Nebalia sp.		X
Mysidacea		
Eucopia sp.		X
Acanthomysis nephrophthalma		X
A. dybowskii		X
A. pseudomacropsis		X
A. stelleri		X
Boreomysis knicaidi		X
Holmesiella anomala		X
Neomysis rayii		X
Pseudomma truncatum		X
Cumacea		
Lamprops quadriplicata typica		X
Leucon nasica orientalis		X
L. fulvus		X
L. sp.		X
Eudorella pacifica		X
Eudorellopsis deformis		X
Diastylis bidentata		X
D. alaskensis		X

TABLE III-1

CONTINUED

Taxa	Common	Rare
Amphipoda		
Argissa hamatipes		X
Corophium sp.		X
Guernea sp.		X
Rhachotropis natator		X
Pontoporeia femorata		X
Photis sp.		X
Ischyrocerus commensalis		X
I. spp.		X
Protomedia sp.		X
Anonyx lilljeborgi		X
Eusirella multicalceola		X
Cyclocaris guilelmi		X
Cyphocaris challengeri		X
C. anonyx		X
Koroga megalops		X
Lepidepedcreum kasatka		X
L. comatum		X
Orchomene lepidula		X
O. nugax		X
Melphidippa sp.		X
Bathymedon obtusifrons		X
B. nanseni		X
Monoculodes diamesus		X
M. packardi		X
M. zernovi		X
Westwoodilla coecula		X
Paraphoxus sp.		X
Stenopleustes glaber		X
Dulichia sp.		X
Melphidippa sp.		X
Metopa alderi		X
Stenula sp.		X
Scina borealis		X
Hyperia medusarum		X
Hyperoche medusarum		X
Parathimisto libellula	X	
P. pacifica	X	
Primno macropa		X
Euphausiacea		
Euphausia pacifica		X
Thysanoessa inermis	X	
T. longipes	X	
T. raschii	X	
T. spinifera		X

TABLE III-1

CONTINUED

Taxa	Common	Rare
Decapoda		
Pandalus borealis		X
P. sp.		X
Eualus macilenta		X
Paracrangon echinata		X
Paralithodes camtschatica		X
Chionoecetes spp.		X
Hyas spp.		X
Telmessus cheiragonus		X
Erimacrus isenbeckii		X
Chaetognatha		
Eukrohnia hamata	X	
E. bathypelagica		X
Sagitta elegans	X	
Chordata		
Larvacea		
Fritillaria borealis		X
Oikopleura spp.	X	
Teleostei		
Clupea harengus pallasi		X
Mallotus villosus		X
Bathylagus pacificus		X
B. stilbius schmidti		X
Stenobrachius leucopsarus		X
Theragra chalcogramma		X
Sebastes spp.		X
Liparis spp.		X
Nectoliparis pelagicus		X
Atheresthes stomias		X
Hippoglossoides elassodon		X

TABLE III-2

ZOOPLANKTON AND MICRONEKTON SAMPLED WITH A 2-M NIO TRAWL IN THE SOUTHEASTERN BERING SEA; MAY 1975-APRIL 1976

Taxa	Common	Rare
Cnidaria		
Hydrozoa		
Aglantha digitale	X	
Perigonimus brevironis		X
Perigonimus c.f. P. yoldia arcticea		X
Perigonimus multicirratus		X
Calycopsis nematophora		X
Bougainvillia superciliaris		X
Rathkea jaschnowi		X
Corymorpha flammea		X
Coryne principes	X	
Ptychogena lactea		X
Eirene indicans		X
Aegina rosea		X
Aequores forskalea		X
Pantachogan haeckeli		X
Melicertum campanula		X
Botrynema burcei		X
Halicreas minimum		X
Crossota brunnea		X
Scyphozoa		
Periphylla hyacinthina		X
Atolla wyvillei		X
Chrysaora melanaster	X	
Chrysaora helvola		X
Cyanea capillata	X	
Phacellophora camtschatica		X
Aurelia limbata		X
Siphonophora		
Dimophyes arctica		X
Vogtia serrata		X
Ramosia vitiazi		X
Rosacea plicata		X
Chaetognatha		
Sagitta elegans		X
Eukrohnia spp.		X
Sagitta scrippsae		X
Mollusca		
Galiteuthis armata		X
Chiroteuthis veranyi		X
Gonatus fabricii		X
Gonatus magister		X
Gonatopsis sp.		X

TABLE III-2

CONTINUED

Taxa	Common	Rare
Clione limacina		X
Limacina heliciana		X
Annelida		
Polychaeta		
Tomopteris septentrionalis		X
Hesperone complanata		X
Chaetozone setosa		X
Krohnia excellata		X
Lopadorrhynchidae spp.		X
Antinoella sarsi		X
Nereis pelagica		X
Crustacea		
Copepoda		
Calanus cristatus	X	
Eucalanus bungii bungii	X	
Euchaeta elongata		X
Pachyptilus pacificus		X
Candacia columbiae		X
Euphausiacea		
Euphausia pacifica		X
Tessarabrachion oculatus		X
Thysanoessa raschii	X	
Thysanoessa inermis	X	
Thysanoessa spinifera		X
Thysanoessa longipes	X	
Isopoda		
Ilyarachna sp.		X
Synidotea bicuspida		X
Mysidacea		
Acanthomysis stelleri		X
Acanthomysis dybowskii		X
Pseudomma truncatum		X
Neomysis rayii		X
Neomysis czerniawskii		X
Holmesiella anomala		X
Eucopia sp.		X
Boreomysis kincaidi		X
Boreomysis californica		X

TABLE III-2

CONTINUED

Taxa	Common	Rare
Cumacea		
Diastylis bidentata	X	
D. alaskensis		X
Leucon quadriplicata typica		X
Amphipoda		
Hyperiidea		
Parathemisto pacifica	X	
Parathemisto libellula	X	
Hyperia medusarum		X
Hyperia springera		X
Hyperoche medusarum		X
Primno macropa		X
Phronima sedentaria		X
Hyperia galba		X
Paraphronima crassipes		X
Scina borealis		X
Scina rattrayi		X
Archoeoscina steenstrupi		X
Parathemisto japonica		X
Gammaridea		
Anonyx nugax		X
Cyphocaris challengeri		X
Byblis gaimardi		X
Protomedia sp.		X
Metopa alderi		X
Monoculodes zernovi		X
Ampelisca macrocephala		X
Westwoodilla coecula	X	
Dulichia unispina		X
Pontoporeia femorata		X
Bulichia arctica		X
Melitoides makarovi		X
Rhachotropis oculata		X
Pleustes panopla		X
Monoculoides diamesus		X
Rhachotropis natator		X
Priscillina armata		X
Eusirella multicalceola		X
Parandania boecki		X
Anonyx compactus		X
Stenopleustes glaber		X
Melita dentata		X
Paramphithoe polyacantha polyacantha		X
Monoculopsis longicornis		X
Anisogammarus macginitiei		X

TABLE III-2

CONTINUED

Taxa	Common	Rare
Gammaridea (cont'd)		
Hippomdeon kurilicus		X
Orchomene c.f. O. lipedula		X
Pontogenia ivanovi		X
Atylus bruggeni		X
Atylus collingi		X
Socarnes bidenticulatus		X
Ischerocerus anguipes		X
Melphidippa goesi		X
Cyclocaris guilelmi		X
Decapoda		
Pasiphaea pacifica		X
Cancer sp.		X
Crangon dalli		X
Argis lar		X
Hymenadora frontalis		X
Eualus macilenta		X
Eualus stonyei		X
Pandalus goniurus		X
Pandalus borealis		X
Sergestes similis		X
Chionoecetes spp.	X	
Erimacrus isenbecki		X
Erimacrus isenbecki		X
Telmessus cheirigonus		X
Telmessue cheirigonus		X
Paralithodes camtschatica		X
Paralithodes camtschatica		X
Hyas sp.		X
Pandalus montagui tridens		X
Pandalopsis spp.		X
Chordata		
Cyclostomata		
Lampetra tridentatus		X
Teleostei		
Mallotus villosus	X	
Lycodes palearis		X
Lumpenus maculatus		X
Reinharditius hippoglossoides	X	
Liparis herschelinus		X
Agonus acipenserinus		X
Theragra chalcogramma		X
Liparis dennyi		X

TABLE III-2

CONTINUED

Taxa	Common	Rare
Teleostei (cont'd)		
Clupea harengus pallasi		X
Lumpenus medius		X
Artediellus pacificus		X
Stenobrachius leucopsarus	X	
Bathylagus pacificus		X
Bathylagus alascanus		X
Ptilichthys goodei		X
Stenobrachius nannochir		X
Nectoliparis pelagicus		X
Bathylagus stilbius schmidti	X	
Hippoglossus stenolepis		X
Malacocottus zonurus		X
Hemilepidotus sp.		X
Chauliodus macouni		X
Bathymaster signatus		X
Triglops pingeli		X
Ammodytes hexapterus		X

The 1-m net samples were dominated by copepods (41 species; 8 common) while the mid-water trawl took more "jellyfishes", amphipods, and finfishes. Euphausiids, annelids, and molluscs appeared in roughly similar proportions by gear type. In cases where the life history stages varied greatly in size (i.e. euphausiids), the 1-m net most representatively sampled the juveniles while the trawl took the adults in greater number.

Thirty-three categories including 23 species, 9 genera or larger composites, and total dry weight were examined statistically to determine if patterns of abundance related to season or regime were discernable within the variance structure of the collection. In the formal analysis of variance considering three cruises and four regimes, a significant cruise effect ($p < 0.05$) is evident for 22 categories, a regime effect is apparent for 10 taxa. When four cruises and three regimes are examined using the same analysis, 24 categories exhibit a significant cruise effect, 28 show regime effects, and the interaction term is apparent for 14. The results of this statistical treatment demonstrated that seasonal and spatial fluctuations occur in the distribution of most common species or composites, and that for some the time-space distributions are very complex.

When these distributions were further sorted by regime, several general distributions emerged (Table III-3). Sixteen taxa were usually found in greatest abundance in the open ocean regime seaward of the shelf break. This group includes the ecologically important copepods *Calanus cristatus*, *Calanus plumchrus*, *Eucalanus b. bungii* and *Metridia lucens*, the pteropods *Clione limacina* and *Limacina helicina*, the euphausiid *Thysanoessa longipes*, and the amphipod *Parathemisto pacifica*.

TABLE III-3

DISTRIBUTION PATTERNS BY REGIME FOR NUMERICALLY DOMINANT ZOOPLANKTON AND MICRONEKTON GROUPS IN THE SOUTHEAST BERING SEA

A. Usually Most Abundant in the Open Ocean

Dimophyes arctica
Clione limacina
Limacina helicina
Conchoecia spp.
Calanus cristatus
C. plumchrus
Eucalanus b. bungii
Larvacea (juveniles)
Metridia lucens
Parathemisto pacifica
Euphausiid (eggs and larvae)
Thysanoessa longipes
Eukrohnia hamata
Chaetognath (juveniles)
Oikopleura spp.
Theragra chalcogramma

B. Usually Most Abundant in the Outer Shelf

Oithona spinirostris
Thysanoessa inermis
Majiidae (larvae)

C. Usually Most Abundant in the Central Shelf

Calanus glacialis
C. marshallae
Pseudocalanus spp.
Parathemisto libellula
Thysanoessa raschii
Sagitta elegans

D. Usually Most Abundant in the Northern Coastal Area

Acartia longiremis

E. No Consistent Regime Affinity

Aglantha digitale
Calanus spp. (juveniles)
Copepod nauplii
Thysanoessa spp. (juveniles)
T. spinifera
Oithona similis

F. Absent in the Northern Coastal Regime

Dimophyes arctica
Clione limacina
Calanus cristatus
C. plumchrus
Eucalanus b. bungii
Oithona spinirostris
Parathemisto pacifica
Thysanoessa inermis
T. longipes
T. spp. (juveniles)
Eukrohnia hamata
Theragra chalcogramma

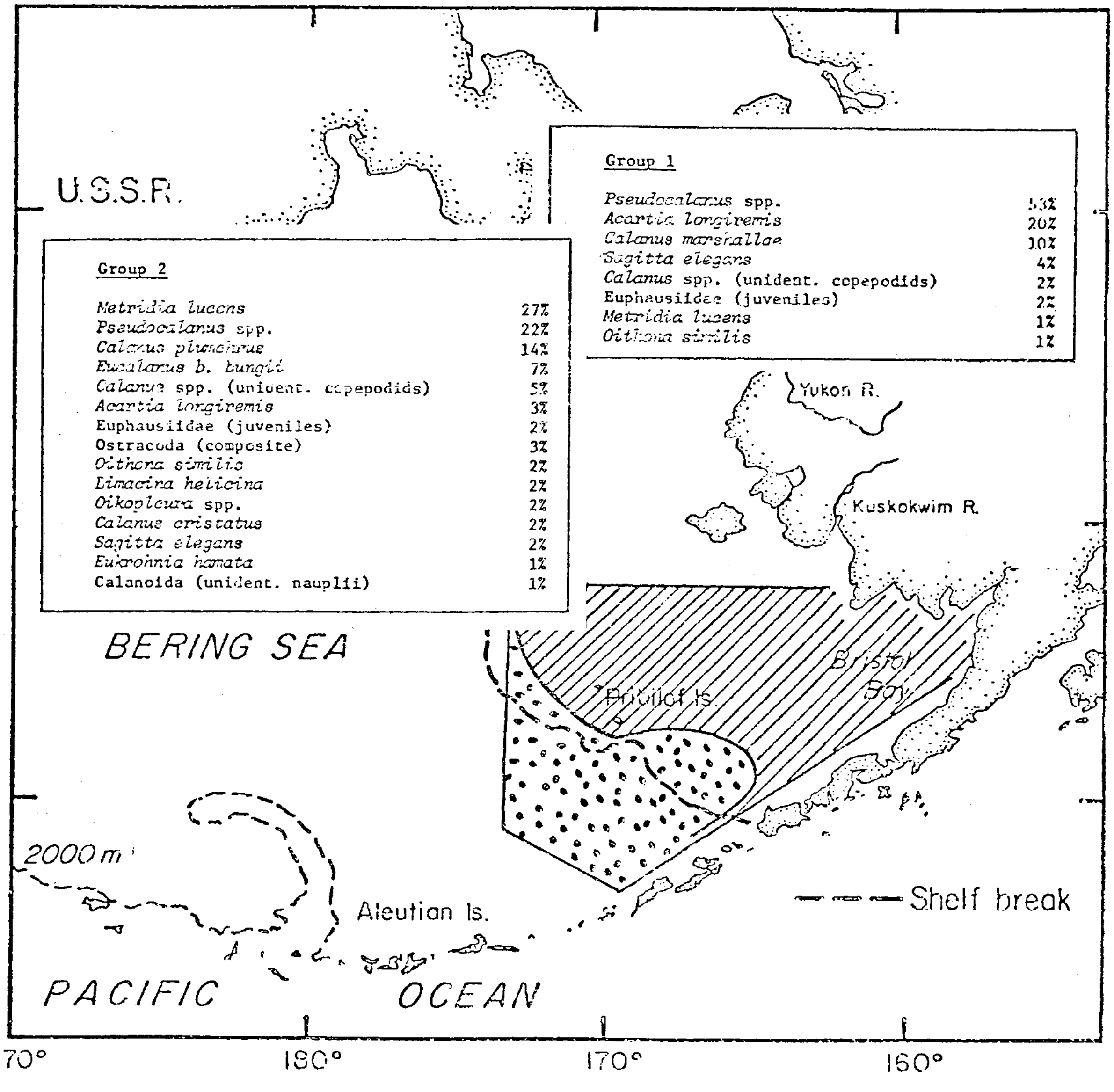
The copepod *Oithona spinirostris*, the euphausiid *Thysanoessa inermis*, and spider crab (Majiidae) larvae, mostly *Chionoecetes* spp., selected the outer shelf regime, while the central shelf water mass favored the copepods *Calanus glacialis*, *Calanus marshallae* and *Pseudocalanus* spp., the amphipod *Parathemisto libellula*, the euphausiid *Thysanoessa rashii* and the arrow worm *Sagitta elegans*.

Of the entire dominant group, only the copepod *Acartia longiremis* seemed to profer the northern coastal regime. In fact, twelve categories were completely absent from this shallow water at all times of the year.

Average dry weight as g/m^2 pooling all cruises, ranges from 3.87 in the open ocean to 2.54 in the outer shelf, down to 2.00 in the central shelf, and finally to 0.79 in the coastal zone shallower than 50 m (Fig. III-2)

However, when this data is reduced to estimates per unit volume (mg/m^3) accounting for an average depth fished in each regime (200 m, 150 m, 75 m, 25 m), the pattern is reversed with the coastal areas exhibiting about 32, the central shelf 27, the outer shelf 17, and the open ocean 19. Expressed in this manner, the various regimes differ in biomass per unit volume by less than a factor of 2.0. Pooling dry weight values (g/m^2) for all regimes within each cruise, the average seasonal variation over the year ranges from a high of 3.72 in May-June, to 1.17 in November.

Within and among the spatial regimes most populations exhibited a strong seasonal component associated with annual reproduction or migration into and/or away from ice area. Those categories which were obvious composities of early life history stages [i.e. juvenile *Calanus* spp., copepod nauplii, euphausiid eggs, larvae, and juvenile, spider crab larvae (Majidae), immature chaetognaths, and larval fish (*Theragra chalcogramma*)] are examples.



Group 1

Pseudocalanus spp.	53%
Acartia longiremis	20%
Calanus marshallae	10%
Sagitta elegans	4%
Calanus spp. (unident. copepodids)	2%
Euphausiidae (juveniles)	2%
Metridia lucens	1%
Oithona similis	1%

Group 2

Metridia lucens	27%
Pseudocalanus spp.	22%
Calanus plumchrus	14%
Eucalanus b. bungii	7%
Calanus spp. (unident. copepodids)	5%
Acartia longiremis	3%
Euphausiidae (juveniles)	2%
Ostracoda (composite)	3%
Oithona similis	2%
Limacina helicina	2%
Oikopleura spp.	2%
Calanus cristatus	2%
Sagitta elegans	2%
Eukrohnia hamata	1%
Calanoida (unident. nauplii)	1%

Figure III-2. Distributions of shelf (Group 1, lined) and oceanic (Group 2, dotted) assemblages from R-mode cluster analysis of 1-m net catches.

An R-mode cluster analysis was employed to search for distribution properties of the system independent of the statistical strata imposed for the Analysis of Variance. Pooling all cruises provided 133 stations scattered across the shelf and open ocean (exclusive of the 1977 ice-edge samples). Grouping of stations based on "alikeness" measured by ranking the percent occurrence of the dominant species revealed 7 associations (Table III-4). Two of these groupings, numbers one and two resembled in their locations, the large-scale distributions of temperature and salinity in outer Bristol Bay. Group one, dominated by *Pseudocalanus* spp. was represented by 69 stations occurring over the central and coastal regimes of the research area. Group two, dominated by *Metridia lucens* clustered 40 stations which were located almost exclusively seaward of the middle of the outer shelf regime (Fig. III-2). Spatially, these groups fall very closely into the oceanic Bering Sea/Alaska Stream water bathing the slope and outer shelf of Bristol Bay, and the central shelf water province of the southeast Bering Sea.

Ice-Edge Ecosystem

Ninety-seven taxa were sorted from 261 closing vertical tows obtained in the ice-edge zone and adjacent waters in the spring of 1977 (Table III-5). Only 14 of these categories occurred as abundantly as 10 organisms per cubic meter, 5 were recorded in excess of 100 per cubic meter, and only 1, *Pseudocalanus* spp., occasionally occurred in numbers of 1000 per cubic meter or more. Since the edge zone formed well north of the southern shelf break following the relatively mild winter of 1976-1977, the animal plankton community in the underlying water column was reflective of a mixture of oceanic and shelf species.

TABLE III-4

CLUSTER GROUPING BASED ON ALIKENESS OF DOMINANT SPECIES COMPOSITION

A. Cluster Group One; 69 Locations

Pseudocalanus spp.
Calanus marshallae
Calanus spp. (unident. copepodids)
Metridia lucens
Acartia longiremis
Sagitta elegans
Euphausiidae (unident. juveniles)
Oithona similis

B. Cluster Group Two; 40 Locations

Metridia lucens
Calanus plumchrus
Calanus spp. (unident. copepodids)
Euphausiidae (unident. juveniles)
Oithona similis
Oikopleura spp.
Sagitta elegans
Calanoida (unident. nauplii)
Pseudocalanus spp.
Eucalanus bungii bungii
Acartia longiremis
Ostracoda (composite)
Limacina helicina
Calanus cristatus
Eukrohnia hamata

C. Cluster Group Three; 5 Locations

Euphausiidae (unident. juveniles)
Calanus glacialis
Acartia longiremis
Calanus spp. (unident. copepodids)
Pseudocalanus spp.
Calanoida (unident. nauplii)
Oithona similis
Calanus marshallae

D. Cluster Group Four; 7 Locations

Oithona similis
Pseudocalanus spp.
Eucalanus bungii bungii
Calanoida (Unident. nauplii)
Calanus marshallae
Metridia lucens
Calanus plumchrus
Euphausiidae (unident. juveniles)
Ostracoda (composite)
Chaetognatha (unident. juveniles)

E. Cluster Group Five; 4 Locations

Calanus marshallae
Sagitta elegans
Acartia longiremis
Pseudocalanus spp.
Eucalanus bungii bungii

F. Cluster Group Six; 6 Locations

Asteroidea (composite)
Pseudocalanus spp.
Euphausiidae (unident. juveniles)
Acartia longiremis
Larvacea (unident. juveniles)

TABLE III- 4

CONTINUED

G. Cluster Group Seven; 2 Locations

Calanoida (unident. nauplii)
Pseudocalanus spp.
Euphausiidae (unident. juveniles)
Ostracoda (composite)
Metridia lucens
Oithona similis
Eucalanus bungii bungii
Calanus plumchrus

TABLE III-5

COMPARATIVE ESTIMATES OF STANDING STOCKS OF ZOOPLANKTON AND MICRONEKTON SAMPLED WITH A 1-M NET IN THE ICE-EDGE ZONE OF THE SOUTHEASTERN BERING SEA: MARCH, APRIL, MAY 1979

	No./m^3		
Taxa	>10	>100	>1000
Cnidaria			
Hydrozoa			
Perigonimus multicirratus			
Bougainvillia superciliaris			
Obelia longissima			
Ptychogena lactea			
Aglanthe digitale	X		
Dimophyes arctica			
Trachynemidae (unident.)			
Scyphozoa			
Chyrsaora melanaster			
Ctenophora			
Beroe spp.			
Annelida			
Polychaeta			
Typhloscolex muelleri			
Tomopteris septentrionalis			
Nereimyra multipapillata			
Scalibregma inflatum			
(Unident. composite)	X		
Mollusca			
Gastropoda			
Limacina helicina	X		
Clione limacina			
Crustacea			
Ostracoda			
(Unident. composite)	X		
Copepoda			
Harpacticoida			
(Unident. composite)			
Calanoida			
Calanus cristatus			
C. glacialis	X	X	
C. marshallae			
C. plumchrus	X		

TABLE III-5

CONTINUED

Taxa	No./m^3 >10	>100	>1000
Calanoida (cont'd)			
Microcalanus spp.			
Pseudocalanus spp.	X	X	X
Aetideidae (unident.)			
Bradyidius saanichi			
Euchaeta elongata			
Scolecithricella minor	X		
Eurytemora herdmani			
Metridia lucens	X	X	
Acartia longiremis	X	X	
(Unident. copepodids)			
Cyclopoida			
Oithona similis	X		
Isopoda			
Cryptoniscidae			
Mysidacea			
Acanthomysis dybowskii			
A. pseudomacropsis			
A. stelleri			
Neomysis rayii			
Pseudomma truncatum			
Cumacea			
Lampropos spp.			
Leucon nasica			
L. nascoides			
L. spp.			
Eudorella pacifica			
Eudorellopsis integra			
E. deformis			
E. spp.			
Diastylis alaskensis			
Amphipoda			
Monoculopsis longicornis			
Westwoodilla caecula			
Byblis gaimardi			
Orchomene spp.			
Ischyrocerus spp.			

TABLE III-5

CONTINUED

Taxa	No./m^3		
	>10	>100	>1000
Amphipoda (cont'd)			
Protomedia spp.			
Anonyx spp.			
Melita formosa			
Podoceridae (unident.)			
Pleustidae (unident.)			
Stenopleustes glaber			
Stenothoidae (unident.)	X		
Eusiridae (unident.)			
Rhacotropis oculata			
R. spp.			
Stenopiidae (unident.)			
Oedicerotidae (unident.)			
Bathymedon nonseni			
Arrhis luthkei			
Monoculodes diamesus			
M. intermedius			
M. zernovi			
M. spp.			
Metopa alderi			
Parathimisto libellula			
P. pacifica			
P. spp. (unident. juveniles)			
Primno macropa			
Protoceropsis spp.			
Euphausiacea			
Thysanoessa inermis			
T. raschii			
(unident. juveniles)			
Decapoda			
Majidae			
Paguridae			
Eualus macilenta			
Pandalidae			
Crangonidae			
Caridea			
Chaetognatha			
Eukrohnia hamata			
Sagitta elegans	X		

TABLE III-5

CONTINUED

Taxa	No./m^3		
	>10	>100	>1000
Chordata			
Larvacea			
Fritillaria borealis			
Oikopleura spp.			
Teleostei			
Cyclopteridae (unident.)			
Gadidae (unident.)			
Cottidae (unident.)			
Stichaeidae (unident.)			
Pleuranectidae (unident.)			
Lumpenus sp.			
(Unident. eggs)	X	X	

An Analysis of Variance for 8 locations, 2 depths (0-25, 26-50 m) and 2 times (day and night), performed on 9 of the 14 common taxa (> $10/m^3$) demonstrated an effect associated with location for all taxa (Table III-6). Six categories exhibited a significant depth by location interaction, while 3 organisms had obvious time, location by time, and depth effects. There was no case of a time by depth interaction, and the 3-way interaction term was evident for only 2 categories.

An analysis considering 2 locations, 4 depths (0-25, 26-50, 51-75, 76-100 m) and 2 times (day and night) revealed considerably more complexity (Table III-7). In this case, the effect of depth was significant for all taxa examined, while location was important for 8 of 11 categories. The depth by location interaction was apparent for 7 taxa. Day or night effected the catch of 6 categories, and a time by depth interaction was significant for 3. The 3-way interaction was only observed for 3 categories.

The depth preferences of the common zooplanktons indicate several patterns (Table III-8). Although euphausiids were never taken in great abundance in the 1-m net, the trend toward highest numbers in the surface waters at night was clearly evident in the catches. It cannot be said whether these more active swimmers were actually moving up into the water column at night, or simply avoiding the net near the surface during the day.

DISCUSSION

It is not surprising that many of the numerically dominant species sampled in the upper 200 m of the southeastern Bering Sea are also reported as dominant and ecologically important in the northwestern Pacific,

TABLE III-6

ANALYSIS OF VARIANCE FOR TWO LOCATIONS, FOUR DEPTHS AND TWO TIMES: APRIL-MAY 1977

Taxonomic Category	Source of Variation						
	Location F[3] df	Depth[1] F df	Time[2] F df	Location/Depth F df	Location/Time F df	Depth/Time F df	Location/Depth/Time F df
Crustacea							
Copepoda							
Acartia longiremis	** 7,32	** 1,32	NS 1,32	** 7,32	NS 7,32	NS 1,32	NS 7,32
Calanus glacialis	** 7,32	NS 1,32	* 1,32	** 7,32	NS 7,32	NS 1,32	* 7,32
Calanus plumchrus	* 7,32	NS 1,32	NS 1,32	NS 7,32	NS 7,32	NS 1,32	NS 7,32
Metridia lucens	** 7,32	NS 1,32	** 1,32	NS 7,32	** 7,32	NS 1,32	NS 7,32
Oithona similis	** 7,32	* 1,32	NS 1,32	** 7,32	NS 7,32	NS 1,32	NS 7,32
Pseudocalanus spp.	** 7,32	NS 1,32	NS 1,32	** 7,32	NS 7,32	NS 1,32	NS 7,32
Scolecithricella minor	** 7,32	NS 1,32	NS 1,32	NS 7,32	NS 7,32	NS 1,32	NS 7,32
Chaetognatha							
Sagitta elegans	** 7,32	NS 1,32	NS 1,32	** 7,32	* 7,32	NS 1,32	NS 7,32
Chordata							
Teleostei							
Fish eggs (unident.)	** 7,32	** 1,32	* 1,32	** 7,32	* 7,32	NS 1,32	NS 7,32

[1] 0-25 m; 26-50 m.

[2] Day; Night.

[3] * = $P \leqslant 0.05$; ** = $P \leqslant 0.01$; NS = $P > 0.05$.

TABLE III-7

ANALYSIS OF VARIANCE FOR TWO LOCATIONS, FOUR DEPTHS AND TWO TIMES: APRIL-MAY 1977

	Source of Variation						
Taxonomic Category	Location F[3] df	Depth[1] F df	Time[2] F df	Location/Depth F df	Location/Time F df	Depth/Time F df	Location/Depth/Time F df
Cnidaria							
Hydrozoa							
Aglantha digitale	NS 1,15	** 3,15	NS 1,15	** 3,15	NS 1,15	** 1,15	NS 3,15
Mollusca							
Pteropoda							
Limacina helicina	NS 1,15	** 3,15	** 1,15	NS 1,15	NS 1,15	** 1,15	* 3,15
Crustacea							
Copepoda							
Acartia longiremis	** 1,15	** 3,15	NS 1,15	* 3,15	NS 1,15	NS 1,15	NS 3,15
Calanus glacialis	** 1,15	** 3,15	* 1,15	NS 3,15	NS 1,15	NS 1,15	NS 3,15
Calanus plumchrus	** 1,15	** 3,15	NS 1,15	NS 3,15	NS 1,15	NS 1,15	NS 3,15
Metridia lucens	NS 1,15	** 3,15	** 1,15	* 3,15	NS 1,15	** 1,15	NS 3,15
Oithona similis	* 1,15	** 3,15	NS 1,15	* 3,15	NS 1,15	NS 1,15	NS 3,15
Pseudocalanus spp.	** 1,15	** 3,15	** 1,15	** 3,15	* 1,15	NS 1,15	* 3,15
Scolecithricella minor	** 1,15	* 3,15	NS 1,15	NS 3,15	NS 1,15	NS 1,15	NS 3,15
Chaetognatha							
Sagitta elegans	** 1,15	** 3,15	** 1,15	* 3,15	NS 1,15	NS 1,15	NS 3,15
Chordata							
Teleostei							
Fish eggs (unident.)	** 1,15	** 3,15	* 1,15	** 3,15	* 1,15	NS 1,15	* 3,15

[1] 0-25; 26-50; 51-75; 76-100 m.

[2] Day; Night

[3] $* = P \leq 0.05$; $** = P \leq 0.01$; NS = $P > 0.05$.

TABLE III-8

VERTICAL DISTRIBUTIONS OF ELEVEN COMMON ZOOPLANKTERS FOR THE ICE-EDGE ZONE OF THE SOUTHEAST BERING SEA APRIL-MAY 1977

A. Usually Most Abundant Above 50 m

Oithona similis
Acartia longiremis
Fish eggs
Pseudocalanus spp.

B. Usually Most Abundant At Mid-Depth, 25-75 m

*Aglantha digitale**
Calanus glacialis
Calanus plumchrus

C. Usually Most Abundant Below 50 m

*Limicina helicina**
Scolecithericella minor
*Metridia lucens**
Sagitta elegans

* Denotes vertical migrator found shallower at night than during daylight hours.

the northern Gulf of Alaska and the western Bering Sea (Minoda, 1971; Cooney, 1975; LeBrasseur, 1965). The general counter-clockwise surface circulation provides a near shelf and coastal "river in the sea" which carries plankton populations to the north from the subarctic current around the periphery of the northern Gulf where the Alaska Stream then moves them westward along the Aleutian Chain and eventually into the Bering Sea. This biological continuity was observed over the shelf south of Hinchinbrook Entrance to Prince William Sound in the northern Gulf of Alaska where the species composition was found to be nearly identical to that reported at the Canadian offshore weather station P some 800 nautical miles upstream (Cooney, 1975). The numerically common oceanic copepods *Calanus cristatus*, *Calanus plumchrus*, *Eucalanus b. bungii* and *Metridia lucens*, the amphipod *Parathemisto pacifica*, the chaetognaths *Eukrohnia hamata* and *Sagitta elegans*, and the pteropods *Clione limacina* and *Limacina helicina* are all major constituents of the holoplankton in the shelf and open ocean waters between station P and the Pribilof Islands.

The unobtrusive fauna found in association with the ice-edge zone of the southeast Bering Sea occurs more in response to the overall distribution of water mass properties than in relation to the presence of the edge zone. During years with cold winters, the southern most terminus of ice intrudes the outershelf and oceanic water at the shelf break. In this region, the cold ice-related environment overlies warmer Bering Sea/Alaska Stream water and a well defined 2-layered system is observed. Here, the typical oceanic community is present in the deeper warmer water, with fewer species occurring in the cold under-ice watermass that can extend down to 80 m. There are some organisms (euphausiids, amphipods, and *Metridia* *lucens*) which migrate dielly into the colder surface waters. Following warmer winters, the edge zone rarely builds into the outer shelf regime and so is primarily associated with the central shelf pelagic fauna, described previously as being less diverse and without the dominant interzonal copepods.

The major ramification of these differences is in the way in which the pelagic consumer assemblage is able to utilize the yearly production originating in the photic zone. As has been noted, the oceanic north pacific grazing community appears as progeny from overwintering populations deep in the water column. The presence of these organisms early in the season assures a very close coupling between the producers and consumers. Such is apparently not the case in the southeast Bering Sea where the relative stability of the two dominant water masses (ocean and shelf) apparently prevents or greatly reduces the mixture of faunas in the early spring. No onshore advective system such as occurs in the northern Gulf of Alaska is present between the Pribilof Islands and Unimak Pass to move the oceanic community over the shelf.

Therefore, during the period of the spring bloom, April through May, a very great percentage of the organic matter synthesized in the water column shallower than about 100 m is essentially ungrazed and sinks to the sea bed as direct input to the benthos. Walsh *et al.*, 1978, indicate that at times, a similar phenomena occurs in the New York Bight area off the eastern continental shelf of New York. At time less than 1-7 percent of the primary production is incorporated in the water column by grazers; the remainder sinks to the sea bed.

The southeast Bering Sea appears essentially to be a region in which two very different food webs are sustained by primary production. Seaward of the 100 m contour, the oceanically dominated pelagic community, "soaks up" a large percentage of the annual production supporting a diverse and abundant fauna, particularly at higher trophic levels. The walleye pollock, (*Theragra chalcogramma*), is a key element in this pelagic system. Over the shallow shelf, the less diverse grazing community in the water (dominated by small copepods) leaks much of the production to the bottom. Here, stocks of crabs, clams, and bottom fishes reflect the nature of the detritally driven benthic assemblage. The degree to which the distribution of benthic feeding assemblages conform to the oceanic/shelf watermasses is quite remarkable (H. Feder, personal communication).

The importance of the ice-edge zone as it relates to the zooplankton and micronekton communities is seemingly in its position from year to year relative to the two major water types it occurs over. Birds and mammals foraging in the edge zone will encounter different food species depending on whether the edge begins in association with the oceanic system (cold winters) and then retreats northward over the shelf, or form only over the shelf. Walleye pollock, the oceanic euphausiids *Thysanoessa longipes* and *Thysanoessa inermis* and the amphipod *Parathemisto pacifica* are ocean species and would be expected seaward of the 100 m contour. The euphausiid *Thysanoessa raschii*, and the amphipod *Parathemisto libellula* are two large forage species found over the central shelf.

Fish eggs and larvae are important elements of the seasonal plankton in both the oceanic and shelf regimes. Following the very cold winter of 1975-1976, early observation in March revealed the presence of very high concentrations of fish eggs in the surface waters of the edge zone near the Pribilof Islands. Later examination of these eggs indicated most were from spawning populations of walleye pollock, which move into the outer shelf to reproduce as early as February each year (T. Nishiyama, personal communication). The fate of these eggs rising from spawners near the bottom and encountering the ice above is unknown.

The dominance of the small copepod *Pseudocalanus* spp. is of considerable importance to the survival of larval fishes in outer Bristol Bay. Clarke (1978) demonstrated that the first feeding newly hatched walleye pollock were dependent almost entirely on the eggs and nauplii of *Pseudocalanus* spp. Cooney *et al.* (1979) observed that *Pseudocalanus* spp. populations were highest in the vicinity of the inner front production zone (about 100-80 m depth contours) even though a great percentage of the phytoplankton bloom in progress there was sinking out of the photic zone. Apparently, this small copepod is able to obtain a good ration from the smaller constituents of the bloom but not able to couple effectively with the larger diatoms. The genus occurs in all oceanic regimes and at all depths above 200 m. It is probably one of the most energetically important microconsumers in the Bering Sea.

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CHAPTER IV

ORGANIC MATTER SYNTHESIS AND TRANSFER PROCESSES IN THE ICE EDGE ECOSYSTEM

INTRODUCTION

The edge of the seasonal ice on the Bering Sea shelf is a region of intense biological activity in the spring, and is of crucial importance to this marine ecosystem, affecting components ranging from marine birds and mammals to benthic communities. It may, in fact, represent the environment in which the majority of the annual *in situ* carbon synthesis occurs in the S. E. Bering Sea shelf area. Break-up of the ice is not a uniform process of retreat, but occurs periodically with wind and wave action, and very often areas covered with ice persist to the south of other areas in which ice is no longer present. Since in our work the role of the retreating ice edge and the potential vulnerability of the ice-edge ecosystem to impact was the major emphasis, a brief background discussion will preceed a summary of our findings. The data have almost all been reported previously, and here an attempt is made to synthesize the information. We will show that areas of broken ice seem to provide a mechanism for an intense surface bloom, whereas little production occurs in the water column below the ice in spite of high post-winter nutrient levels. This is clearly due to the restricted light penetration through the ice. Following the break-up of the large ice plates into ice chunks with open spaces between which allows light penetration, when mixing is still attenuated due to the presence of ice, an intense bloom occurs. Areas of ice slush are particularly suitable for diatom growth, and photographs taken from a helicopter in a clear day clearly have shown that the chlorophyll content of this ice was already very high on the day following a night storm which formed such slush. The system, thus, is primed and ready to bloom.

The southeast Bering Sea shelf is a broad (≈500 km) shallow (shelf break ≈150 m) highly productive region that has been studied extensively by OCSEAP. The results of these and other studies show the oceanographic, meteorological and ice conditions to be extremely seasonal. In addition, in the last few years (≈1975-present) there seems to be a strong fluctuation in the mean weather or short-term climate superimposed on the seasonal signal. This is hypothesized to have an effect on the shelf circulation including ice coverage.

In considering the overall circulation of this region of the eastern Bering Sea, it has been suggested that there are three fronts on this shelf, all approximately parallel to the bathymetry. (A front here is defined as a strong horizontal gradient of a parameter, [eg $S^{\circ}/_{oo}$].) Schumacher *et al.* (1978) illustrate a structural front at about 50 m depth while Coachman and Charnell (1979) consider a double front system with an inner front at 100 m depth and an outer front at the shelf break (about 150 m). Schumacher *et al.* suggest that the 50 m front is a narrow transition zone that separates a well-mixed coastal domain from a two-layered central shelf region. The front does not separate two distinct water masses but rather a seasonally varying balance between buoyant energy input and tidal stirring that allows the formation of seasonally differing water masses. In addition, Schumacher *et al.* find that ice cover influence and salinity distribution is important in the frontal structure but that mean flow is small (2<cm/sec).

Coachman and Charnell (1979) provide a rather complete summary of the oceanographic regime of outer Bristol Bay. The shorter time scale circulation of this section of the southeast Bering Sea shelf is dominated by tides and wind events. However, the longer time scale mean flow is weak, on the order of 1-2 cm sec^{-1} moving from the southeast to the northwest parallel to the shelf bathymetry. This has the effect of decoupling the transport of mass characteristics (S°/₀₀, T°C etc) from the mean advection (see eg. Csanady, 1976) and makes their movement a function of diffusion.

The diffusive transport of salt and heat in the case of this broad shallow shelf is perpendicular to the shelf bathymetry between a fresher, colder <u>shelf water</u> and a warmer, more saline <u>Alaska Stream/Bering Sea</u> source water off the shelf. The interaction of these water masses occurs between the 100 m isobath and the shelf break. As previously mentioned, this zone contains two fronts, one over the 100 m isobath and the other over the shelf break, separated by a 50-100 km wide transition zone with no frontal characteristics. The Bering Sea/Alaska Stream water intrudes as a bottom layer shoreward to the inner front. Above this intrusion, but beneath 30 m, the shelf water moves seaward. Coachman and Charnell (1979) conclude that this 50-100 km transition zone is an area in which the two water masses actually meet and mix *via* layering. This layering is expressed as fine structure (1-10 m) instabilities in a layer beneath the surface wind mixed layer and above a bottom tidally mixed layer.

Reed (1978) considered changes in heat content in two 1° X 1° areas in the region of the "inner front" of Coachman and Charnell. Due to the low net flow in the region, advection of heat was neglected. His data also suggested that gain of heat through horizontal diffusion had little effect on the heat budget and that net radiation is typically the dominant heat flux in the southeast Bering Sea in summer. During the early fall, evaporation and heat conduction fluxes became significant due to increased wind speed and rapid cooling of the overlying atmosphere. In winter, because of the high latitude and extensive ice cover, the net heating is relatively low in comparison to other open ocean areas. The conclusion drawn is that net heat gain or loss here is primarily through air-sea interaction.

Relatively little work has been done on relationships between the ice cover and weather in the Bering Sea. Konishi and Saito (1974), using 12 years of data, state that stagnant weak weather fronts and lows frequently exist along the ice edge in the PROBES area in the Bering Sea. They suggest that low pressure systems flowing northward over the Aleutians in the Bering Sea become stationary in the vicinity of drift ice and dissipate. Conversely, low pressure systems and accompanying fronts that move southward over the Bering Sea gain in force over the warm sea surface in the vicinity of the ice edge. Konishi and Saito (1974) conclude that a stagnant frontal zone is always found at the southern edge of the sea ice, and lows are seen to move along the frontal zone. Moreover, the occluding low pressure will at times move westward and in this way the sea ice may have the effect of blocking low pressure system migration.

Muench and Ahlnäs (1976) observed ice movement and distribution in the Bering Sea using satellite imagery from March to June 1974. They found ice movement was southerly in response to northerly winds until late April after which variable ice motion reflected variable winds.

Johnson and Sackel (1976) have pointed out a climatic shift which occurred in the early 1970's in the Bering Sea which has had a drastic effect on some Alaska fisheries. The low salmon catches in 1973-74 are attributed to the effects of the unusually cold winters of 1971-72 in the Bering Sea. The onset in the decline of SST coincides with anomalous southward penetration of the ice pack (Kukla and Kukla, 1974). McLain and Favorite (1976) related the cold SST to large scale changes in the atmospheric circulation which caused northerly wind over the Bering Sea. Niebauer (1978) has further related a subsequent rise in sea surface temperature in the Bering Sea to, again, large scale changes in the atmospheric circulation which caused southerly flow over the Bering Sea.

The importance of sea ice and the ice-edge to primary production has been discussed previously for the Bering Sea by McRoy and Goering (1974). These authors attributed a substantial primary productivity contribution by algae growing in the ice cover in immediate contact with the sea water, amounting to as much as 44 mg $C/m^3 \cdot$day. They have also described an annual sequence of events in the spring beginning with the ice algae bloom, followed by an ice-edge bloom and finally by a regular spring bloom. With the exception of the spring bloom, our results substantiate this postulated sequence. However, these are not original comments on the role of ice. Zenkevitch (1963) states that the development of the phytoplankton of the arctic basin is closely bound up with ice conditions and that the main development of the spring plankton (mainly diatoms) coincides with the melting of the ice and the penetration of light into the water column. Most of the published discussion relating to ice and primary production has, however, referred to the ice algae, and for these there is a considerable volume of information. Clearly, such production in the lower layers of ice occurs throughout all polar oceans. In northern areas covered by seasonal ice, this ice production occurs somewhat before break-up of the ice, although our recent observations for the antarctic waters suggest that there such activity persists throughout the entire austral summer. This difference between arctic and antarctic waters is possibly related to the more adequate nutrient availability in the antarctic. With respect to ice margin observations for the antarctic, Ivanov (1964) has emphasized the uniformity in phytoplankton populations with latitude except at the ice edge, where the noted intense blooming of phytoplankton in the pack ice region and assumed it due to the liberation of algae growing in the ice. The relationship between seeding from the ice and ice-edge blooms is not clear; whereas some evidence exists for seeding from ice algae, Horner and Alexander (1972) have noted that the species of algae in the water both during and after the ice-algae bloom in the Chukchi Sea were not the same as those of the ice community itself, and that the ice community was dominated by benthic rather than pelagic forms. The ice community was dominated by pennate diatoms, more characteristic of the benthic than the pelagic environment, and these authors therefore discounted the importance of seeding from the ice. It is suffice here to say that both the ice and the ice-edge communities have been reported, but the ice community has received more study than has the phenomenon of the ice edge bloom. Since the first comment by Gran (1904) on ice diatoms, the phenomenon of algal growth in ice has received considerable attention. The ice-edge system demands availability of ships on a standby basis, since the timing of events varies from year to year, and the planning of cruises cannot be made in advance. From this point of view, the availability of ship support during several months of the spring season each year throughout the duration of this project has allowed a previously unattainable intensity of study and coverage of the spring ice edge-bloom throughout three years.

RESULTS

The results are presented in two sections: 1) historical large scale temperature, weather and ice changes, and 2) ice edge hydrography for 1975-77.

Large Scale Fluctuations

The dramatic changes in sea surface temperature (SST) over the past 16 years on the southeast Bering Sea shelf are illustrated in Figure IV-1. The mean annual SST was 4.1°C in 1963, rising to 5.4°C in 1967 before falling to 2.8°C in 1975. Since 1975, there has been a rapid rise reaching 4.8°C in 1977. Figure IV-2 shows these trends in the monthly mean SST. It is interesting to note that the June record is significantly warmer than the February-May data. January (not plotted) is of the same approximate level as June suggesting the February-May is the oceanographic winter on the shelf.

Figure IV-1 illustrates the bottom temperatures on the shelf which generally follow the trend of the SST and are significantly correlated with the SST. This suggests that the process that causes fluctuations in SST also causes fluctuations throughout the water column. Reed's (1978) work, along with the strong correlation between June shelf bottom water temperature and the previous winters degree-day data (Coachman and Charnell, 1979) suggest that the cause may be found in the climate (or fluctuations in climate) of the region.

To outline this theory, Figure IV-3 illustrates the monthly mean 700 mb pressure chart in the winter of 1974-1975 showing essentially meridional flow from the arctic south into the Bering Sea. Some of the flow then turns east and flows into the southeast Bering Sea. This cold arctic air appears to cool the underlying Bering Sea. The onset in the decline of SST coincides with anomalous southward penetration of the ice pack (Kukla and Kukla, 1974)

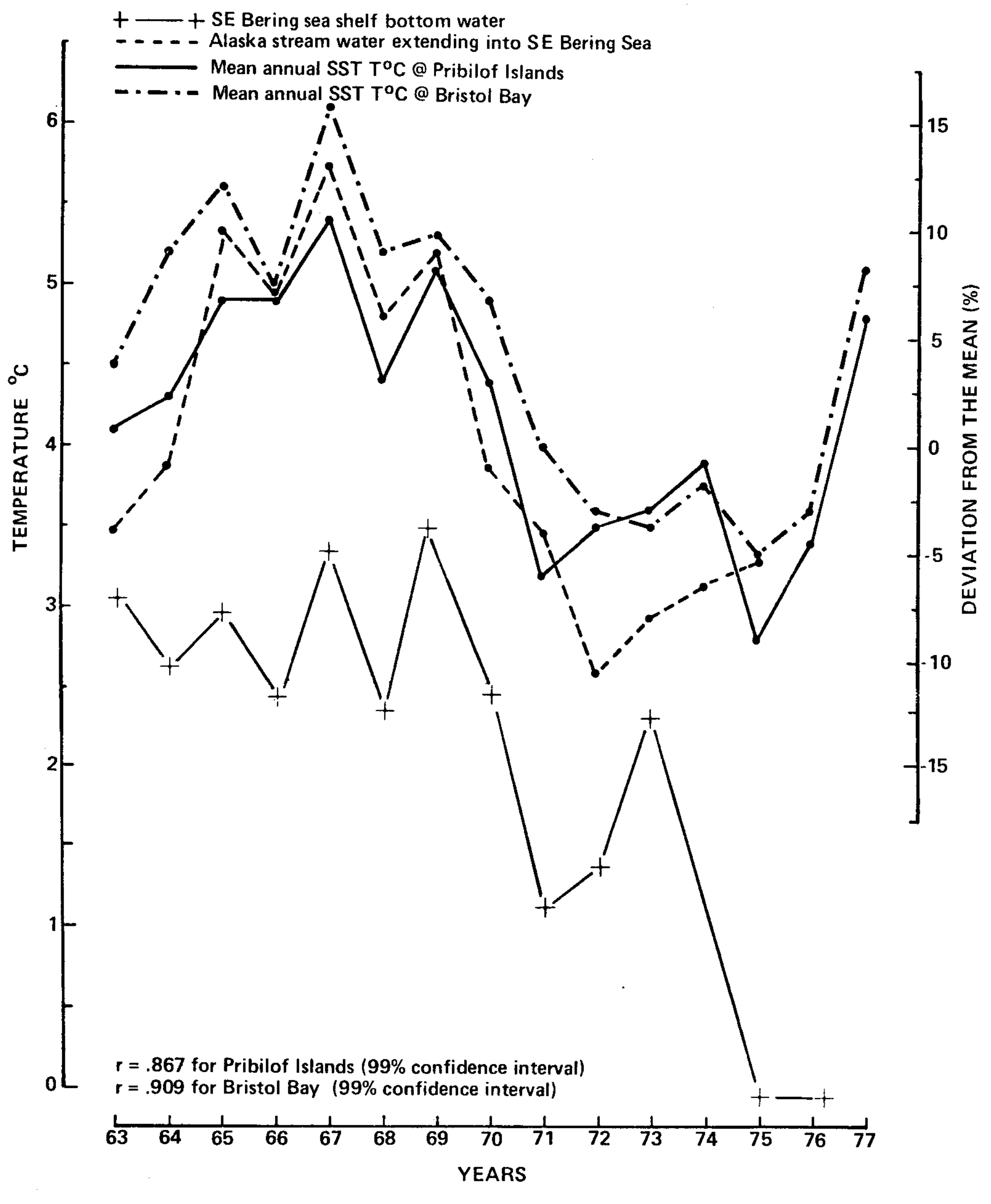


Figure IV-1. Mean annual sea surface and sea bottom temperatures for the S. E. Bering Sea.

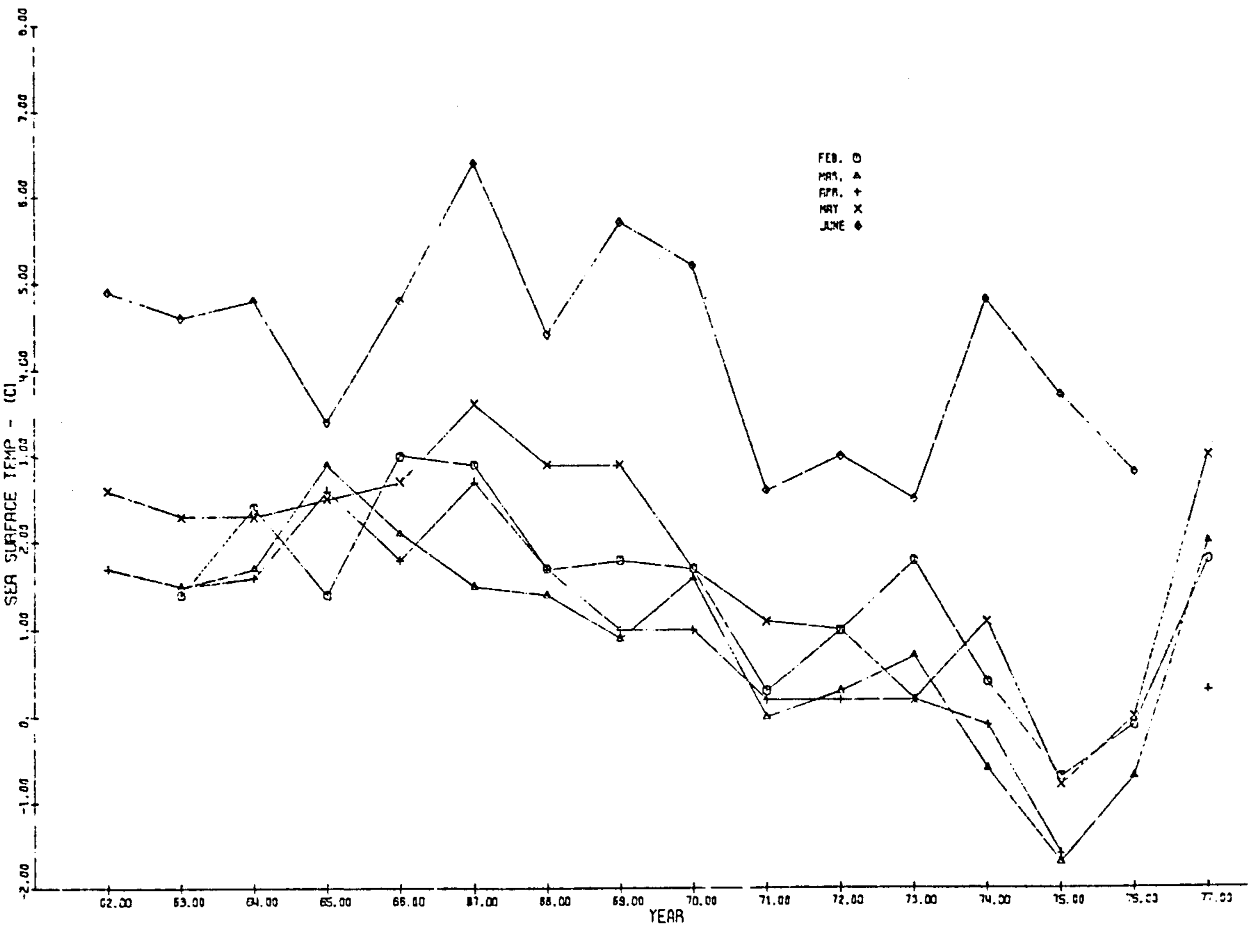
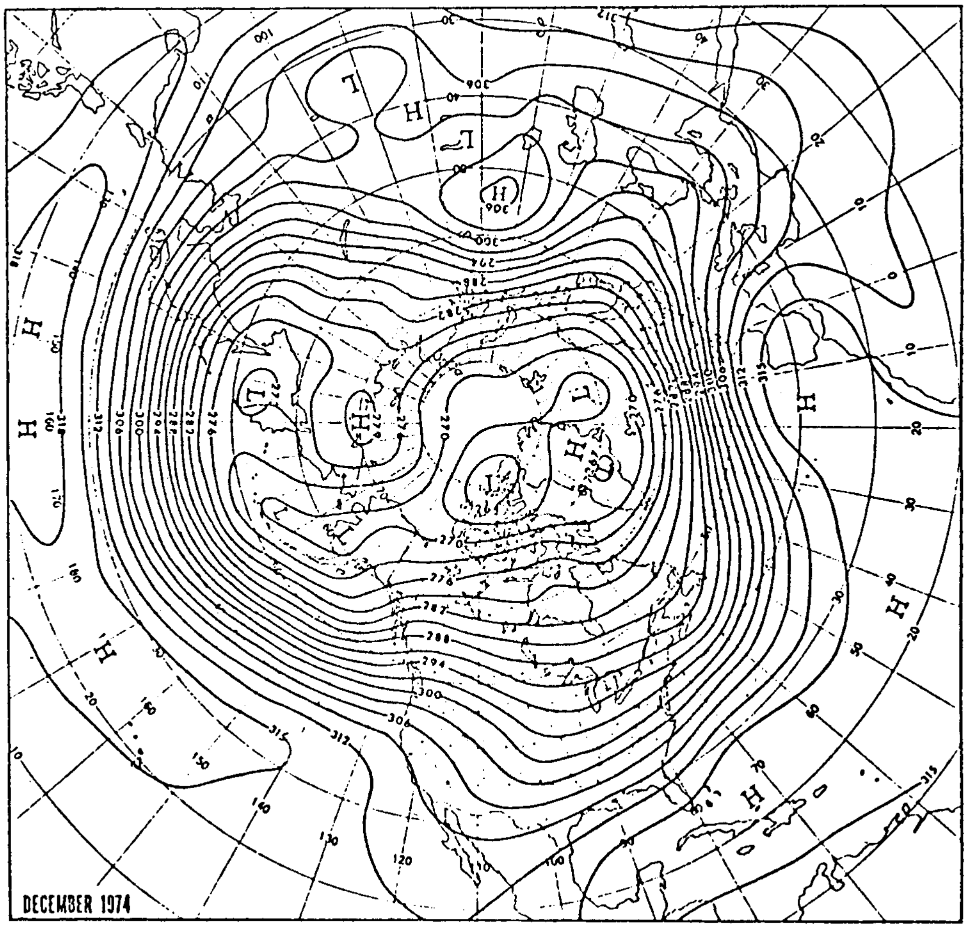


Figure IV-2. Mean monthly sea surface temperatures for the S. E. Bering Sea.



Mean 700 mb height contours (dekameters) for December 1974.

Figure IV-3. Monthly mean 700 mb pressure chart (Taubensee, 1975).

or perhaps, vice versa. Typical ice conditions for 1975 are illustrated in Figure IV-4 which shows ice extending 10-45 nautical miles south of Pribilofs on the western edge of the shelf and covering part of Bristol Bay to the east. Figures IV-1 and IV-2 illustrate the cold SST of this time period. The extremely low SST in 1975 may be due both to southward movement of the ice around the Pribilofs and to air sea interaction.

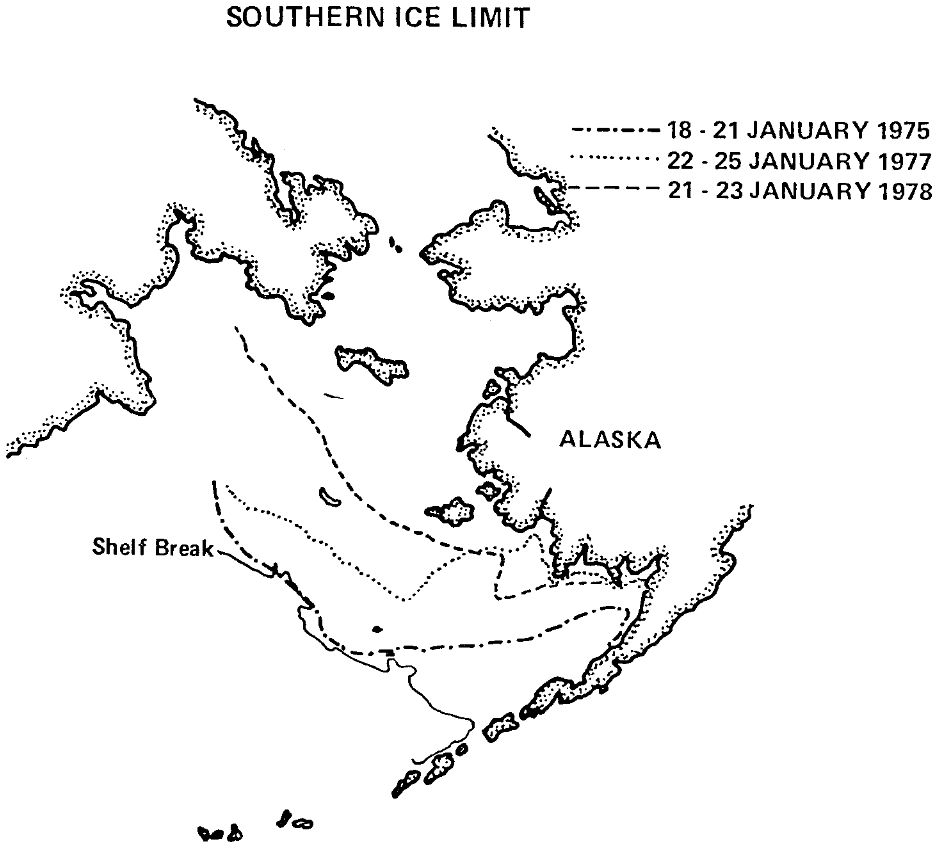
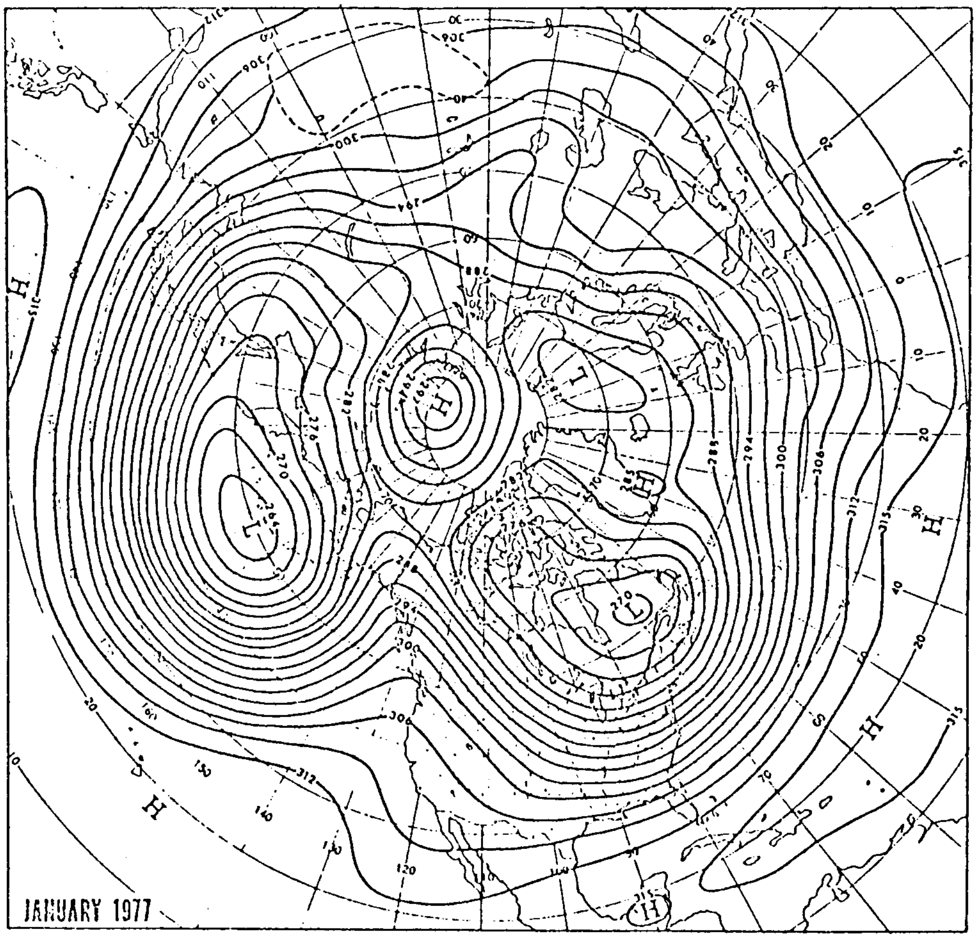


Figure IV-4. Southern ice limit for 1975, 1977, 1978.

Figure IV-5 illustrates the mean 700 mb contours for February 1977 which shows the Aleutian Low over the western Aleutians and strong meridional flow into the southeast Bering Sea from the north Pacific. Namias (1978) has suggested that SST patterns in the north Pacific in November 1976, foretold the strong and persistent air flow from the south over the Bering Sea during the winter of 1976-1977. These air flow patterns can explain,

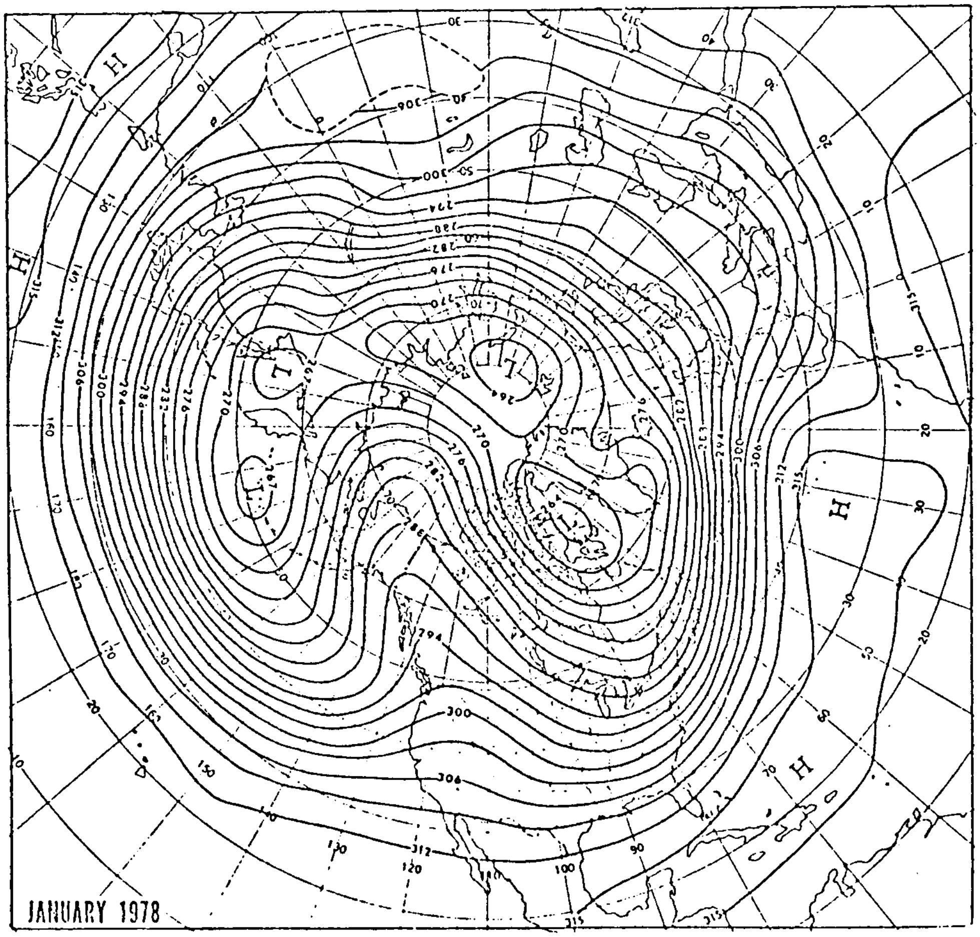


Mean 700 mb height contours (dekameters) for January 1977.

Figure IV-5. Monthly mean 700 mb pressure chart (Wagner, 1977).

to a large measure, the high SST in the Bering Sea. Figure IV-4 illustrates the ice conditions showing the position of the ice to be much farther north than the colder year of 1975. Specifically the ice edge is on the order of 2° or 120 nautical miles north of the Pribilofs on the western shelf and is almost excluded from Bristol Bay to the east.

Figure IV-6 shows the 700 mb situation for 1978 which is similar in some respects to 1977. The SST (Figures IV-1 and IV-2) and ice edge position



Mean 700 mb contours (dam) for January 1978.

Figure IV-6. Monthly mean 700 mb pressure chart (Wagner, 1978).

(Figure IV-4) for 1977 and 1978 are similar. Note that the ice edge is nearly 3° or 180 nautical miles north of the Pribilofs in 1978.

The point is that such dramatic changes in the ecosystem environment must be taken into account when conducting relatively short-term (on the order of 2-3 years) experiments on the ecosystem inhabitants (e.g. sampling and mapping primary productivity in the ice edge of the Bering Sea).

Ice-Edge Hydrography

Against this background of the larger scale weather, sea temperature and ice fluctuations, we consider the ice edge hydrographic data that were collected on the OCSEAP Bering Sea cruises in May 1975 and March-April 1976 and 1977. The approximate times of these data are indicated in Figure IV-7 which also shows monthly mean SST and degree-day data for the Pribilof Islands. The SST plot shows the oceanographic winter of 1975 to be abnormally cold. 1976 was not quite so cold overall but remained colder farther into spring. Nineteen seventy seven was near normal with shorter time scale fluctuations.

The 1975 degree-day curve shows an abnormally cold November 1974-March 1975 but returns to normal by April. In 1976 the months of January-May were below normal while for the winter of 1976-77, only November and December were below normal. As with the larger scale data shown in the preceding section, these fluctuations in the degree-days correlate quite well with the 700 mb flow. Inspection of Figure IV-7 suggests that the SST follows fluctuations in degree-days with a 1-2 month delay.

The hydrography of 1975 were collected late in the Bering Sea oceanographic winter that was abnormally cold and the ice edge (Figure IV-8) was still quite far south. The hydrography in 1976 were collected 1-2 months earlier in an abnormally cold winter that lasted longer (ie, into May). In this case the ice edge was farther south almost to the shelf break (Figure IV-9). The 1977 hydrography were collected at the same time of the year as that of 1976 but the winter was considerably milder so that the ice edge was much farther north than the two previous years (Figure IV-10).

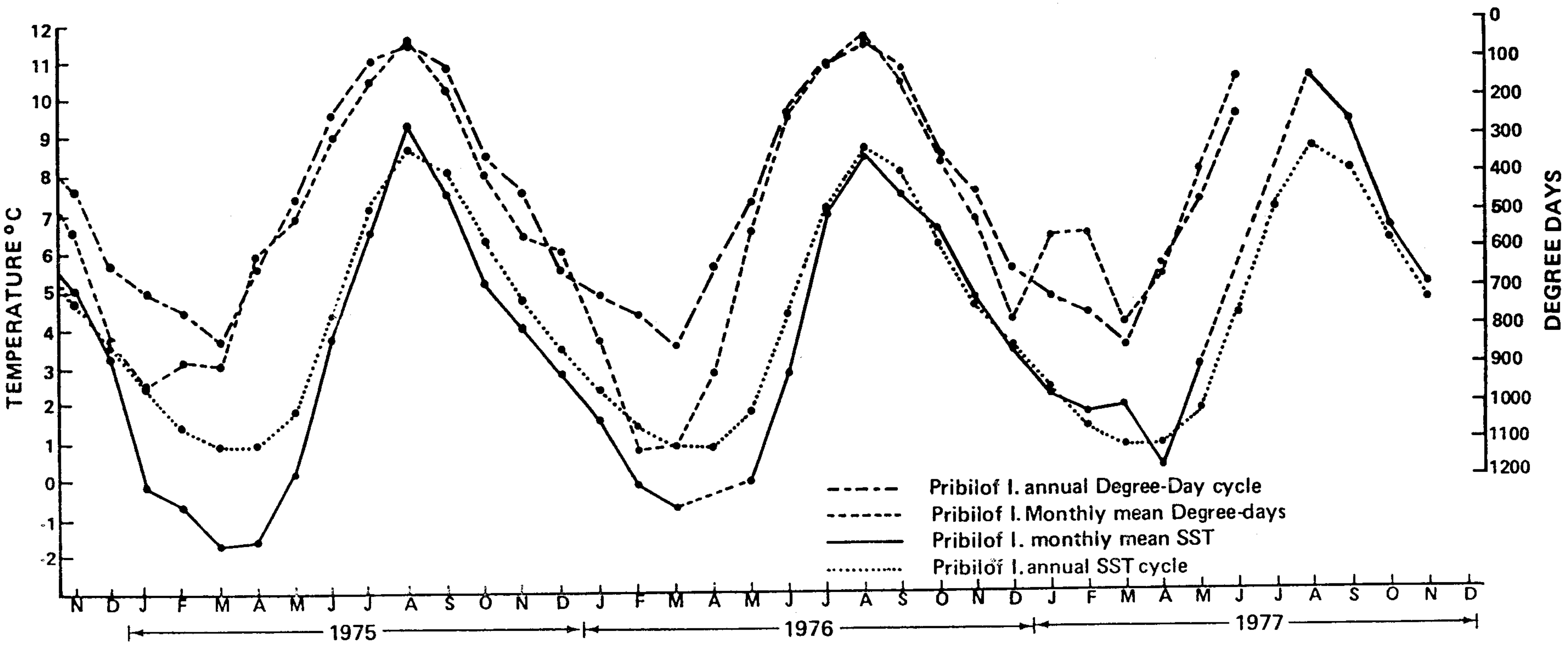


Figure IV-7. Monthly mean sea surface temperatures and degree-day data for the Pribilof Islands for 1975-1977.

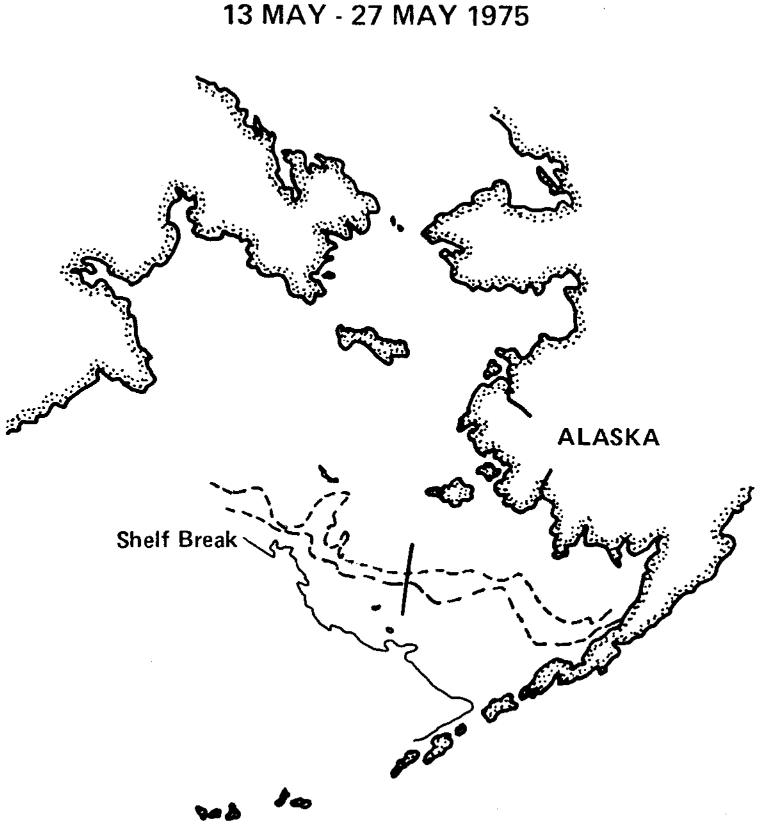


Figure IV-8. 1975 ice edge cruise showing transect.

The position of the temperature, salinity and sigma-t sections (Figure IV-11) for 1975 is shown in Figure IV-8 to be far up on the shelf. The ice edge temperatures are on the order of -0.5 to -1.3 °C but decrease with depth to -1.6 to -1.7 °C at 65-70 meters. Farther away from the ice, the surface temperatures reach 0.1°C. Salinities in the ice are on the order of 31.2°/₀₀ rising with depth to 32.0°/ ₀₀ at the bottom and rising with distance away from the ice to a maximum of 31.8°/₀₀. The thermocline, halocline and hence pycnocline are at 20-30 m depth extending throughout the section although they are most developed at and within the ice edge. All the water found here is the <u>shelf water</u> of Coachman and Charnell (1979).

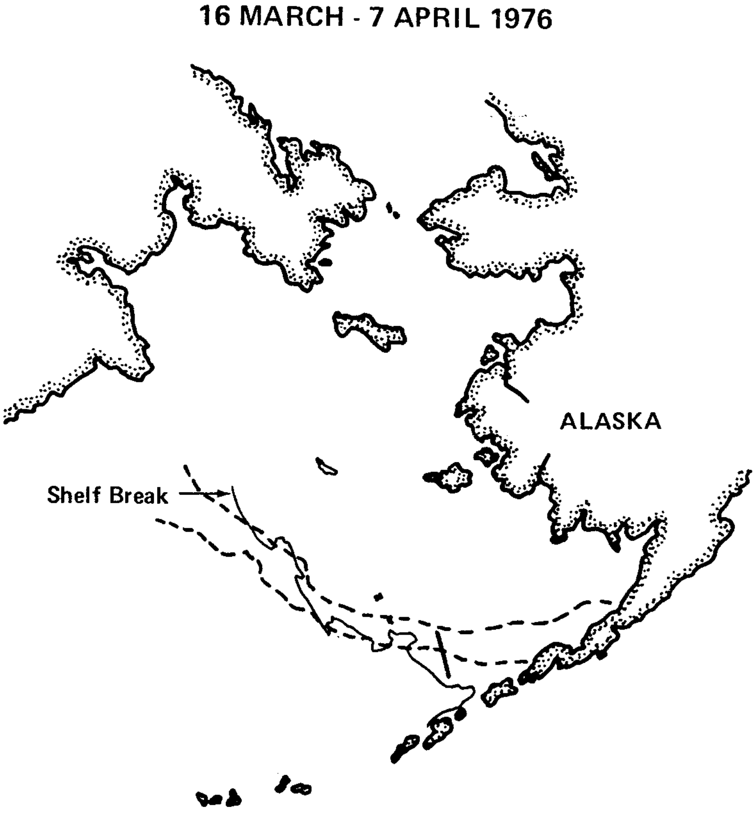


Figure IV-9. 1976 ice edge cruise track showing transect.

The sections for 1976 are farther south near the shelf break (Figure IV-12). The upper layer (0-60 m) shape of the isotherms is similar to that in 1976 as are the ice edge temperatures. However, the vertical temperature gradient is reversed. There is now a strong thermocline much deeper at 70-90 meters with <u>Gulf of Alaska - Bering Sea</u> source water (T°C = 3-4°C) below. The salinity data display these same characteristics of low $S^{\circ}/_{\circ\circ}$ ($31.7^{\circ}/_{\circ\circ}$) at the ice edge increasing both with distance from the ice and with depth. A strong halocline is present at 70-90 meters with the source water ($S^{\circ}/_{\circ\circ} > 32.0$) beneath. The density data also shows the strong pycnocline at 70-90 m.

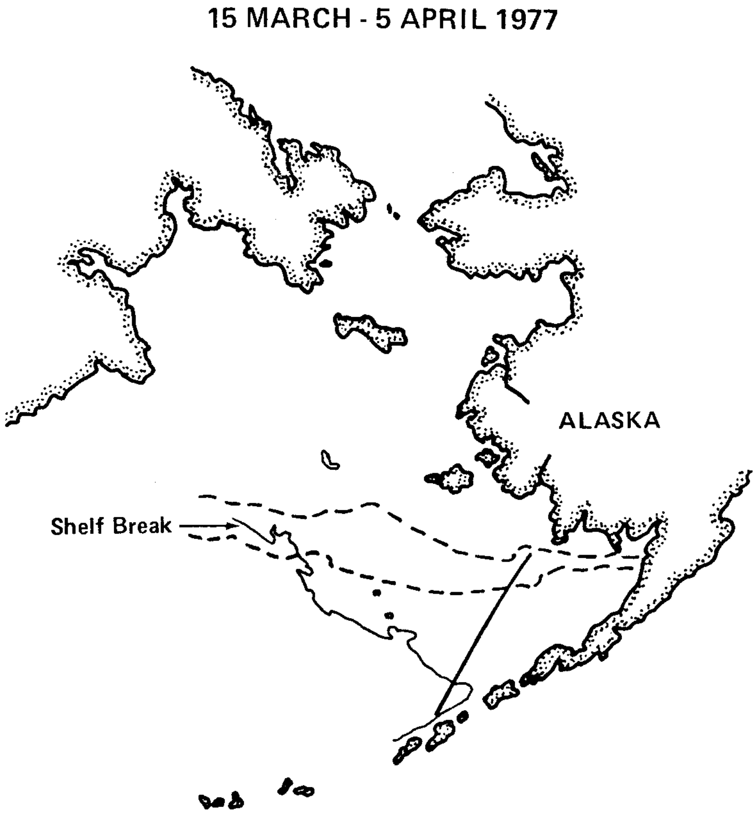


Figure IV-10. 1977 ice edge cruise track showing transect.

The 1977 data constitute a much longer section (Figures IV-10 and IV-13) ranging from off shelf up to the 40 m isobath. The ice edge temperatures (-1.4°C) and salinites (31.6$^{\circ}/_{\circ\circ}$) are similar to those of 1975-1976. The water out to about station 19 looks vertically mixed with a horizontal gradient. This gives the appearance of a rather diffuse frontal zone (see eg. Shumacher *et al.*, 1978). The two front systems of Coachman and Charnell

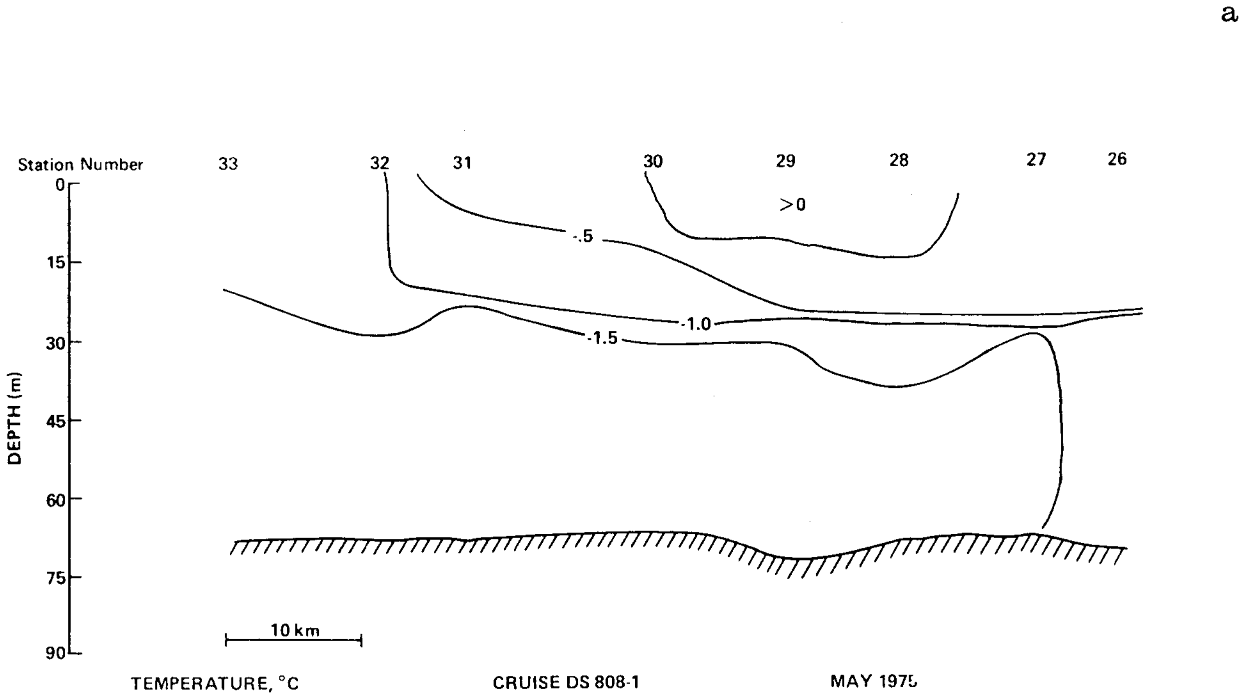
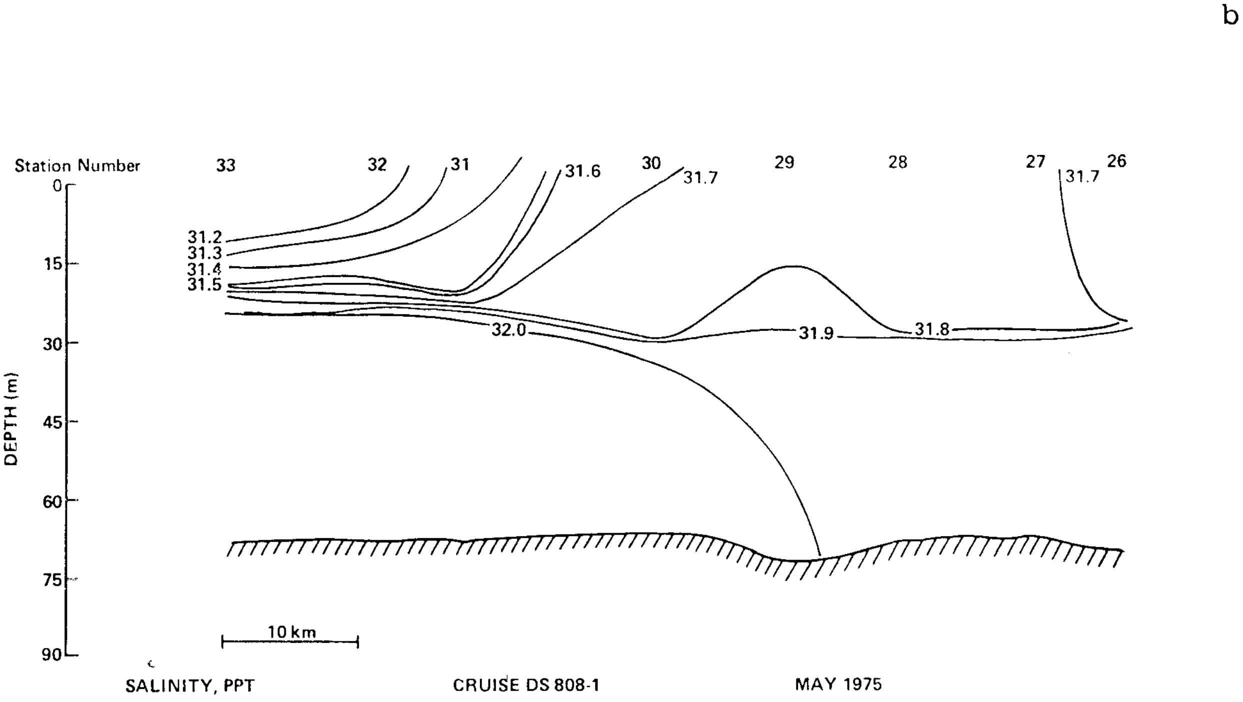


Figure IV-11. Cross section of (a) temperature, (b) salinity, (c) sigma-t, (d) nitrate, (e) ammonia and (f) chlorophyll 1975.



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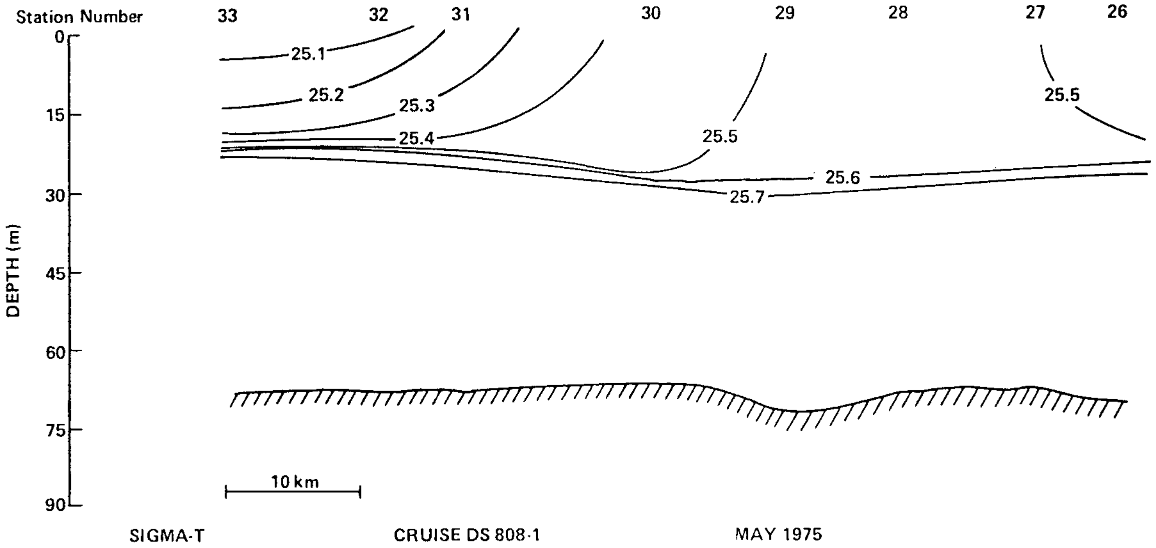
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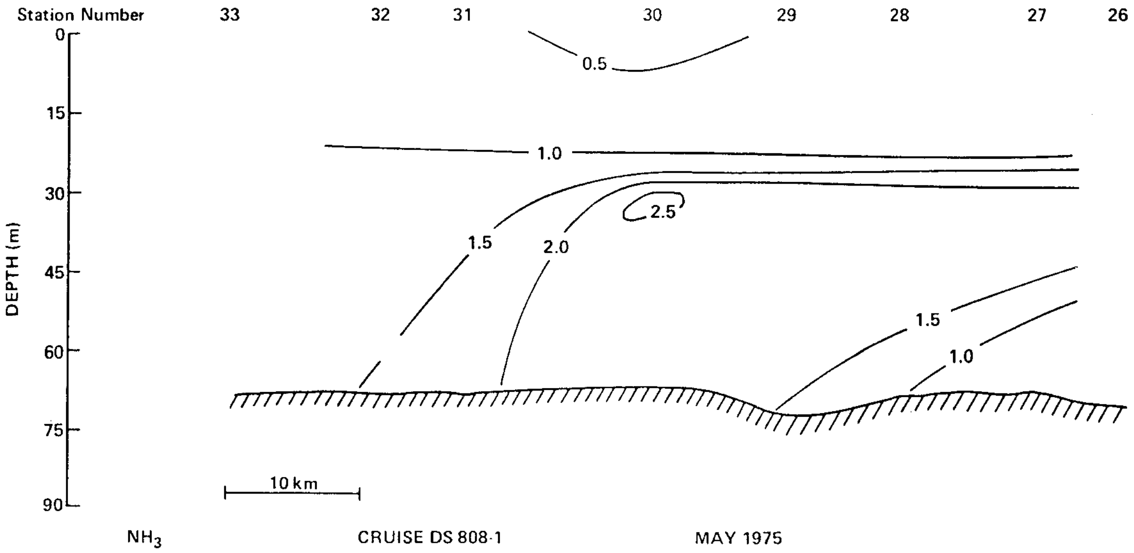
32
31
30
29
28
27
26
0
15
30
45
60
75
90
DEPTH (m)
25.1
25.2
25.3
25.4
25.5
25.5
25.6
25.7
10 km
SIGMA-T
CRUISE DS 808-1
MAY 1975

d


Station Number
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32
31
30
29
28
27
26
0
15
30
45
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75
90
DEPTH (m)
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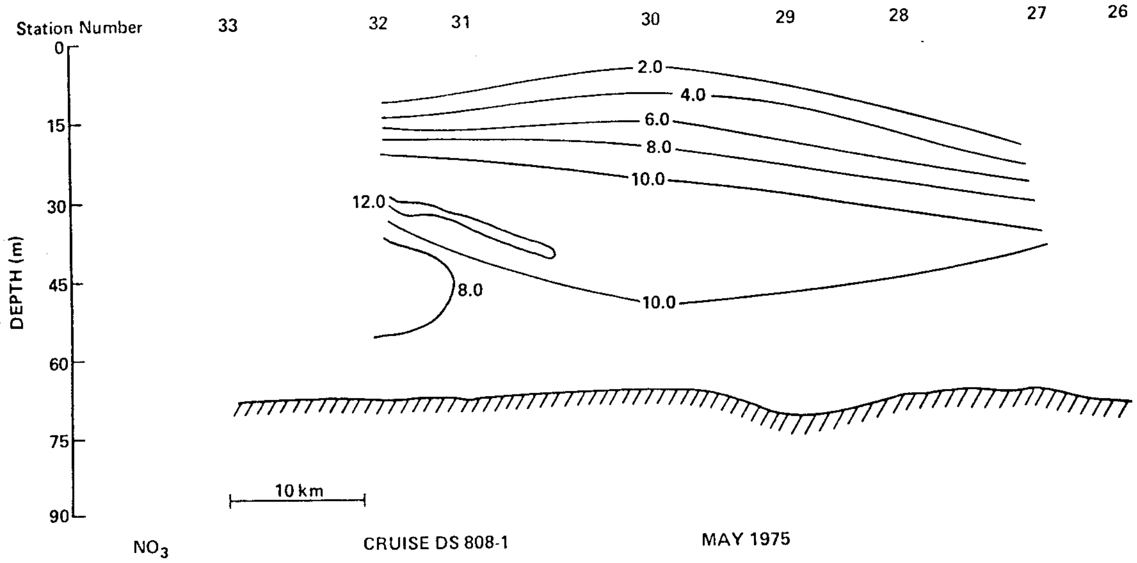
1.5
2.0
2.5
1.5
1.0
10 km
NH3
CRUISE DS 808-1
MAY 1975

e



Station Number
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30
29
28
27
26
0
15
30
45
60
75
90
DEPTH (m)
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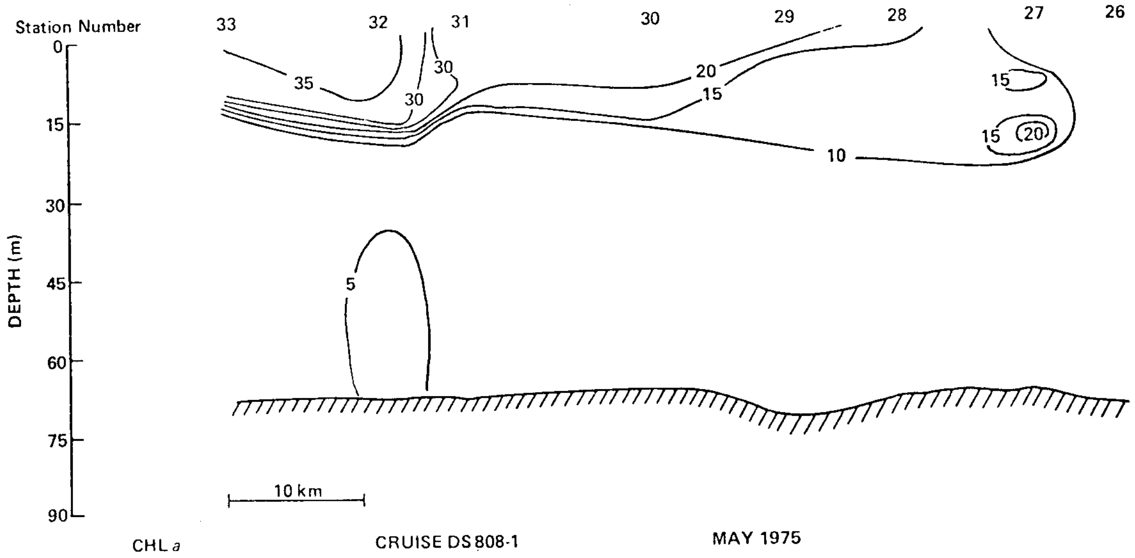
8.0
10.0
10 km
NO_3
CRUISE DS 808-1
MAY 1975

f



Station Number
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31
30
29
28
27
26
0
15
30
45
60
75
90
DEPTH (m)
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30
30
20
15
10
15
15
20
5
10 km
CHL *a*
CRUISE DS 808-1
MAY 1975

a

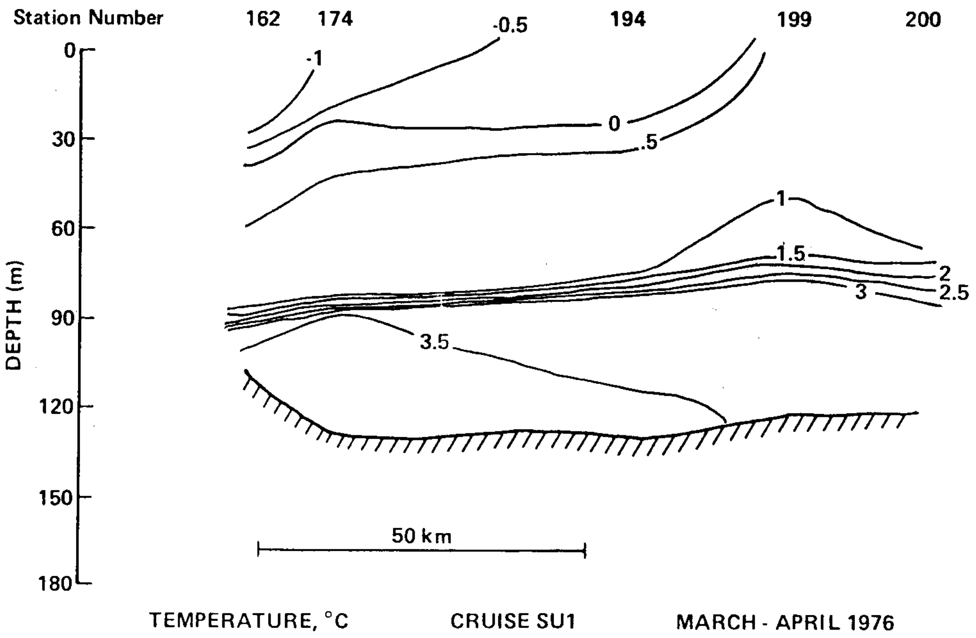
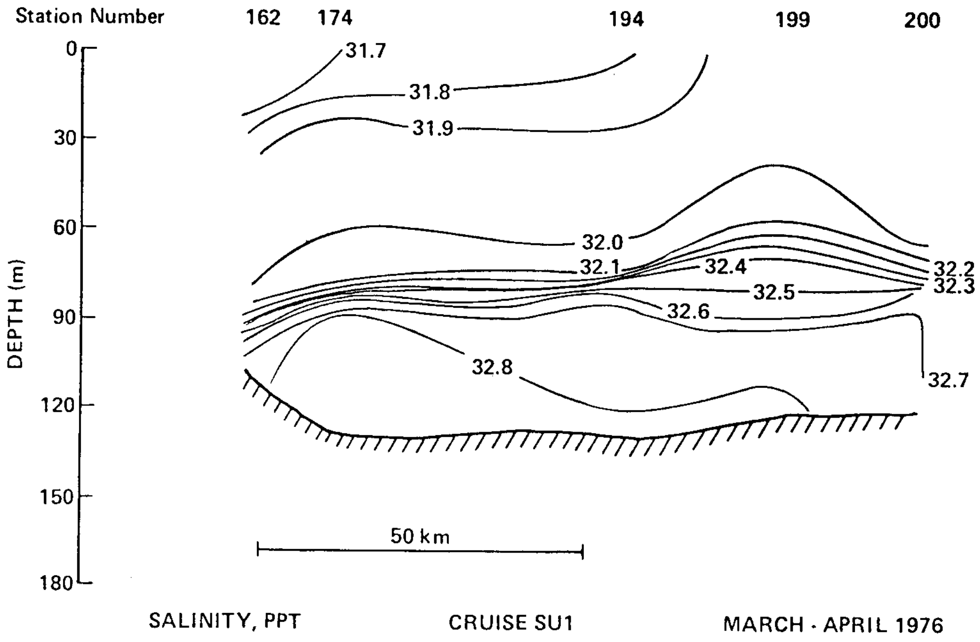


Figure IV-12. Cross section of (a) temperature, (b) salinity, (c) sigma-t, (d) nitrate, (e) ammonia and (f) chlorophyll 1976.

b



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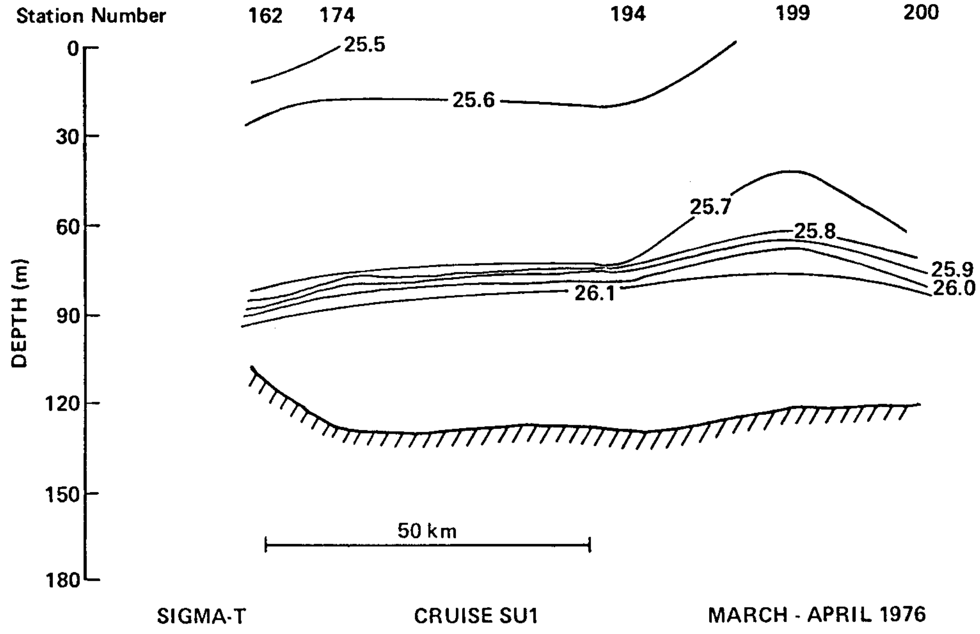
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199
200
0
30
60
90
120
150
180
DEPTH (m)
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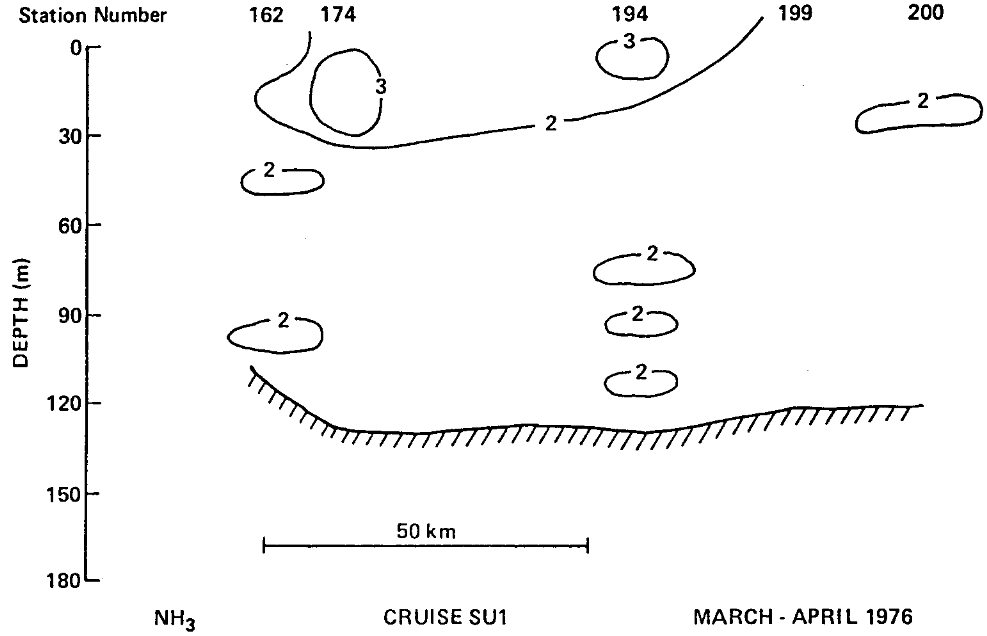
25.6
25.7
25.8
25.9
26.0
26.1
50 km
SIGMA-T
CRUISE SU1
MARCH - APRIL 1976

d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194
199
200
0
30
60
90
120
150
180
DEPTH (m)
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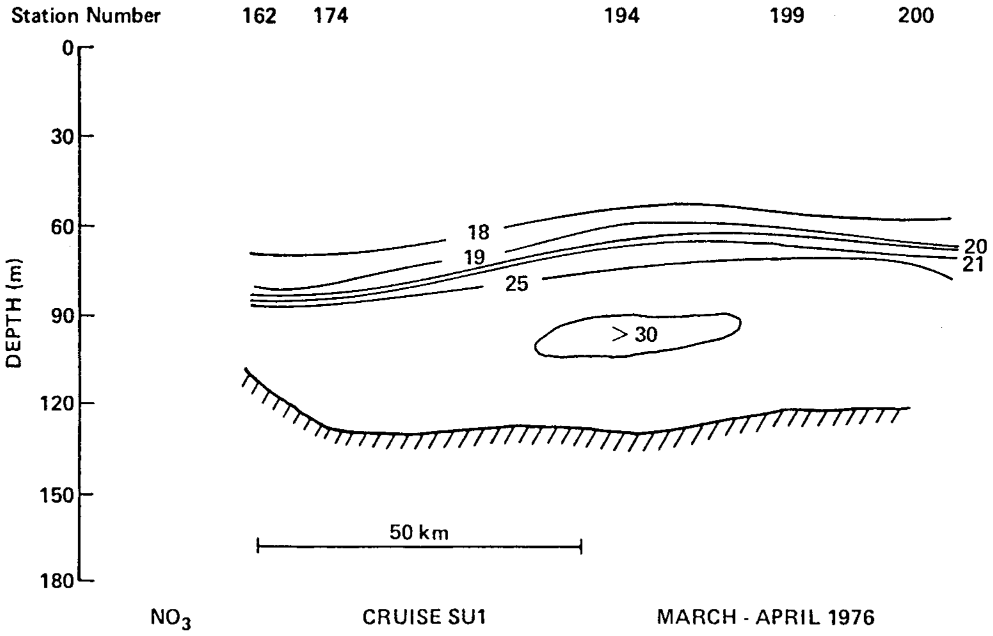
3
2
2
2
2
2
2
2
50 km
NH_3
CRUISE SU1
MARCH - APRIL 1976

e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199
200
0
30
60
90
120
150
180
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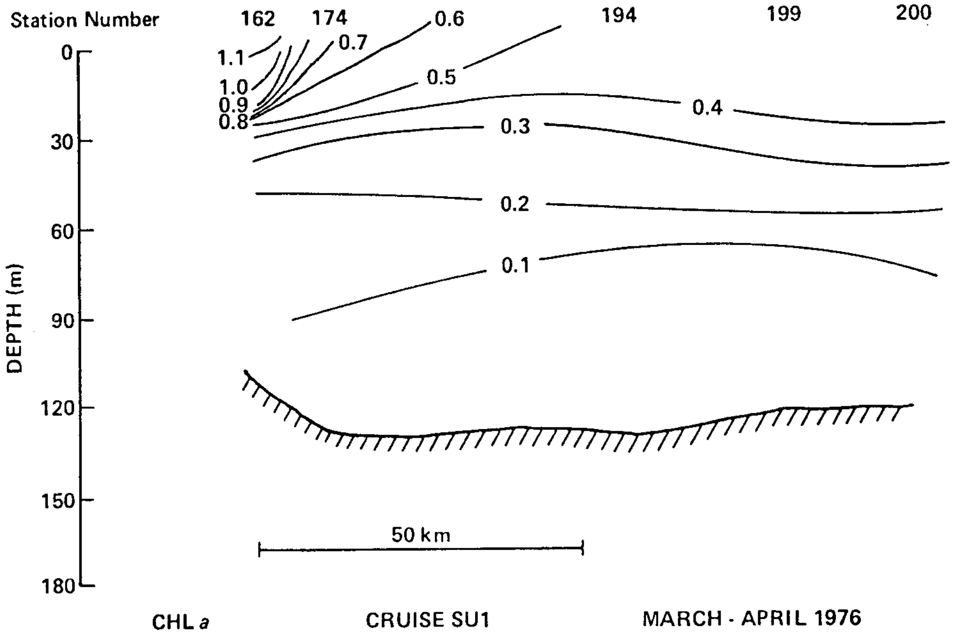
19
25
20
21
> 30
50 km
NO3
CRUISE SU1
MARCH - APRIL 1976

f


Station Number
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199
200
0
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60
90
120
150
180
DEPTH (m)
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1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
50 km
CHL a
CRUISE SU1
MARCH - APRIL 1976

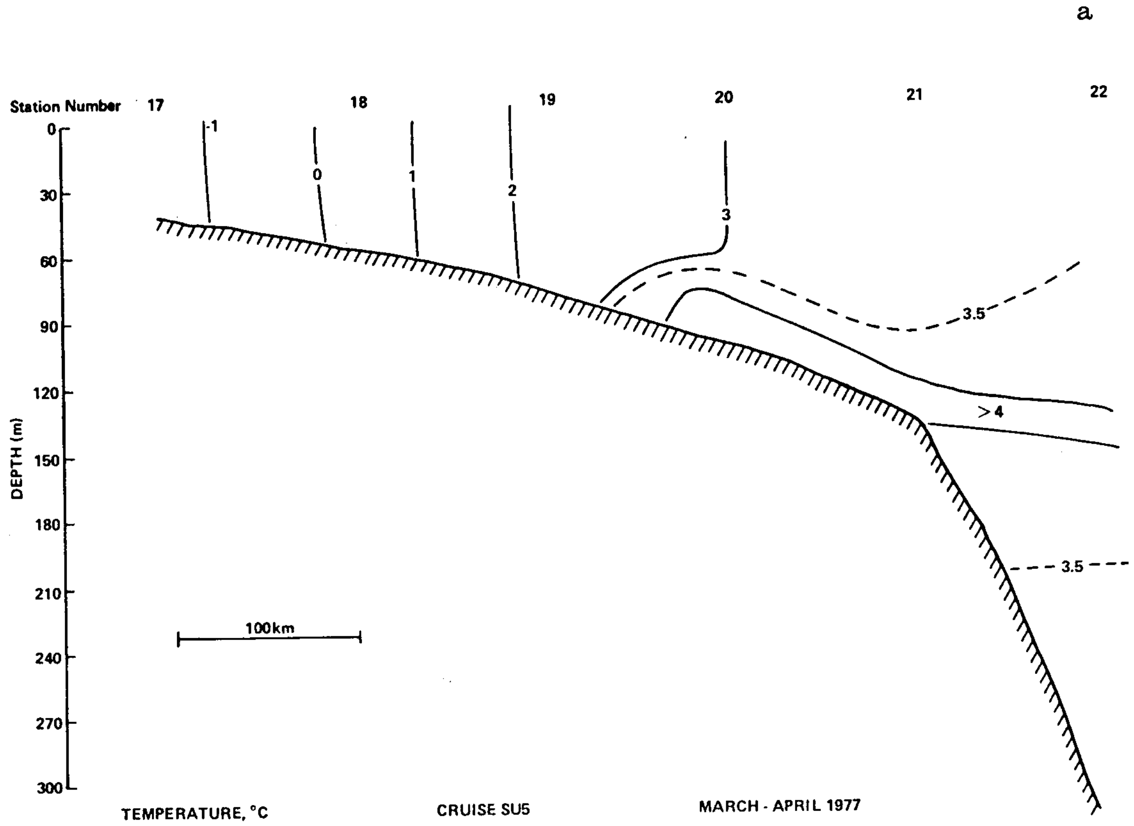
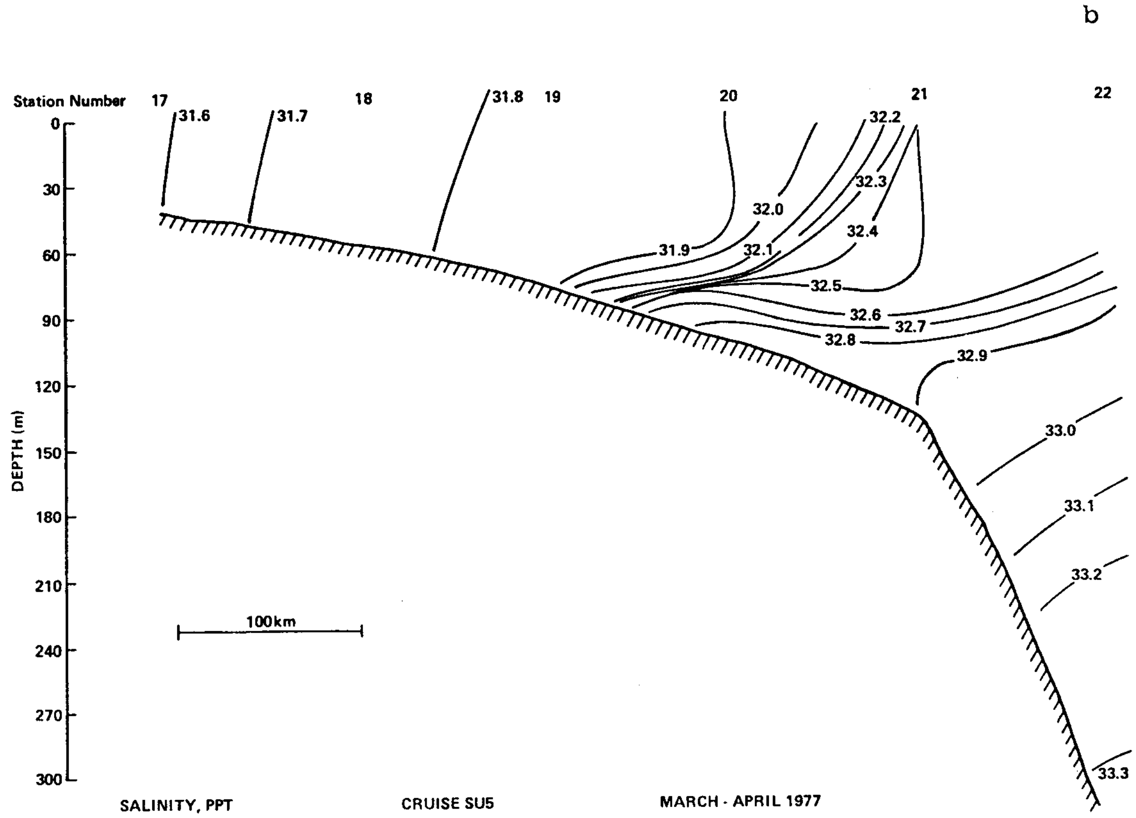
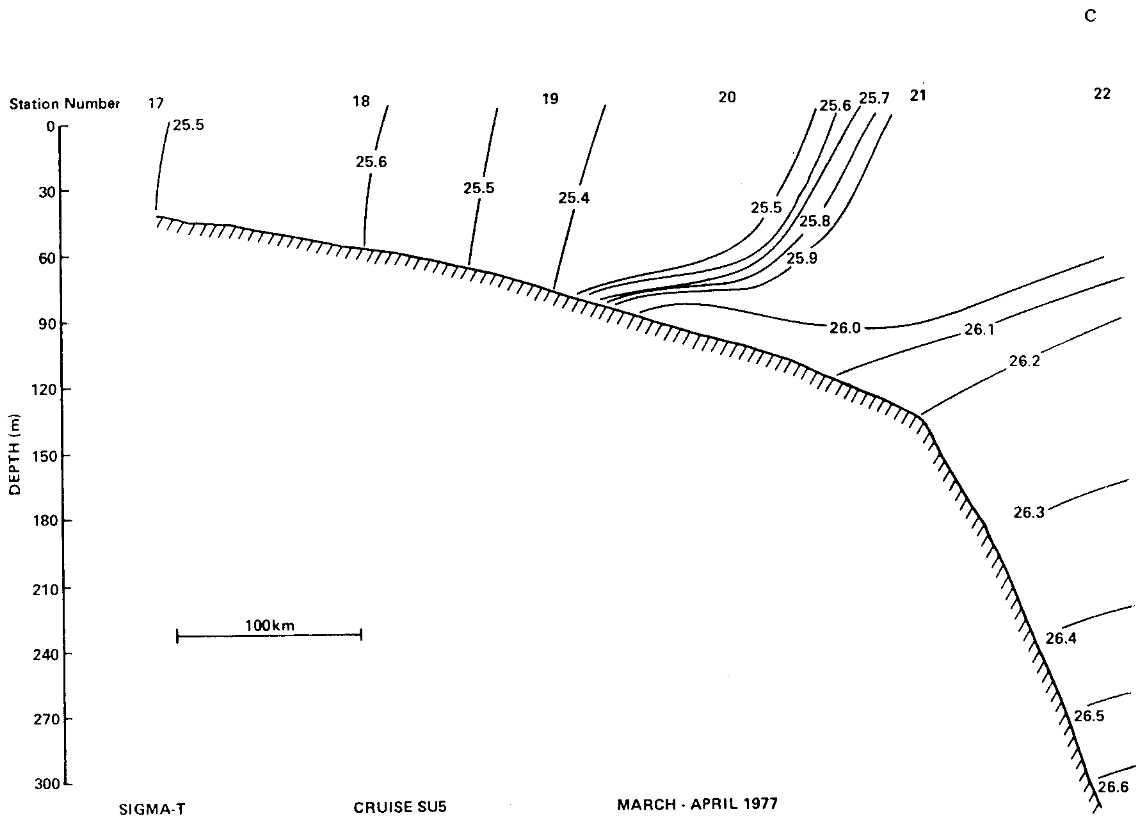


Figure IV-13. Cross section of (a) temperature, (b) salinity, (c) sigma-t, (d) nitrate, (e) ammonia and (f) chlorophyll 1977.




c
Station Number
17
18
19
20
21
22
DEPTH (m)
0
30
60
90
120
150
180
210
240
270
300
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CRUISE SU5
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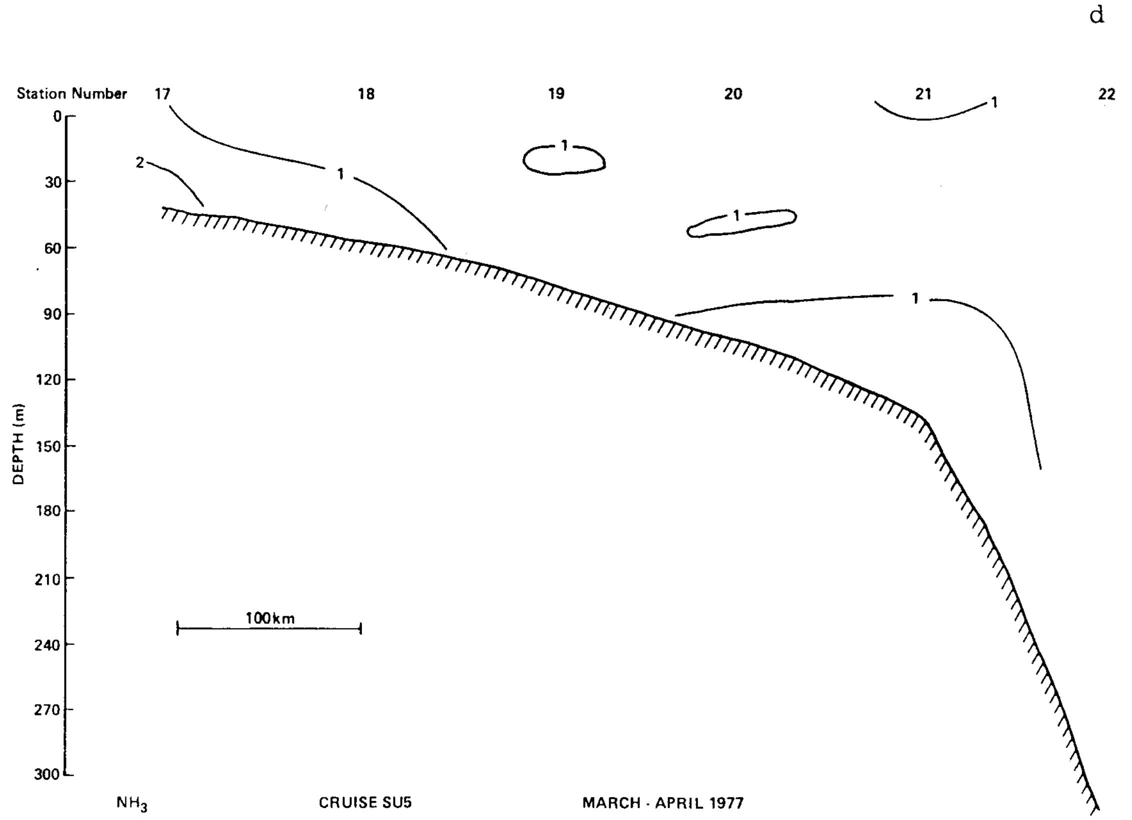
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DEPTH (m)
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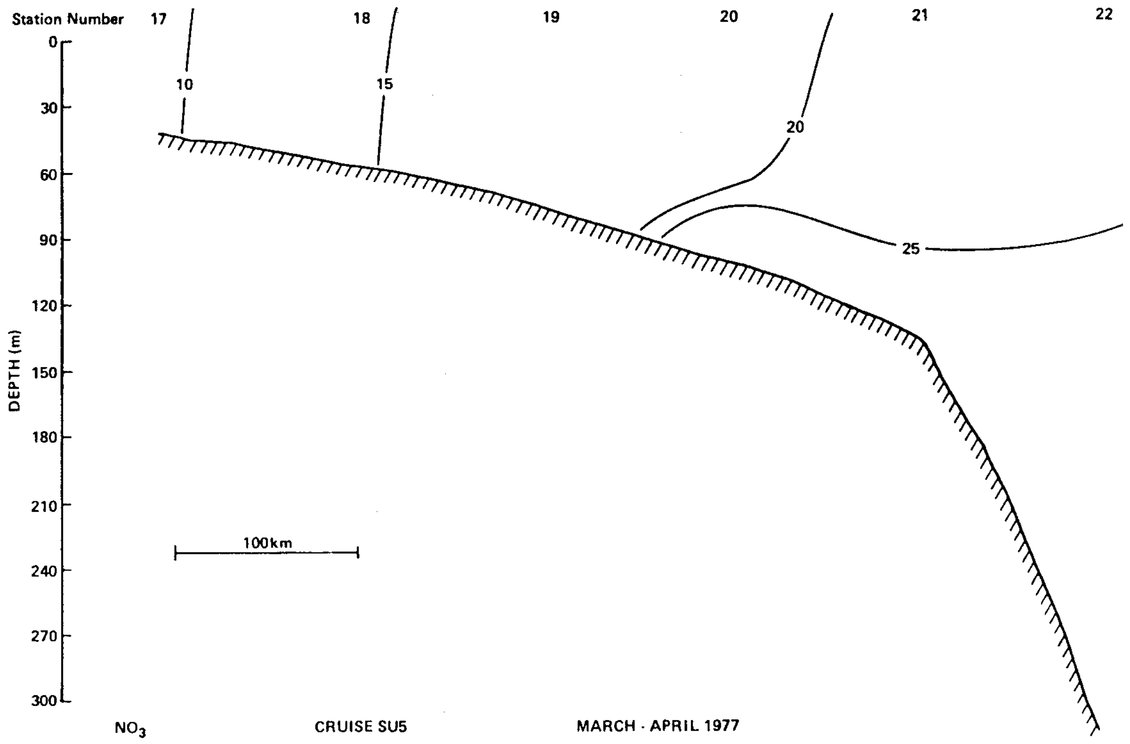
MARCH - APRIL 1977

e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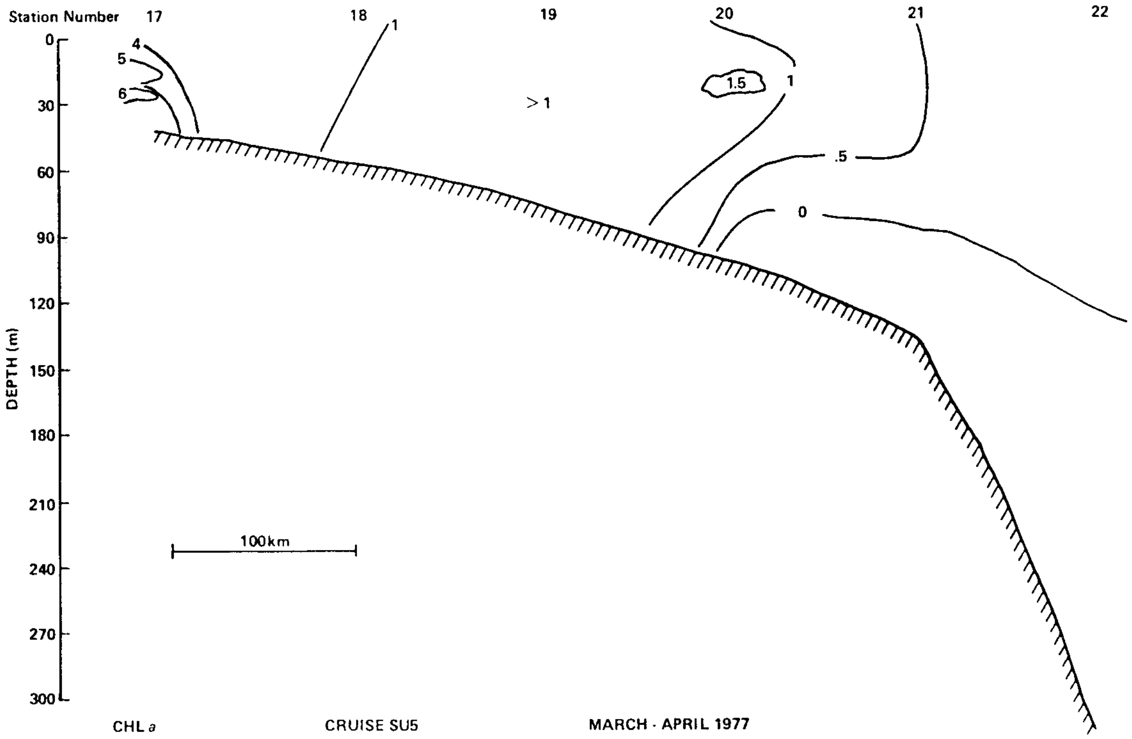
MARCH - APRIL 1977

f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CRUISE SU5
MARCH - APRIL 1977

(1979) is apparent with the inner front in temperature and salinity between stations 19 and 20 on the bottom. The outer front is evident in the surface layers (especially $S^\circ/_{\circ\circ}$) between stations 20 and 21. The whole shelf section, except right at the ice, is much warmer than the previous years. Especially remarkable is the core or layer of greater than 4°C water running up on the shelf at about 100 m.

Ice Algae Production

Regardless of the position of the ice edge, by the time the ice-edge bloom is initiated, major production of algae within the sea ice is no longer underway, although a small amount of coloration may still be present. Frequently, algae are seen growing in melt pools on the ice surface, and these are sloughed off into the sea surface, but the major epontic growth is not evident. In 1977, we were able to carry out a survey of a portion of the Bering Sea shelf further to the north of the ice edge using a UH-IH helicopter during the first week in April. An intensive study was carried out to determine the distribution of chlorophyll at the ice-seawater interface in this region concurrently with an ice edge cruise further south at the active ice margin. The flights were conducted from Nome, and covered an area extending from 64°15'36"N to 62°52'30"N in latitude and from 166°15'36"W to 163°20'06"W in longitude. Thirty-one stations were occupied within this area, and superimposed on this broad survey grid were two areas with more closely spaced clusters of stations in order to determine more local variability. For a map of the stations, see Figure IV-14. SIPRE ice cores were collected at each station and the lower portions analyzed for chlorophyll *a* content, the length of coloration recorded, and a sample of seawater was taken from the surface through the hole for nutrient determination.

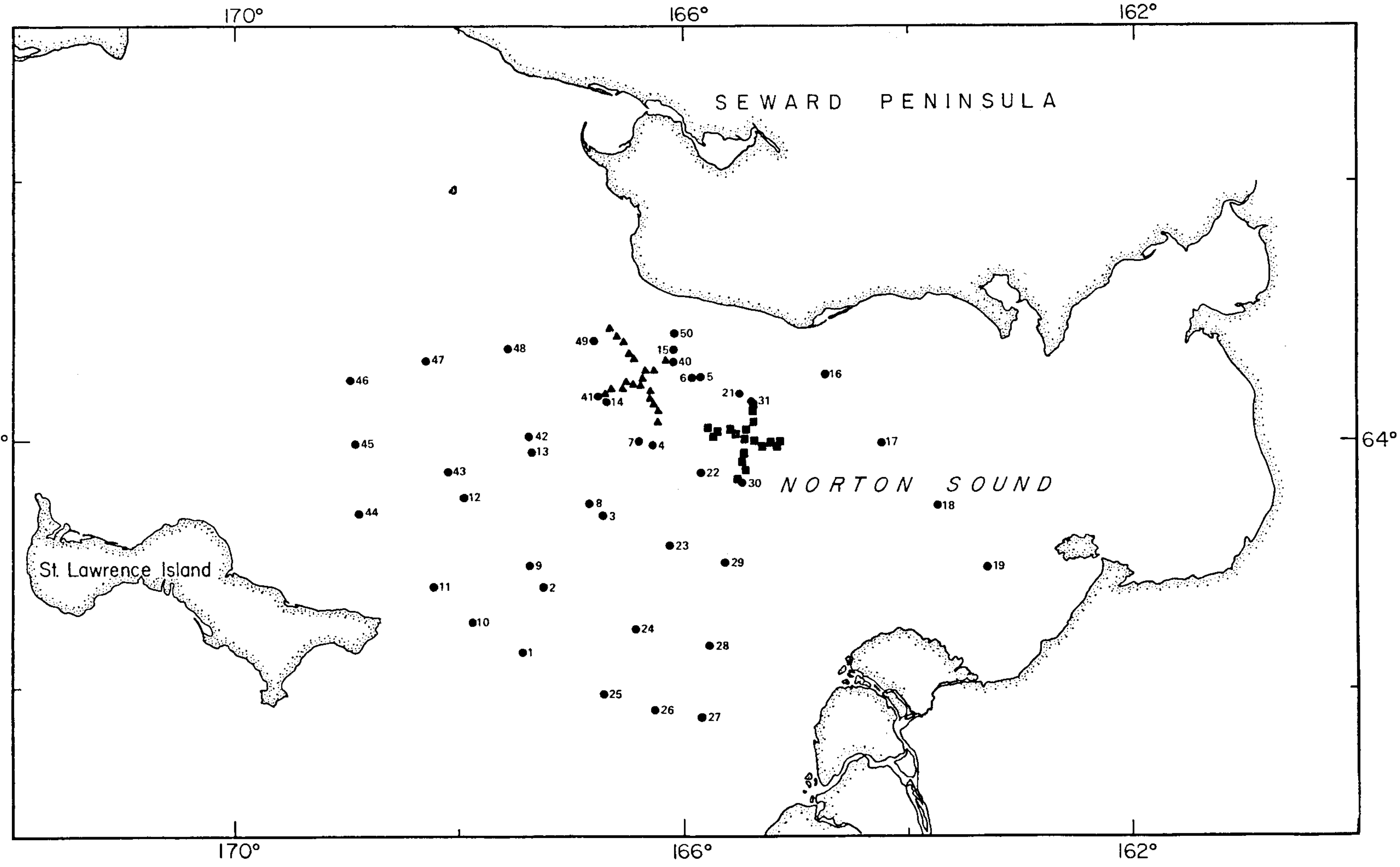


Figure IV-14. Ice algae survey stations, April 1977.

There was extreme variability among stations in terms of chlorophyll content of the bottom ice. For example, although high values were found at one of the most southern stations (96.8 mg/m^3 chlorophyll *a*), one of the lowest was in the same area at the same time (0.30 mg chlorophyll *a*/m^3). Overall, the chlorophyll *a* content of the ice varied from 0.0 to 213.7 mg/m^3, with extreme patchiness both on an overall and on a local scale. An area of very intensive brown ice at the northern end of the study area had 0.5 to 30 cm of color within each core, and under these circumstances as much as 64 mg chlorophyll *a*/m^2 sea surface could be found, as an upper limit. A summary of the findings is presented below:

All Stations
n=63

Mean chlorophyll content of bottom ice	23.1 mg/m^3
Standard deviation	40.9 mg/m^3
Range	0.0 - 213.7 mg/m^3

Station Cluster 1
n=18

Mean chlorophyll content of bottom ice	12.0 mg/m^3
Standard deviation	17.6 mg/m^3
Range	0.0 - 73.9 mg/m^3

Station Cluster 2 (Along edge of shelf at entrance to Norton Sound)
n=14

Mean chlorophyll content of bottom ice	62.3 mg/m^3
Standard deviation	63.9 mg/m^3
Range	4.9 - 85.1 mg/m^3

The generally higher mean chlorophyll content of the ice at the edge of the Norton Sound shelf could be due either to timing or to location. In any event, significant levels of chlorophyll occurred in the ice in the area between Norton Sound and St. Lawrence Island, extending into the Sound, during the first week in April. We do not know how long this chlorophyll growth persists, but judging from our experience in the Beaufort-Chukchi Sea we suppose that it could persist and be active for a period of about a month (Horner and Alexander, 1972; Clasby, Horner and Alexander, 1976). During this time it would certainly account for a significant proportion of the annual production in this shelf area, especially in view of our previous observations that during the summer months primary production is low in this area (V. Alexander, unpublished data from the 1974 Bering Sea cruise of the R/V *Alpha Helix*). Our chlorophyll maxima exceed those found in the Chukchi Sea ice off Barrow, but are of the same order of magnitude (30.49 mg/m^3 during the peak of the Chukchi Sea bloom in May).

Nutrient analyses have shown that at the time nitrate concentrations ranged from 2.5 to 8.6 μg-atoms/liter, ammonia from 1.4 to 4.7 μg-atoms/liter, phosphate from 0.8 to 1.7 μg-atoms/liter and silicate from 12.2 to 42.1 μg-atoms/liter. Thus, there is no evidence for any nutrient depletion at this time. More detailed seasonal coverage of the Bering Sea ice bloom will be difficult to obtain due to the high cost and unavailability of the appropriate logistic support. However, we have now obtained more spatial coverage than has ever previously been available. It may therefore be appropriate to suggest that the intensity of the "ice bloom" in the shallower waters of the shelf, particularly in the Norton Sound area, is such that it would have a major impact on the annual energy budget of the marine ecosystem in the area. Pollution could present a serious problem in such an area in terms of its impact on the annual production cycle if it were to come into contact with the ice/seawater boundary layer.

Ice-Edge Primary Production

We have found the most intense primary production to occur at the ice-edge just prior to break-up. Three years coverage during the critical spring period as well as comparative data from other time of year have given us a rather detailed picture of the seasonal cycle and as a result of this we have been able to estimate the relative contribution from this spring ice edge regime compared with the remainder of the year on the S. E. Bering Sea shelf. Surface chlorophyll values frequently exceeded 20 mg/m^3 and primary productivity exceeded 25 mg $C/m^3 \cdot hr$, and although such rates were not sustained for a very long period of time a substantial contribution is possible due to the intensity of the photosynthetic activity. Resampling of a bloom area showed that chlorophyll had declined to an average of less than 1 mg/m^3 in less than three weeks.

In the shelf-break area to the south of the ice edge, an open water phytoplankton bloom occurs, extending over a wide area along the entire length of the shelf, with local maxima in activity in coastal areas and around the Pribilof Islands (Figure IV-15). The peak of the ice-edge bloom occurs in late May, which is only slightly after the peak of the open water bloom in late April to early May. Although the peak of the ice-edge bloom occurs later, activity along the ice edge is already well above standing winter levels in March when open water productivity is minimal (Figure IV-16). The ice-edge bloom extends away from the ice to a distance of from 30 to 50 miles, but the depth structure of the activity as well as the population composition changes as distance from the ice edge increases. Figure IV-17 shows depth profiles of primary productivity and chlorophyll at three stations along a transect during the May 1975 *Discoverer* cruise.

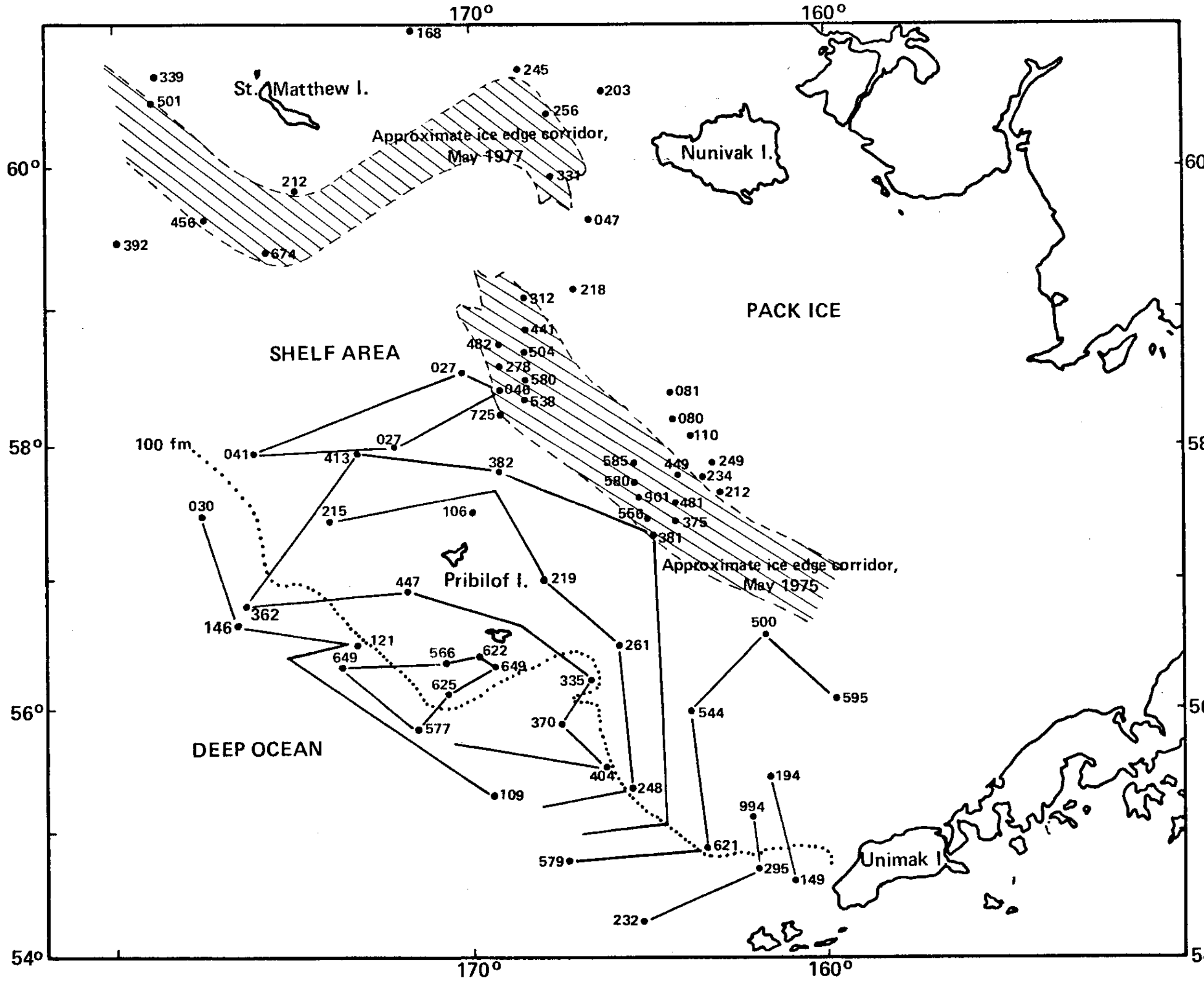


Figure IV-15. Integrated chlorophyll *a* distribution on the Bering Sea shelf.

The high activity near the surface was evident, but the chlorophyll concentration had dropped considerably by the time a station 25 miles from the edge was reached.

We have looked at the structure of the water column along transects intercepting the ice edge. It becomes clear that there is a shallow zone (less than 30 m in depth) which is under influence of ice. This occurs regardless of the overall physical regime in the area of the ice edge. In Figures IV-11-13 we have plotted up the overall information for selected

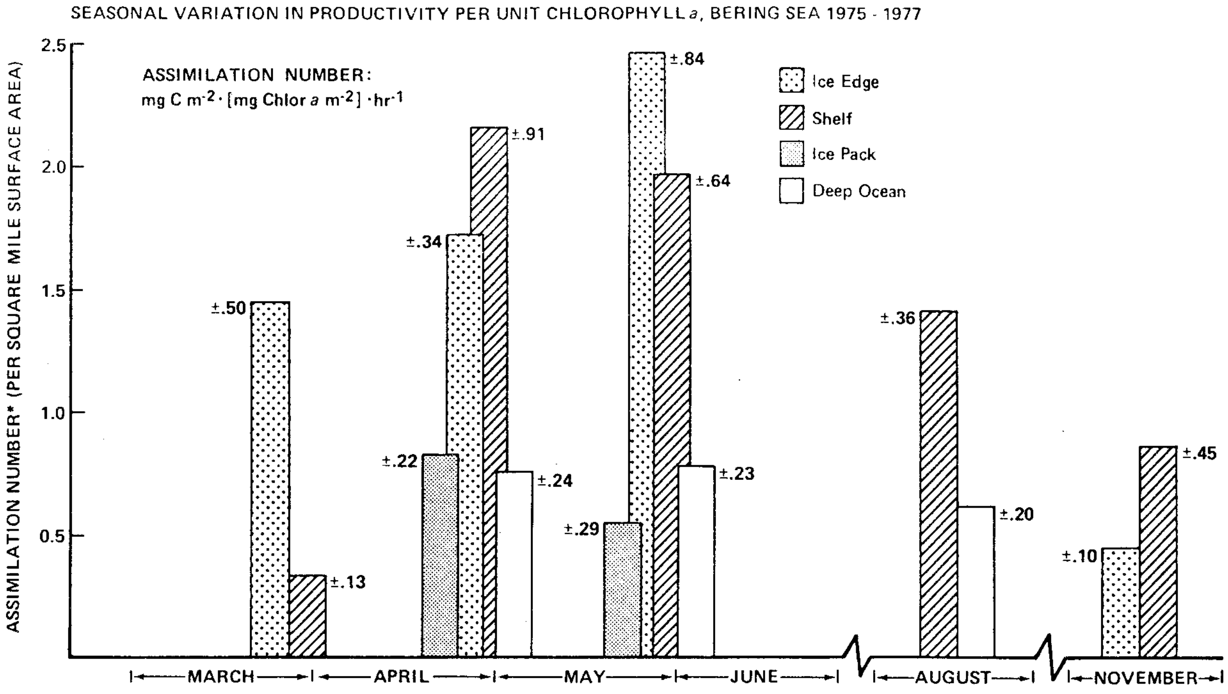


Figure IV-16. Seasonal variation in primary production per unit chlorophyll *a*.

transects sampled during the three years. The ice edge was in different positions during the three years, which was in part due to the different temperature regimes, but also to some extent due to timing. The 1975 transect shows that near the ice edge, the sea temperature dropped with depth, and there is no evidence for source water intruding under the ice-dominated water. In 1976, the more usual situation of an increase in temperature with depth occurred, and at 90 meters there was a thermocline with source water evident below it. To some degree this could have been due to the fact that the 1975 transect was done at a time when the ice was much further north on the shelf. The biological data show that the bloom

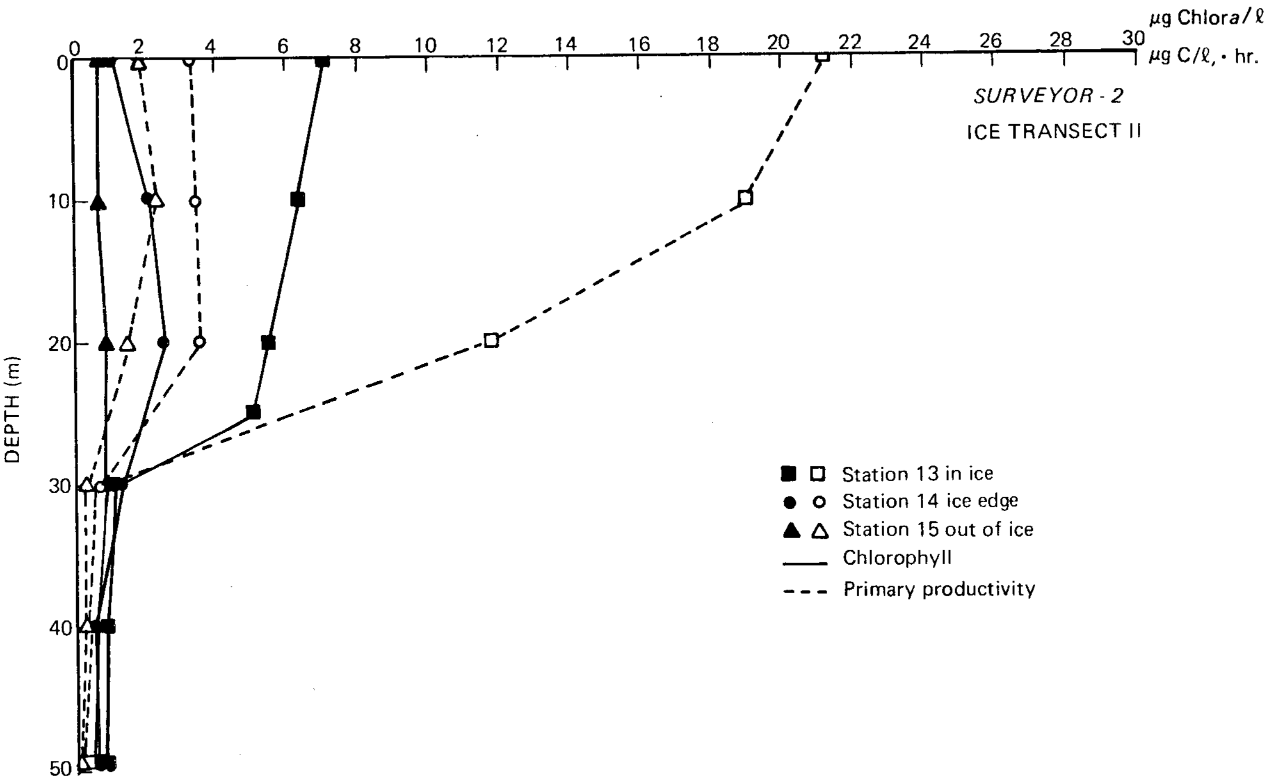


Figure IV-17. Depth profiles of primary production and chlorophyll at three stations at different distances from the ice edge.

had progressed further during this sampling, since the chlorophyll was very high and the nitrate levels near the ice edge had been reduced significantly. In the 1977 transect, the ice is once again far north, this time due to very light ice conditions and a high sea surface temperature. This is a very long section, extending far out towards the shelf break, and the transect shows rather clearly the location of the major fronts, and the warm source water appearing over the edge of the shelf. The ice-edge bloom is not very intense at this time, compared for example with the 1975 transect, but is in the early stages of development, and has already caused a decline in nitrate concentrations near the ice edge.

The phytoplankton bloom, then, develops in the surface layers in the immediate vicinity of the ice. Where the ice-edge bloom has already been underway and the ice is receding, the chlorophyll, as distance from the ice increases, tends to be somewhat mixed down with a less distinct maximum and a more even distribution throughout the surface waters. Figure IV-18 shows a transect for chlorophyll and nitrate at the surface and 10 meter depths. Clearly, nitrate has become depleted near the ice edge at both depths, but increases by the outermost station, where chlorophyll levels are quite low. Figure IV-19 looks at the information summarized above in a slightly different way. It shows primary productivity and chlorophyll at three stations; one in the ice, one at the ice edge, and one away from the ice. This suggests a tremendous enhancement of primary productivity related at least in part to a very high photosynthetic activity per unit chlorophyll in the top 20 meters near the ice. This high efficiency for chlorophyll (high assimilation number) is confirmed in Table IV-1, which shows a tendency for open sea values to be low in comparison.

The information obtained on nutrient distributions strongly suggests that depletion of nitrate is a major limiting factor to spring production, especially at the ice edge. Seasonal distributions of nitrate and ammonia yield some interesting observations (Figure IV-20). Nitrate concentations in spring, at the beginning of the bloom period, are uniform with depth, although somewhat lower in the ice covered areas than in the open water (15-25 μg-atoms/liter in open water, 5-15 μg-atoms/liter in ice covered areas). Although the differences in ammonia concentrations are not so distinct, the general trend appears to be opposite to that for nitrate, and ammonia concentrations are higher in ice-covered areas than in the open

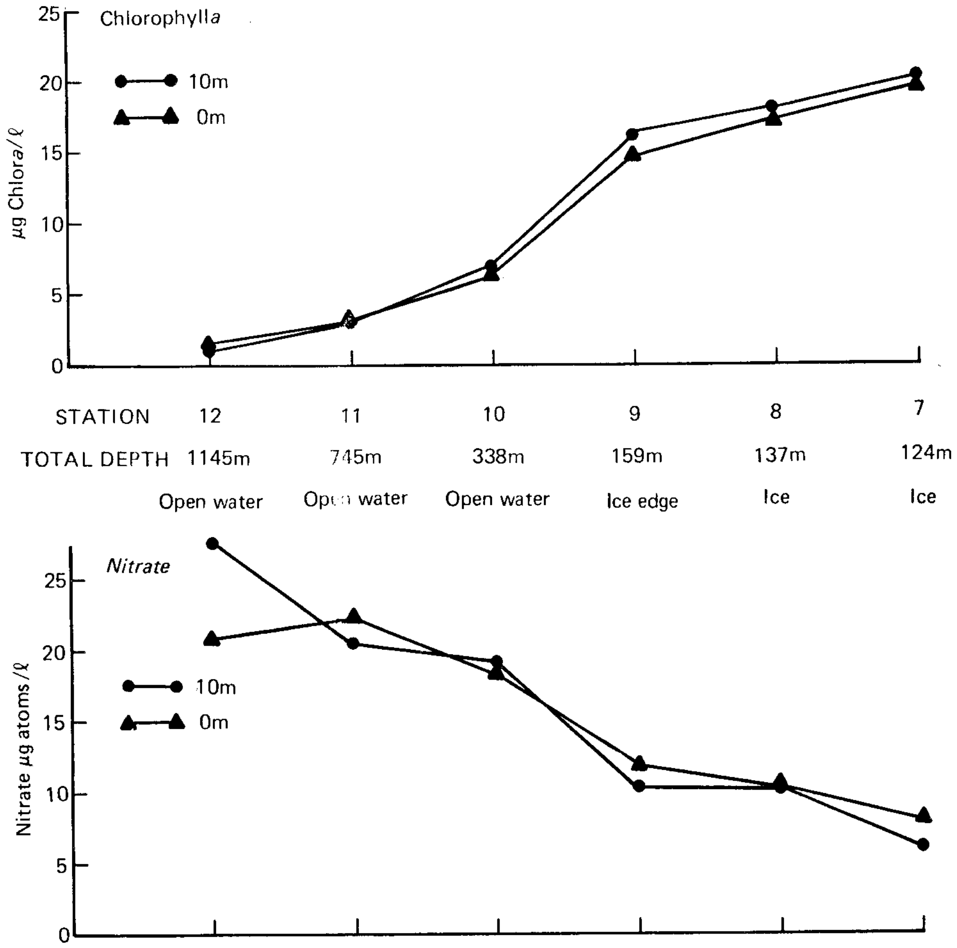


Figure IV-18. Transect showing chlorophyll *a* and nitrate at 0 and 10 m depths away from the ice.

a

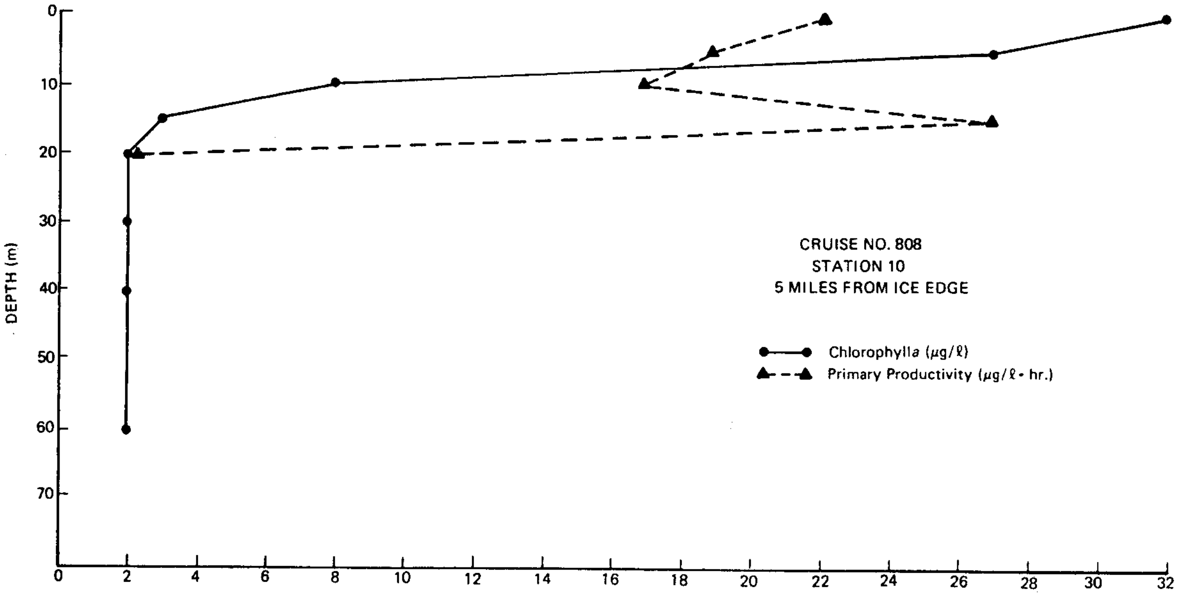
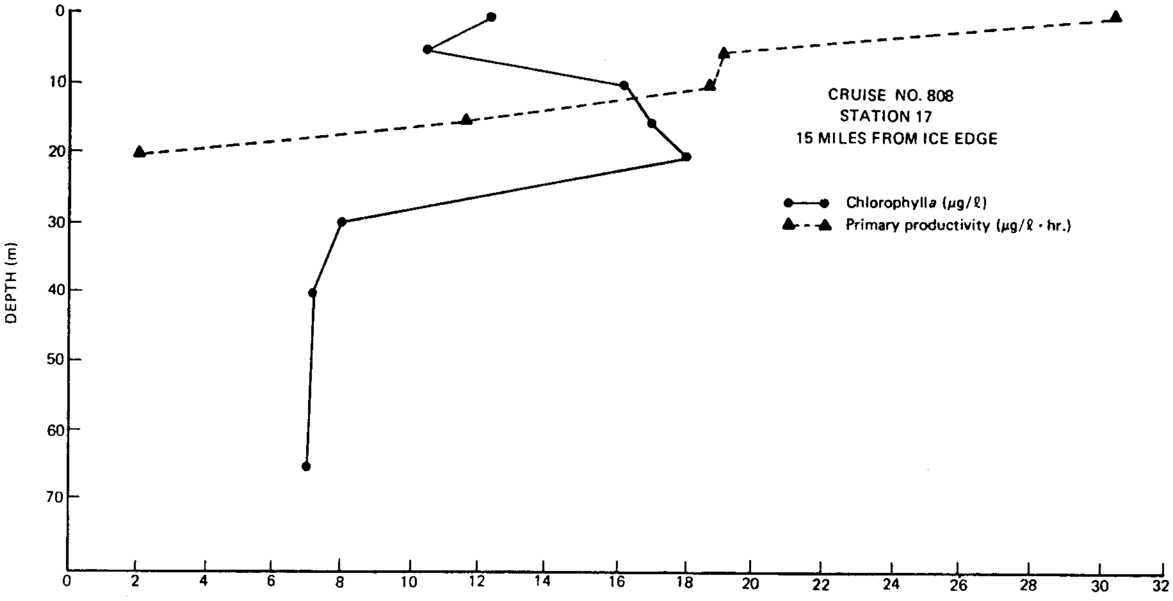


Figure IV-19. Depth profiles for 3 stations [(a) in ice, (b) at ice edge and (c) away from ice] showing primary productivity and chlorophyll *a*.

b



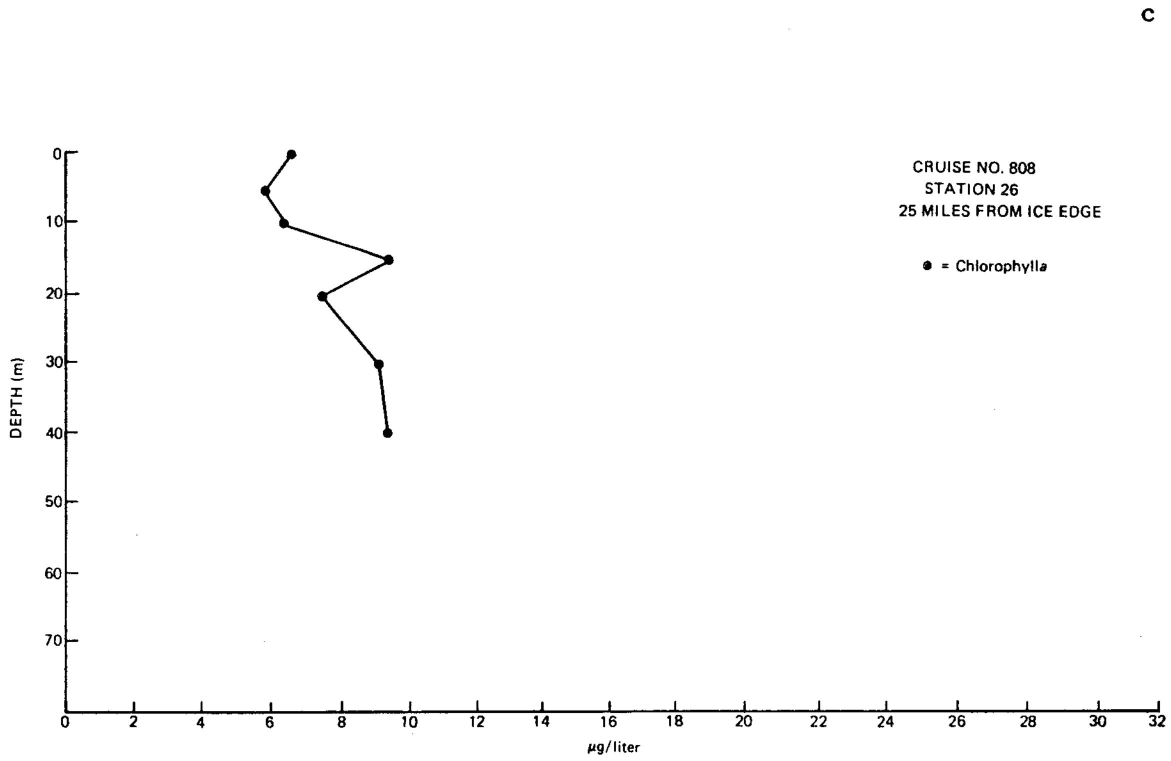


TABLE IV-1

SEASONAL VARIATION IN PRIMARY PRODUCTIVITY PER UNIT CHLOROPHYLL *a* PER HOUR
BERING SEA 1975, 1976, 1977

Time	Locations	Assimilation Number $\bar{X}$	S.D.	No. of Stations
March & early April	Ice Stations	1.44	± .50	17
Cruises: SV-1, 1976	Shelf Stations	0.34	± .13	5
SV-5, 1977				
April & early May	Ice Edge	1.73	± .34	4
Cruises: SV-2, 1976	Ice Pack	0.84	± .22	8
SV-6, 1977	Shelf	2.16	± .91	6
	Deep Ocean	0.76	± .24	6
May & early June	Ice Edge	0.56	± .29	13
Cruises: 808, 1975	Ice Pack	2.46	± .84	6
DS-4, 1977	Shelf	1.96	± .64	10
	Deep Ocean	0.78	± .23	4
August				
Cruises: 810, 1975	No Ice Sta.	--	--	0
	Shelf	1.41	± .36	6
	Deep Ocean	0.62	± .20	6
November	Ice Edge	0.45	± .10	2
Cruises: 815, 1975	Shelf	0.86	± .45	7

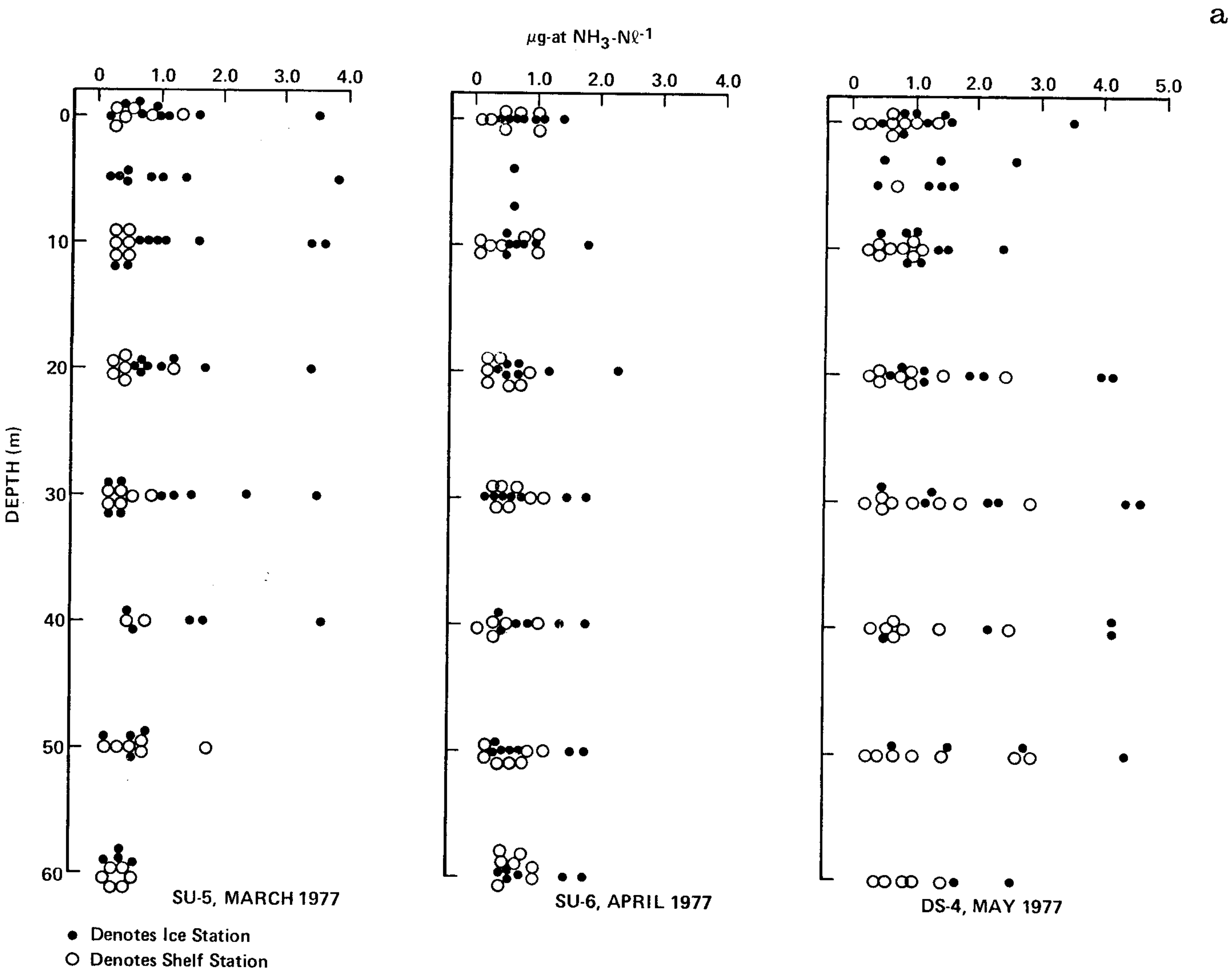
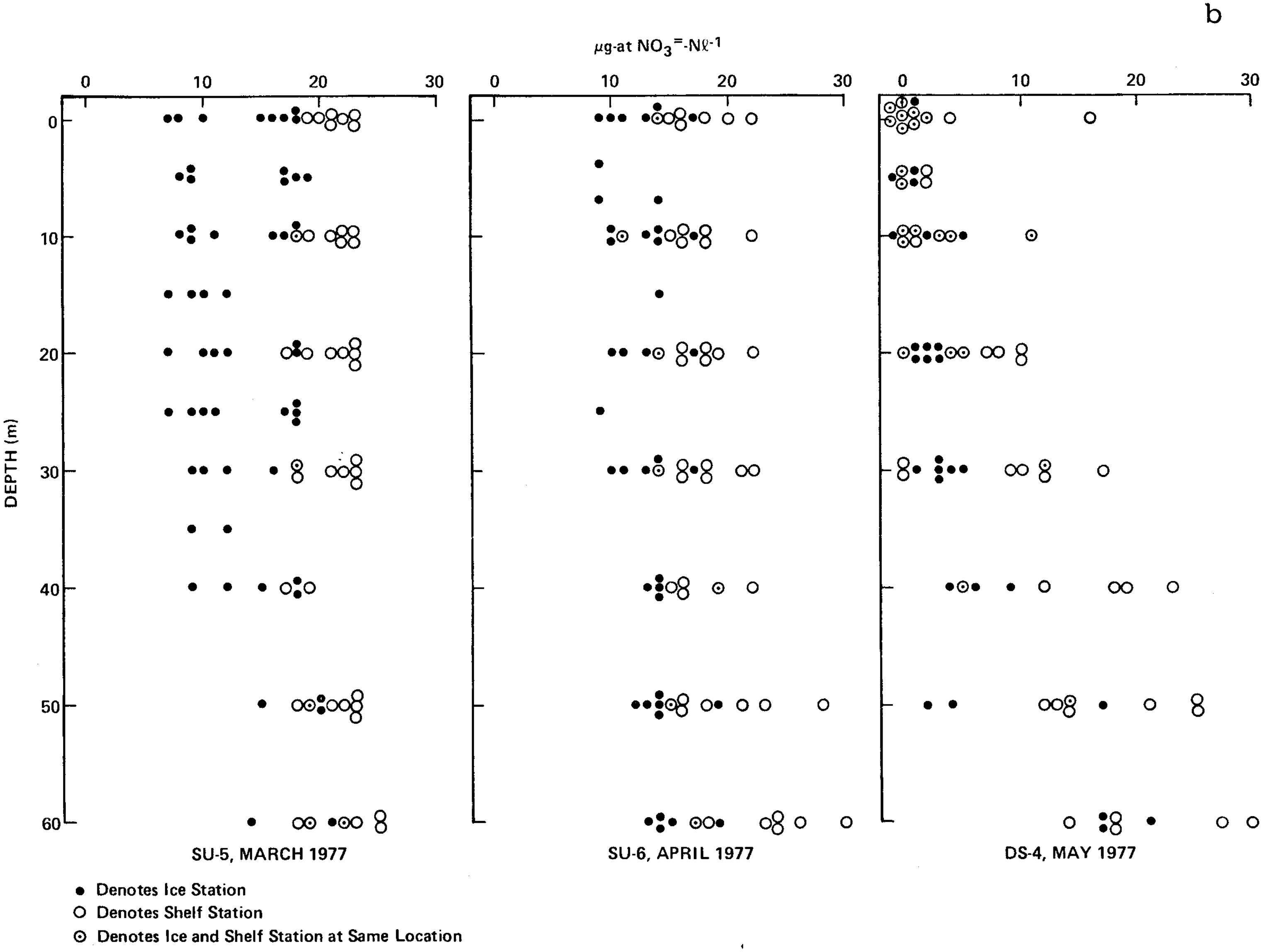


Figure IV-20. Depth profiles in nitrate and ammonia with season.



SU-5, MARCH 1977

SU-6, APRIL 1977

DS-4, MAY 1977

water. As the bloom progresses, following the establishment of stratification near the ice edge, ammonia concentrations tend to increase. An increase is also evident in areas of open water. The source of this increase is not clear, although in ice-dominated areas, *in situ* ammonification is possibly the mechanism.

Two different mechanisms, then, appear responsible for the two major blooms. This is reflected in the different population composition which has been addressed in Chapter 2 above. The significance of spring production in the annual cycle is shown in a simplified way in Figure IV-21, which shows calculations based on the three years work on the percentages of the total annual carbon input through primary productivity into the Bering Sea shelf ecosystem in the St. George's basin area. Sixty-five percent of the input occurs during the spring bloom period, with the largest input in the May ice-edge bloom period.

Organic Matter Transfer to Pelagic Grazers

A major feature of the zooplankton and micronekton communities of the southeast Bering Sea is the relative isolation of the major open ocean and shelf groups. As pointed out previously, the absence of large numbers of "interzonal" or oceanic grazers in waters shallower than about 80 m is reflective of the extremely sluggish hydrographic exchange between the ocean and shelf. In effect, the well developed open Bering Sea grazing community, which appears mostly as juvenile forms rising from deep overwintering populations as early as midwinter, is unable to effectively invade the shelf. Conversely, the shelf grazers are dominated by small copepods which overwinter as adults and which must first feed before reproducing. These differences in species composition seem to significantly affect the degree

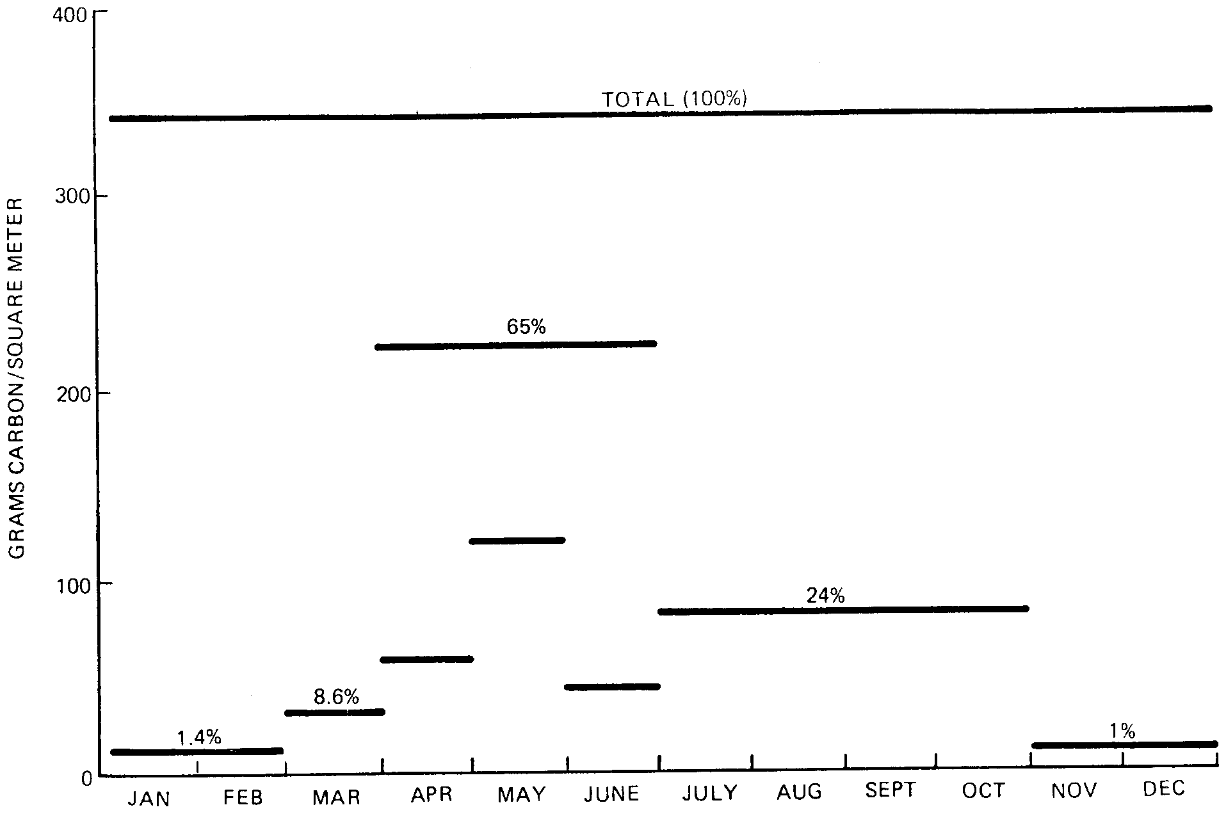


Figure IV-21. Annual distribution of primary production, S. E. Bering Sea shelf.

of coupling between the annual production of plant matter and the pelagic herbivores. The open ocean is apparently the more efficient system with small losses of unconsumed carbon escaping the upper 200 m. Shallower than 80 m, the larger elements of the phytoplankton bloom seem to be "uncoupled" from the grazing pressure and free to sink to the sea bed.

Therefore, the ice edge ecosystem will be relatively more or less coupled to water column production on the basis of its geographic location. During cold years when the ice extends to the shelf break or beyond, the edge zone will be influenced an oceanic community. Following warmer fall/winter seasons, the edge zone will occur considerably further north and thus interact only with the shelf animal plankton and micronekton.

The resulting organic matter exchange processes and the utilization of blooms are quite different in these two extreme cases. Over the shelf the "small" copepod dominated system skews the grazing pressure to the smaller plant cells in the primary producer group. The larger cells and active chain formers then "bloom" in the classic sense and a great percentage of this material sinks unutilized from the water column as direct input to the shelf benthos. Over the oceanic water mass, the edge zone will interact with a much more diverse grazing community. Here, a much greater percentage of the water column plant production is utilized directly, with losses to the deep shelf or slope negligible, at least early in the season.

For comparative purposes, some estimates of herbivore ingestion can be made from information and experiments conducted in the edge zone (1976-1977). These estimates suffer from several unknowns; the greatest of which are errors in measuring herbivore standing stock followed by problems associated with direct ingestion incubations of plant cells and grazers. The former is uncertain because an unknown percentage of the actual herbivore population either passes through the mesh used to collect specimens (0.333 mm), or avoids the slowly towed vertical nets. The latter is biased because of the artificial nature of the incubation with relatively small volumes (1-201) used to derive ingestion rates. All things considered, the errors in the methodology probably result in underestimates of utilization; the bias is not expected to be greater than a factor of 10. In view of these constraints, several values are presented as estimates of water column ingestion by season and regime (Table IV-2). These values are derived under the assumption that a pelagic herbivore ingests the equivalent of about 2.5% of its body carbon per day (Dagg, pers. comm.). Formalin dry weight values, measured during 1975-76 as part of the survey of animal plankton in the southeast Bering Sea, were converted to carbon for the purpose of these calculations.

The resulting estimates seem very low compared with values of daily carbon production particularly in the edge zone and would more than substantiate the notion that a considerable fraction of the spring phytoplankton bloom is unused in the water column. Even if these are increased by a factor of 10 (i.e. .5-1.5 gC/m^2 day^{-1} in the open ocean and .1-.3 gC/m^2 day^{-1} over the central shelf) the resulting ingestion would still represent less than 25% of the carbon production utilized above the sea bed. This result is in

TABLE IV-2

ESTIMATES OF ORGANIC MATTER INGESTION BY PELAGIC GRAZERS IN THE SOUTHEAST BERING SEA, 1975-76

Ingestion; MgC/m^2/day

Regime	March-April	May-June
Open Ocean	24.6* (50)**	76.4 (152)
Outer shelf	7.6 (16)	58.5 (118)
Central shelf	14.7 (30)	7.1 (14)
Northern coastal	- -	6.6 (14)

* ingestion computed as 2.5% of zooplankton standing stock carbon

( )** ingestion computed as 5.0% of zooplankton standing stock carbon agreement with work recently reported for the New York Bight which indicated as little as 2-10% of the bloom in early spring and late summer was consumed above the sea bed (Walsh *et al.*, 1978).

Our direct measures of ingestion using Coulter counter techniques on natural assemblage from several depths in the photic zone in the edge zone during May-June 1977 ranged from about 0.25 to 2.5 μgC/l hr^{-1}. Considering a 20 m photic zone and continuous feeding over 24 hrs, this amounts tc a range of ingestion from 0.096 to 0.960 gC/m^2/day or no more than (1-15)% of the daily plant production.

These direct observations substantiate the view that shelf ecosystems in general, and the southeast Bering Sea specifically, exhibit rather "leaky" pelagic communities that allow much of the pelagically derived organic matter to fall directly to the sea bed. The most generally accepted reason for this uncoupling is that most shelf grazers must first feed before reproducing, and the small overwintering populations are unable to fully utilize the early portion of the production cycle. Unlike the northern Gulf of Alaska, the southeast Bering Sea lacks a strong advective mechanism (i.e. slope current) which would move the oceanic community over the shelf to augment the grazing components of the shelf assemblage in late winter and early spring. The resulting benthic shunt of organic matter may explain the rich and diverse animal assemblege occurring on the shelf in this region.

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CHAPTER V

ICE EDGE MODEL

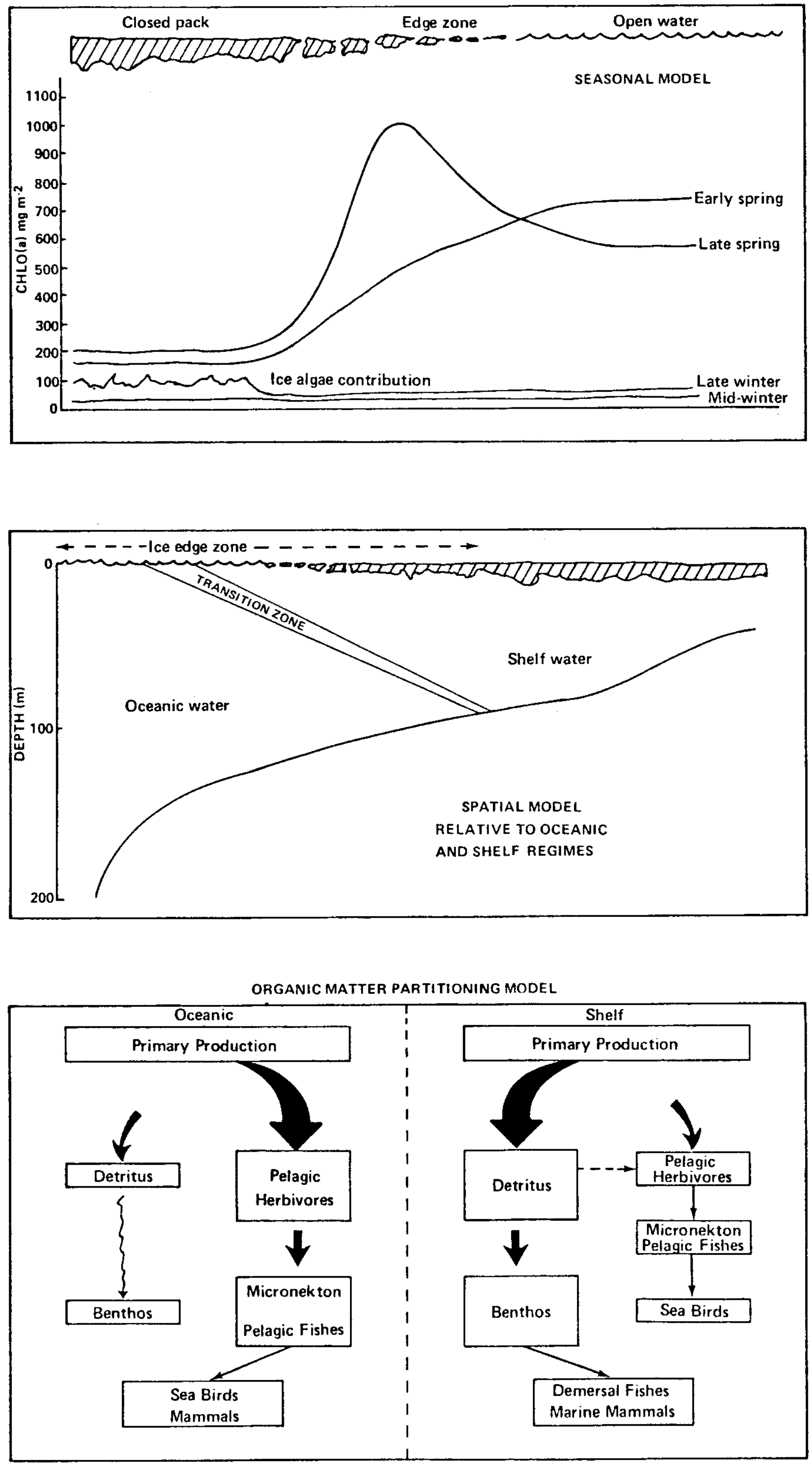

Figure V-1. Conceptual model of the ice-edge ecosystem depicting the seasonal variations in plant stocks, the position of the edge zone relative to the shelf and oceanic waters, and the flow of organic matter in pelagic food webs.

The general elements of the ice-edge ecosystem can be described within the framework of a spatial and temporal conceptual model (Fig. V-1). As noted previously, the position of the edge zone relative to the shelf break in the southeast Bering Sea is related to the severity of the preceeding winter since it appears the duration and strength of the seasonal cooling cycle determines the location of the most southern terminus of the pack. There is growing evidence that cycles of above or below average water temperatures are related to periodicity in the long-term atmospheric circulation over the northern North Pacific Ocean. For periods of one or more years, the atmospheric distribution of spatial pressure patterns forms a more southerly or northerly mean air flow above the ocean surface. Under conditions of flow from the south, the southeastern portion of the outer shelf area is influenced by a larger component of Bering Sea/Alaska stream water. Under these conditions the winters are warm and the seasonal ice is restricted to more northerly shelf regions (the situation for this and the last two years). During periods of mean air flow from the north, the converse is true. The cooling cycle is longer and more intense, influencing waters further to the south. During these years, the edge zone can extend as far as the shelf break and, under some wind conditions beyond, and the ice itself may persist over some portions of the shelf through late spring and early summer.

In midwinter with snow cover and low incident incoming radiation, the ice pack acts as an extremely effective shade for the underlying water column. It is not until late winter and early spring that sufficient light penetrates to promote the growth of the algal community living in the lower portions of the sea ice. This event marks the beginning of the annual production cycle in the region. In our work we have observed chlorophyll levels as high as 70 mg/m^2 of sea ice, although the distribution of the chlorophyll is very patchy. It is likely that the material produced in the ice is grazed either while still in position (juvenile fishes, amphipods, polychaetes) or by the planktonic community as the ice disintegrates, releasing the cells into the water. Although we have no quantitative information on this, it is reasonable to assume that at least part of the carbon finds its way to the benthic environment.

Further increases in radiation allow the beginning of a bloom under the ice and in the open water south of the edge zone. However, the most dramatic event does not occur until the edge begins to break-up over wide areas of the shelf.

As the ice separates into smaller flows, light penetration into the sea is significantly increased while at the same time wind mixing continues to be minimized by the partial ice cover. Under these conditions, an extremely intense bloom occurs. Nitrate concentrations of up to 18 µg-atoms/m^3 and the stable shallow layer at the surface under direct influence of the ice set the optimal conditions. The bloom is probably short lived, and possibly persists for only two weeks or so. The distribution of this activity over the Bering Sea shelf depends on the mode of ice disintegration, but we assume that the ice breaks up over a considerable area simultaneously. The bloom extends as far as 50 nautical miles from the ice edge, although with a decrease in intensity with distance and with a greater vertical distribution. It reaches its greatest intensity within the ice pack, where carbon fixation rates as high as

600 mg/m^2•hr have been measured 20 miles into the broken ice, and 725 mg C/m^2•hr 30 miles into the ice during an April cruise.

An open water bloom occurs away from the ice edge in response to the balance between light and stability as observed elsewhere in the northern North Pacific. Sixty-five percent of the annual primary production on the Bering Sea shelf occurs during the months of April, May and June.

The transfer of organic matter, formed at the ice edge, to primary consumers or higher trophic levels is dependent to some extent upon the structure of the underlying water column grazing community. During cold years when the edge extends to the oceanic water mass, the early portion of edge-zone bloom is grazed by a diverse and abundant copepod assemblage characterized by the immature and adult forms of *Calanus plumchrus*, *Calanus cristatus*, *Eucalanus b. bungii*, *Metridia lucens* and *Pseudocalanus* spp. These copepods range in size from 0.7 to 8.0 mm and are capable of ingesting most of the wide spectrum of particle sizes associated with a bloom. As a result, a relatively large percentage of the water column and ice related production is shunted into a pelagic food web.

During relatively warm years or following the northward recession of the ice edge over the shelf, the composition of the water column grazing community charges. The shelf copepods are numerically dominated by two small species or composites, *Acartia longiremis* and *Pseudocalanus* spp. Together with *Calanus marshallae* and *Calanus glacialis* these organisms seem to be considerably less efficient at harvesting the organic matter in this region, most of which settles to the bottom as direct input to the benthos.

The phenomenon of the edge recession must also effect the availability of food type and abundance for birds and marine mammals using the edge zone in the spring. Shipboard observations of bottom trawl catches and the results of occasional midwater trawling coupled with onsite stomach analyses demonstrated that the food composition differed with location along the edge zone. At stations shallow enough not to be influenced by oceanic water (∿ 70 m or less) Walleye pollock were generally replaced by caplin, and *Parathemisto libellula*, a large hyperiid amphipod became more abundant. Also, the dominant euphausiid over outer shelf, *Thysanoessa longipes* gives way to *Thysanoessa inermis* and *Thysanoessa raschii* over the shallower regions of the shelf. Except for the auklets, birds and mammals feeding along the edge zone utilized micronekton (euphausiids and amphipods) and fishes which were one-year-old or older. Thus, most of the forage species for higher trophic levels are survivors from the previous years production cycle and occur independently of present conditions of the year.

CHAPTER VI

APPLICABILITY TO OVERALL OUTER CONTINENTAL SHELF DEVELOPMENT

In this section, we will address the questions posed in the Objectives in Chapter I, and relate our findings to potential problems.

1. The ice-edge primary production is extremely important seasonally, contributing a substantial proportion of the annual carbon input. The most intense development occurs in breaking-up sea ice along the margins. This could be considered a critical time for the shelf region (April-May). Furthermore, production in the lower layers of the ice cover also is important early in the spring, and this could be especially vulnerable to oil spills, since the oil would tend to form pools under the ice. Since this population undoubtedly removes nutrients from seawater below the ice, it is dependent on uninterrupted contact with this water.

2. The ice-edge region, during spring bloom time, lacks the larger grazing components of the animal population.

3. As a result of this, the phytoplankton population is not effectively grazed, or such grazing as occurs almost certainly selectively removes the smaller flagellates. The bulk of the spring production sinks to the shelf bottom and represents input to the benthos or to the pelagic system only by resuspension. Thus, any contamination occurring in the surface waters would migrate to the deeper water and afeect the benthic communities also.

4. The intensity of the ice-edge production is related to the development of a shallow (10 m) surface layer which is separated from the deeper layers by a salinity difference, primarily, but also by a temperature discontinuity. The amount of mixing is obviously a critical question here, so that weather conditions could markedly affect the timing and intensity of the bloom. After a storm, a restablishment of the stability can result

in extremely high activity due to nutrient availability plus damping of circulation by the physical presence of ice.

5. The position of the ice edge with respect to the shelf break is probably critical in determining the fate of the organic matter produced. At the shelf break, more large-sized animals could be present, and the grazing on the bloom could both reduce the total biomass but also extend the time span of the highly productive period. Further on the shelf, the production would represent input to the benthos. The majority of the production in the ice probably also represents input to the bethic system.

ANALYSIS OF HARRISON BAY ZOOPLANKTON SAMPLES

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Methods

Zooplankton samples were collected by LGL personnel at eight stations in Harrison Bay (Table 1), 8-9 Aug 1980. All samples were collected with a 0.75 m ring net, mesh size 308 μm. One vertical and one double oblique tow were taken at each station. However, the boat drifted with the wind so most of the vertical tows had some horizontal component as well. Maximum depth of tow was generally 6-9 m.

Three apparently benthic samples were also sent to us for analysis. These samples, all from station 5, did not have haul sheets, so we do not know how they were collected. Perhaps they were collected when the plankton net inadvertently dragged along the bottom or perhaps they were sent to us by mistake. We assumed they were benthic samples from the presence of sediment and other debris and the number of burrowing amphipods.

Except for the double oblique tow from sta 6 that was split with a Folsom plankton splitter (McEwan *et al.* 1954), all organisms other than copepods were identified from the whole sample. Copepods were subsampled using an automatic pipet. All sorting and counting were done using dissecting microscopes. Compound microscopes were used to verify identifications when necessary. References used to identify the organisms are listed in Table 2.

Equations used to calculate the number of animals per unit volume were:

1. Volume of water filtered (V):
    a. Double oblique tow: V = (ship speed) x (duration of tow) x (mouth area of net)
    b. Vertical tow: V = (sampling depth) x (mouth area of net)
2. Mouth area of net $= \pi r^2 = \pi(\frac{.75}{2})^2$
3. Concentration (m^3)
    a. Non copepods: $\text{Conc } (m^3) = \frac{(A)\ (2^n)}{V}$
    b. Copepods: $\text{Conc } (m^3) = \frac{(A)\ (\frac{\text{sample vol}}{\text{vol pipetted}})}{V}$

where A = number of animals counted; V = volume of water filtered, and n = the number of splits.

Results and Discussion

Copepods were by far the most abundant organisms in the plankton samples (Table 3). *Pseudocalanus elongatus*, with all stages present, was the dominant species. Other copepod species present in large numbers were *Microcalanus pygmaeus*, especially stage V; *Derjuginia tolli*, all stages; *Metridia longa*, especially stages II and III; and *Calanus hyperboreus*, stages I, II, and III.

Other abundant taxa were hydrozoans, *Mysis* spp. juveniles, and juvenile amphipods from several genera. Other taxa were present and sometimes abundant, *i.e.*, unidentified barnacle larvae in the vertical tow at sta 8.

Table 1. Collection information for zooplankton samples collected in Harrison Bay, 8-9 Aug 1980.

Sta	Date (GMT)	Time (GMT)	Latitude (N)	Longitude (W)	Max Depth Tow (m)
1	9 Aug	0105	70°45'	151°53'	6
2	9 Aug	0240	70°40'	151°46'	6
3	9 Aug	0432	70°37.3'	151°28.7'	6
4	10 Aug	0235	70°43'	151°47'	8
5	10 Aug	0204	70°40'	151°35'	9
6	10 Aug	0340	70°36.7'	151°13.9'	9
7	10 Aug	0704	70°35'	151°30'	9
8	10 Aug	0805	70°35'	150°15'	9

Table 2. References used to identify zooplankton species collected in Harrison Bay, 8-9 Aug 1980.

- General
  - Broad, A. C., *et al.*, 1979
  - Cooney, R. T., and J. J. Crane, 1972
  - Hyman, L. H., 1951, 1959
  - MacGinitie, G. E., 1955
  - Smith, D. L., 1977

- Cnidaria
  - Carlgren, O., 1933
  - Hartlaub, C., 1933
  - Kramp, P. L., 1961
  - Naumov, D. V., 1960
  - Shirley, D. W., and Y. M. Leung, 1970

- Annelida
  - Dales, R. P., 1957
  - Hartman, O., 1959
  - Yingst, D. R., 1972

- Mollusca
  - Leung, Y. M., 1971

- Arthropoda - Crustacea
  - Sars, G. O., 1900b

- Arthropoda - Crustacea - Ostracoda
  - Howe, H. V., 1962
  - Leung, Y. M., 1972c
  - Sars, G. O., 1928
  - van Morkhoven, F., 1962, 1963

- Arthropoda - Crustacea - Copepoda
  - Jaschnov, W. A., 1947, 1955
  - Lang, K., 1948
  - Sars, G. O., 1903-1911

- Arthropoda - Crustacea - Cirripedia
  - Hoek, P. P. C., 1913

- Arthropoda - Crustacea - Mysidacea
  - Holmquist, C., 1959
  - Leung, Y. M., 1972b
  - Zimmer, C., 1909

- Arthropoda - Crustacea - Cumacea
  - Sars, G. O., 1900a

- Arthropoda - Crustacea - Isopoda
  - Sars, G. O., 1899

Table 2. (cont.)

Arthropoda - Crustacea - Amphipoda
  Bernard, J. L., 1969
  Bousfield, E., 1979
  Chevreux, E., 1906
  Gurjanova, E., 1951
  Sars, G. O., 1895
  Schellenberg, D., 1929
  Tencati, J. R., 1970

Arthropoda - Crustacea - Decapoda
  Hart, J. F. L., 1960, 1971
  Haynes, E. B., 1973
  Motoh, H., 1973

Arthropoda - Crustacea - Euphausiacea
  Leung, Y. M., 1970

Chaetognatha
  Dawson, J. K., 1971

Chordata - Larvacea
  Leung, Y. M., 1972a

Chordata - Pisces
  Ehrenbaum, E. H., 1909
  Musienko, L. N., 1970
  Rass, T. S., 1949

Table 3. Abundance (number per 1000 m^3[*]) of zooplankton taxa found in net hauls from Harrison Bay, 8-9 Aug 1980. All samples collected with a 0.75 m ring net, mesh size 308 μm. Where no number is present, no animals were found.

Station Number	1	1	2	2	3	3	4	4
Taxon Tow Type[†]	V	DO	V	DO	V	DO	V	DO
Cnidaria - Hydrozoa								
Aeginopsis laurentii	2593	226	741	10		59	530	239
Aglantha digitale	1111	50						25
Eumedusa birulai								
Euphysa flammea	370							
Halitholus cirratus		50	741	30	370	151		63
Obelia sp.								
Plotocnide borealis	741	25					265	25
Sarsia princeps		25			370		265	
Actinula larvae		251						163
Nematoda - unidentified	1111							
Annelida - Polychaeta								
Iospilidae	22222		370	20			265	
Polynoidae	370							
Unidentified larvae	11111	478	370	90		8	530	704
Mollusca								
Gastropoda								
Pteropoda								
Limacina helicina		25				17		25
Unidentified veliger larvae		25						13
Bivalvia - unidentified larvae				10				

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[*] Volume of double oblique tows estimated as ship speed x mouth area of net x duration of tow; volume of vertical tows estimated as depth x mouth area of net

[†] V = vertical tow; DO = double oblique tow

Table 3. (cont.)

Taxon	Station Number Tow Type†	1 V	1 DO	2 V	2 DO	3 V	3 DO	4 V	4 DO
Arthropoda - Crustacea									
Ostracoda									
Conchoecia sp.			25						
Polycope sp.									
Cyprideis sorbyana		1481							
Cytheridea papillosa		4815			10				
Cytheromorpha fuscata		2593							
Cytherideidae		2963			20			265	
Bythocytheridae									38
Copepoda									
Calanus glacialis	II								
Calanus hyperboreus	III		7039	1852	201		2933	2652	1257
	II			35185	4223	240741	6285	2652	8798
	I			3704	1006	18518	1257	5305	
Pseudocalanus elongatus	VI f	2325926	194067	33333	7843	2796296	68292	623342	212418
	VI m			1852			838		
	V f	44444	3017		201			2652	1257
	V m		1006				838	2652	1257
	IV f	14815	2001	20370	5631	629630	7542	5305	5028
	IV m			27778	4022	685185	7122	5305	7542
	III	162963	8044	233333	43841	2018518	31423	106101	62846
	II			16666	4625	74074	6285	103448	22624
	I					18518		2562	
Microcalanus pygmaeus	VI f							5305	
	VI m								1257
	V f	59259	1006					5305	1257
	V m							23873	1257
Derjuginia tolli	V f								
	V m								
	IV f	74074						18568	3771
	IV m	59259	3017		201	55556		15915	6285
	III	59259	1006		402	74074		31830	7542

Table 3. (cont.)

Taxon	Station Number	1	1	2	2	3	3	4	4
	Tow Type[†]	V	DO	V	DO	V	DO	V	DO
	II					18518	419	7958	
	I								
Eurytemora herdmani	VI f	14815			201				
	VI m								
Metridia longa	V m						419		
	IV f						419		
	IV m	14815			201	55556	838		1257
	III	14815		1852		74074	838	5305	1257
	II	29630	2011		201				
Limnocalanus macrurus	VI f								
	V f			3704	201			2652	
	V m		1006	3704			419		
	IV f							2652	5028
	IV m						419	2652	
	III								
	II				201		419		
Acartia bifilosa	VI m								
Acartia clausii	VI m			1852					
	IV f			1852					
	IV m			1852					
Acartia longiremis	VI f				201		419		
	IV f								1257
	IV m					18518			1257
Oithona similis	VI f								1257
Harpacticus uniremis	VI f	14815						2652	1257
	VI m							2652	
	V f								1257
Cirripedia - unidentified nauplii								265	264

Table 3. (cont.)

Station Number	1	1	2	2	3	3	4	4
Taxon Tow Type†	V	DO	V	DO	V	DO	V	DO
Mysidacea								
Mysis litoralis f								13
Mysis litoralis m								25
Mysis litoralis juvenile								
Mysis spp. juvenile			21481	151	14074	8		
Unidentified damaged mysids								
Cumacea								
Leuconidae								13
Diastylidae	1111							
Isopoda								
Unidentified epicaridean larvae	741	50		20		17		38
Amphipoda								
Gammaridea								
Onisimus glacialis juvenile	1111	50					265	13
Onisimus litoralis f								13
Metopa sp. juvenile		25						
Acanthostepheia behringiensis								13
Monoculodes sp. juvenile	20741	25						666
Monoculodes sp. damaged								13
Oedicerotidae juvenile	13704		370	30				188
Apherusa glacialis f								
Apherusa glacialis juvenile		50		30			265	63
Apherusa megalops juvenile								
Weyprechtia pinguis m								
Weyprechtia pinguis juvenile								
Marinogammarus sp. *cf.* juvenile								
Gammaridae juvenile damaged								
Hyperiidea								
Parathemisto abyssorum juvenile								
Hyperia galba f								
Hyperia galba m						8		
Hyperia galba juvenile						8		

Table 3. (cont.)

Taxon / Station Number / Tow Type†	1 V	1 DO	2 V	2 DO	3 V	3 DO	4 V	4 DO
Unidentified hyperiid larvae	370	25	370					13
Decapoda								
Anomura								
Paguridae - unidentified zoea	1852	151			1481	126	265	88
Brachyura								
Hyas sp. stage I zoea						8		
Caridea								
Hippolytidae - unidentified zoea	741	25						13
Euphausiacea								
Thysanoëssa raschii juvenile								13
Calyptopis stage III								
Unidentified crustacean larvae								
Unidentified crustacean eggs	1111	1408			370		7958	1458
Chaetognatha								
Sagitta elegans	1111	201					1592	364
Unidentified immature chaetognaths								13
Chordata								
Larvacea								
Fritillaria borealis	1481	50			370		1592	867
Pisces (larvae)								
Cyclopteridae								
Gadidae							265	
Unidentified damaged larvae								
Other organisms								
Foraminifera	18148							138
Trochophore larvae	370	25						50

Table 3. (cont.)

Taxon	Station Number Tow Type†	5 V	5 DO	6 V	6 DO	7 V	7 DO	8 V	8 DO
Cnidaria - Hydrozoa									
Aeginopsis laurentii		1980	855	6188	4290	12871	2278	26238	1043
Aglantha digitale			13	248		248	15	495	38
Eumedusa birulai		248		248		248			
Euphysa flammea									25
Halitholus cirratus		495	188	1733	2011	2723	603	2228	75
Obelia sp.									13
Plotocnide borealis		248	25	495		248	136	248	50
Sarsia princeps		495		248	134	248		495	
Actinula larvae		990	126	3218	3888	11634	1840	10396	1358
Nematoda - unidentified							15		
Annelida - Polychaeta									
Iospilidae									
Polynoidae									
Unidentified larvae		5693	75	1485	536	1238	60	2475	327
Mollusca									
Gastropoda									
Pteropoda									
Limacina helicina		248		248		495	75	495	13
Unidentified veliger larvae						743	30		
Bivalvia - unidentified larvae									

Table 3. (cont.)

	Station Number	5	5	6	6	7	7	8	8
Taxon	Tow Type†	V	DO	V	DO	V	DO	V	DO
Arthropoda - Crustacea									
Ostracoda									
Conchoecia sp.									
Polycope sp.				248					
Cyprideis sorbyana									
Cytheridea papillosa									
Cytheromorpha fuscata									
Cytherideidae									
Bythocytheridae		248							
Copepoda									
Calanus glacialis	II		1257				3771		
Calanus hyperboreus	III	86634	8798	24752	12569			123762	1257
	II	37129	2514		8379		7542	24752	3142
	I								628
Pseudocalanus elongatus	VI f	1893564	358220	5866337	2547344	4084158	1591252	6311881	166541
	VI m	24752		24752	8379	24752	3771		628
	V f	12376	7542	24752	4190		41478	24752	628
	V m	12376	11312	24752	12569	99010	116893		
	IV f	24752	36450	198020	83794	49505	184766	247525	13198
	IV m	37129	57818	396040	150830	74257	297888	198020	7542
	III	569307	142031	767327	356125	866337	241327	1757426	60960
	II	49506		24752		99010			1257
	I								
Microcalanus pygmaeus	VI f							24752	1257
	VI m								
	V f	24752		24752				24752	1257
	V m	49506		24752				24752	2514
Derjuginia tolli	V f	12376							
	V m							24752	628
	IV f	24752			50276	123762	7542		1885
	IV m	86634		49505	46087	272277	18854		2514
	III	86634	2514	420792	113122	396040	33937	247525	2514

Table 3. (cont.)

Taxon	Station Number	5	5	6	6	7	7	8	8
	Tow Type†	V	DO	V	DO	V	DO	V	DO
	II	222772		346535	92174	99010	3771		1257
	I				4190				
Eurytemora herdmani	VI f							49505	
	VI m		1257						
Metridia longa	V m								
	IV f								
	IV m							24752	1257
	III	24752	2514	24752	12569	74257	3771	247525	5656
	II	12376			4190		3771	74257	1885
Limnocalanus macrurus	VI f		1257		4190				
	V f	12376							
	V m		1257			24752	7542	24752	
	IV f				4190		3771		
	IV m						3771		
	III		1257		4190				
	II								
Acartia bifilosa	VI m						3771		
Acartia clausii	VI m								
	IV f								
	IV m								
Acartia longiremis	VI f								
	IV f								
	IV m				4190				
Oithona similis	VI f					24752			628
Harpacticus uniremis	VI f								
	VI m								
	V f								
Cirripedia - unidentified nauplii			38			1733	106	13366	1571

Table 3. (cont.)

Taxon	Station Number Tow Type†	5 V	5 DO	6 V	6 DO	7 V	7 DO	8 V	8 DO
Mysidacea									
Mysis litoralis f									
Mysis litoralis m									
Mysis litoralis juvenile						495			
Mysis spp. juvenile		495	666	14356	57919	24010	1659	248	
Unidentified damaged mysids						2228			
Cumacea									
Leuconidae									
Diastylidae									
Isopoda									
Unidentified epicaridean larvae		743	38	2228		1238	90	990	88
Amphipoda									
Gammaridea									
Onisimus glacialis juvenile		248							
Onisimus litoralis f									
Metopa sp. juvenile							15	248	13
Acanthostepheia behringiensis									
Monoculodes sp. juvenile		495							
Monoculodes sp. damaged									
Oedicerotidae juvenile		990							
Apherusa glacialis f						248	15	495	38
Apherusa glacialis juvenile		1485	63	248		248	15	990	63
Apherusa megalops juvenile				248	268				
Weyprechtia pinguis m			25				15		
Weyprechtia pinguis juvenile				248		248	15	248	
Marinogammarus sp. *cf.* juvenile			13				15		
Gammaridae juvenile damaged				248					
Hyperiidea									
Parathemisto abyssorum juvenile							15		
Hyperia galba f			25	248	268	248	30		
Hyperia galba m					134			248	
Hyperia galba juvenile					268	743	15	248	13

Table 3. (cont.)

Taxon / Station Number / Tow Type†	5 V	5 DO	6 V	6 DO	7 V	7 DO	7 V	7 DO
Unidentified hyperiid larvae	248	38			248	30	248	
Decapoda								
Anomura								
Paguridae, unidentifed zoea	495	214	990	402	248	362	2970	214
Brachyura								
Hyas sp. stage I zoea		25	248			15	248	
Caridea								
Hippolytidae - unidentified zoea		38				60		38
Euphausiacea								
Thysanoëssa raschii juvenile					248		495	
Calyptopis stage III					248			
Unidentified crustacean larvae			248	268	743	30		38
Unidentified crustacean eggs	1238	1269	248	536	743	2081	1238	75
Chaetognatha								
Sagitta elegans	248		495		248	15	743	
Unidentified immature chaetognaths						15		
Chordata								
Larvacea								
Fritillaria borealis	2970	767	3713	402	1980	468	18812	2313
Pisces (larvae								
Cyclopteridae		25		536	743	90	248	25
Gadidae			248		248	106	495	75
Unidentified damaged larvae							248	
Other organisms								
Foraminifera	743	25	248		248			
Trochophore larvae		13	495	134	495	256	495	138

It is likely that *Pseudocalanus elongatus* and *Derjuginia tolli* breed in Harrison Bay because both young copepodid stages and mature adults were present at the same time. More than one immature stage of several other species was present, suggesting that at least part of their life cycle is adapted for survival in shallow water.

Calanus hyperboreus, *Microcalanus pygmaeus*, and *Metridia longa* are known to breed independently of their food supply (Heinrich 1962), with *C. hyperboreus* and *M. longa* apparently not feeding extensively until stage II or III (Hansen *et al.* 1971). Adults of these two species were collected only in one of the benthic samples.

Calanus glacialis was present as stage II copepodids in two samples. Grainger (1965) reported that stage I copepodids developed from nauplii in late July and early August, with stage II's developing in early September. He suggested that this species probably overwintered as stage III with development continuing during a second summer. This species is reported to breed when phytoplankton is abundant (Heinrich 1962).

Calanus hyperboreus stages I, II, and III were found in most plankton tows, but adult females (stage V) were only found in a benthic sample. This species probably also overwinters as stage III (Hansen *et al.* 1971). In the Gulf of Maine, this species lives below the photic zone, coming to the surface only during the spring phytoplankton bloom (Conover 1967). In laboratory experiments Conover (1967) found that adequate egg production could occur even when food was scarce or absent.

Pseudocalanus elongatus was the dominant species in all of the plankton hauls. Few adult males were present, but many of the adult females were carrying eggs attached to the genital segment and eggs could be seen in the oviducts. Ussing (1938) reported *P. elongatus* to be abundant in all seasons in East Greenland fjords with a population explosion in July and August. This agrees witn RU 359's data from Stefansson Sound where *P. elongatus* was the most abundant species in Nov 1978, March and May 1979, and off Narwhal Island in Apr, May, and Jun 1980 (Horner and Schrader 1981).

Microcalanus pygmaeus is considered to be a deep-living animal (Ussing 1938). Only adults and stage V individuals were found in the Harrison Bay samples. It apparently develops during winter and is not dependent on phytoplankton for food.

The distribution of *Derjuginia tolli* is closely related to the presence of brackish water (Jaschnov 1947). It has been reported from the High Polar Basin, but Johnson (1963) considered it to be an expatriate from coastal areas.

Eurytemora herdmani is another brackish water species occurring in coastal waters of northeastern and northwestern North America and northeastern Asia, but it is not found in fresh water or water with very low salinity (Wilson and Tash 1966, Johnson 1966). Adults were found in Harrison Bay and females carried eggs.

Metridia longa was present in all the plankton tows from Harrison Bay. An adult male was found in one of the benthic samples. This species was common during winter in East Greenland fjords (Ussing 1938). Spawning occurred in August, with most of the adults dying in Sep-Oct. Eggs and nauplii descended to deeper water where development occurred in winter. Distinct diurnal migrations occurred in late summer as soon as there was a difference between night and day (Ussing 1938). *Metridia longa* apparently does not feed much until stage II or III (Hansen *et al.* 1971).

Limnocalanus macrurus, present in all Harrison Bay samples, has a widespread, circumpolar distribution and occurs in fresh as well as brackish water (Holmquist 1970).

Adult males of *Acartia bifilosa* were found in the double oblique tow from sta 7. It is a brackish water species, common in the northern Baltic (Segerstråle 1957) and has been reported to be abundant in some northwestern Alaska lagoons (Johnson 1961). It is probably an expatriate in Harrison Bay.

Acartia clausii and *A. longiremis* were not abundant in Harrison Bay. *Acartia clausii* is considered to be an inshore, estuarine species (Willey 1920), while *A. longiremis* is a widespread, neritic species (Johnson 1961).

Oithona similis is a small-sized, common, boreal cyclopoid species that was rare in Harrison Bay samples probably because of the relatively large meshed net we used.

Harpacticus uniremis is a widespread, littoral harpacticoid species, probably caught when the net was towed near the bottom or contained debris to which the animal was attached.

All of the hydrozoans are common, widespread species in Arctic coastal seas. *Aeginopsis laurentii* and *Aglantha digitale* are common pelagic species, while *Halitholus cirratus*, *Plotocnide borealis*, and *Sarsia princeps* are meroplanktonic species having pelagic medusae and attached polyp stages. *Halitholus cirratus* is reported to occur in freshened water in bays and at river mouths. All of these species have been reported from plankton samples collected previously by RU 359.

Polychaete larvae were most abundant at sta 1, but were present at all stations. Larvae are pelagic while adults may be either pelagic or benthic. Pelagic barnacle larvae were also present, primarily at sta 7 & 8. Adult barnacles are benthic. The ostracods, most abundant at sta 1, are probably also benthic species.

Most of the mysids and amphipods collected in Harrison Bay were juveniles; none were present in large numbers, although this may be an artifact caused by our sampling gear. All have been reported from previous OCSEAP samples. Juvenile mysids were most abundant at sta 2, 3, 6, & 7. Juvenile amphipods were most numerous at sta 1. Decapod zoea were present in low numbers at all stations. Unidentified crustacean eggs were also common at all stations.

Chaetognaths were present at all stations except 2 & 3 and were identified as *Sagitta elegans*, a common nearshore species.

Fritillaria borealis was the only larvacean in these samples and was present at all stations except sta. 2.

Fish larvae were most abundant at stations 7 & 8. Larvae were identified only to family with Cyclopteridae and Gadidae being present.

With the exception of the copepod *Acartia bifilosa* and perhaps some of the Ostracoda, all of the species identified in these samples have been reported previously from the Beaufort Sea by OCSEAP investigators. The presence of many juveniles among the larger crustaceans and young stages of many copepods relatively late in the season suggests that much development must occur during winter when food from phytoplankton productivity is low. Or if development does not occur, then the juveniles and young must be able to overwinter at low metabolic rates. Some copepods have young stages that apparently do not feed much (Hansen *et al.* 1971) and others, such as *Calanus hyperboreus*, can complete their life cycles using stored lipids as a carbon source (Conover 1967). It is not known what most animals do in winter. Schneider and Koch (1979) have shown that few amphipods are able to utilize carbon from terrestrial sources. It is gradually becoming known that some copepod species may be more opportunistic feeders than previously thought. Berk *et al.* (1977) have reported ciliates to be an important food source for one species of *Eurytemora* and suggested that they might be important for copepods in general. Ciliates have not been studied at all by OCSEAP investigators, and nothing is known about their occurrence or importance in Beaufort Sea coastal areas, although they have been abundant in some phytoplankton net samples from the Barrow area and in some ice cores collected for ice algae studies (Horner personal observations). They are known to utilize bacteria and particulate organic material as well as diatoms, flagellates, and other ciliates as food sources (Fenchel 1968). Perhaps they help provide a carbon source when phytoplankton carbon is not available.

Animals found in the three benthic samples are listed in Table 4. The numbers given are the number of specimens counted in the entire sample. Numbers per unit volume cannot be calculated because there is no haul data. Most of the species are benthic ones.

Acknowledgements

LGL personnel collected the samples and sent them to us. Marc Weinstein identified the non-copepod organisms and provided the table of references used for identification. Gayle Heron identified the copepods and provided the information and references on life history, food habits, and ecology.

Table 4. Relative abundance* of animals found in samples taken at station 5, Harrison Bay, 14 Aug 1980. Method of collection unknown. Where no number is present, no animals were found.

Taxon Sample Number	1	2	3
Cnidaria - Hydrozoa			
Aeginopsis laurentii	1	3	1
Nematoda - unidentified		21	27
Annelida - Polychaeta			
Unidentified benthic spp.	14	51	32
Mollusca - Bivalvia - unidentified	4	7	1
Arthropoda - Crustacea			
Ostracoda			
Cyprideis sorbyana	1		
Copepoda			
Calanus hyperboreus VI f		1	
V m		1	
III	4		2
Pseudocalanus elongatus VI f	1	1	
Euchaeta glacialis IV f	1		
Limnocalanus macrurus V f			1
Metridia longa VI m		1	
Mysidacea			
Mysis spp. juveniles	10	17	33
Cumacea			
Diastylidae female		2	
juveniles	7	14	16
Amphipoda			
Gammaridea			
Aceroides latipes female (gravid)		1	
female	1	8	11
male	2	7	6
juvenile	2	12	12
Paroediceros lynceus juvenile		1	
Oedicerotidae juvenile			5
Apherusa megalops juvenile			2
Unidentified crustacean eggs		25	56
Priapulida			
Halicryptus spinulosus		1	
Chordata - Pisces			
Gadidae		1	
Foraminifera	9	23	14

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* Numbers given are number counted in entire sample. Lack of haul data prevents calculation of abundance per unit volume. Most animals are benthic.

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BEAUFORT SEA PLANKTON STUDIES: WINTER-SPRING STUDIES IN STEFANSSON SOUND AND OFF NARWHAL ISLAND NOVEMBER 1978-JUNE 1980

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Final Report
Outer Continental Shelf Environmental Assessment Program
Research Unit 359

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I. Summary of objectives, conclusions, and implications with respect to OCS oil and gas development.

A. Objectives

Our objectives were to 1) determine the relative contribution of the ice algae, phytoplankton, and benthic microalgae to primary production in the Beaufort Sea coastal zone during the winter-spring period of ice cover; 2) determine the species composition of these communities and the degree of linkage or interaction between them; 3) follow the development of the spring ice algal bloom and determine the environmental factors controlling the timing, distribution, and magnitude of this bloom; and 4) assess the winter density distribution and environmental requirements of zooplankton, phytoplankton, and ichthyoplankton in the nearshore Beaufort Sea.

B. Conclusions

1. Ice algae were responsible for nearly all primary production during the winter-spring period, with only minimal contribution from the phytoplankton and benthic microalgae. The bulk of this production took place from April to June and amounted to *ca.* 0.7 g C m^{-2}. In addition, an unknown amount of primary production probably occurred in the ice during the fall of 1980. The only published reference to a fall bloom in the ice of the Beaufort Sea is that of Hsiao (1980). Although higher rates of production take place in the water column and perhaps the benthos during the open water period, ice algae are the prime source of carbon during *ca.* 30% of the period in which primary production may occur.

2. The ice algal community was composed primarily of pennate diatom species typical of the under-ice community in other arctic areas. These same species dominated the phytoplankton in early spring, but cells were unhealthy and appear to have originated in the ice, being only temporary members of the phytoplankton. Small microflagellates, < 6 µm in diameter, were abundant in both the ice and water column, but they do not appear to be photosynthetic, and their importance as a food source is not known, although some copepod species apparently prefer them. Some ice algal species occurred in the benthic microalgal community, but most of these species were represented by dead or moribund cells and may be considered detrital. The benthic microalgal community formed a separate assemblage, with high standing stocks that lay dormant during the winter period, but are known to be important primary producers during the summer.

3. Light appears to be the major environmental factor controlling primary production during this period. The ice algal bloom is initiated by increasing solar radiation in spring and the distribution and magnitude of the bloom is determined largely by ice turbidity and snow cover which limit light transmission through the ice. Production in the water column and benthos in early spring is inhibited by shading from the ice algal layer when it is present.

4. Ice algae provide a rich food source for animals, such as protozoans, copepods, nematodes, and amphipods that live in direct

association with the underside of the ice. Ice algae are also a major source of living and detrital material for animals living in the water column and benthos.

5. Although data given here do not indicate it because we did not sample the spring phytoplankton bloom, there is a definite species difference between the ice algal bloom and the phytoplankton bloom in the water column, with pennate diatoms dominating the ice community and centric diatoms dominating the phytoplankton (water column) community. There is also a time lag with the ice algae occurring in April-June and the phytoplankton occurring during and after breakup when sufficient light reaches the water column.

6. Copepods are the most abundant zooplankton both in terms of number of animals and species and are present throughout the winter-spring period. All life cycle stages are present. Some species apparently prefer microflagellates that are present all winter as a food source. Other important components of the nearshore zooplankton community are amphipods and mysids, but they were never caught in large numbers, perhaps because of our collecting methods. Hydrozoans became abundant in spring.

C. Implications

The ice algal community occurs as a layer only a few centimeters thick on the under surface of the ice in spring and would be directly susceptible if an oil spill came in contact with the ice. The oil could damage or destroy the ice algae by direct toxic effects, by limiting exchange with the underlying seawater, or by reducing light levels. Oil-related activity prior to the development of the bloom could affect ice algal production by increasing ice turbidity from oil or suspended sediments in the ice that would reduce light transmission through the ice and thus limit algal growth.

There are no other sources of primary production during the early spring, therefore, animals present that depend on primary production for their food supply and spend a significant or critical portion of their life cycles associated with the ice would be seriously affected. This could have serious implications farther up the food chain for fishes, birds, and mammals that depend on these invertebrates for their food.

Phytoplankton and benthic microalgae, while not present in large numbers during the spring, would be affected by direct toxic effects and reduced light levels. These factors could, perhaps, destroy or severely impair seed stock that normally produce the spring phytoplankton bloom and the summer benthic microalgal populations.

The effects of an oil spill could be quite local, but could also spread over a wide area depending on environmental conditions. A spill in tne fall could affect primary productivity of a whole season by damaging ice algal seed stocks. Whether early and timely cleanup would reverse this affect is not known, nor is it known what affects residual pollutants may have on the microalgal populations in the ice, water column, or benthos. Relatively rapid generation times of microalgae and some zooplankton would alleviate the effects of an oil spill in a short period of time in temperate regions, but generation times for most microalgal species found in the Arctic are not known, and some important zooplankton species are known to take at least two years to complete their life cycles.

II. Introduction

A. General nature and scope of the study

The sources of primary productivity and carbon pathways that support the ecosystem of the nearshore Beaufort Sea are poorly understood. In particular, there is a gap in our knowledge of the system during the winter-spring period of ice cover, which accounts for the majority of the annual cycle.

One of the major components of the nearshore ecosystem that has not been intensively studied is the algal community living in and on the underside of sea ice, along with those organisms that are sometimes associated with it such as amphipods and perhaps fish. It is not known how important the ice algae are as a food source in the nearshore area, but their presence about two months before the phytoplankton bloom in the water column must lengthen the growing season for those animals that are able to utilize them.

In addition, benthic microalgae have been shown to account for a significant amount of the total productivity of some nearshore ecosystems, including the nearshore Chukchi Sea near Barrow, Alaska (Matheke and Horner 1974). Its importance in the nearshore Beaufort Sea ecosystem is not known.

Our objective was to assess the winter density distribution and environmental requirements of zooplankton and phytoplankton in the nearshore Beaufort Sea, and to undertake an integrated study of ice algae, water column, and benthic microalgae production to provide comparisons among these habitats and allow us to assess the relative importance of these communities during the critical spring growing season. Cooperative studies with RU's 6 and 537 were designed to provide information on the benthic invertebrate community and its utilization of the ice algae and benthic microalgae, help determine the degree of linkage between the ice algae and benthic microalgal communities, determine the areal extent and patchiness of the ice algae, and the carbon pathways in the system, thus providing a relatively complete study of the winter-spring ecosystem.

B. Specific objectives

1. Determine the primary productivity, standing stocks (plant pigments and cell numbers), and species composition of the ice algal, phytoplankton, and benthic microalgal communities in the Stefansson Sound area.

2. Assess the relative importance of these communities.

3. Follow the development and decay of the spring ice algal bloom.

4. Determine the species composition and abundance of the zooplankton community.

5. Measure environmental parameters, such as light, temperature, salinity, nutrient concentrations, and snow cover, that may affect these communities.

6. Complete and submit a final summary report on winter-spring studies.

C. Relevance to problems of petroleum development

As oil development is planned for the nearshore waters of the Beaufort Sea, and exploration drilling is likely to occur primarily in winter, it is important to assess the biological importance of the area and to determine the ecosystem's vulnerability to oil-related activities during the ice covered months of the year.

Microalgae associated with the underside of the ice appear to be responsible for the bulk of the primary production that supports the nearshore ecosystem during the period. An understanding of the dynamics of this community, and the fauna closely associated with it, is important in assessing periods that may be particularly sensitive to the effects of oil-related activity. In addition, a better understanding of the relative roles of the ice algae, water column, and benthic communities is important in predicting the probable effects of an oil spill on the nearshore ecosystem during the winter-spring period.

D. Acknowledgements

Winter sampling in Nov 1978, Feb and Mar 1979 was done by Tom Kaperak, who also identified the non-copepod zooplankton. Gayle Heron identified the copepods. May 1979 sampling was done by diver Jim Hanes and Rita Horner, who also analyzed the plant pigment and standing stock samples from all the Stefannson Sound samples. Kendra Daly collected the one zooplankton sample from May 1979.

Gary F. Smith, Coastal Environmental, Bellingham, WA., redesigned and fabricated the ice sampler-incubation chambers and provided the divers, Ron Poirot and Jim Dougherty, for the Apr-Jun 1980 sampling period. Carl Schrader and Dave Murphy spent 2.5 mo at Prudhoe Bay doing the field sampling and then analyzed the samples in Seattle. Ron Atlas and Paul Hill analyzed the benthic microalgae productivity samples; Gayle Heron identified the copepods. Kate Persons and Steve Petersen provided logistic support at Prudhoe Bay. Personnel from RU 6 also helped in the field. NOAA helicopter pilots and mechanics provided transportation and logistic support, and, for several weeks until we got adequate stoves, provided heaters for the field site.

III. Current state of knowledge

A. Biota

In the nearshore Beaufort Sea area, early reports from the Canadian Arctic Expedition in 1913-1918 were primarily taxonomic studies (Bigelow 1920; Shoemaker 1920; Willey 1920; Schmitt 1919; Mann 1925). Plankton studies in the nearshore area before the late 1960's were limited. Now, information concerning the plankton of this area is gradually accumulating, primarily as a response to increasing oil and gas exploration and development.

In the Harrison Bay-Simpson Lagoon region, Alexander (1974) found the highest primary productivity rates occurred in deeper, more saline water, with maximum productivity occurring in August. Annual productivity in the water column was estimated to be more than 10-15 g C m^{-2}. Nutrient-rich water from the Colville River may, at least in part, be a major factor contributing to the relatively high productivity rates. Species composition of the phytoplankton community varied with depth, season, and year, but many cells were small, in the nanoplankton range. Ice algae, benthic microalgae, and zooplankton were not studied in this area.

Horner *et al.* (1974) described the plankton of Prudhoe Bay in terms of primary productivity, standing stock, species composition, and spatial variability, along with hydrographic conditions. High concentrations of chlorophyll *a* and pennate diatoms were present in the bottom layer of ice in May and June, but no primary productivity measurements were made. However, annual primary productivity of the ice algal community in Prudhoe Bay was estimated to be *ca.* 1 g C m^{-2}.

During the open-water season, three phytoplankton communities were present with pennate diatoms predominating in Prudhoe Bay immediately after breakup; centric diatoms dominating in deeper, more saline water outside the bay; and flagellates dominating in brackish surface water. Productivity was highest in the diatom-dominated communities. Annual primary productivity in the water column inside Prudhoe Bay was calculated to be *ca.* 9 g C m^{-2} and that in the lagoon system to be *ca.* 18 g C m^{-2}. Nutrient concentrations were higher in winter and early spring, with nitrate being rapidly utilized during spring and probably limiting growth in summer. Benthic microalgae were not studied.

Three zooplankton communities were also found, with copepods being numerically dominant in all. Inside Prudhoe Bay, *Acartia clausi* was the most abundant species and meroplanktonic larvae were absent. In the lagoon system, *Calanus glacialis* and *Pseudocalanus minutus* were dominant; small numbers of meroplanktonic larvae occurred near Reindeer Island. Outside the Midway Islands, meroplanktonic larvae became important with decapod, polychaete, and barnacle larvae all present.

The only previous study to compare production of the ice algal, phytoplankton, and benthic communities was done in the nearshore Chukchi Sea at Barrow, Alaska, (Clasby *et al.* 1973; Matheke 1973; Matheke and Horner 1974; Alexander *et al.* 1974). This was also the first study to look at standing stocks (chlorophyll *a* and cell numbers) and primary productivity for all three communities at the same time. In this study, sampling started in Jan-Feb and continued until late Aug in two successive years. Only the period of ice breakup was not covered. *In situ* techniques were devised to measure productivity of the ice (Clasby *et al.* 1973) and benthic (Matheke 1973) microalgal communities so that cells would not be physiologically stressed by being brought from relatively high temperature, low light conditions under the ice to low temperature, high light conditions at the surface. The Barrow studies showed that the ice algal community developed in response to a critical light level in early April; maximum production occurred in late May with a rapid decline in early June as the ice decayed. Production in the water column was low until after the ice algae disappeared and breakup began. Benthic microalgal production was low while ice cover was present with motile, solitary pennate diatoms being the most abundant organisms. After ice breakup, a mat of *Amphipleura rutilans* (Trent.) Cleve developed and was still present when sampling ended in August. The benthic microalgae became the most important source of primary productivity after ice breakup, being eight times that of the ice algae and two times that of the phytoplankton (Matheke and Horner 1974).

The early literature on ice algae has been reviewed extensively (Alexander *et al.* 1974; Horner and Alexander 1972; Horner 1976, 1977; Alexander 1980).

As part of the OCSEAP project, RU 536 collected epibenthic and planktonic invertebrates from many stations in the nearshore Beaufort Sea (Broad *et al.* 1979). *Mysis litoralis* and a number of amphipod species that have also been collected in plankton samples were the most abundant species found in epibenthic sled tows.

LGL (RU 467) found that invertebrates were important in the Simpson Lagoon area if they provided food for fish and birds. Most of the feeding occurred in shallow lagoons and bays in summer and plenty of invertebrates were available for food. LGL also found that primary production by diatoms in summer was the major source of carbon for the system, with ice algae being a secondary source; benthic microalgae were thought to play a small role in the food web (LGL 1981).

Schell (1980a) estimated ice algae annual productivity in Simpson Lagoon, Stefansson Sound, and offshore based on daily productivity measurements (measured in Stefansson Sound by RU 359), literature values, and observed increases in standing stocks, and compared these estimates with values obtained by ^{14}C uptake experiments in other Alaskan areas. He calculated low productivity within Simpson Lagoon, 0.178 ± 0.166 g C m^{-2}; higher rates in Stefansson Sound, 1.43 ± 1.13 g C m^{-2}; and highest rates, 1.69 ± 0.89 g C m^{-2}, offshore.

Farther east in the southern (Canadian) Beaufort Sea, Hsiao *et al.* (1977) found that standing stock in the euphotic zone decreased with increasing distance from shore and the Mackenzie River delta. Diatoms were more abundant near shore, in river mouths, and in surface water at ice stations, while flagellates were more common offshore. Phytoplankton was more abundant above 5 m than in deeper water. Primary productivity was also found to decrease with increasing distance from shore and the river mouths, primarily because of higher nutrient concentrations and warmer temperatures in the coastal waters. From Hsiao *et al.*'s (1977) hourly productivity data and assumptions previously used by RU 359 (English and Horner 1977) annual productivity in this area was calculated to be *ca.* 3 g C m^{-2}.

Hsiao (1980) identified 196 species of microalgae from annual shorefast ice in the Canadian Arctic, including the Eskimo Lakes region of the southern Beaufort Sea, Eclipse Sound in the high Arctic; and Frobisher Bay in the eastern Arctic. The ice algal communities developed slowly from late fall through winter, increasing exponentially in early spring, reaching a peak just before the thaw period, and declining rapidly as the ice melted. Standing stock was greatest at the bottom of the ice and pennate diatoms were the most abundant organisms.

Dunbar and Acreman (1980) presented data on standing stocks and species composition of diatoms in sea ice from Robeson Channel and Barrow Strait in the high Arctic, Hudson Bay, and the Gulf of St. Lawrence. Nutrient concentrations in all areas were similar, but chlorophyll *a* was one to two orders of magnitude higher in the northern areas than in the Gulf of St. Lawrence. In the northern areas, pennate diatoms comprised 96-99% of the population, while in the Gulf of St. Lawrence, pennate diatoms comprised 57% of the population with the remainder being planktonic centric species.

B. Nutrients

Inorganic nutrient levels in the surface waters of the Beaufort Sea undergo marked seasonal fluctuations. During the summer, nitrate and phosphate drop to very low or undetectable levels, and the system is considered to be strongly nitrogen limited. This results from high phytoplankton utilization and limited vertical mixing due to high water column stability which develops in response to ice melt and increased insolation (Hufford *et al.* 1974; Aagaard 1977). In the winter when stratification breaks down, nutrient concentrations increase to relatively high levels as a result of increased vertical mixing and regeneration at a time when plant utilization is low.

Schell (1974) has documented the regeneration of nitrogenous nutrients beneath the winter ice cover in shallow, nearshore and estuarine areas. This suggests the possibility that a substantial fraction of the nitrate in arctic coastal waters may be regenerated *in situ* during the winter months rather than deriving from offshore deep-water sources. It is suspected, however, that much of the nutrients regenerated in coastal waters may be transported offshore by thermohaline convective processes during winter (Nov-Mar) (Schell pers. comm.).

Winter nutrient levels near Point Barrow have been reported to range up to 1.7 μg-at ℓ^{-1} phosphate, 9.2 μg-at ℓ^{-1} nitrate plus nitrite, and 35 μg-at ℓ^{-1} silicate (Matheke 1973). Similar values have been reported by Horner *et al.* (1974) for Stefansson Sound. The same authors reported summer levels ranging from 0-0.9 μg-at ℓ^{-1} phosphate, 0-2.7 μg-at ℓ^{-1}

nitrate and 5-28 μg-at ℓ^{-1} silicate.

Upwelling has been documented by Hufford (1974a) along the eastern portion of the shelf and may be a major source of nutrients to the euphotic zone in this region. As a result of local easterly winds, nutrient-rich water from 100-200 m depth is upwelled and advected westward over the mid-portion of the shelf. Observed as far east as Barter Island (144°W), upwelling is largely limited by the amount of open water on which the wind may act. The rather persistent ice cover in the western shelf area may be responsible for the lack of observed upwelling in that region.

Strong onshore-offshore nutrient gradients are often apparent during the summer, due largely to the influence of river runoff. Hufford (1974b) found that in the area between Point Barrow and Barter Island, nitrates decreased from 1.5 μg-at ℓ^{-1} nearshore to very low or undetectable levels near the shelf break. At the same time, he found that river discharge in the area contained 3-15 times the amount of nitrates found in the coastal surface layer. Silicates followed a similar pattern decreasing from 10 μg-at ℓ^{-1} near the mouth of the Colville River, to less than 2 μg-at ℓ^{-1} 100 km offshore. Phosphates deviated strongly from this pattern, being low or not detectable nearshore and increasing to 0.8 μg-at ℓ^{-1} near the shelf break. This pattern reflects the high input of nitrates and silicates by river water and the relative lack of phosphates (Codispoti and Richards 1968; Grainger 1974). River flow is seasonal, however, and the majority of nutrient input from rivers occurs during spring breakup, as has been documented by Hamilton *et al.* (1974) for the Colville River.

In the Canadian Arctic, the Mackenzie River has a substantial impact on the southern Beaufort Sea. Approximately half of the freshwater runoff to the Beaufort Sea flows through this river. The plume generally flows eastward along the coast and is deflected north and westward near Amundsen Gulf to mix with waters of the Beaufort Gyre (O'Rourke 1974). Grainger (1974) found the highest surface nutrients immediately off the river mouths, with concentrations decreasing seaward. With the exception of silicate, nutrients were much higher in the surrounding sea where the river discharges than in the river proper. These high nutrient concentrations may be largely attributed to the estuarine circulation typical of many large rivers (Redfield *et al.* 1963). In this type of circulation, a sub-surface countercurrent forms to replace water entrained in the surface flow causing nutrient concentrations to increase upstream relative to the motion of the surface layer. In addition, microbial activity was found by Griffiths *et al.* (1978) to be very high in the plumes of major rivers and nearshore sediments of the North Slope. Decomposition of river-borne detritus must be a major source of nutrients to the nearshore environment.

IV. Study area

Two areas were sampled (Fig. 1). In Nov 1978, and Feb, Mar, and May 1979, samples were collected in Stefansson Sound near RU 356's dive site 11 (70°19'N, 147°34.4'W) in the boulder patch area. From Apr-Jun 1980, a site was established on a large, flat pan in the shorefast ice *ca.* 300 m seaward of Narwhal Island (70°24.0'N, 147°31.1'W). The Narwhal

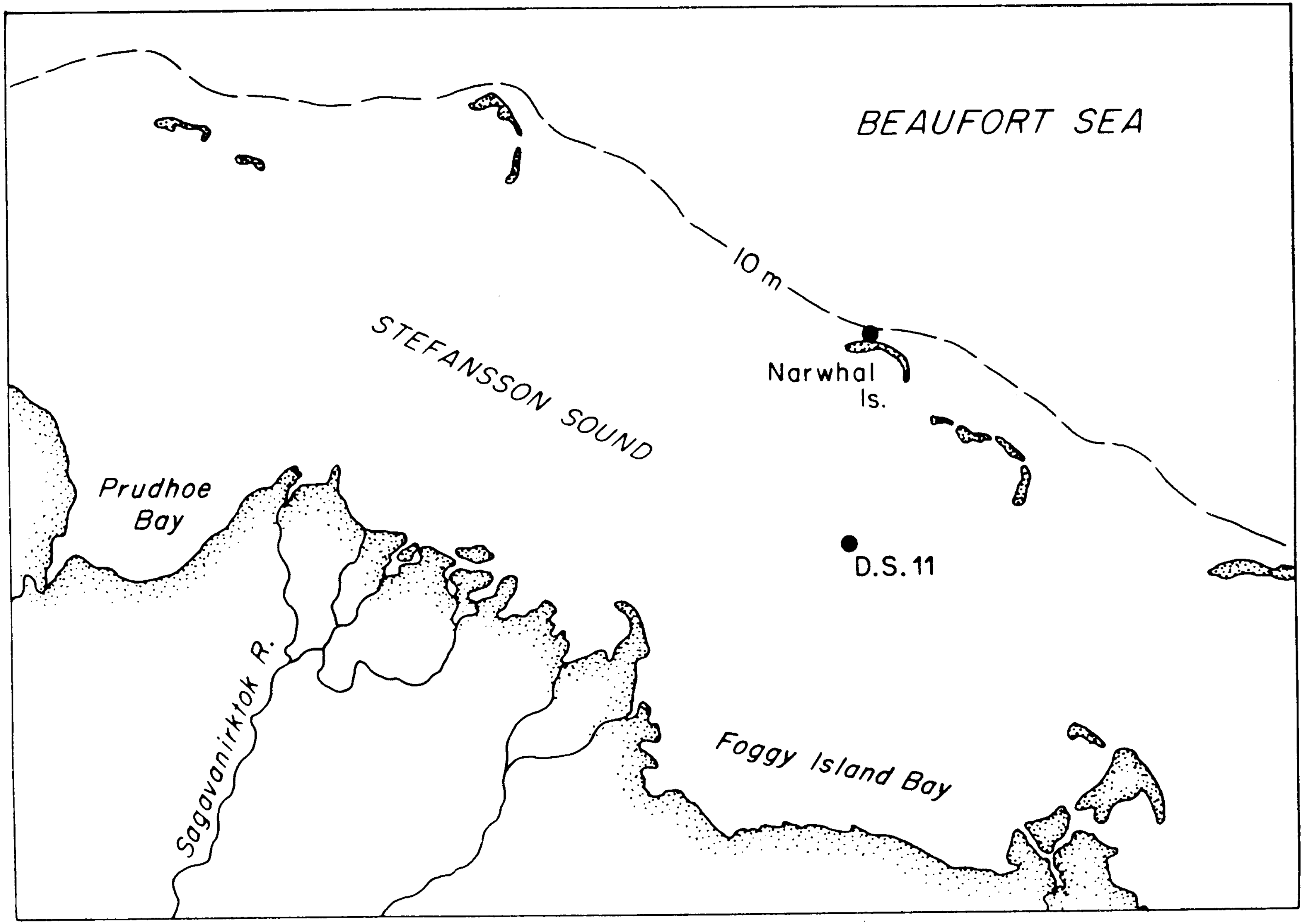

Fig. 1. Location of study sites in Stefansson Sound (1978-1979) and off Narwhal Island (spring 1980).

Island station was occupied jointly with RU 6 (Fig. 2).

V. Sources, methods, and rationale of data collection

A. Sources and rationale

Winter and spring samples were collected in Nov 1978 and Feb, Mar, and May 1979. In order to provide more detailed coverage of the dynamic spring period, a station was occupied at approximately twice weekly intervals from early Apr through mid-Jun 1980. This provided the opportunity to follow the cycle of the ice algal community from its beginning until its disappearance at the end of the bloom, as well as the early development of the spring phytoplankton bloom in the water column and the benthic microalgal bloom.

Sampling during the 1978-79 period was done in the boulder patch area of Stefansson Sound near dive site 11 established by RU 356. This area was selected because of the ability to share logistics support and data with other RU's (6, 356, 537).

In spring 1980, we planned to continue sampling in this area and to add a station outside the barrier islands in an area more typical of the whole lease area that would allow a comparison between the two areas. However, a series of ice cores collected in early April with a SIPRE corer indicated the presence of a layer or layers of sediment in the ice throughout the lagoon system. The sediment layers effectively reduce the amount of light reaching the bottom of the ice where the ice algae are, thus inhibiting their growth. No traces of ice algae were seen on the bottom of the lagoon ice. Relatively clear ice with traces of ice algae were found just seaward of Narwhal Island and we decided to concentrate our efforts at that site. We returned to the boulder patch area once during the study to measure chlorophyll *a* levels in the bottom ice.

We have chosen to separate the presentation of the methods by date and kind of sample collected because sampling methods varied to some extent depending on equipment available and logistics support. In the results and discussion sections, we have chosen to separate the data by sampling location, Stefansson Sound (1978, 1979) and Narwhal Island (1980).

We have studied four distinct communities. The ice algal community consists of diatoms, dinoflagellates, flagellates, and associated invertebrates and sometimes fish that live in the interstitial water between ice crystals. This community, often called the epontic community (Bunt and Wood 1963), occurs on the bottom of sea ice in spring, Mar-Apr to mid-Jun. It is not present in the nearshore area in summer. This community has also been referred to as an upside down benthic community (Mohr 1959).

The phytoplankton community consists of diatoms, dinoflagellates, and flagellates that live in the water column. This community is present in abundance in late spring (breakup) and during the summer. The spring bloom probably occurs during ice breakup, but no data are available from the lease area to support this.

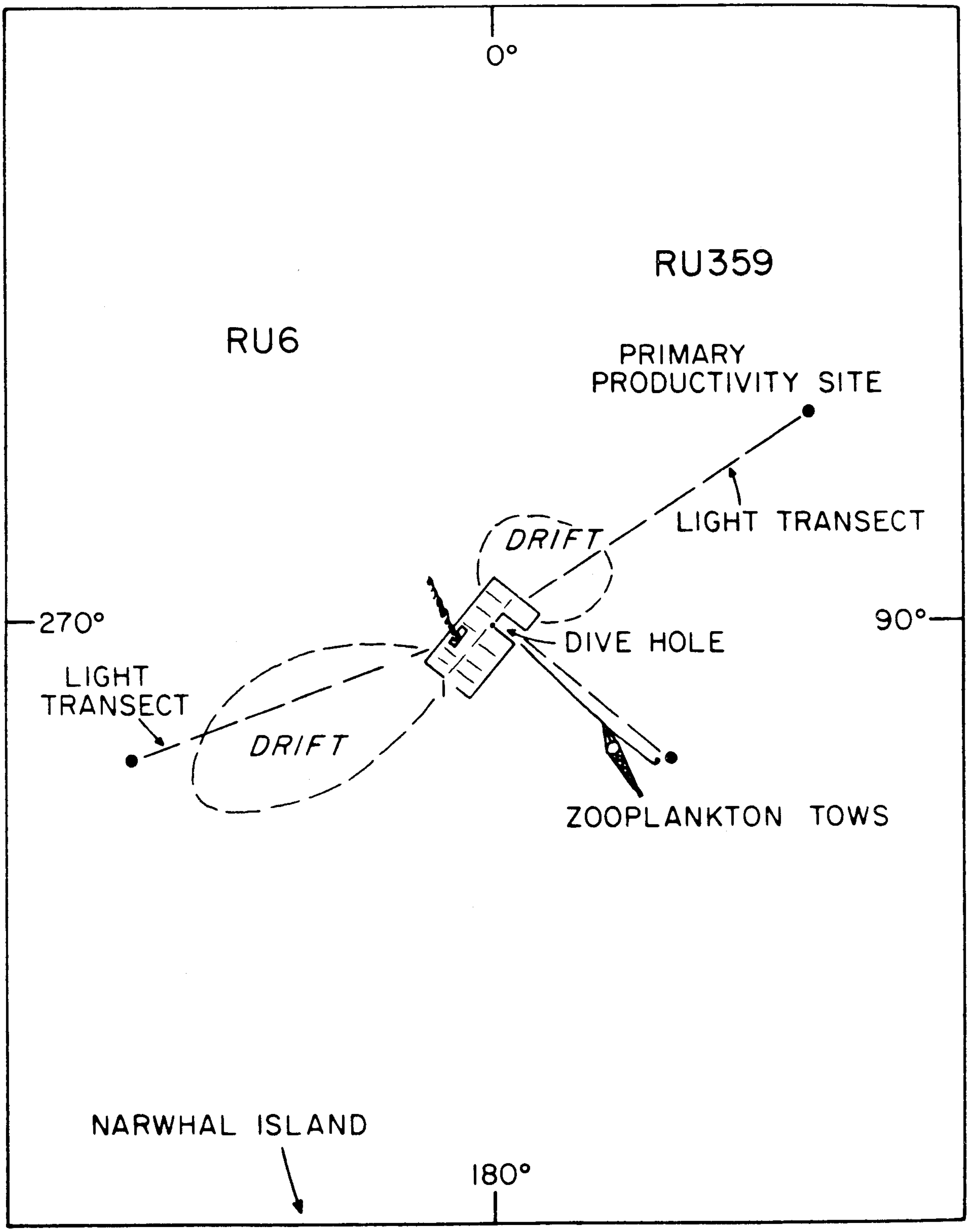

Fig. 2. Schematic diagram of the sampling site off Narwhal Island, spring 1980.

The benthic microalgae are those organisms, usually pennate diatoms, that live attached to or between sediment particles on the sea bed. This community may consist of patches of solitary, motile diatoms, dispersed solitary, motile diatoms, or mats of diatoms where cells are held together in tough mucilagenous filaments.

The zooplankton community consists of those invertebrates that live in the water column. They are present all year with species, life cycle stages, and abundances varying with season.

Separation of these communities is often difficult because diatoms from the ice community may be found in the water column or on the sea bed. This problem is more pronounced with the larger invertebrates such as amphipods because they are more mobile and able to move from one site to another. In the following discussion, we have tried to separate the communities as much as possible and to distinguish between typical ice algae species that might be in the water column temporarily and true planktonic species.

B. Sampling methods

1. Phytoplankton

a. November 1978

Samples were collected daily from 8-16 Nov at dive site 11. Water samples were collected using a plastic water sampling bottle lowered on a hand line. Samples were collected near the underside of the ice (0 m) and near the bottom (4.5 m). Samples for phytoplankton standing stock were poured into 250 ml glass jars and immediately preserved with *ca.* 10 ml 4% formaldehyde buffered with sodium acetate. The remainder of the water samples, usually 3 ℓ, was kept in a cool place until they could be taken to the shore laboratory.

Water collected for plant pigment determinations was filtered through 47 mm, 0.45 μm Millipore filters. Near the end of the filtration process, three drops of a saturated solution of $MgCO_3$ were added and the filter tower was rinsed with filtered seawater. The filters were folded into quarters, placed in labeled glassine envelopes, and frozen in a desicator.

b. February 1979

Only one sample was collected during the period 12-17 Feb because of weather and logistics problems. Water samples were collected through a hole used by LGL and located *ca.* 300 m south of dive site 11. Sampling was done using a plastic water sampling bottle lowered on a hand line. Sampling depths were 0 and 4.5 m. The phytoplankton standing stock samples were poured into 250 ml glass jars and preserved with *ca.* 10 ml 4% formaldehyde buffered with sodium acetate. The samples for plant pigment analysis were kept cool until they could be filtered on shore. The samples were filtered through 47 mm, 0.45 μm Millipore filters. Three drops of a saturated solution of $MgCO_3$ were added near the end of the filtration period, the filter tower was washed with filtered seawater, the filter was removed, folded into quarters, placed in a labeled glassine envelope, and frozen in a desicator.

c. March 1979

Samples were collected five times during the period 11-16 Mar at dive site 11. Samples for phytoplankton standing stock and plant pigment determinations were collected at 0 and 4 m using a plastic sampling bottle lowered on a hand line. The standing stock samples were drained into 250 ml glas jars and immediately preserved with *ca.* 10 ml 4% formaldehyde buffered with sodium acetate. The samples for plant pigment determinations were drained into 4 ℓ polyethylene bottles and kept in a cool place until taken to the shore laboratory where they were filtered through 47 mm, 0.45 µm Millipore filters. Three drops of a saturated solution of $MgCO_3$ were added near the end of the filtration and the filter tower was washed down with filtered seawater. The filter was removed, folded into quarters, placed in a labeled glassine envelope, and frozen in a desicator.

d. May 1979

Water samples were collected in 2 ℓ polyethylene bottles from just under the ice (0 m) and near the bottom (4 m). Portions of these samples were poured into 60 ml reagent bottles, two light and one dark bottle for each depth, and inoculated with 2 ml $Na_2H^{14}CO_3$ solution (*ca.* 5 µCi). The samples were incubated *in situ* by attaching the bottles to a line suspended from the bottom of the ice. Another portion of the water sample was poured into a 250 ml jar and preserved with 5-10 ml 4% formaldehyde for a phytoplankton standing stock sample. The remainder of the sample, usually about 1.5 ℓ, was returned to the shore laboratory.

At the shore laboratory, the remainder of the water sample was filtered through 47 mm, 0.45 µm Millipore filters and the filters frozen for determination of plant pigments. Some of the filtered water was put into 250 ml polyethylene bottles to be used to determine salinity and some filtered water was put into 125 ml polyethylene bottles and frozen to be used to determine nutrient concentrations.

The primary productivity samples were all filtered through 25 mm, 0.45 µm Millipore filters which were rinsed with 5 ml 0.01 N HCl and 5 ml filtered seawater before being placed in labeled glass scintillation vials.

All samples were returned to Seattle for analysis.

e. April-June 1980

Water samples for phytoplankton studies were collected with a PVC sampling bottle from just below the ice (0 m) and from 1 m above the bottom (7 m). Two-liter polyethylene bottles were rinsed and filled with water from each depth and a portion was used immediately for primary productivity experiments. The remainder of each sample was kept cool and dark in an ice chest until returned to the shore laboratory for analysis of plant pigments; portions were also preserved for standing stocks, nutrient, and salinity determinations.

To determine rates of primary productivity, 60 ml glass-stoppered reagent bottles (two light, one dark for each depth) were rinsed and filled to the shoulder with sample. Each bottle was inoculated with 2 ml ^{14}C-bicarbonate solution (*ca.* 5 µCi), stoppered, and mixed. Samples were incubated for 3-4 hr at the sampling depths in clear plastic tubes suspended from a line anchored to the ice with an ice piton. Dark bottles were incubated in a darkened chamber at 0 m depth. Light, measured within the diving shelter, was comparable to under ice levels which reduced the problem of light-shock when bringing the samples to the surface. At the end of the incubation period, the samples were retrieved and kept in a darkened ice chest until processed at the shore laboratory, usually within 1-2 hr.

At the shore laboratory, primary productivity samples were filtered through 25 mm, 0.45 µm Millipore filters, rinsed with 5 ml 0.01 N HCl and filtered seawater, and placed in labeled glass scintillation vials that were returned to Seattle for analysis. The 2 ℓ polyethylene bottle containing water from each depth was shaken and 250 ml poured into 250 ml glass jars and preserved with 10 ml 4% buffered formaldehyde for standing stock analysis.

One liter of water from each sampling depth was filtered through a 47 mm, 0.45 µm Millipore filter for pigment analysis. After *ca.* 100 ml of sample had filtered, filtration was stopped and the filtrate discarded. Filtration was continued until *ca.* 5 ml remained in the filter tower. Some of the filtrate was put into a 250 ml polyethylene bottle for later salinity determination and some was put into a 125 ml polyethylene bottle and frozen to be used to determine nutrient concentrations. Two drops of $MgCO_3$ suspension were added to the filter tower and filtration continued until the filter was just dry. The tower was rinsed with filtered seawater, the filter was removed and folded into quarters, placed in a labeled glassine envelope, and stored frozen in a desicator until pigment determinations were made within two weeks.

2. Ice algae

a. May 1979

The ice algae were sampled by SCUBA divers using a combination incubation chamber-sampler used in previous studies (Clasby *et al.* 1973; Alexander *et al.* 1974). The chamber was constructed of 4.8 cm diameter plexiglass core tube lining 4 cm in length. The area of this sampler was 18.10 cm^2 and the volume 70 ml. One end was closed with a plexiglass plate fitted with a rubber septum, and the top of the sampler was serrated to cut into the ice. To place the chamber, a diver removed the septum, which allowed water to evacuate, and screwed the sampler into the underside of the ice to a depth of 2 cm. The septum was then replaced and a syringe used to inoculate the chamber with 2 ml ^{14}C-bicarbonate solution (*ca.* 5 µCi). In order to keep the ^{14}C solution from freezing in the hypodermic syringe, each syringe filled with ^{14}C solution was placed in a plastic container partially filled with hot water which the diver took down to the experimental site. The syringe was pumped several times to help insure mixing of the isotope with the ice algae. Two light and one dark chamber were used. After a 3-4 hr incubation period, a heavy, metal spatula was used to chip away ice from around the chamber and sever the top of the core. The sample was retained in the chamber by a core cap. Dark uptake rates were determined in a darkened chamber that was capped and suspended from an ice piton immediately following inoculation. These chambers were also used to collect samples for plant pigment, standing stock, nutrient, and salinity determinations. Following retrieval, the ice cores were transferred to 250 ml glass jars. Primary productivity samples were immediately preserved with 5 ml 4% formaldehyde buffered with sodium acetate to prevent further uptake of the isotope by the cells. One additional core was immediately preserved with 5 ml 4% buffered formaldehyde to be used for standing stock analysis. The remaining cores were returned to the shore laboratory for further processing.

At the shore laboratory, primary productivity samples were filtered through 25 mm, 0.45 μm Millipore filters, rinsed with 5 ml 0.01 N HCl and 5 ml filtered seawater, and placed in labeled scintillation vials for determination of carbon uptake. The remaining cores were filtered through 47 mm, 0.45 μm Millipore filters and the filters were frozen for pigment analysis. The water was put into two 125 ml polyethylene bottles; one bottle was frozen to be used for nutrient determinations and one was to be used for salinity determination. All samples were returned to Seattle for analysis.

b. April-June 1980

For the spring 1980 sampling period, the ice incubation chamber was redesigned to accomodate a greater range of ice conditions and to minimize sample loss during core extraction and capping (see Appendix I). The new chamber has an area of 20.43 cm^2 and a volume of 85 ml.

Two new features were incorporated into this chamber. It was provided with a holder equipped with four threaded stainless steel pins adjusted to protrude *ca.* 2 cm from the chamber mouth. The chamber could then be hammered into the ice where the pins would anchor it securely. In addition, a scraper was designed with a locking pin that fit into a guide in the holder. At the end of the incubation period while the chamber was still anchored to the ice, the pin was started into the guide and the core severed as the scraper was pushed into place, sealing the chamber mouth. The scraper was secured by a handle on the bottom of the holder which was screwed tightly against the pin. The chamber can be returned to the surface with little sample loss. As an added precaution when returning the chambers to the surface, the scraper was held tightly against the chamber mouth to prevent leakage.

To measure dark uptake, a darkened chamber was hammered into the ice and the scraper inserted to enclose the ice sample prior to injecting the isotope. This allowed the chamber to remain in place during the incubation period. As the added weight of the scraper had a tendency to pull the sampler from the ice, a donut-shaped float was placed over the handle of dark chambers to provide additional security.

Following retrieval, the primary productivity samples were immediately transferred to 250 ml opaque jars and two drops of 0.4% $HgCl_2$ were added to kill the cells and prevent further uptake of the isotope. Five additional cores were taken to determine standing stock, plant pigments, particulate carbon, nutrient concentrations, and salinity. All samples were transferred to 250 ml glass jars and kept in the dark in an ice chest until processing at the shore laboratory within 2-3 hr. The additional cores were taken after the incubation period to minimize the time between collecting and processing.

At the shore laboratory the primary productivity samples were filtered onto 25 mm, 0.45 μm Millipore filters, rinsed with 0.01 N HCl and filtered seawater, and placed in glass scintillation vials. Three ice cores were used for determination of plant pigments. Each core was allowed to melt and was filtered onto a 47 mm, 0.45 μm Millipore filter. After *ca.* 5 ml had filtered, filtration was stopped and the filtrate discarded. Filtration was continued until *ca.* 5 ml remained in the filter tower. This filtrate was divided equally between two 125 ml polyethylene bottles for nutrient and salinity determinations, the filtrate from all three cores being combined. Two drops of $MgCO_3$ suspension were added to the filter tower and filtration continued until the filter was just dry. The tower was rinsed with 5 ml filtered seawater and obvious animals (> 1 mm) were carefully removed. The filters were folded into quarters, placed in labeled glassine envelopes, and stored frozen in a desicator until pigment determinations were made within two weeks. Nutrient samples were immediately frozen. The core to be used for standing stock determination was preserved with 10 ml 4% formaldehyde buffered with sodium acetate.

One ice core, to be used by RU 537 for particulate carbon determination, was filtered through a 25 mm Gelman glass fiber filter provided by RU 537. The sample was filtered to dryness and the tower rinsed with 5 ml filtered seawater. Conspicuous animals (> 1 mm) were removed with forceps and the filter, folded into quarters, was placed in a labeled glassine envelope and stored frozen.

3. Benthic microalgae (spring 1980)

Benthic primary productivity was measured using field techniques described by Matheke (1973). The incubation chambers consisted of 3.4 cm diameter plastic cylinders closed at one end with a plastic sheet drilled to accept a No. 00 rubber stopper. A sidearm with a rubber sleeve-type serum bottle stopper was located near the top of each cylinder. The bottom of the cylinder was beveled to minimize disturbance of the sediment when the diver placed it in the bottom. With the rubber stopper removed, the cylinder was pushed *ca.* one-half way into the sediment. The rubber stopper was inserted into the top of the chamber and 2 ml ^{14}C-bicarbonate solution (*ca.* 5 μCi) was injected through the serum bottle stopper with a syringe. The chambers were then pushed further into the sediment to ensure penetration of the isotope. The isotope was detected in the 1-2 mm layer when incubation chambers were treated this way (Leach 1970). Two light and one dark chamber were used. After a 3-4 hr incubation period, the chambers were capped with rubber stoppers and returned to the surface where two drops of concentrated H_3PO_4 were added to kill the algae. The cores were left in the incubation chambers and stored upright in an ice chest until processing 2-3 hr later.

On shore, the water was suctioned from the top of the core, the volume recorded, and then filtered through a 47 mm Whatman GFC glass fiber filter. The tower was rinsed with 5-10 ml filtered seawater, the filter was removed, folded into quarters, and placed in a labeled plastic petri dish. The top 1 cm of sediment was cut off with a sharp spatula and transferred to a labeled petri dish. Filter and sediment samples were kept frozen for later analysis.

Samples were collected for pigment and standing stock analysis using 3.8 cm diameter plastic core tubes beveled at the bottom. The cores were pushed into the sediment to a depth of *ca.* 5 cm, the upper end was capped with a rubber stopper, and the corer withdrawn until the bottom of the corer could be closed with another rubber stopper. In the laboratory, the supernatant water was drawn off and the top 1 cm of each core was removed. One sample was placed in a plastic petri dish and frozen for later pigment analysis; another was to be used for sediment size analysis. One core section was transferred to a 250 ml glass jar to which 25 ml filtered seawater and 25 ml 4% formaldehyde buffered with sodium acetate were added to be used for standing stock analysis.

4. Zooplankton

a. November 1978

Zooplankton samples were collected using a 0.75 m ring net with a mesh size of 308 μm and an open area ratio of 2:1. Vertical tows were made by lowering the net to the bottom and retrieving by hand at a constant rate. Horizontal tows were made by extending a stationary line from the sampling hole to an ice piton located on the surface *ca.* 12 m away. The net ring was clipped to a pulley on this line, pulled backward to the ice piton, and then forward to the sampling hole. Slack in the stationary line caused an unknown amount of deviation from a constant depth of tow, but the deviation was assumed to be minimal and was ignored. All net tows were timed with a stopwatch to obtain an approximate speed of tow.

The net was washed by dipping it several times in the hydrohole. The collection cup was then placed in a plastic bucket and removed from the net. Samples were warmed slowly when ice occurred in the collection cup. Samples were concentrated by gently swirling the collection cup and were then poured into 250 ml glass jars. A label with the collection data was placed in the jar and the sample was preserved with 13 ml 37% formaldehyde buffered with 5 ml each saturated sodium acetate and sodium borate solutions. Seawater was added if necessary to fill the jar and the jar was tightly capped for storage and shipping to Seattle.

A 0.25 m ring net with mesh size of 46 μm was used to scrape the underside of the ice for epontic organisms. In the first attempt, the net was towed behind a diver swimming immediately under the ice, but swimming speed was not fast enough to keep the net horizontal and against the underside of the ice. On the second try, two 250 ml jars partially filled with water were taped to one leg of the net bridle and to the collection jar to provide flotation, but the diver still could not keep the net against the ice. An ice sample was collected by leaving the flotation jars empty and increasing the towing speed by pulling the diver in by his safety line. Samples were poured into 250 ml jars and preserved with 20 ml 4% formaldehyde buffered with sodium acetate.

b. February 1979

No zooplankton samples were collected because of weather and logistics problems.

c. March 1979

Zooplankton samples were collected with a 0.75 m ring net with a mesh size of 209 μm. The net was lowered to the bottom and vertically hauled to the surface by hand. Hauls were timed using a stopwatch to obtain the approximate speed of tow. The net was washed by dipping it several times in the hydrohole and the samples were drained into a plastic bucket. If necessary, the samples were warmed slowly to melt any ice. The samples were concentrated by gently swirling in the net collection cup and were preserved in 250 ml jars with 10 ml 37% formaldehyde buffered with 5 ml each saturated sodium acetate and sodium borate solutions. Seawater was added if necessary to fill the jars and they were tightly capped for storage.

d. May 1979

One zooplankton sample was collected with a 0.5 m ring net, mesh size 209 μm. The net was lowered to the bottom and vertically hauled to the surface. The net was washed by dipping it several times in the hydrohole. The sample was concentrated by gently swirling in the net collection cup and was preserved in a 250 ml jar with 10 ml 37% formaldehyde buffered with sodium acetate.

e. Spring 1980

Zooplankton was sampled with a 0.75 m ring net having a mesh size of 308 μm. The net ring was attached to a line and pulley system anchored to a post placed through the ice 14 m from the dive hole. The net was lowered through the dive hole and hauled horizontally as quickly as possible to the pulley and back, fishing at an average depth of 2 m. Net tows were timed to obtain an approximate speed of tow (*ca.* 0.3 m sec^{-1}). The net was washed by dipping it several times in the dive hole. The sample cup was removed and warmed slowly if much ice was present. Samples were concentrated by gently swirling the collection cup and then poured into 250 ml glass jars. Samples were stored in an ice chest until processed on shore where a label was placed in the jar and the sample was preserved with 25 ml 37% formaldehyde buffered with sodium acetate.

5. 24 hr primary productivity studies (spring 1980)

At *ca.* bi-weekly intervals, replicate water, ice, and benthic primary productivity incubation chambers were placed and inoculated. One set was allowed to incubate for the normal 4 hr period as part of the regular sampling regime; the second set was retrieved on the following day after a 24 hr incubation period. All samples were treated as described for the 4 hr incubations.

6. Light (spring 1980)

Light intensity was measured with a LI-COR underwater quantum sensor, Model LI-192S, and a quantum radiometer-photometer, Model LI-185A, (LI-COR, Inc., Lincoln, NE.). This sensor measures light intensity in the 400-700 nm waveband, which is the waveband used by plants for photosynthesis. Measurements were in microeinsteins m^{-2} sec^{-1}, where one microeinstein equals 6.02×10^{17} photons. Accuracy is stated as ± 7%. This meter was intercalibrated on 28 May 1980 with a Protomatic Underwater Photometer used by RU 537 that measured light intensity in lux.

Submarine light was measured immediately after placement of the ^{14}C incubation chambers and again just prior to their retrieval. All measurements were made within 1 m of the chambers, and care was taken to avoid errors due to shading and sediment suspended by the diver. With the sensor directed upward, light was measured directly beneath the ice, both before and after removal of the ice algal layer. Light reaching the benthos was measured near the bottom directly above the ^{14}C incubation chambers. Surface light outside the dive shelter was also measured, with the sensor held vertically *ca.* 2 m above the snow surface.

To assess the effect of snow depth on light penetration and algal growth, a series of transects was begun on 28 Apr and continued at *ca.* biweekly intervals through 3 Jun. Transects were taken in two locations: through a semi-permanent snow drift that formed in the lee of the tent, and through the area from which the majority of the ice samples were collected (*ca.* 15 m north of the tent). Each transect was marked by a permanent post placed through the ice and visible from both the surface and underside of the ice. A line marked at 0.5 m intervals was anchored to the reference post and secured to the tent frame. The surface light intensity was recorded, and snow depth measured, at 1 m intervals along the transect line for a distance of 25 m. Measurements were made at 0.5 m intervals along the portion of the transect that passed through the drift. Immediately following the surface transect, the line was removed and secured by a diver to the reference post under the ice and to the tent frame. Light intensity was measured at the same points along the line as the surface transect, both before and after removal of the ice algal layer.

7. Surface weather observations (spring 1980)

Surface weather observations were taken within one hr of the placement of productivity chambers. Surface water temperature was measured with a laboratory thermometer held just beneath the surface of the water in the dive hole, and read while submerged. Air temperature was measured with the same thermometer suspended 0.5 m from the tent on the windward side in the shade. Five minutes were allowed for equilibration. The wind direction was determined using a hand held compass, and speed was estimated using Deadhorse Airport weather reports and the helicopter air speed indicator as guides. Local weather, cloud type, and percentage cover were also recorded. Ice thickness was recorded by divers from a reference post marked at 1 cm intervals which was placed through the ice (Appendix II-1).

C. Analytical methods

1. Ice algae and phytoplankton

a. Primary productivity

Primary productivity samples were counted in Seattle using a Packard Tri-Carb Liquid Scintillation Spectrometer with 10 ml Aquasol (New England Nuclear, Boston, MA.) as the scintillation cocktail. Samples were counted for 50 min or to 50,000 counts. Phytoplankton carbon uptake was calculated using the equation:

$$\text{Carbon uptake (mg C m}^{-3}\text{ hr}^{-1}) = \frac{(L-D)\ (W)\ (1.05)}{(R)\ (T)}$$

where L = average of two light bottle counts in disintegrations per minute (dpm); D = dark bottle count (dpm); W = weight of carbonate carbon in mg C m^{-3} (determined by multiplying the salinity, °/₀₀, X 810 [G. C. Anderson pers. comm.]); 1.05 = ^{14}C isotope factor; R = activity of the ^{14}C added; and T = incubation time (hr).

Precision at the 1.5 mg C m^{-3} hr^{-1} level is in the range: mean of n determinations is $\pm\ 0.15/n^{1/2}$ mg C m^{-3} hr^{-1} (7 hr incubations, 5 μCi added) (Strickland and Parsons 1968).

Ice algal carbon uptake was calculated using the equation:

$$\text{Carbon uptake (mg C m}^{-2}\text{ hr}^{-1}) = \frac{(L-D)\ (W)\ (1.05)}{(R)\ (A)\ (T)}$$

where L = average of two light bottle counts in disintegrations per minute (dpm); D = dark bottle count (dpm); W = weight of inorganic carbon per sample; 1.05 = ^{14}C isotope factor; R = activity of the ^{14}C added; A = area of core (m^2); and T = incubation time (hr).

b. Plant pigments

Filters were ground in 7-9 ml 90% acetone with a teflon tissue grinder for about 4 min. The samples were then centrifuged for 10 min. The supernatant liquid was decanted into a clean centrifuge tube, 1 ml 90% acetone was added to the filter residue and it was centrifuged again for about 5 min. The liquid was added to the first supernatant liquid and the total sample centrifuged again for about 10 min.

The extracts were made up to 10 ml with 90% acetone and measured in a Turner Model 111 fluorometer with the scale zeroed against 90% acetone. A second measurement was made after 2 drops of 0.1 N HCl were added to the extract. Chlorophyll *a* and phaeopigment concentrations were calculated using the equations:

$$\text{mg Chl } a \text{ m}^{-3} = \frac{\dfrac{Fo/Fa_{max}}{(Fo/Fa_{max}) - 1}\,[K_x\,(Fo - Fa)]}{L}$$

$$\text{mg Phaeo m}^{-3} = \frac{\dfrac{Fo/Fa_{max}}{(Fo/Fa_{max}) - 1}\,(K_x)\,[Fo/Fa_{max}\,(Fa) - Fo]}{L}$$

where Fo = fluorometer reading before acidification; Fa = fluorometer reading after acidification; Fo/Fa_{max} = maximum chlorophyll/phaeopigment ratio (1.91); K_x = calibration constant (assumes 10 ml extract); L = volume of water filtered in liters (Lorenzen 1966).

To express the concentration of plant pigments obtained from ice cores as mg pigment m^{-2}, the expression (A x 1000) was substituted for the volume of water filtered (L) in the above equations. A = area of the core (m^2).

The limit of detection depends on the volume of water filtered and the sensitivity of the fluorometer. About 0.01 mg chl *a* m^{-3} should be detectable with a 2 ℓ sample.

c. Nutrients and salinity

Nutrient and salinity samples were returned to the University of Washington, Department of Oceanography Chemistry Laboratory for analysis. The nutrient samples were analyzed using autoanalyzer techniques; salinity samples were analyzed using a whetstone bridge (Pavlou 1972).

d. Standing stock

Standing stock samples were analyzed with a Zeiss phase contrast inverted microscope following the method of Utermöhl (1931). Large and rare phytoplankton organisms (> 100 μm) were counted at 156 X magnification in 50 ml Zeiss counting chambers and small, abundant organisms (< 100 μm) were counted at 390 X magnification in 5 ml Zeiss counting chambers. Usually 1/5 of the chamber was counted.

Ice algae were counted at 390 X magnification in 5 ml Zeiss chambers; usually 1/10 of the chamber was counted. Samples with very high density were diluted 1:5 with distilled water before settling. Many species are difficult or impossible to identify in water mounts, therefore a second set of subsamples was acid cleaned and permanently mounted in Euparol vert resin on microscope slides. Higher magnifications, up to 2000 X, could be used with these slides. Line drawings were made of some species to aid in identification.

References used to identify the phytoplankton and ice algae included Cleve and Grunow (1880); Cleve (1894-1895); Van Heurck (1896): Hustedt (1930, 1959-1962); Schiller (1933-1937); Cupp (1943); and Hendey (1964).

Species diversity of the ice algal community was calculated using the Shannon-Wiener diversity index (H), which is widely used in phytoplankton community studies (Fager 1972; Poole 1974):

$$H = - \sum_{i}^{s} (n_i/N) \ln (n_i/N)$$

where n_i = number of cells of the ith species; N = total number of cells; and s = number of species.

2. Benthic microalgae

a. Primary Productivity

The amount of ^{14}C incorporated by benthic microorganisms was determined at the University of Louisville, Louisville, KY, using the wet oxidation technique described by Atlas and Hubbard (1974). Carbon uptake was calculated using the equation:

$$\text{Carbon uptake } (\text{mg C m}^{-2} \text{ hr}^{-1}) = \frac{(L-D)\ (W)\ (1.05)}{(R)\ (A)\ (T)}$$

where L = average of two light bottle counts in disintegrations per minute (dpm); D = dark bottle count (dpm); W = inorganic carbon per sample; 1.05 = ^{14}C isotope factor; R = activity of ^{14}C added; A = sample area (m^2); and T = incubation time (hr).

b. Plant pigments

Before analysis, the samples were thawed in the dark at 5°C. Each sample was weighed and mixed in the petri dish and two subsamples (*ca*. 2 g) were removed and weighed. Subsamples were ground with a mortar and pestle for *ca*. 1 min in 3 ml 90% acetone, washed into a 15 ml centrifuge tube, and the volume brought to 15 ml with 90% acetone. The samples were extracted in the dark at 5°C for 17-20 hr, and were shaken 1 hr after the beginning of the extraction and at the end of the extraction period. Samples were centrifuged for 15 min, and the extract volume determined by subtracting the sediment volume from the total volume. Fluorescence was measured in a Turner Model 111 fluorometer with the scale zeroed against 90% acetone. A second measurement was made after acidification with 2 drops 1 N HCl. Chlorophyll *a* and phaeopigments were calculated using an adaptation of Lorenzen's equations (Lorenzen 1966):

$$\text{mg Chl } a \text{ m}^{-2} = \frac{\dfrac{Fo/Fa_{max}}{(Fo/Fa_{max}) - 1} \; K_x \, (Fo - Fa) \left(\dfrac{Wc}{Ws}\right) \left(\dfrac{V}{10}\right)}{1000 \text{ A}}$$

$$\text{mg Phaeo m}^{-2} = \frac{\dfrac{Fo/Fa_{max}}{(Fo/Fa_{max}) - 1} \; (K_x) \, [Fo/Fa_{max} \, (Fa) - Fo] \left(\dfrac{Wc}{Ws}\right) \left(\dfrac{V}{10}\right)}{1000 \text{ A}}$$

where Fo = fluorometer reading before acidification; Fa = fluorometer reading after acidification; Fo/Fa_{max} = maximum chlorophyll/phaeopigment ratio (1.89); K_x = calibration constant; A = area of the core sample (1.13×10^{-3} m^2); Wc = weight of core (g); Ws = weight of subsample (g); and V = volume of extract (ml).

c. Standing stock

The top 1 cm of the benthic cores was rinsed into a graduated cylinder and diluted to 1 ℓ with distilled water. The samples were mixed by vigorous stirring and bubbling air from a glass tube extending to the bottom of the cylinder. One ml subsamples were drawn from the middle of the cylinder with a pipette and added to 50 ml Zeiss counting chambers which were then filled with distilled water and allowed to settle for 24 hr. The samples were counted at 400 X magnification using a Zeiss pnase contrast inverted microscope (Utermöhl 1931). Normally, 1/10 of the chamber was counted.

3. Zooplankton

All zooplankton samples were first sorted for large, rare organisms such as mysids, amphipods, euphausids, shrimp, and fish eggs and larvae. The samples were split in a Folsom plankton splitter (McEwan *et al.* 1954) until a subsample containing *ca.* 100 specimens of the most abundant remaining taxa was obtained. Subsamples were successively sorted until at least 100 specimens of each taxon were counted and identified. Counts and identifications were done using dissecting microscopes. Identifications were done using dichotomous keys and by comparison with descriptions and illustrations in the literature.

For copepods, samples that had previously been sorted for larger animals were subsampled with a calibrated automatic pipette to obtain a subsample containing about 100 specimens of the most abundant copepod species. Copepods were identified, counted, and recorded by sex and copepodid stage.

The number of animals per 1000 m^3 was calculated using the equations:

$$V \, (m^3) = \text{haul length (m)} \times \text{mouth area } (m^2)$$

$$\text{Number } (1000 \, m^3) = \frac{(A)\,(1000)}{V} \times 2^n$$

where V = volume of water filtered; A = number of animals counted; and n = number of times the sample was split.

References used to identify zooplankton are listed in Table 1.

4. Light

Percentage surface light was calculated according to the equation:

$$\% \text{ surface} = \frac{I}{Io} \times 100$$

where I = light intensity ($\mu E\ m^{-2}\ sec^{-1}$) measured at depth; Io = incident radiation ($\mu E\ m^{-2}\ sec^{-1}$) measured above the ice.

The diffuse attenuation coefficient $k_{(m^{-1})}$, was calculated from the relationship:

$$\frac{I}{Io} = 10^{-kz}$$

or

$$k = \frac{-\log \frac{I}{Io}}{Z}$$

where I = light intensity ($\mu E\ m^{-2}\ sec^{-1}$) measured in the bottom ice above the ice algal layer; Io = incident radiation ($\mu E\ m^{-2}\ sec^{-1}$) measured above the ice; and Z = total thickness of the ice plus snow depth (m).

In the text, the diffuse attenuation coefficient ($k_{m^{-1}}$) is referred to as the extinction coefficient.

VI. Results

A. Stefansson Sound, 1978-1979

1. Phytoplankton and ice algae

Phytoplankton levels in Stefansson Sound were low during the winter period (Tables 2-3). In November, 1978, unidentified flagellates, mostly < 6 μm in diameter, were the most common organisms. A few diatoms, including spores of *Chaetoceros* spp., and cells of *Navicula* spp. and *Nitzschia* spp., were also present. Although the diatoms contained chloroplasts, they did not appear to be healthy. Chlorophyll *a* levels were low.

Phytoplankton levels remained low in February and March with unidentified small flagellates being the most numerous organisms. A few pennate diatoms were also present. In February, there were many small detritus

Table 1. References used to identify zooplankton from Narwhal Island, spring 1980.

- Cnidaria - Hydrozoa
  - Kramp, P. L., 1961
  - Shirley, D. W., and Y. M. Leung, 1970

- Ctenophora
  - Leung, Y. M., 1970b

- Arthropoda - Crustacea - Copepoda
  - Heron, G. A., and D. M. Damkaer, 1976
  - Jaschnov, W. A., 1948
  - Lang, K., 1948
  - Lindberg, K., 1953
  - Sars, G. O., 1903-1911
  - Sars, G. O., 1913-1918
  - Sars, G. O., 1921

- Arthropoda - Crustacea - Mysidacea
  - Banner, A. H., 1948a, b
  - Leung, Y. M., 1972b
  - Sars, G. O., 1870

- Arthropoda - Crustacea - Amphipoda
  - Bernard, J. L., 1969
  - Gurjanova, E., 1951
  - Sars, G. O., 1895
  - Tencati, J. R., 1970

- Arthropoda - Crustacea - Euphausiacea
  - Banner, A. H., 1950
  - Leung, Y. M., 1970a
  - Zimmer, C., 1933

- Chaetognatha
  - Dawson, J. K., 1971

- Chordata - Larvacea
  - Leung, Y. M., 1972a
  - Lohmann, H., 1933

Table 2. Phytoplankton and ice algae data from Stefansson Sound, 1978-1979.

	Standing Stock (Total cells/liter)		Chl *a* (mg m^{-3})		(mg m^{-2})	Phaeo (mg m^{-3})		(mg m^{-2})	Prim Prod (mg C m^{-3} hr^{-1})		(mg C m^{-2} hr^{-1})
Date	0 m	4 m	0 m	4 m	ice	0 m	4 m	ice	0 m	4 m	ice
8 Nov 78	26000	14000	0.06			0.07					
9	24000	18000	0.02	0.02		0.12	0.12				
10			0.06	0.06		0.06	0.08				
11			0.05	0.05		0.04	0.05				
12			0.06	0.04		0.07	0.06				
13			0.06	0.04		0.05	0.06				
14			0.07	0.04		0.05	0.05				
15			0.05	0.06		0.06	0.06				
16	46000	46000	0.06	0.06		0.05	0.05				
15 Feb 79	36000	22000	0.02	0.01		0.07	0.04				
12 Mar 79	46000	34000	0.01	0.00		0.03	0.02				
13			0.00	0.01		0.02	0.03				
14	ice core 38000		0.00	0.01		0.03	0.03				
15			0.01	0.01		0.03	0.07				
16	60000	82000	0.01	0.01		0.03	0.03				
15 May 79	3 ice cores*				2.87			4.32			1.50
18	162000	38000	0.42	0.17		1.13	0.24		0.16	0.12	1.42
	3 ice cores*				2.70			3.36			
19			0.67	0.24		1.05	0.43		0.16	0.80	0.31
	3 ice cores*				2.53			2.83			
20	208000	36000	1.19	0.23		0.89	0.33		0.11	0.26	1.42
	ice core 23070000										
	4 ice cores*				3.01			1.99			

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* average values

Table 3. Phytoplankton and ice core standing stock (cells ℓ^{-1}) from Stefansson Sound, 1978-1979.

	8 Nov 78		9 Nov 78		16 Nov 78		15 Feb 79		12 Mar 79	
Taxon	0 m	4 m	0 m	4 m	0 m	4 m	0 m	4 m	0 m	4 m
Diatoms										
Amphiprora spp.										
Amphiprora hyperborea										
Chaetoceros spp.	2000		2000			8000	2000			2000
Chaetoceros septentrionalis										
Cylindrotheca closterium		2000						2000		
Gyrosigma spp.										
Licmophora spp.										
Melosira spp.										
Navicula spp.				2000						
Navicula marina										
Navicula pelagica										
Nitzschia spp.										
Nitzschia cylindrus										
Nitzschia delicatissima										
Nitzschia seriata cf.										
Thalassiosira spp.										
Thalassiosira antarctica cf.										
Thalassiosira gravida										
Tropidoneis sp.										
Unidentified pennate diatoms										
< 10 µm		2000								
11 - 20 µm										
21 - 30 µm										
31 - 40 µm										
41 - 50 µm										
51 - 75 µm										
76 - 100 µm										
101 - 150 µm										

Table 3. (cont.)

Taxon	8 Nov 78		9 Nov 78		16 Nov 78		15 Feb 79		12 Mar 79	
	0 m	4 m	0 m	4 m	0 m	4 m	0 m	4 m	0 m	4 m
Unidentified flagellates										
< 10 μm	20000	10000	20000	14000	44000	36000	32000	18000	40000	22000
11 - 20 μm					2000				2000	
21 - 30 μm	2000									
31 - 40 μm										
41 - 50 μm										
Identified flagellates										
Calycomonas gracilis										
Unidentified choanoflagellates								2000	4000	6000
Unidentified cryptomonads										
Chrysophyta										
Dinobryon petiolatum										
Euglenophyta										
Unidentified euglenoid *cf.*										
Euptreptiella sp. *cf.*										
Urceolus sp.										
Chlorophyta										
Platymonas sp. *cf.*	2000		2000							
Pyrrophyta										
Unidentified dinoflagellates				2000		2000	2000			
Gonyaulax sp.										
Peridinium spp.										

Table 3. (cont.)

	14 Mar 79	16 Mar 79		18 May 79		20 May 79	20 May 79	
Taxon	ice core	0 m	4 m	0 m	4 m	ice core	0 m	4 m
Diatoms								
Amphiprora spp.						50000		
Amphiprora hyperborea						60000	6000	
Chaetoceros spp.	4000					280000	4000	
Chaetoceros septentrionalis							2000	
Cylindrotheca closterium		2000		4000		80000	12000	4000
Gyrosigma spp.					2000	130000	2000	
Licmophora spp.						530000	2000	
Melosira spp.						40000		
Navicula spp.	2000					550000	2000	
Navicula marina						80000		
Navicula pelagica						860000		
Nitzschia spp.	2000	2000	2000	8000		2560000	10000	
Nitzschia cylindrus	2000			14000		5880000		
Nitzschia delicatissima							4000	
Nitzschia frigida				6000		6080000	14000	
Nitzschia seriata cf.				6000			12000	
Thalassiosira spp.	6000							
Thalassiosira antarctica	12000							
Thalassiosira gravida								
Tropidoneis sp.						10000		
Unidentified pennate diatoms								
< 10 μm	2000		2000	2000	2000	190000	2000	
11 - 20 μm	6000			2000		850000		
21 - 30 μm						870000	4000	
31 - 40 μm			8000	4000		320000		
41 - 50 μm						200000	2000	2000
51 - 75 μm						350000		
76 - 100 μm						30000		
101 - 150 μm						80000		

Table 3. (cont.)

Taxon	14 Mar 79	16 Mar 79		18 May 79		20 May 79	20 May 79	
	ice core	0 m	4 m	0 m	4 m	ice core	0 m	4 m
Unidentified flagellates								
< 10 µm	2000	46000	64000	84000	34000	2740000	98000	28000
11 - 20 µm		2000		8000		320000	6000	
21 - 30 µm						20000	4000	
31 - 40 µm						10000	2000	
41 - 50 µm						20000		
Identified flagellates								
Calycomonas gracilis								2000
Unidentified choanoflagellates		6000						
Unidentified cryptomonads			2000			20000	2000	
Chrysophyta								
Dinobryon petiolatum							2000	
Euglenophyta								
Unidentified euglenoid *cf.*				2000				
Euptreptiella sp. *cf.*				2000		10000	2000	
Urceolus sp.						30000		
Chlorophyta								
Platymonas sp. *cf.*				4000		50000	2000	
Pyrrophyta								
Unidentified dinoflagellates		2000	4000	2000		60000	2000	
Gonyaulax sp.							2000	
Peridinium spp.				14000		20000	8000	

particles in the water sample collected from just beneath the ice (0 m) which made phytoplankton counting difficult. The detritus particles probably came from dirty brash ice that formed a thick layer on the underside of the ice (Dunton pers. comm.). Not as much detritus was found in the sample collected near the sea bed. Chlorophyll *a* levels were barely detectable.

By March, the number of individual diatom cells and the number of diatom species increased with species that are common in the spring beginning to appear. Chlorophyll *a* levels were still low.

One ice core collected by RU 6 on 14 Mar was analyzed. The core, about 30 cm long and 2.5 cm in diameter, was collected from the brash ice layer on the underside of the ice. *Navicula* sp., *Nitzschia* spp., and unidentified pennate diatoms were present, along with *Thalassiosira* spp. The large amount of detrital material made positive identification of the *Thalassiosira* spp. impossible.

By May, more diatom cells were present in the water column, including species of *Chaetoceros, Cylindrotheca, Navicula,* and *Nitzschia*. Unidentified flagellates, usually < 10 μm in diameter, were abundant, along with a few cryptomonad, chrysophyte, and euglenoid species. Unidentified *Peridinium* spp. and other unidentified dinoflagellates were present in low numbers. Chlorophyll *a* levels in the water column were still low, but beginning to increase slightly.

An ice core collected on 20 May contained more than 23 x 10^6 cells per liter, including diatoms and flagellates. *Nitzschia* spp. were the most abundant organisms with *Nitzschia frigida* and *N. cylindrus* comprising nearly 50% of the total population. Both of these species are common in the ice in the Barrow area with *N. frigida* found in large numbers only in the ice, while *N. cylindrus* is also a prominent component of the phytoplankton in spring (Alexander *et al.* 1974; Horner 1976). Other typical ice organisms found included *Eutreptiella* sp., and *Urceolus* sp. *Eutreptiella* sp. is sometimes found in the water column also, but only when ice is present (Horner unpubl. obs.). Neither of these species occurred in large numbers. Chytridiaceous fungi were found to be parasitizing some of the pennate diatoms.

Chlorophyll *a* levels in the ice cores were variable and phaeopigments were high (Table 2).

Primary productivity was low in the water column, averaging about 0.15 mg C m^{-3} hr^{-1}. In the ice, primary productivity was much higher. On 15, 18, and 20 May, productivity was consistantly near 1.5 mg C m^{-2} hr^{-1}, but on 19 May, productivity was only 0.3 mg C m^{-2} hr^{-1} probably because of the patchy distribution of the ice algae. On an areal basis (mg C m^{-2} hr^{-1}) ice algal primary production was approximately twice that of the water column.

2. Nutrients and salinity

Nutrient and salinity data from May 1979 are given in Table 4. On 18, 19, and 20 May, a lens of low salinity water (*ca.*

Table 4. Nutrient and salinity data from Stefansson Sound, May 1979. Where no number is present, no sample was taken.

Date	Nutrient Concentrations (μg-at ℓ^{-1}) NO_3	NO_2	NH_3	PO_4	SiO_4	Salinity (°/₀₀)
15 May						
0 m						
4 m						
ice	1.35	0.14	2.68	1.38	19.90	
18 May						
0 m	1.55	0.04	1.07	0.20	24.06	18.28
4 m	4.69	0.17	0.84	1.42	13.34	35.20
ice	1.19	0.06	2.85	0.74	20.62	15.26
19 May						
0 m	1.57	0.06	1.68	0.39	26.27	18.32
4 m	4.72	0.16	0.24	0.95	13.23	35.19
ice	1.24	0.05	1.87	0.50	21.02	15.94
20 May						
0 m	1.01	0.05	1.04	0.24	24.53	16.57
4 m	4.46	0.16	0.79	0.91	13.43	34.76
ice	0.76	0.06	2.66	0.46	20.56	14.05

16-18°/₀₀) was detected at the surface, which resulted from mixing with fresh water from the Sagavanirktok River, flowing into the sound *ca.* 10 km to the south. The sea ice had not started to melt. Salinities from ice cores were lower than surface water values, probably because of dilution from melting ice in the core samples.

Phosphate, nitrate, and nitrite concentrations were highest in the water column at 4 m. Silicate concentrations were highest at 0 m, which may have been due to the influence of the Sagavanirktok River, as silicate content of rivers draining into the Beaufort Sea is known to be high (Hufford 1974b). The concentration of ammonia in the ice, *ca.* 2-3 μg-at ℓ^{-1}, was approximately twice the surface water level, and probably resulted from excretion by fauna associated with the bottom of the ice, reflecting the relatively high biological activity of this zone.

3. Zooplankton

Forty-nine categories, including 37 species and 12 other categores, including larval stages or where identification was made to genus or other higher taxonomic level, were identified in zooplankton samples collected in Nov 1978, Mar and May 1979 in Stefansson Sound (Table 5). Relative abundance and distribution through time are given in Table 6.

Copepods were the most abundant organisms collected in Nov 1978. *Pseudocalanus elongatus* was the dominant species. It was present as stages III, IV, V, and VI, and both males and females were present. Stage II copepodids were found once. *Pseudocalanus major* was also abundant with stages II, III, IV, V, and VI and both males and females being present. *Derjuginia tolli* was present as stages IV females, V mostly females, and VI males and females, while *Acartia longiremis* was present as stage VI males and females. Other copepods were present in small numbers. The only cyclopoid copepod was *Oithona similis* with abundant adult females being found twice.

Other animals present included *Mysis* spp., the amphipods *Anonyx nugax, Boeckosimus plautus, Onisimus litoralis,* and *Orchomenella pinguis*, and the chaetognath *Sagitta elegans*. None of these animals was very abundant.

In Mar 1979, *Pseudocalanus elongatus* was still the dominant copepod with stages I, II, III, IV, V, and VI all being present. Other copepods included *Calanus glacialis* stages I, II, and III; *Microcalanus pygmaeus* stages III, IV males and females, V males and females, and VI only females; *Pseudocalanus major* as stages I and III, and IV and V males and females; *Eurytemora richingsi* stages III, IV mostly females, and V females; *Metridia lucens* stages I, II, and III; and many unidentified nauplii. The presence of early life history stages may indicate some reproduction occurred during the winter. The cyclopoid *Oithona similis* as stages II, III, IV, and V females and VI males and females and *Oncaea borealis* as adult males and females were present usually in low numbers.

Also in March, a few hydrozoans were present along with some polychaete larvae. A cladoceran, *Eubosmina longispina*, was found once and ostracods were also found once. A few amphipods were present and a few *Sagitta elegans*.

Table 5. Zooplankton species from samples collected in Stefansson Sound, Nov 1978, Mar and May 1979.

- Cnidaria - Hydrozoa
  - *Halitholus cirratus* Hartlaub
  - *Sarsia tubulosa* (M. Sars)
  - Unidentified Hydrozoa

- Ctenophora
  - *Pleurobrachia pileus* (O. F. Müller)

- Nematoda - unidentified species

- Annelida
  - Polychaeta - unidentified larvae

- Arthropoda - Crustacea
  - Cladocera
    - *Eubosmina longispina* (Leydig)
  - Ostracoda - unidentified species
  - Cirripedia
    - *Balanus* sp. nauplii
    - Unidentified larvae
    - Unidentified parasitic larvae
  - Isopoda - unidentified epicaridean parasite
  - Copepoda
    - Calanoida
      - *Calanus glacialis* Jaschnov
      - *Calanus hyperboreus* Krøyer
      - *Microcalanus pygmaeus* (G. O. Sars)
      - *Pseudocalanus elongatus* (Boeck)
      - *Pseudocalanus major* G. O. Sars
      - *Derjuginia tolli* (Linko)
      - *Eurytemora richingsi* Heron and Damkaer
      - *Metridia longa* (Lubbock)
      - *Metridia lucens* Boeck
      - *Limnocalanus macrurus* G. O. Sars
      - *Acartia longiremis* (Lilljeborg)
    - Cyclopoida
      - *Oithona similis* Claus
      - *Cyclopina gracilis* (Claus)
      - *Cyclopina* sp. A
      - *Cyclopina* sp. B
      - *Cyclopinodes* sp. A
      - *Oncaea borealis* G. O. Sars
    - Harpacticoida
      - *Pseudobradya minor* (T. & A. Scott)
      - *Harpacticus superflexus* Willey
      - *Tisbe furcata* (Baird)

Table 5. (cont.)

Mysidacea
Mysis litoralis (Banner)
Mysis oculata (Fabricius)
Mysis relicta (Lovén)
Amphipoda
Gammaridea
Atylus carinatus (Fabricius)
Weyprechtia pinguis (Krøyer)
Anonyx nugax (Phipps)
Acanthostepheia behringiensis (Lockington)
Boeckosimus plautus (Krøyer)
Onisimus glacialis Sars
Onisimus litoralis (Krøyer)
Orchomenella pinguis Boeck
Lagunogammarus wilkitzkii (Birula)
Hyperiidea
Parathemisto libellula (Lichtenstein)
Euphausiacea
Thysanoessa raschii (M. Sars)
Unidentified calyptopis

Chaetognatha
Sagitta elegans Verrill

Chordata - Larvacea
Fritillaria borealis Lohmann

Table 6a. Relative abundance and distribution through time of zooplankton taxa other than copepods collected in Stefannson Sound, 1978-1979. Nov 1978 samples collected with a 0.75 m ring net, mesh size 308 μm; Mar and May 1979 samples collected with a 0.5 m ring net, mesh size 216 μm. Where no symbol is present, no animals were found. P = < 1000; Δ = 1001 - 5000; O = 5001 - 10000; x = > 10001.

Taxon								Nov							
	8	8	9	9	10	10	11	11	12	12	13	13	14	14	14
Cnidaria - Hydrozoa															
Aeginopsis laurentii															
Euphysa flammea															
Halitholus cirratus															
Sarsia tubulosa															
Unidentified Hydrozoa															
Ctenophora															
Pleurobrachia pileus															
Polychaeta - unidentified larvae									P						
Arthropoda															
Cladocera															
Eubosmina longispina															
Ostracoda - unidentified															
Cirripedia															
Balanus sp. nauplii															
Unidentified larvae					P								Δ		
Unidentified parasitic larvae															
Isopoda															
Unidentified epicaridean parasite															
Mysidacea															
Mysis litoralis						P					P	P	P		
Mysis oculata									P				P		
Mysis relicta		P			P								Δ		
Unidentified species	P				P								P		

Table 6a. (cont.)

								Nov							
Taxon	8	8	9	9	10	10	11	11	12	12	13	13	14	14	14
Amphipoda															
Gammaridea															
Atylus carinatus				P							P	P			
Weyprechtia pinguis															
Lagunogammarus wilkitzkii															
Anonyx nugax			P	P				P							
Acanthostepheia behringiensis		P													
Boeckosimus plautus			P	Δ		P	Δ	P	P	P		Δ			
Onisimus glacialis															
Onisimus litoralis								P			Δ	Δ			
Orchomenella pinguis									P		P	P			
Unidentified species													P		
Hyperiidae															
Parathemisto libellula		P													
Euphausiacea															
Thysanoëssa raschii															
Unidentified calyptopids															
Chaetognatha															
Sagitta elegans	P				P						P	P	Δ		
Unidentified animals	P				P								P		
Unidentified invertebrate eggs													O		

Table 6a. (cont.)

Taxon			Nov							Mar					May
	14	15	16	16	16	12	12	13	13	14	14	15	16	16	16
Cnidaria - Hydrozoa															
Aeginopsis laurentii															
Euphysa flammea															
Halitholus cirratus							P	P			Δ				
Sarsia tubulosa								P							
Unidentified Hydrozoa										P					
Ctenophora															
Pleurobrachia pileus		P													
Polychaeta - unidentified										P		P			
Arthropoda															
Cladocera															
Eubosmina longispina									P						
Ostracoda - unidentified									P						
Cirripedia															
Balanus sp. nauplii						Δ									
Unidentified larvae															
Unidentified parasitic larvae													P		
Isopoda															
Unidentified epicaridean parasite													P		
Mysidacea															
Mysis litoralis		P	Δ												
Mysis oculata															
Mysis relicta															
Unidentified species															

Table 6a. (cont.)

Taxon			Nov							Mar					May
	14	15	16	16	16	12	12	13	13	14	14	15	16	16	16
Amphipoda															
Gammaridea															
Atylus carinatus															
Weyprechtia pinguis		P													
Lagunogammarus wilkitzkii			P												
Anonyx nugax			P		P										
Acanthostepheia behringiensis															
Boeckosimus plautus			Δ		P										
Onisimus glacialis										P					
Onisimus litoralis											P	P			
Orchomenella pinguis			P		P										
Unidentified species										P					
Hyperiidae															
Parathemisto libellula															
Euphausiacea															
Thysanoëssa raschii			P												
Unidentified calyptopids															
Chaetognatha															
Sagitta elegans			P		Δ						P		P		
Unidentified animals															
Unidentified invertebrate eggs			O												

Table 6b. Relative abundance and distribution through time of copepods collected in Stefansson Sound, 1978-1979. Nov 1978 samples collected with a 0.75 m ring net, mesh size 308 μm; Mar and May 1979 samples collected with a 0.5 m ring net, mesh size 216 μm. Where no symbol is present, no animals were found. P = < 1000; Δ = 1001 - 5000; O = 5001 - 10000; x = 10001 - 20000; ● = 20001 - 50000; + = > 50001; m = male; f = female.

Taxon								Nov							
	8	8	9	9	10	10	11	11	12	12	13	13	14	14	14
Calanoida															
Calanus glacialis VI m															
f															x
III m															
f	●														
II															x
I															
Calanus hyperboreus V m															
f	●														
Microcalanus pygmaeus VI m															
f															x
V m															
f															
IV m															
f															
III m															
f															
Pseudocalanus elongatus VI m					●	●		●		●	●	x		+	
f	●	●	+	+	+	+	+	+	+	+	+	+	+	+	+
V m	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
f	+	+	+	+	+	+	+	+	●	+	+	+	+	+	●
IV m	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
f	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
III m															
f	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
II	●														
I															

Table 6b. (cont.)

											Nov						
Taxon			8	8	9	9	10	10	11	11	12	12	13	13	14	14	14
Pseudocalanus major	VI	m												●	+		
		f	●			●	●						x		+		
	V	m	+				+								+		●
		f	●			●	+				●				●		●
	IV	m	+				+									+	
		f	+				+									+	
	III	m															
		f	+				+										
	II		●														
	I																
Derjuginia tolli	VI	m	●					●		●	●					+	
		f	●						●							+	x
	V	m	●														
		f						●	●			●				+	x
	IV	m															
		f	●								●						
Eurytemora richingsi	V	m															
		f															
	IV	m															
		f	●														
	III	m															
		f															
Metridia lucens	VI	m															
		f			●												
	III	m															
		f															
	II																
	I																
Limnocalanus macrurus	VI	m	●														
		f	●				●								x	●	x
Acartia longiremis	VI	m							●	●				x			
		f		x		●	●		●			●			x	●	

Table 6b. (cont.)

Taxon								Nov							
	8	8	9	9	10	10	11	11	12	12	13	13	14	14	14
Unidentified nauplii															
Cyclopoida															
Oithona similis VI m															
f						●									
V m															
f												x			
IV m															
f															
III m															
f															
Cyclopina gracilis VI m															
f															
Cyclopina sp. A VI m															
f															
Cyclopina sp. B VI m															
f															
Cyclopinodes sp. A VI m															
f															
Oncaea borealis VI m															
f															
Harpacticoida															
Pseudobradya minor juveniles															
Harpacticus superflexus VI m															
f															
juveniles															
Tisbe furcata VI m															
f															

Table 6b. (cont.)

Taxon			Nov					Mar									May
			14	15	16	16	16	12	12	13	13	14	14	15	16	16	16
Calanoida																	
Calanus glacialis	VI	m															
		f															
	III	m															
		f												Δ			
	II																
	I													P		P	
Calanus hyperboreus	V	m															
		f	O														
Microcalanus pygmaeus	VI	m															
		f						P	P	P				P	P	P	
	V	m														P	
		f						P									
	IV	m												P		P	P
		f						P		P							Δ
	III	m														P	
		f								Δ				P	P		P
Pseudocalanus elongatus	VI	m	x		●	x						P					Δ
		f	+	+	+	+	+				P		P	P	P		Δ
	V	m	+	+	+	+	+	Δ	O			O	Δ	Δ	Δ		O
		f	+	+	+	+	+	P				P	Δ	P	P		Δ
	IV	m	+	+	+	+	+	x	x	O	P	x	●	O	x	O	Δ
		f	+	+	+	+	+	●	●	O	O	●	+	O	x	O	O
	III	m															
		f	+	+	+	+	+	+	+	●		●	+	●	●		Δ
	II							O	O	O	P	O	O	P	Δ	Δ	
	I							Δ	Δ	Δ		P	Δ	P		P	Δ

Table 6b. (cont.)

			Nov					Mar									May
Taxon			14	15	16	16	16	12	12	13	13	14	14	15	16	16	16
Pseudocalanus major	VI	m					x										
		f															
	V	m	●							P			O				
		f	+	●	●		x						P				
	IV	m	+							Δ							
		f	x							Δ							
	III	m															
		f								P							
	II																
	I									P							
Derjuginia tolli	VI	m															
		f	●														
	V	m															
		f															
	IV	m															
		f															
Eurytemora richingsi	V	m															
		f										P					
	IV	m												P			
		f						P				P		Δ		P	
	III	m															
		f									P						
Metridia lucens	VI	m															
		f															
	III	m															
		f						P		P							
	II								Δ	P	P			P			
	I							P			P						
Limnocalanus macrurus	VI	m			x												
		f				x											
Acartia longiremis	VI	m												P			Δ
		f		●		x	x										P

Table 6b. (cont.)

Taxon	Nov					Mar									May
	14	15	16	16	16	12	12	13	13	14	14	15	16	16	16
Unidentified nauplii						O	O	O	O	x	x	O	Δ	O	●
Cyclopoida															
Oithona similis VI m											P	P	P		Δ
f											Δ	Δ	Δ		●
V m											x	x	O		
f															x
IV m											x	O	O		
f															Δ
III m															
f											P		P		Δ
Cyclopina gracilis VI m															
f															Δ
Cyclopina sp. A VI m															P
f															Δ
Cyclopina sp. B VI m															
f															Δ
Cyclopinodes sp. A VI m															
f															Δ
Oncaea borealis VI m												P	Δ		
f											Δ	P			
Harpacticoida															
Pseudobradya minor juveniles															●
Harpacticus superflexus VI m															Δ
f															P
juveniles															●
Tisbe furcata VI m															P
f															

Only one sample was collected in mid-May in conjunction with another project. *Pseudocalanus elongatus* was still the most common animal with stages I, III, IV, V, and VI males and females being present. A few *Microcalanus pygmaeus* stages III and IV were present along with stage VI *Acartia longiremis* males and females. The cyclopoids *Oithona similis* as stages III, IV, and V females and stage VI males and females; and *Cyclopina gracilis*, *Cyclopina* spp. and *Cyclopinodes* sp. stage VI's were also present. The harpacticoid, *Harpacticus superflexus*, was relatively common as juveniles and adult males and females.

B. Narwhal Island, spring 1980

1. Primary productivity

During April, ice algal productivity was low, < 0.2 mg C m^{-2} hr^{-1} (Table 7, Fig. 3). Productivity began to increase during the first week in May when submarine light levels increased (Fig. 3), and reached a peak of 0.8 mg C m^{-2} hr^{-1} on 8 May. A week of stormy weather with fog and blowing snow followed. When sampling resumed, submarine light had dropped to one-half the previous level and productivity to *ca.* 0.1 mg C m^{-2} hr^{-1}. Presumably in response to increasing light levels, productivity increased to a high of 2.7 mg C m^{-2} hr^{-1} on 29 May. On this date, snow was completely gone from the surface of the ice and overflow from the Sagavanirktok River was first noticed by the divers. By the next sampling day, the soft bottom layer of ice containing the ice algae had begun to dissociate from the ice and formed a slush layer loosely associated with the undersurface of the ice. Small pieces of this slush layer clouded the water column. Productivity dropped during the following week, but increased to 2.6 mg C m^{-2} hr^{-1} on 7 Jun, comparable to the previous high level. By 11 Jun, the underside of the ice had begun to melt and erode, and the algal layer was no longer evident.

Surface and 7 m water column productivity values were integrated to give productivity on a m^2 basis to allow comparison with ice algal and benthic microalgal communities (Fig. 3). Surface and 7 m water column productivity are also give on a m^3 basis (Fig. 4a).

Water column productivity was low, < 0.2 mg C m^{-3} hr^{-1}, during April and the first half of May, but increased during late May and early June. Two productivity peaks were evident, 22 May and 7 Jun, which coincided with periods of high ice algal productivity. The highest productivity, 0.4 mg C m^{-3} hr^{-1}, occurred at 0 m on 7 Jun and probably resulted from the ice algal layer that was rapidly disintegrating into the water column. Productivity occurred primarily at 0 m, with productivity at 7 m near the limit of detection throughout most of the study.

Benthic productivity remained near or below the limit of detection, *ca.* 0.01 mg C m^{-2} hr^{-1}, throughout the study. Light reaching the benthos was only *ca.* 0.2% of surface levels, and probably limited growth. Although light levels in the ice increased as the snow melted, shading from the growing ice algal layer prevented an increase in light at depth.

Daily and total primary productivity contributed by the ice algae,

Table 7. Summary of data from Narwhal Island, spring 1980. Where no number is present, no sample was taken. 0 and 7 m productivity and plant pigment data are in mg m^{-3}. * indicates questionable data; + = based on 24 hr incubation; – = dark uptake greater than light.

Sta	Date	Depth	Light	Chl a	Phaeo	Prim Prod	Salinity	NO_3	NO_2	NH_3	PO_4	SiO_4
		(m)	(% sfc)	(mg m^{-2})		(mg C m^{-2} hr^{-1})	(°/₀₀)		(μg-at ℓ^{-1})			
1	10 Apr	ice		1.2	0.1	0.14	34.503	10.6	0.13		1.08	25
		0		0.1	0.1	0.01	35.213	10.1	0.07	0.01	1.27	22
		7		0.1	0.0	–	35.712	10.6	0.10	0.00	1.30	23
		sed										
2	12	ice										
		0		0.4	0.0	0.01^{+}	34.962	10.3	0.08	0.18	1.34	23
		7		0.1	0.0	0.01^{+}	35.312	10.3	0.08	0.00	1.25	23
		sed				–						
3	14	ice				0.05	33.731	10.3	0.10	0.75	1.08	24
		0		0.1	0.0	0.01	34.772	10.3	0.07	0.00	1.43	23
		7		0.0	0.0	–	35.077	10.5	0.08	0.00	1.29	23
		sed		0.7	1.5	–						
4	17	ice		0.4	0.1	0.03	33.825	10.6	0.10	1.12	4.06^{*}	23
		0		0.1	0.0	0.04	34.911	10.5	0.06	0.01	1.33	23
		7		0.0	0.0	–	35.264	10.6	0.09	0.00	1.32	24
		sed		13.3	5.0	< 0.01						
5	19	ice		0.4	0.0	0.08	34.020	10.3	0.07	0.59	10.50^{*}	24
		0		0.1	0.1	0.05	34.745	10.2	0.05	0.10	3.31^{*}	23
		7		0.0	0.0	0.01	35.528	10.8	0.09	0.00	4.55^{*}	24
		sed		0.9	1.6	< 0.01						
6	24	ice		2.4	0.2	0.07	32.582	9.9	0.11	0.69	1.17	23
		0		0.1	0.0	0.04	34.240	10.2	0.04	0.05	1.63	23
		7		0.1	0.0	0.01	35.312	11.0	0.09	0.00	1.49	24
		sed		6.8	3.1	< 0.01						

Table 7. (cont.)

Sta	Date	Depth	Light	Chl a	Phaeo	Prim Prod	Salinity	NO_3	NO_2	NH_3	PO_4	SiO_4
		(m)	(% sfc)	(mg m^{-2})		(mg C m^{-2} hr^{-1})	(°/∘∘)		(µg-at ℓ$^{-1}$)			
7	28	ice				0.01^+						
		0	0.34			0.01^+						
		7				-						
		sed				-						
8	29	ice	0.06	0.0	0.0	0.02	31.646	10.3	0.13	0.77	1.03	24
		0	0.02	0.2	0.1	0.06	34.332	10.3	0.05	0.02	11.82^*	24
		7	0.08	0.1	0.1	-	35.176	10.8	0.08	0.00	3.60^*	24
		sed		1.4	1.5	-						
9	2 May	ice	0.65	8.3	1.2	0.22	33.069	9.0	0.23	0.54	4.40^*	20
		0	0.52	0.2	0.1	0.01	34.381	10.0	0.07	0.14	15.63^*	24
		7	0.21	0.1	0.0	-	35.320	10.7	0.08	0.14	25.26^*	26
		sed		9.5	5.8	-						
10	5	ice	1.37	4.3	0.3	0.35	33.046	9.0	0.17	0.74	4.94^*	21
		0	0.87	0.3	0.1	0.01	34.436	9.7	0.06	0.06	1.49	23
		7	0.20	0.3	0.2	-	35.593	10.8	0.08	0.01	1.39	24
		sed		8.3	4.2	0.01						
11	6	ice	0.89			0.33^+						
		0	0.84			0.04^+						
		7	0.18			0.01^+						
		sed				$< 0.01^+$						
12	8	ice	0.81	2.2	0.3	0.77	32.632	9.6	0.28	0.76	1.13	23
		0	0.49	0.2	0.2	0.05	34.571	9.6	0.08	0.09	1.36	23
		7	0.24	0.0	0.0	-	35.707	11.0	0.07	0.08	1.49	24
		sed		1.4	1.8	0.02						

Table 7. (cont.)

Sta	Date	Depth	Light	Chl a	Phaeo	Prim Prod	Salinity	NO_3	NO_2	NH_3	PO_4	SiO_4
		(m)	(% sfc)	(mg m^{-2})		(mg C m^{-2} hr^{-1})	(°/oo)	(µg-at ℓ^{-1})				
13	15	ice	0.64	1.2	0.1	0.11	33.727	11.0	0.19	0.81	1.18	22
		0	0.37	0.1	0.1	0.07	34.540	9.5	0.07	0.21	1.90	22
		7	0.13	0.3	0.1	-	35.446	10.5	0.08	0.15	1.52	24
		sed		2.5	2.5	0.07						
14	17	ice	0.74	2.5	0.3	0.24	33.046	10.5	0.10	1.48	1.49	23
		0	0.55	0.3	0.1	-	34.340	9.3	0.07	0.16	1.34	22
		7	0.17	0.1	0.1	0.06	35.054	10.1	0.08	0.06	1.36	23
		sed		6.0	3.7	-						
15	19	ice	1.16			0.35^{+}						
		0	0.68			0.01^{+}						
		7	0.23			-						
		sed				0.03^{+}						
16	20	ice	1.48	3.9	0.5	0.51	32.648	11.9	0.21	0.64	1.27	23
		0	0.69	0.3	0.1	0.07	34.028	9.4	0.09	0.12	1.74	23
		7	0.24	0.1	0.1	-	34.895	10.1	0.10	0.02	1.41	24
		sed		0.7	1.0	-						
17	22	ice	1.08	14.4	1.5	0.71	31.601	10.7	0.19	0.77	1.36	19
		0	0.72	0.2	0.1	0.21	33.742	9.0	0.08	0.04	1.40	22
		7		0.1	0.1	0.09	34.520	9.6	0.10	0.00	1.42	23
		sed		14.2	7.7	-						
18	24	ice		11.1	0.3	0.55	31.016	14.0	0.28	1.03	2.06	21
		0		0.4	0.1	0.13	33.625	8.9	0.08	0.02	1.60	22
		7		0.1	0.1	0.13	34.326	9.6	0.09	0.02	1.50	23
		sed		7.2	5.2	-						

Table 7. (cont.)

Sta	Date	Depth (m)	Light (% sfc)	Chl a (mg m^{-2})	Phaeo (mg m^{-2})	Prim Prod (mg C m^{-2} hr^{-1})	Salinity (°/oo)	NO_3 (µg-at ℓ$^{-1}$)	NO_2 (µg-at ℓ$^{-1}$)	NH_3 (µg-at ℓ$^{-1}$)	PO_4 (µg-at ℓ$^{-1}$)	SiO_4
19	26	ice	0.87	13.5	1.5	0.38	30.046	16.6	0.20	1.52	1.89	22
		0	0.36	0.8	0.2	0.09	33.595	8.9	0.07	0.00	4.36	22
		7	0.20	0.2	0.1	-	33.877	9.3	0.08	0.00	3.94	23
		sed		6.1	2.9	-						
20	29	ice	1.74	12.7	1.6	2.64	32.318	9.6	0.13	0.54	1.46	20
		0	0.81	0.2	0.1	0.06	34.122	9.1	0.09	0.00	1.36	23
		7	0.59	0.1	0.1	-	34.383	9.5	0.09	0.00	1.40	23
		sed		0.9	0.8	0.02						
21	31	ice	2.00	26.5	3.2	0.77	32.875	17.4	0.32	1.20	1.53	20
		0	0.94	0.5	0.2	0.04	34.208	9.1	0.09	0.03	1.41	23
		7	0.27	0.1	0.1	-	34.345	9.4	0.09	0.00	1.29	23
		sed		16.5	6.0	< 0.01						
22	2 Jun	ice	1.86	20.4	3.4	0.36	31.516	18.0	0.17	0.87	1.68	22
		0	0.50	0.3	0.2	0.05	34.031	8.7	0.09	0.03	1.33	22
		7	0.19	0.1	0.1	0.03	34.497	9.7	0.09	0.01	1.27	23
		sed		10.9	5.6	0.02						
23	3 Jun	ice	1.36			0.72^{+}						
		0	0.33			0.02^{+}						
		7	0.18			0.01^{+}						
		sed				-						
24	5	ice	1.30	12.0	2.0	0.46	31.659	16.1	0.18	1.08	2.28	22
		0	0.56			0.07	33.662	8.2	0.09	0.11	1.11	21
		7	0.14	0.2	0.1	0.16	34.781	10.4	0.10	0.07	16.95*	25
		sed		28.7	6.6	< 0.01						

Table 7. (cont.)

Sta	Date	Sample (m)	Light (% sfc)	Chl *a* (mg m^{-2})	Phaeo (mg m^{-2})	Prim Prod (mg C m^{-2} hr^{-1})	Salinity (°/ₒₒ)	NO_3 (µg-at ℓ^{-1})	NO_2 (µg-at ℓ^{-1})	NH_3 (µg-at ℓ^{-1})	PO_4 (µg-at ℓ^{-1})	SiO_4
25	7	ice	4.01	17.2	2.7	2.60	31.207	9.7	0.22	1.85	1.77	22
		0	2.65	0.7	0.7	0.42	32.911	8.0	0.10	0.43	1.38	21
		7	0.33	0.2	0.2	-	34.725	10.4	0.09	0.00	1.38	24
		sed		17.0	7.9	-						
26	9	ice	1.83	18.0	2.9	1.69	26.383	7.8	0.21	4.33	1.36	21
		0	0.41	1.0	0.1	-	28.192	8.1	0.09	0.64	1.27	20
		7	0.24	0.1	0.1	-	34.541	10.2	0.09	0.00	1.22	23
		sed		4.8	2.7	0.01						
27	11	ice	2.80	0.1	0.0		16.385	7.1	0.09	2.26	2.86	21
		0	1.51	1.4	0.3	0.01	24.086	9.9	0.09	0.64	2.62	23
		7	0.23	0.5	0.1	0.01	33.843	6.8	0.16	0.11	0.88	23
		sed		12.2	6.3	-						

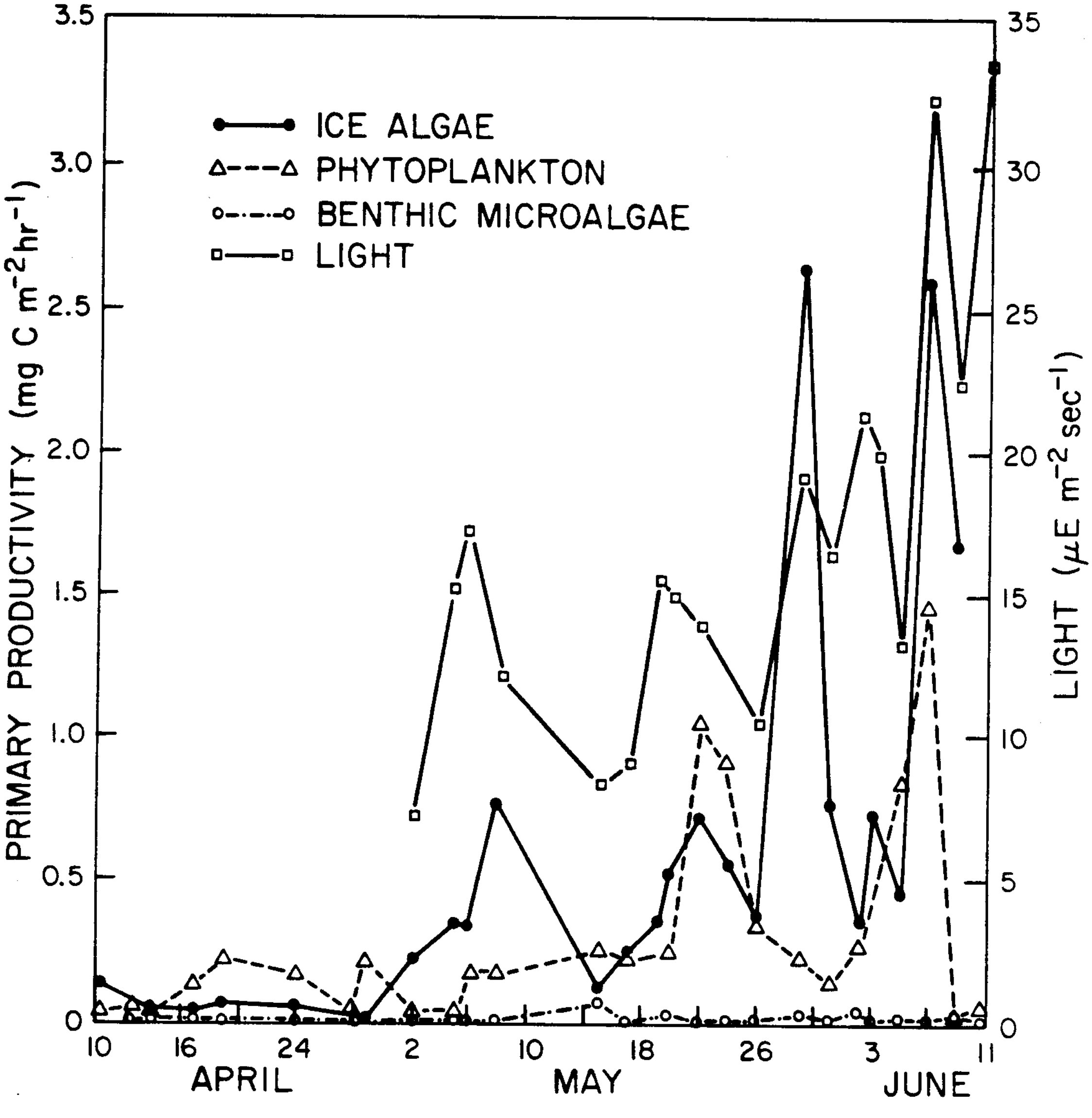

Fig. 3. Primary productivity (mg C m^{-2} hr^{-1}) and incident light intensity (μE m^{-2} sec^{-1}), spring 1980. Productivity of the water column was calculated by integrating productivity at 0 and 7 m.

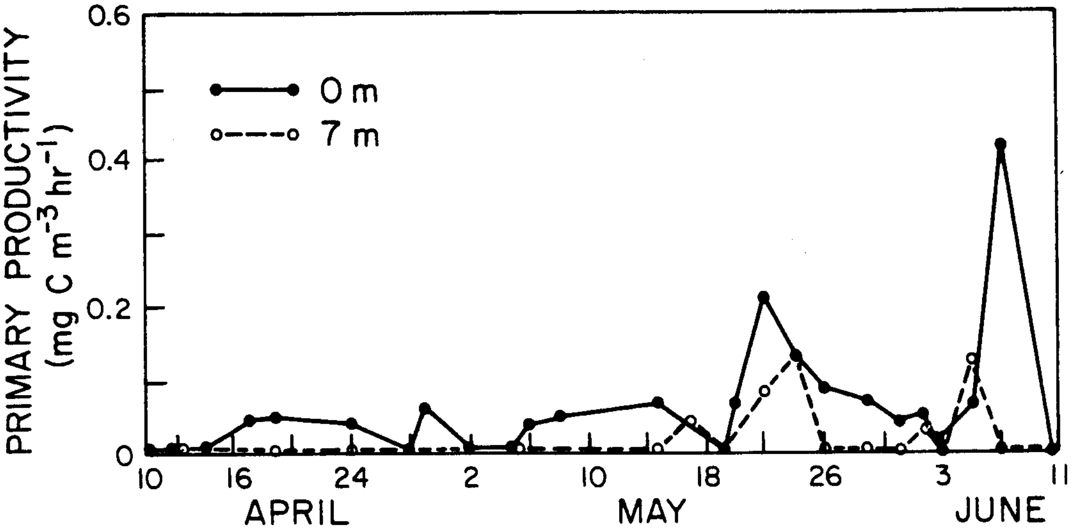

Fig 4a. Primary productivity (mg C m^{-3} hr^{-1}) of the water column at 0 and 7 m, spring 1980.

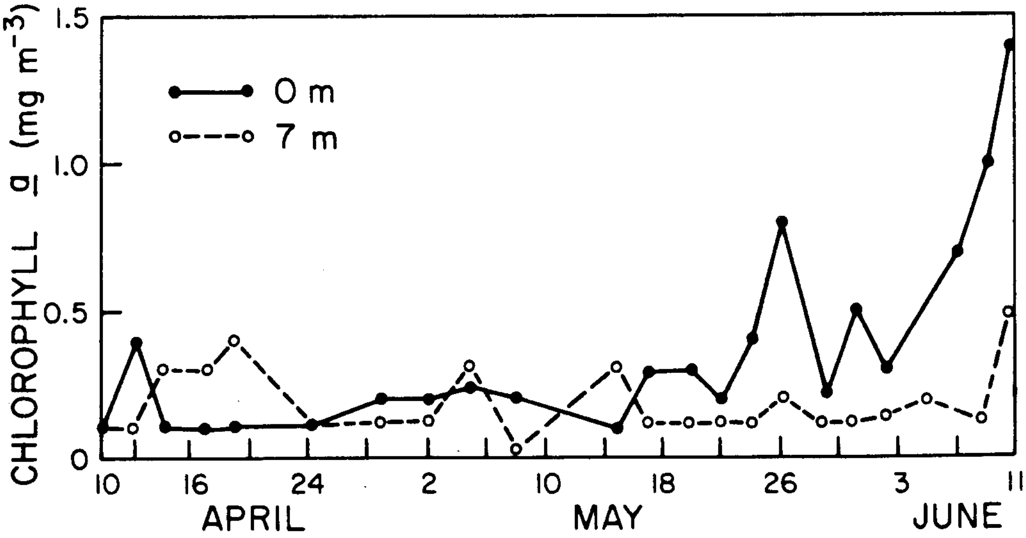

Fig. 4b. Chlorophyll *a* (mg m^{-3}) of the water column at 0 and 7 m, spring 1980.

phytoplankton, and benthic communities during the study period is summarized in Table 8. Production rates based on 4 and 24 hr incubation periods often differed, but these differences are not considered significant in relation to the high variance found among replicate cores and successive sampling days. During this period the ice algal community contributed 688 mg C m^{-2}; the phytoplankton, 380 mg C m^{-2}; and the benthic community *ca.* 12 mg C m^{-2}. Thus, approximately two-thirds of the primary production occurred in the bottom ice, about one-third occurred in the water column, mainly at the surface, and productivity in the benthos was negligible.

2. Plant pigments

Ice algal chlorophyll *a* followed a pattern similar to that shown for primary productivity. Chlorophyll *a* levels were relatively low during April, *ca.* 1 mg m^{-2}, and increased to over 26 mg m^{-2} during the second half of May (Fig. 5). Levels remained fairly constant for *ca.* three weeks and then dropped to near zero at the termination of the bloom on 11 Jun.

Pigment concentrations in the water column remained low throughout most of the study period, rising slightly near the termination of the ice algal bloom. At 7 m, levels were fairly constant, fluctuating between < 0.1 mg m^{-3} to *ca.* 0.4 mg m^{-3} (Fig. 4b). Chlorophyll *a* concentrations at 0 m were about equal to those found at 7 m during April and early May, but increased significantly during the ice algal bloom in late May and early June, reaching a peak of 1.4 mg m^{-3} on 11 June. The high surface levels of chlorophyll *a* near the end of the bloom reflect the large quantity of ice algae dropping from the undersurface of the ice into the water column.

Chlorophyll *a* levels in the sediments were comparable to those found on the undersurface of the ice with both communities showing sharp increases during the late May through early June period. During April, however, benthic chlorophyll *a* levels were *ca.* five times greater than those found in the ice algal community. Fluctuations in chlorophyll *a* levels in the sediments were greater than in the ice, which may be a function of patchiness and differences in sampling technique. Three replicate cores were used to sample the ice algal pigments, but only a single sediment core was taken for benthic pigment determinations.

Because primary productivity in the sediments was negligible, it appears likely that the high chlorophyll is from benthic microalgae remaining in the sediments from the previous season of productivity. This is supported by the high chlorophyll levels in April, when ice algal productivity was low. Subsequent increases in benthic chlorophyll probably resulted from algae falling from the ice, and accumulating in the sediments, as the relative amount of phaeopigments found in the sediments increased during the course of the ice algal bloom.

The relative amount of phaeopigments in the ice was very low compared with the water column and sediments. The ratio Σ phaeopigments:Σ chlorophyll *a* was 0.13 for the ice; 0.40 at 0 m; 0.55 at 7 m; and 0.49 in the sediments, indicating an increase in the relative amount of phaeopigments with depth. As phaeopigments are degradation products of chlorophyll *a*, one would expect this increase with depth because of sinking of fecal

Table 8. Daily and total primary productivity of ice algal, water column, and benthic communities. Daily rates were calculated by multiplying the hourly productivity rate by the day length in hours. Total carbon fixed was calculated by integrating daily rates over the study period. * = based on 24 hr incubation period.

			Prim Prod (mg C m^{-2} day^{-1})	
Date	Day Length (hr)	Ice	Water	Benthos
10 Apr	15.5	2.2	0.62	
*12	15.8		1.10	0
14	16.4	0.8	0.7	0
17	16.6	0.5	2.3	0
19	16.9	1.4	3.6	0
24	17.8	1.2	3.7	0
*28	18.5	0.01	1.0	0
29	18.7	0.4	3.9	0
2 May	19.3	4.2	0.8	0
5	19.9	7.0	0.8	0.2
* 6	20.2	7.9	4.3	0
8	20.7	15.9	3.6	0.4
15	22.8	2.5	5.7	1.6
17	24.0	5.8	5.0	0
*19	24.0	8.4	0.5	0
20	24.0	12.2	6.0	0
22	24.0	17.0	25.2	0
24	24.0	13.2	21.8	0
26	24.0	9.1	7.7	0
29	24.0	63.4	5.0	0.5
31	24.0	18.5	3.4	0
2 Jun	24.0	8.6	6.7	0.5
* 3	24.0	17.3	2.6	0
5	24.0	11.0	19.4	0
7	24.0	62.4	35.3	0
9	24.0	40.6	0	0.2
11	24.0		1.7	0
Total		688	380	12

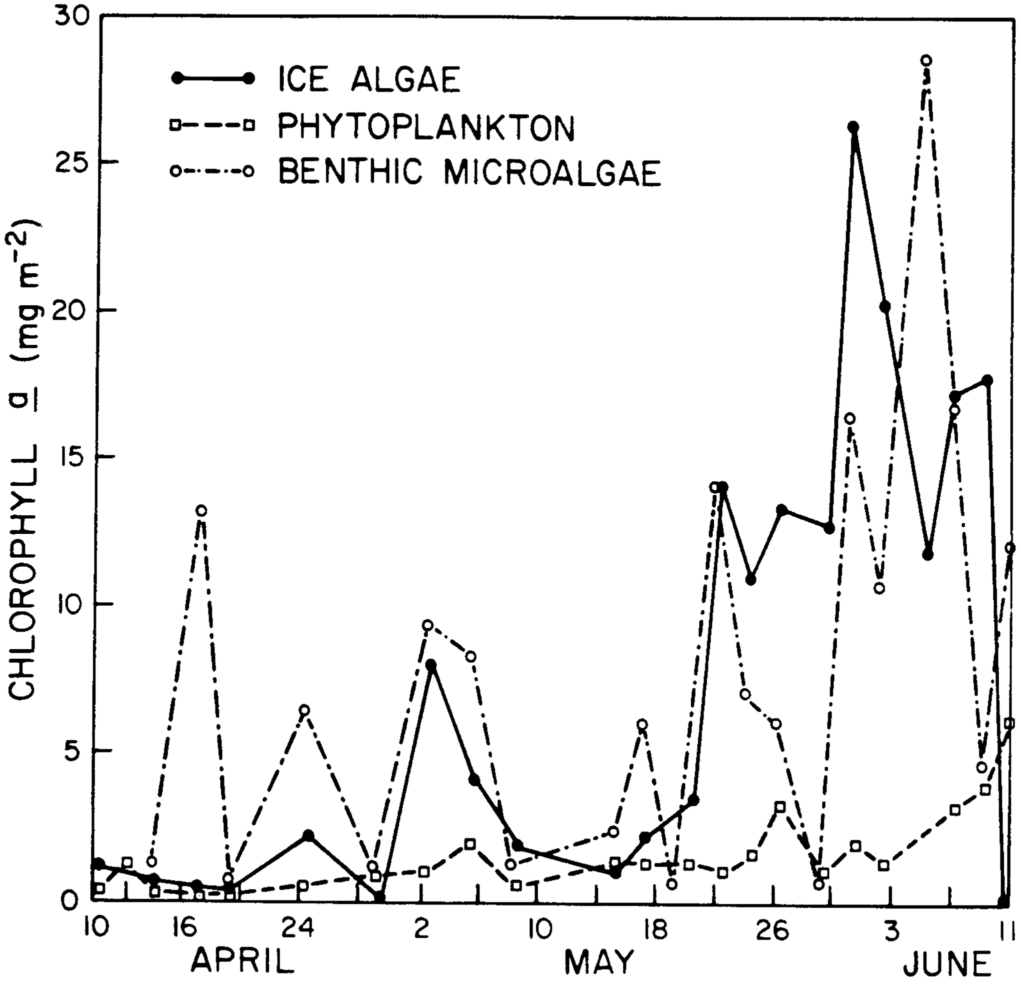

Fig. 5. Chlorophyll *a* (mg m^{-2}), spring 1980. Chlorophyll *a* of the ice algae is the average of three replicate cores; chlorophyll *a* of the benthic microalgae is from one core; chlorophyll *a* of the water column was calculated by integrating values from 0 and 7 m.

pellets from grazing herbivores, and from dead algal cells falling from the ice and water column.

On 11 May, a station inside Stefansson Sound in the boulder patch area was sampled for chlorophyll *a* in the bottom ice. The average concentration from two ice cores was 0.24 mg m^{-2}, which was low compared with the station outside Narwhal Island. The ice in Stefansson Sound was turbid and under-ice light levels were low.

3. Standing stock

a. Cell numbers

Small, unidentified flagellates, mostly < 6 μm in diameter, accounted for *ca.* 50% of the cells in the ice algal community (Fig. 6). The remainder of the cells was predominately pennate diatoms, with low numbers of centric diatoms, dinoflagellates, and other flagellates. In the water column, microflagellates were by far the most numerous organisms, exceeding the concentration of diatoms by an order of magnitude (Fig. 7; Appendix II-2). Although microflagellates are considered to be important primary producers in the ocean (Malone 1971), those found in this study did not appear to be photosynthetic. Cell concentrations at the surface remained nearly constant and did not reflect changes in primary productivity or chlorophyll *a*. Microflagellate concentrations at 7 m declined by an order of magnitude during the ice algal bloom in late May and early June. Microflagellates were not considered further here because they are apparently not photosynthetic.

Ice algal cell concentrations were quite variable, fluctuating between *ca.* 1×10^7 and 1×10^9 cells m^{-2} during the April to mid-May period (Fig. 8, Appendix II-3). Samples collected after 20 May were far less variable, 6.6×10^8 - 1.2×10^9 cells m^{-2}, suggesting a more patchy distribution earlier in the study, and more uniformity during the height of the bloom. Cell concentrations correlated well with levels of chlorophyll *a*.

The concentration of algal cells in the water column was generally at least an order of magnitude lower than that found in either the bottom ice or benthos, averaging *ca.* 1×10^4 cells ℓ^{-1} at the surface and 1×10^8 cells m^{-2} for the entire water column. Cell numbers fluctuated greatly during the April to mid-May period, but stabilized during the ice algal bloom period.

Limited resources permitted the enumeration of only a portion of the benthic standing stock samples, but seven cores were analyzed, corresponding to the highest and lowest levels of chlorophyll *a*. Cell numbers correlated well with chlorophyll *a* values and were as high as those found in the ice algal community. Average cell size in the benthic community, however, was considerably smaller than was found in the ice algal community. Cell concentrations were fairly constant, *ca.* 3×10^8 - 3×10^9 cells m^{-2}, suggesting a more uniform distribution than in the ice algal community.

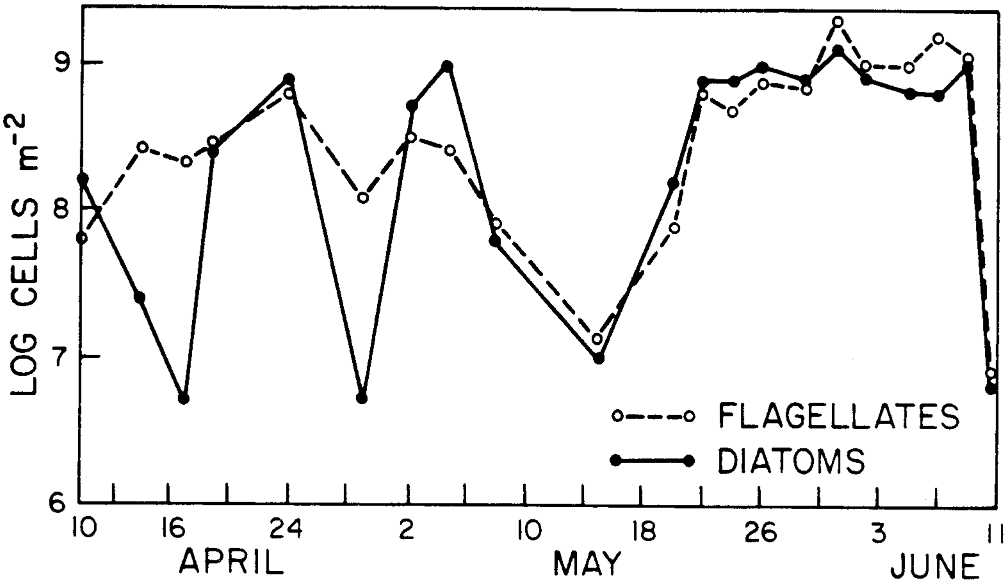

Fig. 6. Concentrations of diatoms and flagellates (log cells m^{-2}) in the ice, spring 1980.

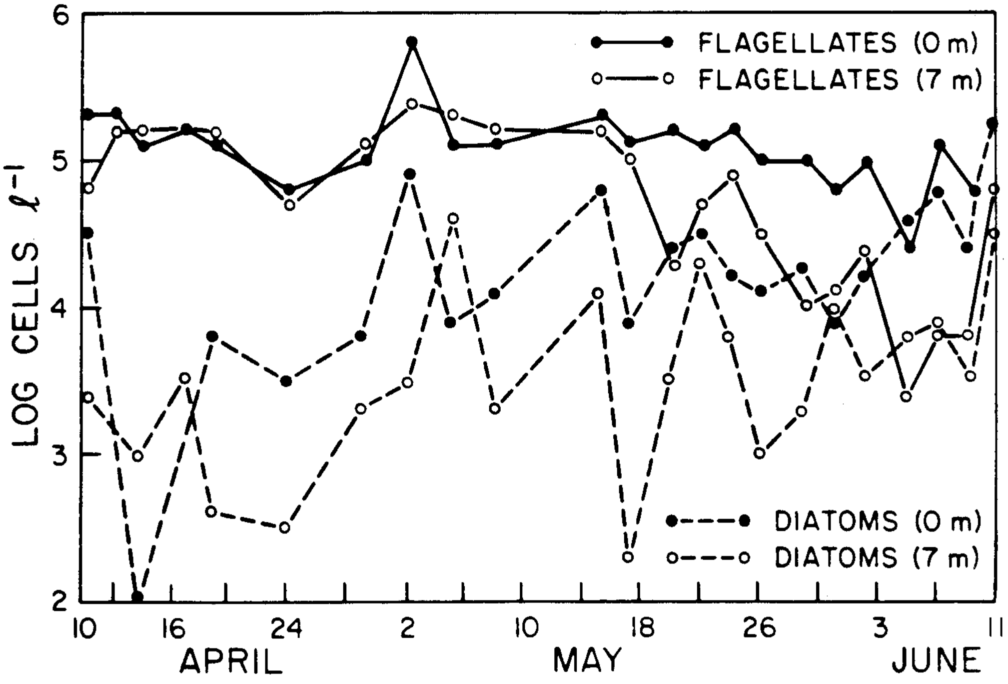

Fig. 7. Concentrations of diatoms and flagellates (log cells ℓ$^{-1}$) in the water column at 0 and 7 m, spring 1980.

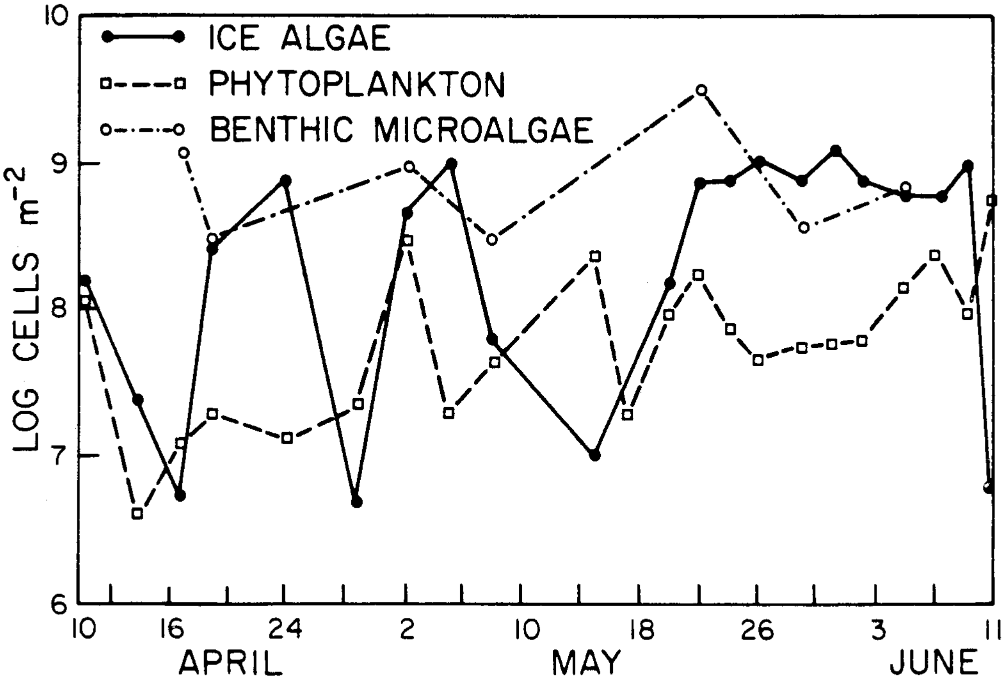

Fig. 8. Concentration of diatoms (log cells m^{-2}) in the ice, water column, and benthos, spring 1980.

b. Species composition

1. Ice algae

Seventy-three taxa including 43 species were identified from ice cores. These included 58 species or genera of pennate diatoms, three centric diatoms, four dinoflagellates, and six flagellates (Tables 9-10). The ice algal community was strongly dominated by pennate diatoms, with a single species, *Nitzschia cylindrus*, accounting for an average of 47% of all diatoms counted. Other pennate diatom species that were numerically important included *Amphora ocellata, Cylindrotheca closterium, Navicula directa, N. transitans,* and *Nitzschia frigida.*

Centric diatoms were represented by few species and in low numbers. *Thalassiosira gravida* was the most common, occurring in one-third of the samples. *Chaetoceros septentrionalis* was found once on 9 June, and other small *Chaetoceros* spp., < 10 µm, were present in three samples.

Dinoflagellates were found in low numbers throughout the study and were predominantly unidentified athecate forms. *Peridinium grenlandicum, Amphidinium* sp., and *Gymnodinium* sp. were also found. Unidentified flagellates, < 6 µm in diameter, were often dominant organisms in the ice. Other flagellates found were *Dinema litorale, Eutreptiella* sp., *Urceolus* sp., *Platymonas* sp., *Cryptomonas* spp., and an unidentified euglenoid.

Changes in community structure and composition were noted during the course of the bloom. During April to mid-May, species diversity was relatively low and was inversely related to cell numbers (Fig. 9). Changes in diversity were due largely to changes in the relative percentage by cell numbers of *Nitzschia cylindrus*. Fluctuation in cell numbers reflect the patchy distribution of the ice algae, suggesting that within patches (high cell numbers) the community was more strongly dominated by *N. cylindrus*. During the second half of May, when chlorophyll *a* and standing stocks increased precipitously and stabilized at high levels, the diversity of the community began to increase. *Nitzschia cylindrus* became less dominant and cells often appeared unhealthy. Both *N. cylindrus* and another dominant species, *Navicula spicula*, were parasitized by chytridiaceous fungi. Several species became common that had not been identified previously, or that had occurred rarely earlier in the study. These included *Achnanthes taeniata, Amphora ocellata, Cylindrotheca closterium, Navicula directa, Nitzschia* sp. A, *Pinnularia quadratarea* var. *kerguelensis, Synedra* sp., and *Thalassiothrix* sp.

A bottom ice sample collected with a SIPRE corer on 9 Nov 1980 by RU 537 contained the same species that made up the spring assemblage. *Nitzschia cylindrus* dominated the community, comprising 92% of the cell numbers.

2. Phytoplankton

Fifty-six taxa, including 35 species, were identified in samples from the water column (Tables 11-12). These species were predominantly the same as occurred in the ice, with pennate diatoms being the dominant group. Unidentified flagellates, < 6 µm in diameter, were also abundant. Only five species were identified from the water

Table 9. Microalgae species from ice cores collected off Narwhal Island, spring 1980.

Pennate diatoms

- *Achnanthes taeniata* Grunow
- *Achnanthes* sp.
- *Amphiprora paludosa* var. *hyperborea* (Grunow) Cleve
- *Amphiprora formosa* Meunier
- *Amphiprora kjellmanii* Cleve
- *Amphora laevis* Gregory
- *Amphora ocellata* Donkin *cf.*
- *Amphora* spp.
- *Cylindrotheca closterium* (Ehrenberg) Reimann & Lewin
- *Diploneis* spp.
- *Eunotia* spp.
- *Fragilaria* spp.
- *Gomphonema exiguum* var. *arctica* Grunow
- *Gomphonema kamtschaticum* Grunow
- *Gyrosigma fasciola* (Ehrenberg) Cleve
- *Gyrosigma spenceri* (W. Smith) Griffith & Henfrey
- *Gyro-Pleurosigma* spp.
- *Licmophora* spp.
- *Navicula bolleana* (Grunow) Cleve *cf.*
- *Navicula cancellata* Donkin
- *Navicula directa* (W. Smith) Ralfs in Pritchard
- *Navicula kjellmanii* Cleve
- *Navicula lyroides* Hendey
- *Navicula maculosa* Donkin
- *Navicula marina* Ralfs
- *Navicula pelagica* Cleve
- *Navicula peregrina* (Ehrenberg) Kützing
- *Navicula peregrina* var. *meniscus* (Schumann) Grunow
- *Navicula spicula* (Hickie) Cleve
- *Navicula transitans* var. *derasa* (Grunow) Cleve
- *Navicula transitans* var. *erosa* (Cleve) Cleve
- *Navicula trigonocephala* Cleve
- *Navicula valida* var. *minuta* Cleve
- *Navicula* sp. A
- *Navicula* sp. B
- *Nitzschia angularis* W. Smith
- *Nitzschia cylindrus* (Grunow) Hasle
- *Nitzschia frigida* Grunow
- *Nitzschia seriata* Cleve
- *Nitzschia sigma* (Kützing) W. Smith *cf.*
- *Nitzschia sigmoidea* (Nitzsch) W. Smith
- *Nitzschia* sp. A
- *Nitzschia* sp. B
- *Nitzschia* spp.
- *Pinnularia quadratarea* (A. Schmidt) Cleve
- *Pinnularia quadratarea* var. *antarctica* (M. Peragallo) Frenguelli & Orlando
- *Pinnularia quadratarea* var. *interrupta* (Cleve) Cleve

Table 9. (cont.)

- *Pinnularia quadratarea* var. *kerguelensis* (Cleve & Grunow) Cleve
- *Pinnularia quadratarea* var. *theelii* (Cleve) Cleve
- *Pseudonitzschia delicatissima* (Cleve) Heiden
- *Rhoiconeis* spp.
- *Stauroneis quadripedis* (Cleve-Euler) Hendey
- *Synedra* spp.
- *Thalassiothrix* spp.
- *Tropidoneis* spp.
- Unidentified pennate diatoms

Centric diatoms
- *Chaetoceros septentrionalis* Østrup
- *Chaetoceros* spp.
- *Thalassiosira gravida* Cleve

Dinoflagellates
- *Amphidinium* sp.
- *Gymnodinium* spp.
- *Peridinium grenlandicum* Woloszynska
- Unidentified dinoflagellates

Flagellates
- *Dinema litorale* Skuja
- *Eutreptiella* sp.
- *Urceolus* sp.
- Unidentified euglenoid sp. A
- *Platymonas* spp.
- Unidentified cryptomonad spp.

Table 10. Relative abundance and distribution through time of microalgae species from ice cores collected by divers off Narwhal Island, spring 1980, and from one core collected with a SIPRE corer in Nov 1980. P = present (< 1%); O = common (1-5%); x = abundant (5-10%); Δ = dominant (> 10%).

Taxon	Apr 10	14	17	19	24	29	May 2	5	8	15	20
Pennate diatoms											
Achnanthes taeniata	P										
Amphiprora alata											
Amphiprora kjellmanii	P	P		P							
Amphiprora paludosa v. *hyperborea*										P	P
Amphora ocellata									O		x
Cylindrotheca closterium	P		Δ		P		P	P	P	P	O
Eunotia spp.	P										
Fragilaria sp.											P
Gomphonema exiguum v. *arctica*	O	O	x	O	O		P	P	P	O	P
Gyrosigma fasciola	P										
Gyro-Pleurosigma spp.	O	P		O	O		P	P	P	P	P
Licmophora spp.	O	x		O	O	O	P	P	P	O	P
Navicula bolleana cf.	P	O		O	P	O	P	P	P	O	
Navicula directa	P						P	O	O	O	O
Navicula kjellmanii											
Navicula maculosa	P										
Navicula marina	P	x	O	P	P		P	P	P	P	P
Navicula pelagica									P		
Navicula spicula	O			O	O	O	Δ	O	O	O	x
Navicula transitans	P	O		P	P				P	O	O
Navicula trigonocephala	P	O	O	P	P		P	P			P
Navicula valida v. *minuta*		O			P		P			O	P
Navicula sp. A	P				P						
Nitzschia angularis											
Nitzschia cylindrus	Δ	Δ	x	Δ	Δ	x	Δ	Δ	Δ	Δ	Δ
Nitzschia frigida	Δ	O		P	Δ		Δ	x	Δ	x	Δ
Nitzschia seriata											
Nitzschia sigma cf.											
Nitzschia sigmoidea								P		P	P

Table 10. (cont.)

Taxon	Apr						May				
	10	14	17	19	24	29	2	5	8	15	20
Nitzschia sp. A									O	O	O
Nitzschia sp. B		O		P	P	O	O	P		P	
Pinnularia quadratarea											
Pinnularia quadratarea v. *kerguelensis*	P										
Pinnularia quadratarea v. *theelii*											
Pseudonitzschia delicatissima	P										P
Stauroneis quadripedis										P	P
Synedra utermöhlii											
Synedra sp.											O
Thalassiothrix spp.	P						P				
Tropidoneis sp.											
Unidentified pennate diatoms	Δ	O	Δ	Δ	x	Δ	Δ	x	O	Δ	x
Centric diatoms											
Chaetoceros gracilis											
Chaetoceros septentrionalis											
Chaetoceros spp.		O	x								
Thalassiosira gravida		P		P	P		P				
Dinoflagellates											
Amphidinium sp.	P							P		P	P
Gymnodinium sp.	P										
Peridinium grenlandicum								P			
Unidentified dinoflagellates		P	P	P	P		P	P		P	O
Flagellates											
Cryptomonad spp.	P		P				P	P			P
Dinema litorale	P				P						
Eutreptiella sp.	P	P	P		P	P	P	P		P	P
Urceolus sp.											
Unidentified euglenoid sp.										P	P
Platymonas spp.									O	P	
Unidentified flagellates (> 6 μm)	O	Δ	P	O	O	O	Δ	x	x	x	x

Table 10. (cont.)

	May					Jun					Nov
Taxon	22	24	26	29	31	2	5	7	9	11	9
Pennate diatoms											
Achnanthes taeniata	O	O			P	O	x	O	O		P
Amphiprora alata											P
Amphiprora kjellmanii											P
Amphiprora paludosa v. *hyperborea*	P	P	P	P				P			P
Amphora ocellata	P	O	x	x	O	O	P	O	O	O	
Cylindrotheca closterium	O	O	O	x	x	O	x	x	O	O	P
Eunotia spp.									O		
Fragilaria sp.		P			O			O		P	P
Gomphonema exiguum v. *arctica*	P	P	P	P	P	O	P	P	O	O	P
Gyrosigma fasciola	P	P	P	P	P			P	P		
Gyro-Pleurosigma spp.	O	O	O	P	P	P	P	P	P	P	P
Licmophora spp.	P	P	P	P	P		P	P	O		
Navicula bolleana cf.	P	P			P	O	O	P	O	O	
Navicula directa	O	x	O	O	x	O	Δ	x	Δ	O	P
Navicula kjellmanii								P			
Navicula maculosa		P		P	P	P	P	P	P		
Navicula marina	P	P	P		P		P	P	P	P	
Navicula pelagica											P
Navicula spicula	O	Δ	Δ	Δ	Δ	O	x	O	O	O	P
Navicula transitans	O	O	x	Δ	O	O	O	O	x	x	P
Navicula trigonocephala	O	P	P		P	P	P	P	P		
Navicula valida v. *minuta*		P	P	P	P	P	P	P	P	O	
Navicula sp. A	P				P						
Nitzschia angularis		P	P	O	P	P					
Nitzschia cylindrus	Δ	Δ	Δ	Δ	Δ	Δ	x	O	x	Δ	Δ
Nitzschia frigida	x		O	O	O	Δ	O	Δ	Δ		P
Nitzschia seriata											O
Nitzschia sigma cf.			P		P	P			P		
Nitzschia sigmoidea	P	P	P		P	P			P		

Table 10. (cont.)

Taxon	May					Jun					Nov
	22	24	26	29	31	2	5	7	9	11	9
Nitzschia sp. A	O	O	P		P	P		P			
Nitzschia sp. B	P		P			P	P				
Pinnularia quadratarea		P	P		P			P	P	P	
Pinnularia quadratarea v. *kerguelensis*		O	O	O	O	O	P	P	O	O	P
Pinnularia quadratarea v. *theelii*								P	P		
Pseudonitzschia delicatissima	P	P	P	O	P		P	P	P		O
Stauroneis quadripedis	P	P	P		P						
Synedra utermöhlii											P
Synedra sp.			P	O	O	O	O	O	O		P
Thalassiothrix spp.	O	P	P	P	P		P	P	O	P	
Tropidoneis sp.	P										
Unidentified pennate diatoms	Δ	x	Δ	Δ	Δ	Δ	Δ	Δ	Δ	Δ	P
Centric diatoms											
Chaetoceros gracilis											P
Chaetoceros septentrionalis									P		P
Chaetoceros spp.				P							
Thalassiosira gravida			O	O	O			P		O	P
Dinoflagellates											
Amphidinium sp.	P				P	P	P	P		P	
Gymnodinium sp.										P	
Peridinium grenlandicum											
Unidentified dinoflagellates	O		P	P	P	P		P			P
Flagellates											
Cryptomonad spp.		P	P	P							
Dinema litorale	P	P	P	P	P	P	P	P	P		
Eutreptiella sp.	P	P		P	P	P	P			P	
Urceolus sp.					P						
Unidentified euglenoid sp.	P	P				P	P	P	P		
Platymonas spp.					O	O	P	P	P	P	
Unidentified flagellates (< 6 μm)	Δ	Δ	Δ	Δ	Δ	Δ	x	Δ	x	Δ	P

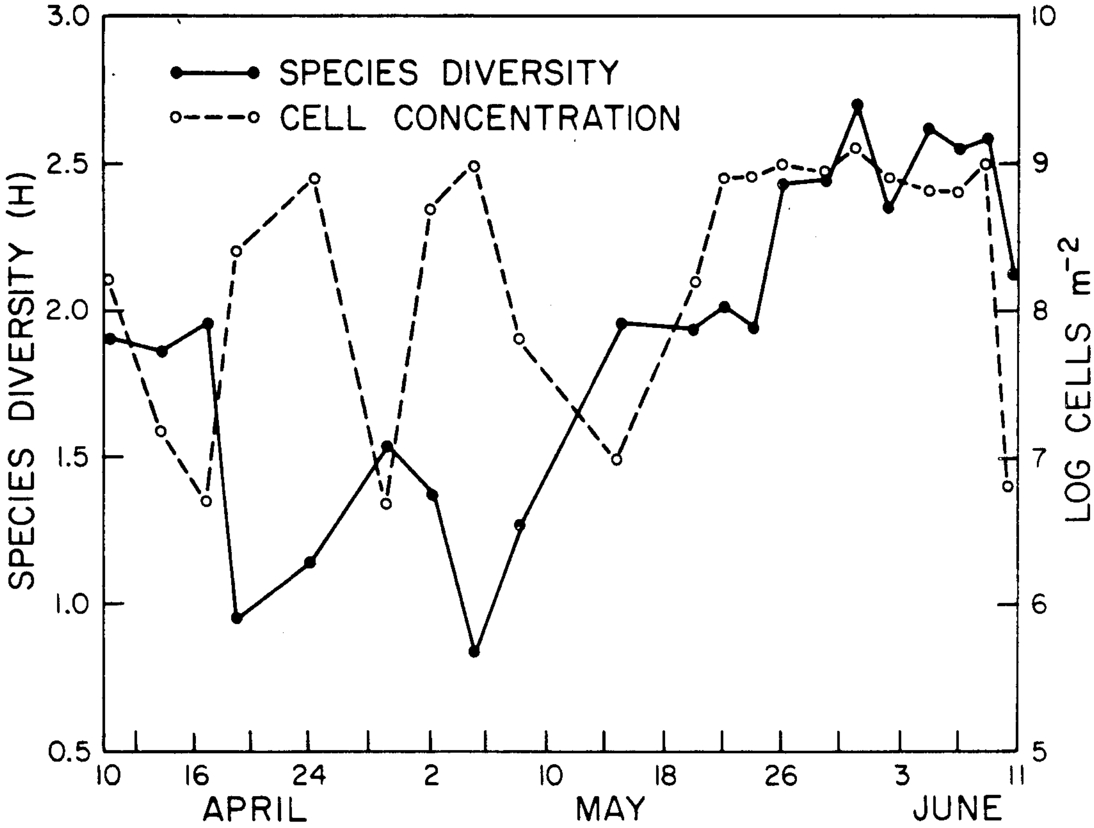

Fig. 9. Shannon-Wiener diversity index and concentration of cells (log cells m^{-2}) in the ice community, spring 1980.

Table 11. Phytoplankton species collected off Narwhal Island, spring 1980.

Pennate diatoms

- *Achnanthes taeniata* Grunow
- *Achnanthes* sp.
- *Amphiprora paludosa* var. *hyperborea* (Grunow) Cleve
- *Amphora ocellata* Donkin *cf.*
- *Amphora* sp.
- *Cylindrotheca closterium* (Ehrenberg) Reimann & Lewin
- *Gomphonema exiguum* var. *arctica* Grunow
- *Gomphonema kamtschaticum* Grunow
- *Gyrosigma fasciola* (Ehrenberg) Cleve
- *Gyro-Pleurosigma* spp.
- *Licmophora* sp.
- *Navicula bolleana* (Grunow) Cleve *cf.*
- *Navicula directa* (W. Smith) Ralfs in Pritchard
- *Navicula kjellmanii* Cleve
- *Navicula lyroides* Hendey
- *Navicula maculosa* Donkin
- *Navicula marina* Ralfs
- *Navicula pelagica* Cleve
- *Navicula spicula* (Hickie) Cleve
- *Navicula transitans* var. *derasa* (Grunow) Cleve
- *Navicula trigonocephala* Cleve
- *Navicula valida* var. *minuta* Cleve
- *Navicula* sp. A
- *Nitzschia angularis* W. Smith
- *Nitzschia cylindrus* (Grunow) Hasle
- *Nitzschia frigida* Grunow
- *Nitzschia seriata* Cleve
- *Nitzschia sigma* (Kützing) W. Smith *cf.*
- *Nitzschia sigmoidea* (Nitzsch) W. Smith
- *Nitzschia* sp. A
- *Nitzschia* sp. B
- *Pinnularia quadratarea* var. *kerguelensis* (Cleve & Grunow) Cleve
- *Pinnularia quadratarea* var. *theelii* (Cleve) Cleve
- *Pseudonitzschia delicatissima* (Cleve) Heiden
- *Rhoiconeis* sp.
- *Stauroneis quadripedis* (Cleve-Euler) Hendey
- *Stauroneis* sp.
- *Synedra* sp.
- *Thalassiothrix* spp.

Centric diatoms

- *Chaetoceros gracilis* Schütt
- *Chaetoceros septentrionalis* Østrup
- *Chaetoceros* spp.
- *Leptocylindrus* sp.
- *Melosira juergensii* Agardh

Table 11. (cont.)

Thalassiosira gravida Cleve
Thalassiosira spp.

Dinoflagellates
- *Amphidinium* sp.
- *Dinophysis arctica* Mereschkowsky
- *Exuviaella* sp.
- *Gymnodinium* sp.
- *Peridinium grenlandicum* Woloszynska

Flagellates
- *Dinema litorale* Skuja
- *Euglena* sp.
- *Eutreptiella* sp.
- *Platymonas* spp.
- Unidentified flagellates (> 6 μm)

Table 12. Relative abundance and distribution through time of phytoplankton species collected at 0 and 7 m off Narwhal Island, spring 1980. P = present (< 1%); O = common (1-5%); x = abundant (5-10%); Δ = dominant (> 10%).

	Apr												May											
	10		14		17		19		24		29		2		5		8		15		20	
Taxon	0	7	0	7	0	7	0	7	0	7	0	7	0	7	0	7	0	7	0	7	0	7
Pennate diatoms																						
Achnanthes taeniata															P							
Achnanthes sp.							P				P											
Amphiprora paludosa v. *hyperborea*																						
Amphora ocellata									P					P	P		P				P	
Amphora sp.	P																		P			
Cylindrotheca closterium							P	P							P	P		P	P		P	
Gomphonema exiguum v. *arctica*	P				P	P	P								P		P		P		P	
Gomphonema kamtschaticum																	P		P	P		
Gyrosigma fasciola																			P			
Gyro-Pleurosigma spp.										P	P			P			P		P		P	
Licmophora sp.	P								P				P				P		P		P	
Navicula bolleana cf.	P								P				P		P	P	P		P		P	
Navicula directa	P		P				x		P										P		P	
Navicula kjellmanii	P																					
Navicula lyroides																						
Navicula maculosa																						
Navicula marina							P				P				P	P			P			
Navicula pelagica																						
Navicula spicula															P	P	P		P		P	
Navicula transitans v. *derasa*	P						P	P	P				P				P	P	P	P	P	
Navicula trigonocephala															P				P			
Navicula valida																						
Navicula sp. A																			P		P	
Nitzschia angularis																						
Nitzschia cylindrus	P												Δ	P	P	Δ	Δ		Δ	P	Δ	x
Nitzschia frigida												P									P	
Nitzschia seriata					P	P	P										P		P			

Table 12. (cont.)

	Apr												May									
	10		14		17		19		24		29		2		5		8		15		20	
Taxon	0	7	0	7	0	7	0	7	0	7	0	7	0	7	0	7	0	7	0	7	0	7
Nitzschia sigma cf.																						
Nitzschia sigmoidea																						
Nitzschia sp. A																	P					
Nitzschia sp. B							P		P	P		P			P						P	
Pinnularia quadratarea v. *kerguelensis*															P	P			P		P	
Pinnularia quadratarea v. *theelii*							P								P	P						
Pseudonitzschia delicatissima																			P		P	
Rhoiconeis sp.																						
Stauroneis quadripedis							P												P		P	
Stauroneis sp.																				Δ		
Thalassiothrix spp.											P				P	P	P		P			
Unidentified pennate diatoms	P	P	P		P	P	P	P	P	P	Δ	O	P	P	P	P		P	P	P	P	
Centric diatoms																						
Chaetoceros gracilis																						
Chaetoceros septentrionalis																						
Chaetoceros spp.																						
Cyclotella sp.																					P	
Leptocylindrus sp.																		P				
Melosira juergensii																						P
Thalassiosira gravida																						
Thalassiosira spp.				P			P								P		P		P			
Dinoflagellates																						
Amphidinium sp.													P				P				Δ	
Dinophysis arctica																						
Exuviaella sp.	P				P																	
Gymnodinium sp.															P							
Peridinium grenlandicum							P		P										P			
Flagellates																						
Dinema litorale																						
Euglena sp.																						
Eutreptiella sp.					P		P		P		P		P	P	P		P		P		P	
Platymonas spp.																			P			
Unidentified flagellates (> 6 μm)	x		x	O	O	O	O	P	P	P	O		O		Δ	P	x	P	x	O	x	

Table 12. (cont.)

	May										Jun									
	22		24		26		29		31		2		5		7		9		11	
Taxon	0	7	0	7	0	7	0	7	0	7	0	7	0	7	0	7	0	7	0	7
Pennate diatoms																				
Achnanthes taeniata			P	P			P													
Achnanthes sp.	P			P											P			P		
Amphiprora paludosa v. *hyperborea*	P			P																
Amphora ocellata	P	P		P			P		P	O	P		P		P	P	P	P	P	
Amphora sp.																				
Cylindrotheca closterium			P		P		P		P	P		P	P		O	P	x		x	P
Gomphonema exiguum v. *arctica*	P		P	P																
Gomphonema kamtschaticum													P							
Gyrosigma fasciola			P																P	
Gyro-Pleurosigma spp.	P	P	P				P			P	P	P	P	P	P	P	P		P	P
Licmophora sp.	P	P	P	P	P		P													
Navicula bolleana cf.	P	P	P	P		P	P			P			P		P		P		P	P
Navicula directa	P	P	P	P			P		P		P	P	P	P	P	P	O	P	P	P
Navicula kjellmanii																				
Navicula lyroides	P																			
Navicula maculosa	P																			
Navicula marina	P	P	P																	
Navicula pelagica																			P	P
Navicula spicula	P	P		P	P	P	P		P	P	P		P	P	O		P	P	P	P
Navicula transitans v. *derasa*	P	P		P	P		P			P	P		P	P	P		P	P	P	P
Navicula trigonocephala	P																			P
Navicula valida	P	P																	P	
Navicula sp. A																				
Nitzschia angularis	P														P				P	
Nitzschia cylindrus	Δ	Δ	Δ	P	Δ	P	O			O	Δ	P	x	O	Δ	P	Δ	P	Δ	Δ
Nitzschia frigida	P		P										P		P	P	O		P	P
Nitzschia seriata			P	P			x								P					

Table 12. (cont.)

	May										Jun									
	22		24		26		29		31		2		5		7		9		11	
Taxon	0	7	0	7	0	7	0	7	0	7	0	7	0	7	0	7	0	7	0	7
Nitzschia sigma cf.																	P		P	
Nitzschia sigmoidea												P		O						
Nitzschia sp. A			P																	
Nitzschia sp. B	P		P	P																
Pinnularia quadratarea v. *kerguelensis*	P	P	P									P			P		P		P	P
Pinnularia quadratarea v. *theelii*																			P	
Pseudonitzschia delicatissima	P	P	P		P	P							P		P		P		O	P
Rhoiconeis sp.	P																			
Stauroneis quadripedis																				
Stauroneis sp.																				
Synedra sp.	P		P						P						P	P	P	P	P	
Thalassiothrix spp.	P		P				P								P	P				
Unidentified pennate diatoms	x	x	P	P			P	P	P	P	Δ	P	O	P	P	x	x	P	P	Δ
Centric diatoms																				
Chaetoceros gracilis							P													
Chaetoceros septentrionalis									O											
Chaetoceros spp.	P						P			Δ					P					
Cyclotella sp.																				
Leptocylindrus sp.																				
Melosira juergensii				P						P									P	
Thalassiosira gravida	P		P		P		P		P		x		O		P	P	P	P	P	P
Thalassiosira spp.	P								P						P				P	
Dinoflagellates																				
Amphidinium sp.	O				P				O		x		P		P					
Dinophysis arctica													P							
Exuviaella sp.													P		P					
Gymnodinium sp.					P															
Peridinium grenlandicum	P												P		P		P		P	P
Flagellates																				
Dinema litorale				P	P										P				P	
Euglena sp.													P		P		P			
Eutreptiella sp.	P		P						P											
Platymonas spp.			P				P		P		O		Δ		Δ		x			
Unidentified flagellates (> 6 μm)	O	P	x	O	P	P	O	P	O	P	x	P	x		x		Δ		x	

column that were not found in the ice algae samples. Four of these species were centric diatoms, *Chaetoceros gracilis*, *Cyclotella* sp., *Leptocylindrus* sp., and *Melosira juergensii*; and a dinoflagellate, *Exuviella* sp. was also found exclusively in the phytoplankton.

Most of the cells found in the water column appear to have originated in the ice. About 50% of the cells in the samples were empty frustules, and many others appeared to be unhealthy, and were often heavily parasitized. *Nitzschia cylindrus* was present in low numbers during April, but became the dominant diatom species during most of May and early June. This was also the dominant species in the ice algal community. In the water column, however, the cells did not appear to be healthy, and had probably fallen from the ice.

3. Benthic microalgae

Cells in seven sediment cores were enumerated and 18 taxa, including 10 species were identified (Tables 13-14). An additional 12 taxa with eight species were identified from empty frustules, but were not represented by living cells. This community consisted almost exclusively of pennate diatoms. The only centric diatom found was a single resting spore of *Chaetoceros* sp. *Dinema litorale* was the only flagellate identified.

Although we were unable to identify the majority of the species present, they were clearly not the same species found in the ice or water column. *Cylindrotheca closterium*, *Navicula cancellata*, *N. directa*, *N. spicula*, *N. transitans* var. *derasa*, *Nitzschia angularis*, and *N. cylindrus* occurred in both the ice and sediments, but comprised a small minority of the cells present in the sediments. *Nitzschia cylindrus*, the dominant species of the ice and water column, was represented by a single pair of cells, that were found near the end of the ice algal bloom and probably had fallen from the ice; they appeared to be unhealthy. Of the taxa represented only by empty frustules, all were members of the ice algal community and probably originated there.

4. Zooplankton

Thirty-two categories including 25 species and seven other categories where identification was made to genus or other higher taxonomic rank, were identified (Table 15). Relative abundance and distribution through time are given in Tables 16a-16b.

Pseudocalanus elongatus was the most common animal in spring 1980. It was present primarily as stages IV, V, and VI males and females with a few younger stages also being present. Other copepods common during this period included *Acartia longiremis* adult males and females; some adult *Pseudocalanus major*, and *Eurytemora herdmani*. Adult *Oithona similis* were present in late May and June. Harpacticoid copepods became more abundant in May and June, including *Harpacticus superflexus* adults and juveniles, and *Helectinosoma neglectum* adults.

Hydrozoans were present throughout the spring, including the meroplanktonic species *Euphysa flammea* and *Halitholus cirratus*, and the holo-

Table 13. Benthic microalgae species collected off Narwhal Island, spring 1980.

Pennate diatoms
- *Achnanthes* sp.
- *Amphora* sp.
- *Cylindrotheca closterium* (Ehrenberg) Reimann & Lewin
- *Diploneis smithii* (de Brébisson) Cleve
- *Diploneis* sp.
- **Gomphonema exiguum* var. *arctica* Grunow
- **Gomphonema kamtschaticum* Grunow
- **Gyrosigma fasciola* (Ehrenberg) Cleve
- **Gyro-Pleurosigma* spp.
- *Navicula cancellata* Donkin
- *Navicula cancellata* var. *skaldensis* Van Heurck
- *Navicula directa* (W. Smith) Ralfs in Pritchard
- **Navicula gracilis* Kützing
- **Navicula peregrina* (Ehrenberg) Kützing
- *Navicula spicula* (Hickie) Cleve
- *Navicula transitans* var. *derasa* (Grunow) Cleve
- *Nitzschia angularis* W. Smith
- *Nitzschia cylindrus* (Grunow) Hasle
- **Nitzschia frigida* Grunow
- **Pinnularia quadratarea* (A. Schmidt) Cleve
- *Stauroneis* sp.
- *Synedra* spp.
- Unidentified tube-forming species
- Unidentified pennate diatoms

Centric diatoms
- **Chaetoceros* sp.
- *Chaetoceros* sp. resting spore
- **Coscinodiscus radiatus* Ehrenberg
- **Thalassiosira* sp.

Flagellates
- *Dinema litorale* Skuja

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* empty frustules only

Table 14. Relative abundance and distribution through time of benthic microalgae species from seven sediment cores collected off Narwhal Island, spring 1980. P = present (< 1%); O = common (1-5%); x = abundant (5-10%); Δ = dominant (> 10%). * indicates only empty frustules present.

	Apr						May				
Taxon	10	14	17	19	24	29	2	5	8	15	20
Pennate diatoms											
Achnanthes sp.							x		P		
Amphora sp.											
Cylindrotheca closterium											
Diploneis smithii			x								
Diploneis sp.											
*_Gomphonema exiguum_ v. _arctica_											
*_Gomphonema kamtschaticum_											
*_Gyrosigma fasciola_											
*_Gyro-Pleurosigma_ spp.											
Navicula cancellata			Δ	Δ			Δ		O		
Navicula cancellata v. _skaldensis_			P				P				
Navicula directa			P								
*_Navicula gracilis_											
*_Navicula peregrina_											
Navicula spicula											
Navicula transitans v. _derasa_			P	P			P				
Nitzschia angularis				P							
Nitzschia cylindrus											
*_Nitzschia frigida_											
*_Pinnularia quadratarea_											
Stauroneis sp.			P								
Synedra spp.											
Unidentified tube-forming species											
Unidentified pennate diatoms			Δ	Δ			Δ		Δ		
Centric diatoms											
*_Chaetoceros_ sp.											
Chaetoceros sp. resting spore			P								
*_Coscinodiscus radiatus_											
*_Thalassiosira_ sp.											
Flagellates											
Dinema litorale									P		

Table 14. (cont.)

	May					Jun				
Taxon	22	24	26	29	31	2	5	7	9	11
Pennate diatoms										
Achnanthes sp.	O									
Amphora sp.							P			
Cylindrotheca closterium				P						
Diploneis smithii	O						O			
Diploneis sp.	O									
**Gomphonema exiguum* v. *arctica*										
**Gomphonema kamtschaticum*										
**Gyrosigma fasciola*										
**Gyro-Pleurosigma* spp.										
Navicula cancellata	x			Δ			Δ			
Navicula cancellata v. *skaldensis*	O						O			
Navicula directa										
**Navicula gracilis*										
**Navicula peregrina*										
Navicula spicula				Δ						
Navicula transitans v. *derasa*	O						P			
Nitzschia angularis	P									
Nitzschia cylindrus							P			
**Nitzschia frigida*										
**Pinnularia quadratarea*										
Stauroneis sp.										
Synedra spp.	P						P			
Unidentified tube-forming species							Δ			
Unidentified pennate diatoms	Δ			Δ			Δ			
Centric diatoms										
Chaetoceros sp.										
Chaetoceros sp. resting spore										
Coscinodiscus radiatus										
Thalassiosira sp.										
Flagellates										
Dinema litorale										

Table 15. Zooplankton species from samples collected off Narwhal Island, spring 1980.

- Cnidaria - Hydrozoa
  - *Aeginopsis laurentii* Brandt
  - *Euphysa flammea* (Linko)
  - *Halitholus cirratus* Hartlaub

- Ctenophora
  - *Pleurobrachia pileus* (O. F. Müller)

- Annelida
  - Polychaeta - unidentified larvae

- Echinodermata - unidentified pluteus larvae

- Arthropoda - Crustacea
  - Isopoda - unidentified larvae
  - Copepoda
    - Calanoida
      - *Pseudocalanus elongatus* (Boeck)
      - *Pseudocalanus major* G. O. Sars
      - *Pseudocalanus minutus* (Krøyer)
      - *Eurytemora herdmani* Thompson & Scott
      - *Eurytemora richingsi* Heron & Damkaer
      - *Metridia longa* (Lubbock)
      - *Acartia longiremis* (Lilljeborg)
    - Cyclopoida
      - *Oithona similis* Claus
      - *Cyclopina gracilis* (Claus)
      - *Cyclopina schneideri* T. Scott
    - Harpacticoida
      - *Harpacticus superflexus* Willey
      - *Helectinosoma neglectum* (G. O. Sars)
  - Mysidacea - unidentified species
  - Amphipoda
    - Gammaridea
      - *Anonyx nugax* (Phipps)
      - *Apherusa glacialis* (Hansen)
      - *Halirages mixtus* Stephensen
      - *Lagunogammarus wilkitzkii* (Birula)
      - *Onisimus litoralis* (Krøyer)
    - Hyperiidea
      - *Hyperia galba* (Montague)
  - Decapoda - unidentified Brachyura
  - Unidentified crustacean eggs

- Chaetognatha
  - *Sagitta elegans* Verrill

- Chordata - Larvacea
  - *Fritillaria* sp.
  - *Oikopleura labradoriensis* Lohmann
  - *Oikopleura vanhöffeni* Lohmann

Table 16a. Relative abundance and distribution through time of zooplankton taxa other than copepods collected off Narwhal Island, spring 1980; Samples collected with a 0.75 m ring net, mesh size 308 μm. Where no symbol is present, no animals were found. P = < 1000; Δ = 1001 - 5000; O = 5001 - 10000; x = > 10001; - = present, but not counted.

		Apr							May			
Taxon	T	10	12	14	17	19	24	29	2	5	8	15
Coelenterata - Hydrozoa												
Aeginopsis laurentii	P				Δ	P	P		P		P	P
Euphysa flammea	Δ	P		Δ	Δ	P	P	Δ	Δ	Δ		Δ
Halitholus cirratus	P	P		P	P	P	P			P	P	P
Ctenophora												
Pleurobrachia pileus						P						
Polychaeta - unidentified larvae	P	P			P	P	P	P		P	P	P
Arthropoda - Crustacea												
Isopoda												
Unidentified epicaridean parasite	P								P			
Unidentified larvae												
Mysidacea - unidentified species												
Amphipoda												
Gammaridea												
Lagunogammarus wilkitzkii			P									
Anonyx nugax	P											
Onisimus litoralis	Δ	Δ	Δ	P			P	P	P	P	P	P
Apherusa glacialis				P		P						
Halirages mixtus	P		P			P	P	O	P		P	P
Hyperiidea												
Hyperia galba												
Decapoda - unidentified species												
Unidentified crustacean eggs				-	-	-	-	-		-		
Echinodermata - plutei				Δ	P		x	x	x	x	x	x
Chaetognatha												
Sagitta elegans						P						
Chordata - Larvacea												
Fritillaria borealis			P	P	Δ	P						
Fritillaria sp.									P		P	Δ
Oikopleura labradoriensis					P				P	P	P	P
Oikopleura vanhöffeni												

Table 16a. (cont.)

Taxon				May						Jun		
	17	20	22	24	26	29	31	2	5	7	9	11
Coelenterata - Hydrozoa												
Aeginopsis laurentii		P	P	P		P	Δ	P	P	P		
Euphysa flammea	Δ	Δ	Δ	P	P	P	P	P	P	P	P	
Halitholus cirratus			P		P		P			P	P	
Ctenophora												
Pleurobrachia pileus			P					P				
Polychaeta - unidentified larvae	P	P	P	P	P	P	P	P	P	Δ		Δ
Arthropoda - Crustacea												
Isopoda												
Unidentified epicaridean parasite				P								
Unidentified larvae					P							
Mysidacea - unidentified species							P					
Amphipoda												
Gammaridea												
Lagunogammarus wilkitzkii					-							
Anonyx nugax												
Onisimus litoralis	P	P	P	P	P	P		Δ	Δ		Δ	P
Apherusa glacialis												Δ
Halirages mixtus	P	P	P	P				P	P	P	Δ	O
Hyperiidea												
Hyperia galba						P						
Decapoda - unidentified species									P			
Unidentified crustacean eggs												
Echinodermata - plutei	x	x	O	P	P	Δ	x	x	P	x		
Chaetognatha												
Sagitta elegans												
Chordata - Larvacea												
Fritillaria borealis					Δ	x	O	Δ	P	Δ		Δ
Fritillaria sp.	P	Δ	Δ	x								
Oikopleura labradoriensis	P		P	P		Δ	O	P		P		
Oikopleura vanhöffeni								P				

Table 16b. Relative abundance and distribution through time of copepods collected at Narwhal Island, spring 1980. Samples collected with a 0.75 m ring net, mesh size 308 μm. Where no symbol is present, no animals were found. P = < 1000; Δ = 1001 - 5000; O = 5001 - 10000; x = 10001 - 20000; ● = 20001 - 50000; + = > 50000.

Taxon			Apr								May			
			T	10	12	14	17	19	24	29	2	5	8	15
Calanoida														
Pseudocalanus elongatus	VI	m	P		P	P					P	P		O
		f	P	P	P	P		Δ	Δ	P	P	P		Δ
	V	m	●	Δ	Δ	x	x	+	+	Δ	●	●	●	●
		f	O	P	P	Δ	Δ	Δ	x	P	O	x	O	x
	IV	m	+	Δ	Δ	x	●	O	O	Δ	●	●	●	●
		f	●	Δ		Δ	x	x	x	Δ	●	x	x	●
	III	m												
		f											P	Δ
	II													Δ
	I													P
Pseudocalanus major	VI	m	Δ								P	P	Δ	
		f							Δ					P
Pseudocalanus minutus	VI	m												
		f												
	V	m												
		f												
Eurytemora herdmani	VI	m												P
		f												
	V	m								P		P		
		f									P	P	P	
	IV	m												
		f												
Eurytemora richingsi	V	m		P										
		f												
Metridia longa	V	m												
		f												
	III	m												
		f												
	II				P	P			P		P			

Table 16b. (cont.)

Taxon				Apr							May			
		T	10	12	14	17	19	24	29	2	5	8	15
Acartia longiremis	VI m	P						Δ	P	P	P	P	Δ
	f	P	P		P	P		Δ	P	Δ	P	P	O
	V m												
	f		P		P	P		P	P			P	P
Cyclopoida													
Oithona similis	VI m												
	f												
Cyclopina gracilis	VI m												
	f												
Cyclopina schneideri	VI m												
	f												
Harpacticoida													
Harpacticus superflexus	VI m											P	P
	f												
	juveniles			P									P
Helectinosoma neglectum	VI m												
	f												
	juveniles								P				

Table 16b. (cont.)

Taxon						May						Jun		
			17	20	22	24	26	29	31	2	5	7	9	11
Calanoida														
Pseudocalanus elongatus	VI	m	O	Δ	+	●	+	x	x	O	Δ	P	Δ	Δ
		f	P	Δ	●	x	●	x	x	x	Δ	Δ	Δ	●
	V	m	●	●	+	+	+	●	x	x	Δ	P	Δ	Δ
		f	●	x	+	+	+	+	●	●	O	Δ	O	x
	IV	m	x	O	+	●	+	O	Δ	Δ	P	P	Δ	Δ
		f	●	x	+	+	+	●	x	●	Δ	P	Δ	O
	III	m		P		Δ				P			P	x
		f												
	II				x	x	●	Δ	Δ	Δ	P	P		O
	I				Δ			P				P		
Pseudocalanus major	VI	m												
		f	P	P		x								
Pseudocalanus minutus	VI	m												
		f	P	P					P					
	V	m							P					
		f												
Eurytemora herdmani	VI	m		P										
		f							P		P		P	P
	V	m												
		f												
	IV	m												
		f												P
Eurytemora richingsi	V	m												
		f												
Metridia longa	V	m												
		f						P						
	III	m												
		f								P	P			
	II													

Table 16b. (cont.)

Taxon						May						Jun		
			17	20	22	24	26	29	31	2	5	7	9	11
Acartia longiremis	VI	m	Δ			Δ			P			P		
		f	Δ	Δ			Δ	Δ	P		P	P	P	
	V	m	P											
		f												
Cyclopoida														
Oithona similis	VI	m		P				P	P		P	P	P	
		f												
Cyclopina gracilis	VI	m										P		
		f												
Cyclopina schneideri	VI	m										P	P	
		f												
Harpacticoida														
Harpacticus superflexus	VI	m		P	Δ		Δ		Δ	P	Δ	O	●	●
		f							x		P	Δ	x	+
	juveniles			P		Δ		P	P		Δ	O	●	●
Helectinosoma neglectum	VI	m								P	P	Δ	P	
		f								P	P	P	P	P
	juveniles										P	P		

planktonic species *Aeginopsis laurentii*. Polychaete larvae were always present, as well as echinoderm plutei, indicating reproduction of these benthic groups. Unidentified crustacean eggs were present during late April.

The amphipods *Onisimus litoralis* and *Halirages mixtus* were common throughout the spring. Present on occasion were *Lagunogammarus wilkitzkii, Anonyx nugax, Apherusa glacialis,* and *Hyperia galba.* The larvaceans *Fritillaria borealis* and *Oikopleura labradoriensis* were usually present.

5. Nutrients and salinity

The concentrations of inorganic plant nutrients are given in Table 7. Data from ice cores should be considered as minimum values because they were obtained from melted cores, that were diluted by an unknown amount from the melting ice.

Nitrate in the water column remained near 10 µg-at ℓ^{-1} throughout the study period, and was *ca.* 1 µg-at ℓ^{-1} higher at 7 m than at the surface (Fig. 10). This is comparable to levels found during the winter near Barrow (Matheke 1973) and near Prudhoe Bay (Horner *et al.* 1974). Water samples collected in Stefansson Sound during May 1979 had significantly less nitrate, *ca.* 1.5 µg-at ℓ^{-1} at the surface and *ca.* 4.5 µg-at ℓ^{-1} at 4 m.

In the ice, the nitrate concentration was approximately equal to surface water levels from April to mid-May. During the peak of the ice algal bloom, mid-May to early June, the concentration increased dramatically to 15-20 µg-at ℓ^{-1} for approximately two weeks, and then declined to previous levels. The source of this nitrate is not known, but may have resulted from brine drainage or microbial activity (Schell 1974). A similar pulse of nitrate was observed in the interstitial water of the sediments and in bottom water near Barrow (Matheke 1973).

Nitrite concentrations remained low and at nearly constant levels. Nitrite was highest in the ice, averaging 0.19 µg-at ℓ^{-1}, and lowest at 0 m, 0.08 µg-at ℓ^{-1}, while at 7 m, the concentration was intermediate, 0.13 µg-at ℓ^{-1}.

Ammonia was highest in the ice, *ca.* 1.2 µg-at ℓ^{-1}, and decreased with depth, averaging 0.14 µg-at ℓ^{-1} at 0 m, and 0.03 µg-at ℓ^{-1} at 7 m. A slight increase in ammonia concentration was seen in the ice during the peak of the ice algal bloom, and high levels, 4.33 µg-at ℓ^{-1}, were found near the end of the bloom on 9 June.

Phosphate concentrations were generally *ca.* 1.5 µg-at ℓ^{-1}, which is similar to winter levels reported from Point Barrow (Matheke 1973) and from Prudhoe Bay (Horner *et al.* 1974). No difference was seen between concentrations in the ice and water column. Several anomalous peaks in phosphate concentration, up to 25 µg-at ℓ^{-1}, were seen, but we have no explanation for these peaks at present.

Silicate concentrations were nearly constant, averaging 22 µg-at ℓ^{-1}

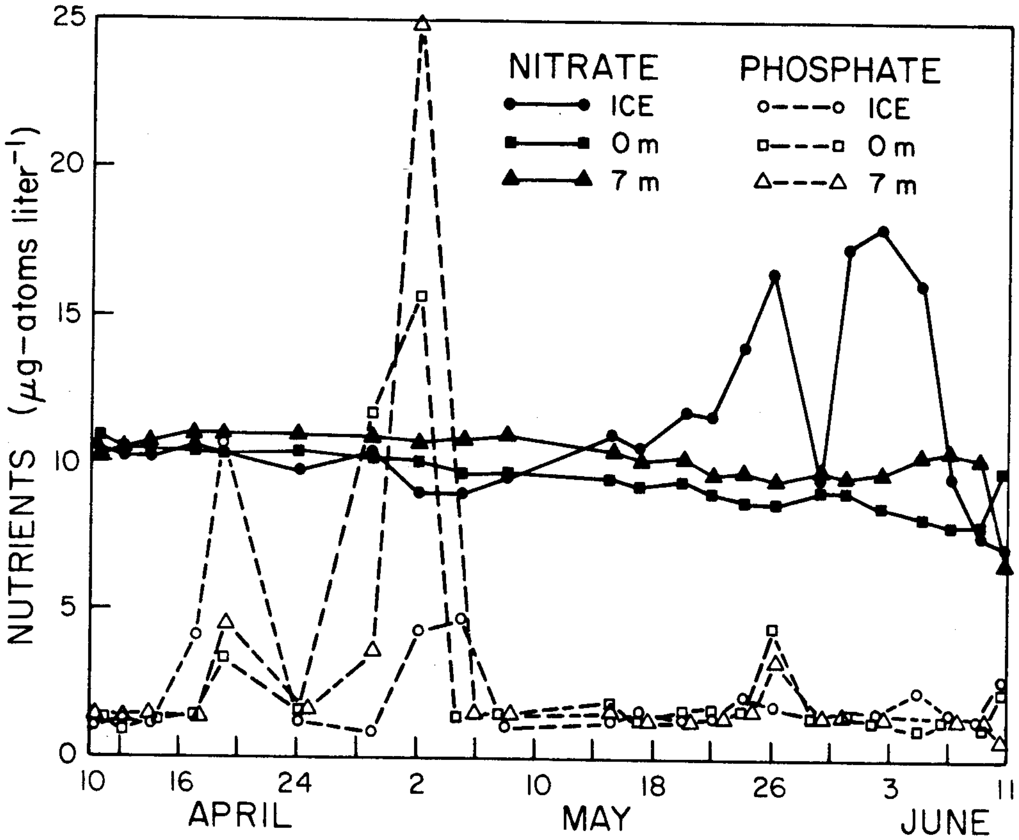

Fig. 10. Nitrate and phosphate concentrations (μg-at ℓ^{-1}) from ice cores and at 0 and 7 m in the water column, spring 1980.

in the ice and at the water surface, being only slightly higher, 24 μg-at ℓ^{-1}, at 7 m.

Salinity was *ca.* 34.5°/₀₀ at the surface, and increased by *ca.* 1°/₀₀ at 7 m (Table 7, Fig. 11). During the last two weeks of May, salinity dropped *ca.* 1°/₀₀, which may have been because of overflow from the Sagavanirktok River. Salinity increased slightly before dropping abruptly in June when the ice began to melt, causing the water column to become highly stratified, with over 10°/₀₀ difference between the surface and 7 m. Salinity in the ice was variable and somewhat lower than at the surface, probably caused by melting ice in the core samples.

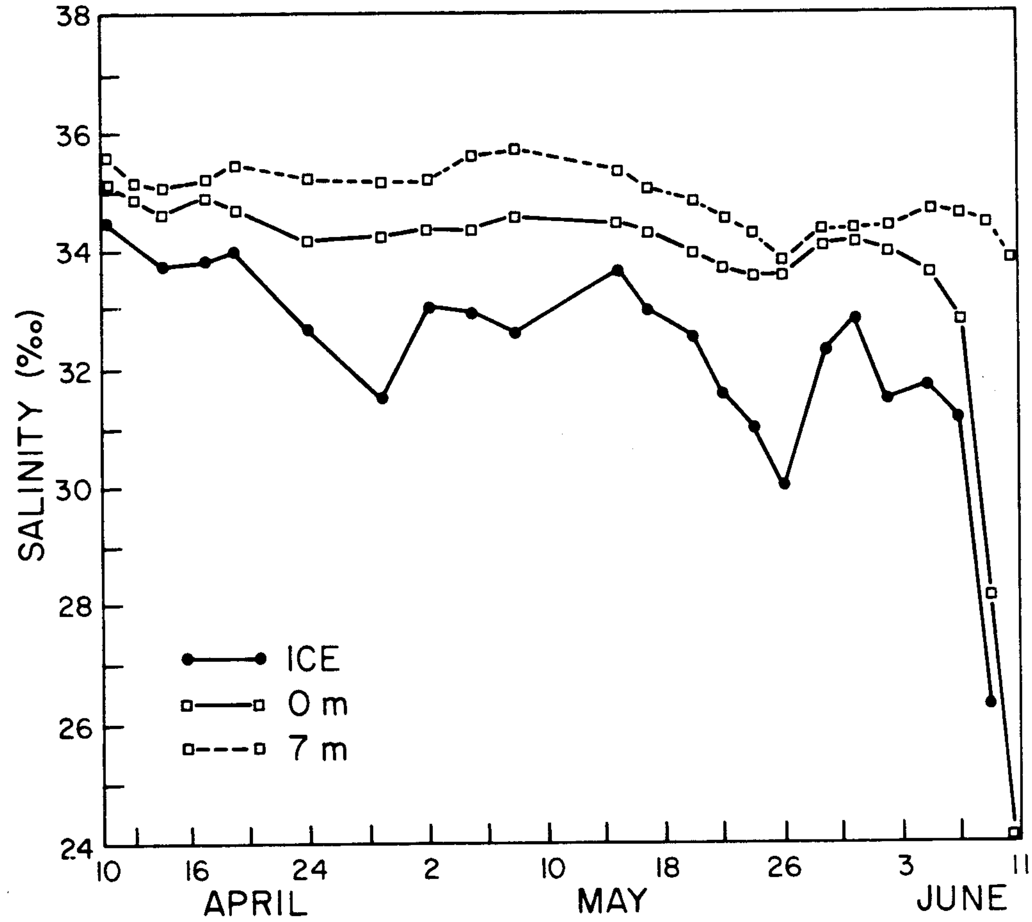

Fig. 11. Salinity (°/₀₀) from ice cores and at 0 and 7 m in the water column, spring 1980.

6. Light

Measurements of incident solar radiation (μE m^{-2} sec^{-1}) and light intensity in the bottom ice above the algal layer, and at 0 and 7 m are presented in Table 17. Light data before 2 May are not available because of a malfunction of the light meter.

Incident light, measured near local apparent noon, was variable and more a function of local weather than of the increasing elevation of the sun with time (Fig. 12). The average surface light intensity was lower during mid-May to early June.

Light penetrating the ice and reaching the top of the algal layer generally fluctuating between 0.5 and 1.5% of surface light during the period of snow cover (Fig. 13). After the snow cover melted (29 May), light levels increased sharply, fluctuating between 1.5 and 4% of surface values. In the water directly beneath the algal layer, 0 m, light levels generally fluctuated between 0.4 and 0.8% of surface light. Levels did not generally increase in response to decreasing snow cover, because of the shading effect of the growing ice algal layer. Light reaching the benthos was very low, remaining at *ca*. 0.2% of surface levels throughout the study. The highest light intensity recorded at 7 m was only 0.6% of the surface level.

In order to describe in more detail the effect of snow depth on subsurface light, a series of six transects was run: four through a snow drift that formed in the lee of the tent, and two directly over the area where primary productivity samples were incubated. The percentage of light transmitted through the ice and snow was measured before and after removal of the ice algal layer, in snow depths ranging from 0-40 cm (Appendix II-4). Given a constant or zero snow depth, light reaching the underside of the ice varied by as much as a factor of 2. The extinction coefficient and percentage of surface light transmitted through the ice and snow are listed in Table 18. Only 3-4 cm of snow was required to reduce light reaching the underside of the ice to < 1%; 6 cm reduced light to 0.5%; and 20 cm reduced light to < 0.1% of surface levels. An inverse relationship was found between snow depth and light attenuation by the algal layer, indicating decreasing algal growth with increasing snow depth.

Table 17. Light intensity, percentage of surface light, and snow depth off Narwhal Island, spring 1980. Data are the average of measurements taken at the beginning and end of primary productivity experiments.

	$\mu E\ m^{-2}\ sec^{-1}$				Percent Surface			Snow Depth
Date	Surface	Ice	0 m	7 m	Ice	0 m	7 m	(cm)
May 2	1125	7.4	5.8	2.4	0.7	0.5	0.2	6.0
5	1075	15.3	9.6	2.2	1.4	1.0	0.2	3.5
6	1385	13.6	12.7	2.5	0.9	0.8	0.2	3.0
8	1375	7.2	10.9	3.3	0.5	0.8	0.2	2.0
15	1275	8.4	4.8	1.7	0.6	0.4	0.1	3.0
17	1250	9.3	4.9	2.1	0.7	0.5	0.2	2.5
19	1350	15.8	9.3	3.1	1.2	0.7	0.2	2.5
20	1035	15.0	7.1	2.4	1.5	0.7	0.2	2.0
22		14.0	9.4		1.1	0.7		3.0
26	1265	10.5	4.4	2.6	0.9	0.4	0.2	1.0
29	1110	19.3	8.8	6.5	1.7	0.8	0.6	0.0
31	835	16.6	7.9	2.3	2.0	0.9	0.3	0.0
Jun 2	1165	21.4	5.8	2.3	1.9	0.5	0.2	0.0
3	1130	16.1	3.9	2.1	1.4	0.3	0.2	0.3
5	975	13.3	5.9	1.4	1.3	0.6	0.1	0.0
7	885	32.4	18.9	2.9	4.0	2.7	0.3	0.0
9	1235	22.3	4.9	3.0	1.8	0.4	0.2	0.0
11	1175	33.7	18.1	2.7	2.8	1.5	0.2	0.0

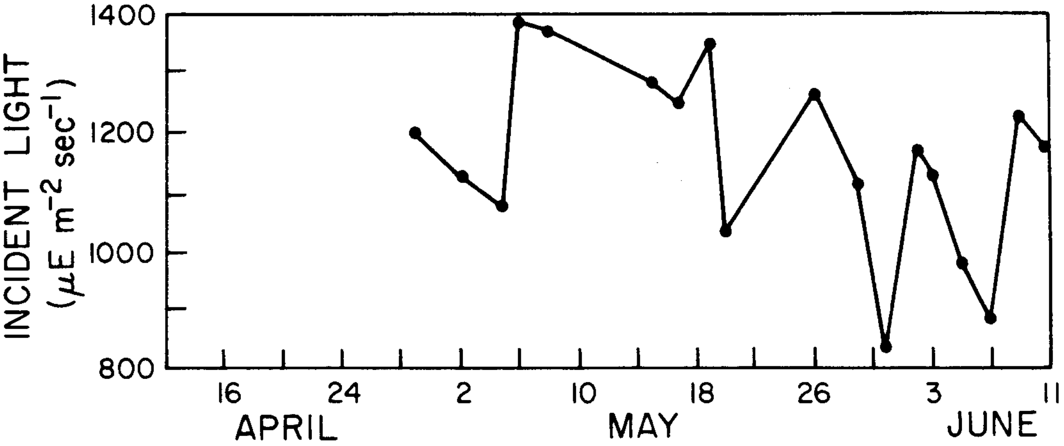

Fig. 12. Incident light intensity (μE m^{-2} sec^{-1}) measured near local apparent noon, spring 1980.

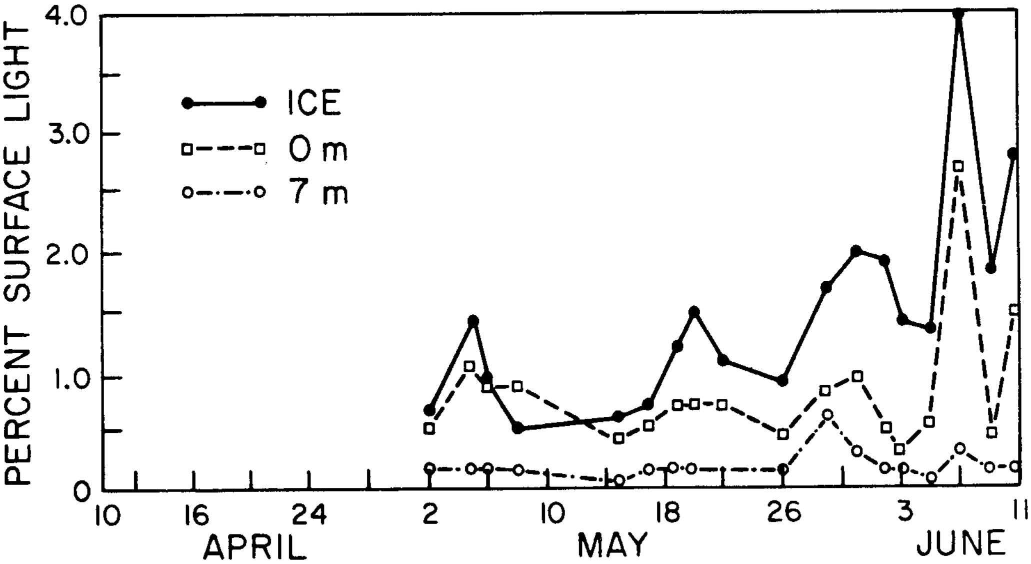

Fig. 13. Percent surface light reaching the ice algal layer and at 0 and 7 m in the water column, spring 1980.

7. Surface weather observations

Surface weather and snow observations are listed in Appendix II-1.

Air temperatures in early April were generally -10 to -20°C, and gradually increased, so that by 24 May, the air temperature was about equal to the surface water temperature, -1.8°C. The highest air temperature was 9.5°C, recorded during a period of clear, calm weather on 9-11 June.

Snow depth was generally 2-5 cm with drifts to 50 cm. Drifts formed at the north and south ends of the tent, but samples were collected in areas free of drifts. The snow began to melt on 26 May and had completely disappeared and melt ponds had begun to form by 29 May. By 9 June, the top of the ice was melting rapidly and the dive hole had become a major drainage point for meltwater.

Sea ice was accreting during most of the study period. The ice thickness was 169 cm on 24 April, and had increased to a maximum of 178 cm on 2 June.

The sky was generally overcast during the study period, and winds were typically 10-20 kt, from 030° magnetic. Blowing snow and fog were common and helicopters were often grounded because of poor visibility. This restricted sampling to periods of clearer weather.

Table 18. Snow depth, mean extinction coefficients (k_{m-1}), and percent surface light for six transects taken during spring 1980. Light measurements were taken above the ice algal layer.

Snow Depth (cm)	Surface Light (%)	k (m^{-1})	Replicates (N)
0	2.10	0.99	21
.25 - .99	1.34	1.14	4
1 - 1.9	1.51	1.06	5
2 - 2.9	1.33	1.09	33
3 - 3.9	0.85	1.18	11
4 - 4.9	0.43	1.35	4
5 - 5.9	0.53	1.30	5
6 - 6.9	0.28	1.55	3
7 - 8	0.43	1.39	3
10 - 11	0.23	1.42	1
12 - 15	0.31	1.38	3
16 - 20	0.13	1.53	7
21 - 25	0.07	1.61	3
26 - 30	0.05	1.73	4
31 - 40	0.02	1.83	6
41 - 50	0.01		6

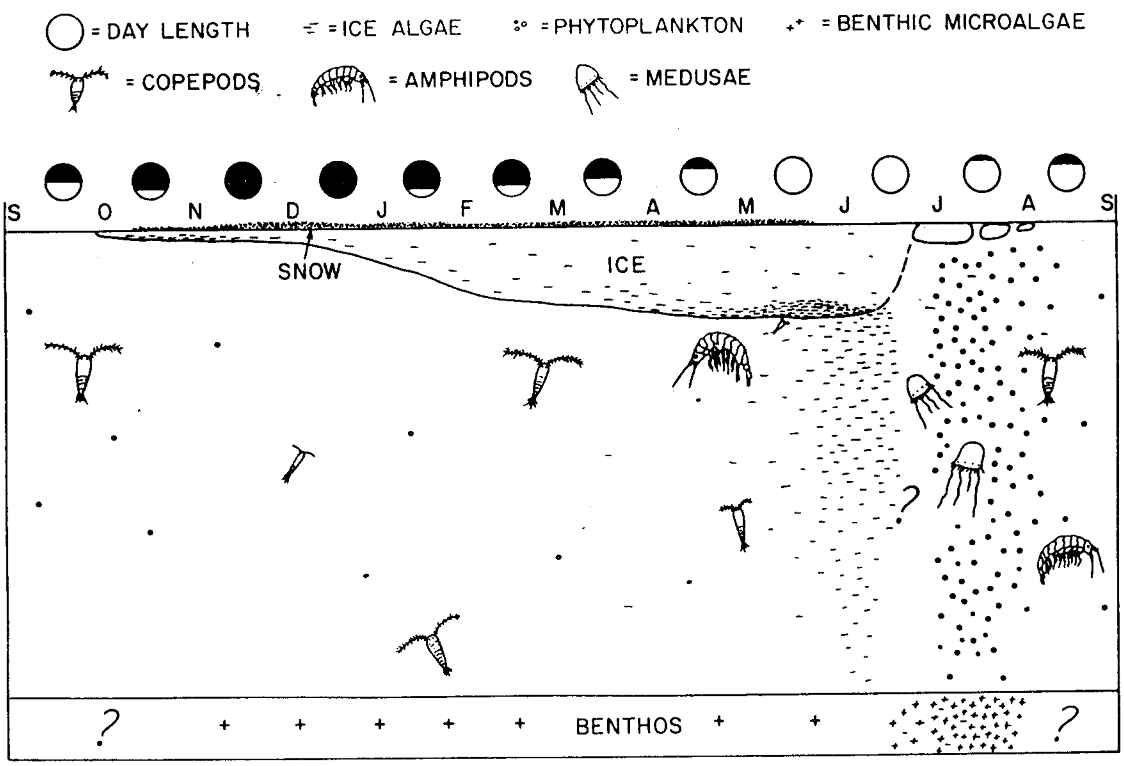

Fig. 14. Schematic representation of the annual cycles of ice algae, phytoplankton, benthic microalgae, and zooplankton in the nearshore area of the Beaufort Sea and Stefansson Sound.

VII. Discussion

Figure 14 is a schematic presentation of the annual cycle of ice algae, phytoplankton, benthic microalgae, and zooplankton for the nearshore area of the Beaufort Sea and Stefansson Sound.

A. Ice algae

Microalgae are present in the sea ice as soon as it forms in the fall with microflagellates being the most abundant organisms (Horner 1976). The origin of the cells is uncertain. Few species of ice algae are members of the fall phytoplankton community which is dominated by centric diatoms (Horner 1969), rather than the flagellates and pennate diatoms found in the ice. It is possible, however, that ice algae species are present in the water column in such low numbers that they are not collected by conventional sampling techniques. As the ice forms, algal cells become trapped in brine pockets and natural selection favors species adapted to this habitat.

Newly formed sea ice may also be seeded from ice algae still associated with drifting pack ice that persists throughout the summer. Meguro *et al.* (1966, 1967) reported a rich ice algal layer 5-30 cm thick in the soft bottom of pack ice off Barrow, Alaska, during July and August that contained species typical of the spring ice algal community (Horner and Alexander 1972). However, it is not known if cells persist in the drifting pack ice as late as freezeup. This mechanism of seeding may contribute to the observed patchy distribution of the ice algae.

Another possible source of seed stock for the ice algae may be from sediments that become resuspended during the fall storms in nearshore areas. However, although some species are common to both habitats, many species found in the ice, including several of the most abundant species, are not found in the sediments (Matheke and Horner 1974). This mechanism would only be operative in nearshore areas where resuspended sediments could reach the surface, or in areas where sediments may be advected by currents.

Growth of the diatoms in the ice in the fall probably continues until mid-November when light becomes limiting, although few reports are available to confirm this. Hsiao (1980) reported a layer of ice algae concentrated near the bottom of sea ice 50 cm thick in late November in the Eskimo Lakes region of the Canadian Arctic. In the western Beaufort Sea, a core taken on 9 November 1980 by RU 537 from our study area off Narwhal Island, contained a rich algal layer in the bottom ice, with diatom concentrations of 1.8 x 10^8 cells m^{-2}, which was comparable to levels found during the 1980 spring bloom. The cells were healthy, and the species composition was similar to that found in the ice the preceeding spring. An autumnal bloom has been reported to be a normal event in Antarctic sea ice (Hoshiai 1977).

Heterotrophy has been suggested as a mechanism by which algae survive the prolonged darkness of Arctic winter (Rodhe 1955; Wilce 1967; Allen 1971). Experiments using a variety of labeled organic substrates and four species of algae isolated from Antarctic sea ice failed to show heterotrophic growth in the dark (Bunt and Lee 1972). They concluded that dark survival for many Antarctic species did not depend on external substrates. In the Arctic, Horner and Alexander (1972) found that heterotrophic metabolism by natural populations of ice algae was negligible, and assimilation of labeled organic substrates was almost exclusively by bacteria.

Recent work on dark survival has shown that many algal species maintain viability for long periods of total darkness. Antia (1976) tested the viability of 37 species of marine planktonic algae from 10 taxonomic classes. Most species maintained viability for 5-6 mo in media free of organic substrates at temperatures ranging from 2-20°C. Benthic species (pennate diatoms) were more resistant, with some species remaining viable for over one year and a few species for up to three years of darkness. At the low temperature, *ca.* -1.8°C, to which ice algae are adapted, metabolic requirements should be low and species should easily tolerate the 4-5 mo of darkness during the Arctic winter.

During the winter, cells are found scattered throughout the ice (Horner 1976; Hsiao 1980), but by mid-March, the algae become concentrated at the bottom of the ice. How the cells become concentrated is not known, but it may be the result of brine drainage and active migration of the algal cells through brine channels. Brine cells are small pockets of hypersaline water formed as salts are excluded during ice formation (Pounder 1965). These pockets migrate downward through the ice by diffusion and gravity. Brine drainage becomes more rapid as the ice warms in spring and microalgae living in the pockets are transported to the bottom of the ice. The diatoms, themselves, may assist this migration because many pennate diatoms are able to move with a slow, gliding movement.

Light is probably the major factor controlling the distribution, development, and production of the ice algal community with growth of the ice algae beginning in spring in response to increasing light. At Barrow, Alexander *et al.* (1974) measured rates of primary production at varying light intensities. Productivity remained < 0.1 mg C m^{-2} hr^{-1} until a threshold level was reached. Above this level, 2.3 and 9.3 $\mu E\ m^{-2}\ sec^{-1}$ in successive years, production was rapid. In Davis Strait, Maclaren Marex (1979) reported maximum productivity at 1.8 $\mu E\ m^{-2}\ sec^{-1}$, but their reported productivity was nearly always < 0.1 mg C m^{-2} hr^{-1}. Off Narwhal Island in spring 1980, productivity began to increase when the light level was 7.4 $\mu E\ m^{-2}\ sec^{-1}$, which is similar to the threshold levels reported by Alexander *et al.* (1974).

In nearshore areas, light may be severely limited by sediments trapped in the ice. In early April 1980, a series of ice cores collected with a SIPRE corer in Stefansson Sound revealed a layer or layers of sediment throughout the lagoon system, and no algal layer was detected. Divers sampled the boulder patch area of Stefansson Sound on 11 May and found only a trace amount of chlorophyll *a* at a time when productivity was high outside the lagoon. This is in contrast to 1979 when in the same area, the algal layer was well-developed, although patchy. Schell (1980a) reported that light attenuation by turbid ice was the controlling factor of ice algal development in Stefansson Sound. It appears that in shallow areas, the distribution of sediments in the ice may largely determine the extent of the ice algal layer, and thus, the spring productivity of the lagoon system.

Where ice does not contain sediment, light attenuation because of snow is the prime factor controlling the distribution and productivity of ice algae. The light attenuating property of snow is very high compared with that of clear sea ice (Thomas 1963). Off Narwhal Island we found that an average of 2% of surface light reached the algal layer when no snow was present, but that 3-4 cm of snow reduced light to < 1%, *ca.* 15 $\mu E\ m^{-2}\ sec^{-1}$; 6 cm to < 0.5%; and 20 cm to < 0.1%. Alexander *et al.* (1974) observed that patchy distribution of the ice algae was correlated with light attenuation due to snow, and found an inverse relation between chlorophyll *a* and snow depth. Transects through snow drifts off Narwhal Island showed the same relationship, with a decrease in the algal layer with increasing snow depth.

At Barrow, maximum productivity occurred at light levels of *ca.* 16-65 $\mu E\ m^{-2}\ sec^{-1}$ (0.3-1.2 ly hr^{-1}) (Alexander *et al.* 1974) and off Narwhal Island at 10-25 $\mu E\ m^{-2}\ sec^{-1}$. Productivity over the entire bloom period was *ca.* 5 g C m^{-2} at Barrow and only 0.7 g C m^{-2} off Narwhal Island. In both areas, productivity increased in response to increasing light levels and maximum productivity occurred after the snow had gone. The observed differences in productivity between the two areas was probably the result of different light levels caused by ice turbidity and snow, with light being more limiting off Narwhal Island.

During early development of the bloom off Narwhal Island, divers noted more algal growth near stalactites that form when brine drains down through vertical channels in the ice (R. Poirot, J. Dougherty pers. comm.). Lewis and Milne (1977) reported increased light levels in stalactites that apparently act as funnels for light penetrating the ice. The higher light levels, and perhaps the increased nutrient concentrations from brine drainage, appear to encourage algal growth which may provide a concentrated food source for grazing invertebrates. Amphipods have been reported living within the crystal structure of the stalactites (Lewis and Milne 1977; Dunton pers. comm.) and have remained at the site after the stalactites were removed, apparently taking advantage of the localized food source.

At the time of the spring ice algal bloom, nutrient concentrations at the water surface were high because of vertical mixing and regeneration during winter when plant utilization is low. Nutrient levels in the ice may be even higher than at the surface because of brine drainage and local recycling. That recycling of nutrients occurs is evidenced by the pulse of nitrate during the bloom (Fig. 10). Nitrate in the ice rose to nearly twice the surface water values and probably resulted from nitrification by the microbial population. Nitrification is the oxidation of ammonia, a product of animal metabolism, to nitrite and nitrate. The ammonia concentration was high during the bloom, which suggests heavy grazing pressure. In the bottom water, 7 m, ammonia remained near the limit of detection throughout the study period, suggesting the relative lack of animal activity at that depth.

River overflow may also have a significant effect on surface nutrient concentrations in the lagoon system. In May 1979, river overflow was evident by a lens of low salinity, nutrient-poor water just below the ice. Nitrate and phosphate concentrations in the surface water were about one-fourth the levels at 4 m. The silicate concentration was higher at the surface, reflecting the high levels of silicate in rivers draining into the Beaufort Sea (Hufford 1974b). Nutrients were probably not limiting, however, because productivity was equal to, or exceeded, productivity off Narwhal Island in 1980.

During the spring bloom off Narwhal Island, surface salinity was fairly constant, 34-35°/oo, until early June when melting ice and river runoff caused salinity to drop below 25°/oo. River runoff was detected *ca.* two weeks before the sea ice began to melt. The algal layer began to soften and dissociate from the harder bottom ice and was easily disturbed by bubbles from the diver's breathing apparatus. Several dominant ice algal species, such as *Nitzschia cylindrus* and *Navicula spicula* appeared to be unhealthy, and productivity dropped for about one week. These events also coincided with the disappearance of the snow and it is likely that increasing radiation contributed to the disintegration of the ice algal layer because of selective absorption by diatoms (Meguro *et al.* 1966, 1967).

Ice diatoms are able to withstand a wide range of salinity. Grant and Horner (1976) measured the salinity tolerance of four species of ice algae collected near Barrow and found rapid growth over a broad range of salinities from *ca.* 10-50°/oo. At *ca.* 60°/oo, growth was limited, and they suggested that high brine cell salinity may limit the upward penetration of ice algae into the sea ice. Schell (1980a, 1980b) suggested that surface water salinity over 40°/oo may have been partly responsible for low ice algal density in Simpson Lagoon when clear ice was present, but this seems unlikely in view of the salinity tolerances reported by Grant and Horner (1976) and because ice algae usually live in brine pockets in the ice.

Off Narwhal Island, the ice algae were associated with the bottom ice in a loose, slush layer for a week after the ice had begun to melt, but by 11 June, no layer was visible and the water was clouded with ice algae. Microscopic examination of cells from the water showed that they were not healthy and primary production in the water column was almost undetectable.

The fate of the ice algae in Stefansson Sound and off Narwhal Island is not known. No data are available after the ice algae leave the ice and there is no information for the period of ice breakup or for the spring phytoplankton bloom. The summer plankton situation near Prudhoe Bay (Horner *et al.* 1974) and beyond the 10 fm line (Horner 1981) have been documented. Perhaps the ice algae cells are rapidly dispersed in the water column and are not collected in water sampling bottles (Horner 1976). Many cells probably do not survive as already suggested. Some cells may settle to the bottom, but the dominant species from the ice are not the same as the dominant species from the benthos (Matheke and Horner 1974).

At Barrow, the ice algal bloom and the spring bloom in the water column are separated by species present and time. The ice community consists primarily of pennate diatoms (Horner and Alexander 1972; Alexander *et al.* 1974), while the spring phytoplankton bloom consists primarily of centric diatoms (Horner 1969). Only one species, *Nitzschia cylindrus*, is common in both the ice and water column communities. The ice algal bloom occurs in April and May, sometimes extending into early June, while the phytoplankton bloom does not start until ice breakup is underway and light is available to the cells in the water column. In shallow, coastal waters the phytoplankton bloom may be delayed somewhat by the low salinity of the water column caused by the melting ice.

Elsewhere, Saito and Taniguchi (1978) reported what they called "ice plankton," or species that probably grew in sea ice, in deeper water in the Bering and Chukchi seas during summer, but whether these cells remain viable and, if brought back into the surface water, they are able to seed new ice in the fall is not known. These authors, however, did not actually sample the ice to determine the species present in the ice.

The species composition of the ice algal community off Narwhal Island and in Stefansson Sound was similar to that reported from other areas of the Arctic (Meguro *et al.* 1966, 1967; Horner and Alexander 1972; Horner *et al.* 1974; Hsiao 1980). The community was dominated by pennate diatom species, and although centric diatoms and dinoflagellates occurred, they were represented by few species and were seldom abundant. Several identifiable flagellate species were present in low numbers, while unidentified flagellates were often abundant. A single pennate diatom, *Nitzschia cylindrus*, accounted for nearly 50% of the population off Narwhal Island. *Nitzschia frigida, Navicula directa, Navicula transitans, Cylindrotheca closterium,* and *Amphora ocellata* were also numerically important species.

Hundreds of diatom species have been identified from Arctic sea ice, but only a few species have been reported as dominant. Of 58 species enumerated from our samples, only six species ever accounted for more than 10% of the cells counted. Horner and Alexander (1972) found that *Nitzschia frigida* was usually the most abundant species at Barrow, but was apparently not found farther offshore by Meguro *et al.* (1966, 1967). It was often important in the community off Narwhal Island, in Stefansson Sound, and in the Canadian Arctic (Dunbar and Acreman 1980; Hsiao 1980). *Navicula marina* was also a prominent member of the community at Barrow, and was often the most abundant species (Alexander *et al.* 1974). This species was found in the community off Narwhal Island, but was never abundant.

Nitzschia cylindrus is frequently reported as a dominant ice algal species and has also been reported as a member of the summer phytoplankton community (Horner *et al.* 1974; Dunbar and Acreman 1980). It is difficult to identify accurately in routine counting and the taxonomy of this and closely related species has recently gone through several changes at the generic level, being transferred from *Fragilaria* Lyngbye, to *Fragilariopsis* Hustedt, to *Nitzschia* Hassall. *Nitzschia cylindrus* is easily confused with *N. grunowii*, which has also been reported as a dominant ice algal species (Horner 1976; Dunbar and Acreman 1980).

Changes in community structure accompanied the development of the bloom off Narwhal Island. During April and early May, the community was strongly dominated by *Nitzschia cylindrus*, but in mid-May this species became less healthy and empty frustules were common in the ice and water column. As the relative numbers of *N. cylindrus* declined, other diatom and flagellate species which had been rare or had not been identified previously became common, and the diversity of the community increased. An increase in standing stock (chlorophyll *a*) accompanied this shift in community structure.

Environmental factors may have contributed to these species changes. Light inhibition has been suggested as a factor limiting the ice algal bloom (Apollonio 1965) and it is possible that increasing light intensity resulting from snow melt may have favored more light adapted species. Salinity declined during the peak of the bloom and, although ice algae are known to tolerate a wide range of salinities (Grant and Horner 1976), the specific requirements of *Nitzschia cylindrus* are not known and the reduced salinity may have been more favorable to the development of other species. The nitrate increase at the same time may have favored species that prefer higher nitrate concentrations.

The development of the spring ice algal bloom off Narwhal Island is similar to that reported by Alexander *et al.* (1974) for the Chukchi Sea near Barrow, which is the only other study to include the complete cycle of the ice algal bloom. Algal biomass (chlorophyll *a*) off Narwhal Island exhibited the same bimodal distribution and timing, and reached comparable peak values. An early peak occurred in late April to early May during both studies, with high values of *ca.* 8 mg chlorophyll *a* m^{-2}. A later and maximum peak occurred at the end of May to early June with 26.5 mg Chl *a* m^{-2} reported at Barrow and 23 mg Chl *a* m^{-2} off Narwhal Island. Primary productivity followed a similar pattern in both studies, remaining relatively low until mid-May and climbing sharply to peak levels with a maximum during the last week of May. Total production for the bloom off Narwhal Island was about one-seventh that reported for Barrow and may have been due largely to lower light levels found off Narwhal Island.

Primary productivity was much lower at Narwhal Island than at Barrow, although both studies reported comparable levels of chlorophyll *a*. This suggests that it is misleading to compare or estimate productivity of different areas based only on measurements of chlorophyll *a*. The difficulties of trying to determine the carbon to chlorophyll ratio (F) used to convert chlorophyll *a* to algal carbon are well-known (Banse 1977). The most important environmental factors that affect this ratio include nutrient concentrations, light, and temperature in that order, but species differences and interactions between factors are also important (Banse pers. comm.). Direct chemical measurements of algal carbon in natural populations are difficult because of the presence of unknown quantities of zooplankton and detrital carbon; the use of glass fiber filters also overestimates algal carbon. There are seasonal variations as well, for example when nutrients are low, the ratio is high. Strickland (1960) thought that choosing conversion factors from environmental data could not be correct to better than a factor of 0.3 to 3 and this has not changed much (Banse 1977).

The carbon to chlorophyll ratio can also be estimated microscopically by counting and measuring cells, determining mass, and converting to algal carbon. This method has serious drawbacks, as well, including the enormous amount of time needed to count and measure cells, the problem of losing unknown numbers and kinds of cells when samples are preserved, and the problem of changes in carbon:cell volume ratio that depends on the growth conditions of the cells (see Banse 1977 for discussion and references).

It is difficult to compare rates of primary productivity measured off Narwhal Island with other areas of the Arctic because few measurements have been made and methods generally have been different. Schell (1980a, b) included a table comparing annual ice algae productivity for areas of the Bering, Chukchi, and Beaufort seas based on literature values from ^{14}C measurements (McRoy and Goering 1976; Alexander *et al.* 1974; Horner *et al.* 1974; Horner 1980) and values calculated from biomass (chlorophyll *a*) measurements. (The annual value of 24 g C m^{-2} from McRoy 1976 [should be McRoy and Goering 1976] should read 24 x 10^6 metric tons and is the calculated annual budget for the whole Bering Sea shelf.) This table suggests that our measured annual productivity off Narwhal Island, *ca.* 0.7 g C m^{-2}, is low when compared with other areas with the exception of Simpson Lagoon, calculated to be 0.18 g C m^{-2}.

Estimates of primary production based on direct ^{14}C measurements, reported from Arctic regions, are listed in Table 19. The highest production was reported from near Barrow and was 2-7 times higher than that from off Narwhal Island. In the Bering Sea and Davis Strait, production was lower than either Stefansson Sound or Narwhal Island by a factor of 10. The literature suggests that the algal production is high along the north coast of Alaska compared with the Bering Sea and Davis Strait, but only a few experiments have been done in most areas. Production off Narwhal Island and in Stefansson Sound was low when compared with Barrow, but relatively high in relation to other areas of the Arctic where primary productivity measurements have been made.

B. Phytoplankton

Phytoplankton was present in low numbers during the winter, with unidentified flagellates, mostly < 10 μm, being the most abundant organisms. By April, diatoms were more abundant, both in numbers and species, but microflagellates were still numerically dominant. Most of the

Table 19. Ice algal primary productivity measured by ^{14}C uptake experiments and chlorophyll *a* values from Arctic regions.

		Primary Productivity				
Location	No. Stations	(max) hr^{-1} (mg C m^{-2})	(max) day^{-1} (mg C m^{-2})	annual (g C m^{-2})	Chl *a* (max) mg m^{-2}	Source
Bering Sea	3		4.8	0.3 *	3.0	McRoy & Goering 1974
Davis Strait	11		2.4		0.8	MacLaren Marex 1979
Davis Strait	5		2.0	0.15	0.5	Andersen 1977
Barrow, Alaska	25	4.56	109 *		30.5	Clasby *et al.* 1973
Barrow, Alaska	15	14.92	358 *	5	23.0	Alexander *et al.* 1974
Stefansson Sound	4	1.50	36	0.9 *	3.0	Horner 1980
Narwhal Island	25	2.70	63	0.7	26.5	This study

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* Values calculated from data presented

diatoms were pennate species that had probably fallen out of the ice. Only a few centric diatom species were present, with *Thalassiosira gravida* becoming more common late in the spring. This species is often abundant during the spring bloom, but none of the other typical spring bloom species occurred during our sampling program.

Chlorophyll *a* was low, < 0.1 mg m^{-3}, during the winter, increasing to 1.4 mg m^{-3} on 11 June, the last sampling day. Phaeopigments were usually high, *ca.* 50%, suggesting that cells were either not photosynthetic, *i.e.*, the microflagellates, or not viable. Microscopic examination showed that many of the diatoms were in poor condition.

Primary productivity in the water column was low, usually < 0.1 mg C m^{-3} hr^{-1}; maximum ^{14}C uptake, only 0.42 mg C m^{-3} hr^{-1}, occurred at the surface on 7 June.

The spring bloom in the water column probably occurs during and just after ice breakup, but more information is needed during this period between the end of the ice algal bloom and breakup to determine the origin and timing.

C. Benthic microalgae

The annual cycle of benthic microalgae has been documented (Matheke and Horner 1974) for the nearshore area near Barrow. Growth was limited during the winter by low light levels, and productivity did not begin until the formation of melt ponds on the ice surface which, along with the disappearance of the ice algae, increased light transmission through the ice. Following breakup of the shorefast ice, benthic microalgae became the most important source of primary production in that nearshore ecosystem. Chlorophyll *a* concentrations were relatively high during the winter months when primary productivity was negligible, and the community was apparently able to survive long periods of darkness. Many of the same species were found in both the bottom ice and sediments, but some of the species in the ice, including several of the most abundant, were not found in the sediment either during or after the bloom in the ice. This suggests that ice algae probably do not contribute significantly to benthic productivity.

Our data agree with Matheke and Horner (1974). Benthic microalgae did not contribute significantly to primary productivity off Narwhal Island during spring. Productivity was limited by low light levels due to snow cover and by shading from the ice algal layer. Light levels remained low, even after melt ponds had formed and the ice algal layer had dissolved, because of shading from algae suspended in the water column. Although productivity was extremely low, chlorophyll *a* concentrations in the sediments were relatively high throughout the spring and increased during maximum development of the ice algal bloom from algal material falling from the ice. The benthic microalgal community contained a distinct flora, dominated by species not found in the ice algal community. Few ice algal species occurred in the sediments, and most were dead or in poor condition. The most abundant species in the ice and water column, *Nitzschia cylindrus*, was represented in the sediments by a single pair of cells that had probably fallen from the ice. Some species, such as *Navicula directa, N. transitans,* and *Cylindrotheca closterium*, were members of both communities, and have also been reported from the sediments and ice at Barrow (Matheke and Horner 1974).

D. Zooplankton

Zooplankton species reported here are common inhabitants of the nearshore Arctic environment. Most have been reported previously in reports from RU 359 and other OCSEAP projects.

During the winter, copepods are by far the most abundant animals in the plankton. Most of the copepods in our winter samples were adults, although some stage II and III individuals of *Pseudocalanus elongatus* and *P. major* were present in November 1978.

In March 1979, young stages of *Calanus glacialis, Microcalanus pygmaeus, Pseudocalanus elongatus, P. major, Metridia lucens,* and *Oithona similis* were present, and early stages were often present, along with adults, as late as May. No really clear progression of stages occurred for any of the copepod species during the almost two years we sampled. Cairns (1967) suggested that *Pseudocalanus elongatus* may take two years to reach maturity, while Grainger (1965) thought *Microcalanus pygmaeus* and *Calanus glacialis* also took two years. This may also be the case with other copepods in our samples where there is no clear progression of stages.

Cyclopoid and harpacticoid copepods were most common in May with both juveniles and adults being present at the same time. *Oithona similis* juveniles and adults occurred in March 1979, as did adults of *Oncaea borealis*.

The most abundant copepod in our samples was *Pseudocalanus elongatus*. It is considered to be widespread in the temperate zone and at high latitudes, being abundant from the North Pacific to the North Atlantic. It is found in cold, surface waters and is more common nearshore where it can be an important food source for fish (Brodskii 1950). Two other *Pseudocalanus* species were identified: *P. major* is a neritic, strictly Arctic species found in less saline water (Brodskii 1950); while *P. minutus*, also known from neritic areas where the salinity is lower, is found from the North Pacific across the Arctic to the North Atlantic (Tidmarsh 1973).

Metridia longa is one of the three dominant copepods in the Arctic and Subarctic (Grainger 1962). It is reported to breed over an extended period in summer (Grainger 1959), but may start as early as March in some marginal areas. We found a few stage II's and III's and stage V females as early as April.

Acartia longiremis is a circumpolar Arctic species that is mostly neritic, but also occurs in surface water offshore. It is often found near melting ice (Johnson 1956). In our samples adults were found in Nov, Mar, Apr, May, and Jun, but were most abundant in Nov.

Two *Eurytemora* species were present in our samples. *Eurytemora* *herdmani* is a littoral species found in less saline water in the Bering Sea and along the Alaskan north coast (Brodskii 1950). Johnson (1956) thought it might be an expatriate from the Bering Sea, and Redburn (1974) found it at Barrow only when the surface water was > 7°C. *Eurytemora richingsi* was described from > 500 m in the central Arctic (Heron and Damkaer 1976), but it has also been reported from shallow water in the Beaufort Sea (English and Horner 1977).

The most common cyclopoid copepod in our samples was *Oithona similis*. Adults were present during all sampling times with stages III and IV present in March. *Oncaea borealis* adult males and females were present in March. Small numbers of other cyclopoids were present in May 1979 and June 1980. The May 1979 tow was a vertical one with the net lowered to the bottom in the Stefansson Sound boulder patch where attached macroalgae were present. The species present are often reported to be found attached to plants and that may account for their occurrence in this sample. The same is also true of the Harpacticoida that were common in the same sample. However, the same harpacticoid species were also present in horizontal net tows collected off Narwhal Island in May and June 1980 where there were no attached macroalgae.

The food habits of many copepods are incompletely known. Food preference is often suggested by the type of mouth parts present (Anraku and Omori 1963), however, recent studies seem to indicate that more than one feeding mode may be used (Heron pers. comm.). *Pseudocalanus* species are apparently filter-feeders, eating diatoms, small protozoans, and scraps of detritus. Deep water species in the same family, such as *Microcalanus pygmaeus*, are mixed feeders, being able to filter out food particles and also to selectively capture prey. They use plant, animal, and detrital foods (Arashkevich 1969; Harding 1974).

Size of food particles is also important. Hargrave and Geen (1970) found that adult *Pseudocalanus minutus* and *Oithona similis* preferred microflagellates in the size range 5-15 μm and microflagellates in this size range were present through the winter-spring period. Copepodids of *P. minutus* were opportunistic feeders and had a higher grazing and ingestion rate per unit body weight than older stages and fed continuously. Copepodids obtained more food on particles < 10 μm than did adults suggesting at least partially separate food niches (Poulet 1977).

Not all copepods utilize whole cells. Some cyclopoids are able to suck out cell contents and thereby make use of much larger cells than if whole cells had to be eaten (Kryuchkova 1974). The extent to which planktonic organisms use dissolved organic matter as food is not known. Perhaps its greatest importance is as a source of vitamins or growth substances (Kryuchkova 1974).

Amphipods and mysids are also important components of the nearshore ecosystem. Of these, *Lagunogammarus wilkitzkii* and *Apherusa glacialis* have been reported from the underside of the ice (Tencati 1970; Dunbar 1954), and *A. glacialis* has also been reported to be pelagic (Lewis 1969). Both are widespread, circumpolar species and generally occur in the upper 200 m. *Lagunogammarus wilkitzkii* produces one brood per year with eggs occurring in December, and some young still in brood pouches as late as June. The life cycle of this animal may be as long as six years, suggesting low production (Tencati 1970). *Apherusa glacialis* also breeds in the area, probably in January-February (Tencati 1970). Barnard (1959) suggested that Arctic cod may selectively feed on this species.

Onisimus litoralis is an abundant, shallow water species usually occurring in brackish water. It is probably near its southern limit of distribution in the Beaufort Sea (Dunbar 1954). *Anonyx nugax* is a circumpolar, Arctic-Subarctic species confined to shallow water on the shelf and extending into the North Sea and the Skagerak. It is a food species for ducks, cod, and bearded seals (Dunbar 1954).

Schneider and Koch (1979) discussed the feeding habits of some nearshore amphipods and mysids. They reported that most of the species studied ingested diatoms and peat, along with crustaceans and polychaetes. They found some suggestion of patterns of food selection, but all of the species studied appeared to be opportunistic feeders with deposit feeding being relatively important. These authors found a high proportion of benthic diatoms being utilized indicating that the benthic diatom community is an important food source for benthic and epibenthic animals, but also reported planktonic diatoms were eaten when they were available.

Hydrozoans became abundant in spring. They are probably not utilized as a primary source of food by other animals, but they do feed on copepods and other small invertebrates.

VIII. Conclusions

A. Ice algae are responsible for nearly all primary production during the winter-spring period, with only minimal contributions from the phytoplankton and benthic microalgae.

B. In addition to providing a rich food source for animals living in direct association with the bottom ice, ice algae provide a major source of living and detrital material for herbivores and detritivores living in the water column and benthos.

C. The ice algal community was composed primarily of pennate diatom species typical of the underice community in other Arctic regions.

D. The phytoplankton in early spring consisted almost entirely of ice algal species, most of which had fallen from the ice, and were not typical of species found during the spring and summer phytoplankton blooms.

E. The benthic microalgal community was composed mainly of species that were not found in the ice or water column. Although some species are common to both the ice and benthic microalgal communities, many ice algal species found in the sediments were unhealthy and had probably originated in the ice. More taxonomic work needs to be done on this difficult group. Using existing techniques, it is difficult to adequately separate algal cells from the sediments, and cell counts are semi-quantitative at best.

F. Copepods were the dominant taxonomic group of zooplankton during the winter-spring period, and are numerically the most important species in the area during the entire year.

IX. Needs for further study

We have documented the development of the ice algal bloom, and the relative contributions of the ice algae, phytoplankton, and benthic microalgae to primary production during much of the winter-spring period, and have gone far in elucidating the interrelationships of these communities. However, several questions remain to be answered.

A. There is a gap in our knowledge of the crucial period following dissolution of the ice algal layer in early June, leading up to the spring phytoplankton bloom after breakup.

1. What is the fate of the ice algae once they leave the ice? Are they rapidly consumed by zooplankton? Do they sink to deeper water? Are they incorporated into the sediments? Are they so diluted in the water column that we don't collect them by conventional sampling methods? Or, do many of the cells die in the low salinity water during ice melt with relatively rapid dissolution of the silica valves?

2. The spring phytoplankton bloom is composed of different species from those found in the ice and water column during the winter, and occurs after the end of the ice algal bloom. What is the origin of these cells? Are spores present in the sediments during winter that are able to germinate in spring in response to some environmental factor? What factors control this bloom?

B. In assessing the contribution of ice algae to the primary production of the nearshore ecosystem, we have concentrated efforts in the winter-spring period. There is evidence, however, that an ice algal layer also occurs in the fall. A sample of bottom ice collected in November 1980 near Narwhal Island contained an algal concentration comparable to that found during the preceeding spring ice algal bloom. Does production occur in the fall? What is the extent of the layer in fall, temporally and spatially? Is it a regular occurrence?

C. Small microflagellates < 6 μm in diameter are present, often in high numbers, in the ice and water column throughout the year. Many of them do not appear to be photosynthetic, and it is possible that they utilize dissolved or particulate organic material as an energy source. These organisms may be an important food source for grazers, and their role in the food chain dynamics of the nearshore ecosystem should be investigated.

D. The benthic microalgae were not very important in the nearshore area during the winter-spring period. At Barrow, however, production in this community in summer is high. Does the same thing happen in the nearshore Beaufort Sea? Does a mat of filamentous diatoms form in summer? Is this mat utilized as a food source by invertebrates?

E. Zooplankton are present all year round. What happens to the populations in summer? When do individual species breed? How long are individual life cycle stages? Do life cycles take more than one year? What food sources are being utilized? Do these sources change during the life cycle? During the year?

F. Perhaps the most critical need with respect to oil and gas development: what are the effects of oil, drilling muds, and other pollutants on the organisms that live in the ice, water column, and benthos? Would they be able to survive a major spill? Could they repopulate an area? How long would recruitment and repopulation take? How would the loss of primary producers at different times of the year affect consumers, particularly higher trophic levels?

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APPENDIX I

An Improved Chamber for in situ Measurement of Primary Productivity of Arctic Sea Ice Algae

G.C. Schrader[1], R.A. Horner[2], and G.F. Smith[3]

Schrader, G.C., R.A. Horner, and G.F. Smith. 1981. An improved chamber for in situ measurement of primary productivity of Arctic sea ice algae.

An incubation chamber was designed to measure rates of carbon uptake of microalgae growing on the underside of Arctic sea ice. SCUBA divers are used to place the chambers, which are secured to the ice with steel pins. The chambers were found to accomodate a wide range of ice conditions, and were superior to the core-liner type chambers used previously.

Key words: Arctic Ocean; Sea Ice Algae; Primary Productivity.

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An Improved Chamber for in situ Measurement of Primary Productivity of Arctic Sea Ice Algae[1]

The occurrence of algae growing in sea ice is a widewpread phenomenon which has been documented in both Arctic (Apollonio 1961; Meguro et al. 1967; Horner 1976; Alexander 1980) and Antarctic regions (Bunt and Wood 1963; Bunt and Lee 1970; Hoshiai 1977). In the Antarctic, Meguro (1962) described a community which occurs in snow that has been flooded by seawater. Hoshiai (1977) reported algae growing in two layers within the ice: an upper layer formed during early ice formation, incorporating components of the fall phytoplankton bloom, and a bottom layer formed on the underside of the ice in spring. The bottom layer is by far the most developed in both Arctic and Antarctic regions, and has been termed the "epontic" community by Bunt and Wood (1963). This community consists primarily of pennate diatoms and flagellates living attached to ice crystals and in brine pockets and interstitial water between crystals.

In the Arctic, little or no growth occurs during the dark winter months, but in the spring increasing insolation triggers a bloom which produces a golden-brown layer several centimeters thick on the underside of the ice. This layer typically persists until early June when the ice begins to soften and melt, and the algae are washed from the ice. During this period ice algal productivity may be quite high. Clasby et al. (1973) reported maximum rates of 4.56 mg C/m^2. hr near Point Barrow, Alaska, with productivity in the ice usually far exceeding that of the underlying water column (Alexander et al.1974). Although this high productivity is of relatively short duration, it is significant in that it extends the period of productivity in the Arctic by several months.

Attempts at measuring the rate of primary production of the ice algal community have employed a variety of strategies, all utilizing modifications of the ^{14}C method of Steemann Nielsen (1952). One approach has been to obtain a sample of the under ice community by coring through the ice from the surface. The lower portion of the core containing ice algae may then be sectioned off and either taken to the laboratory for incubation (Horner and Alexander 1972; Alexander *et al*. 1974) or placed in a chamber, inoculated with isotope, and incubated *in situ* under the ice (MacLAREN MAREX 1979). Ice many meters thick may be sampled from the surface in this manner.

A similar approach was used by Andersen (1977) in a frozen lead in West Greenland where the ice did not exceed *ca*. 40 cm thickness. Blocks of ice were cut and removed, and clear plastic chambers attached to the underside. After inoculation the blocks were replaced and incubated *in situ*. This method is limited however, to ice of less than *ca*. 0.5m thickness.

There are certain problems inherent with surface operated collection techniques which are difficult to overcome. When coring devices are used the delicate structure of the ice algal layer is disturbed, resulting in partial loss of sample and interstitial water. In addition, thermal and light shock are difficult to avoid when bringing the samples to the surface, and ambient conditions are difficult to duplicate in the laboratory.

SCUBA divers were first used by Bunt (1963, 1973; Bunt and Lee 1970) to sample the ice algal community in the Antarctic. Samples were collected by forcing a Van Dorn sampler through the soft ice matrix; incubation was done in the laboratory. This method, however, did not overcome many of the problems encountered with surface coring devices.

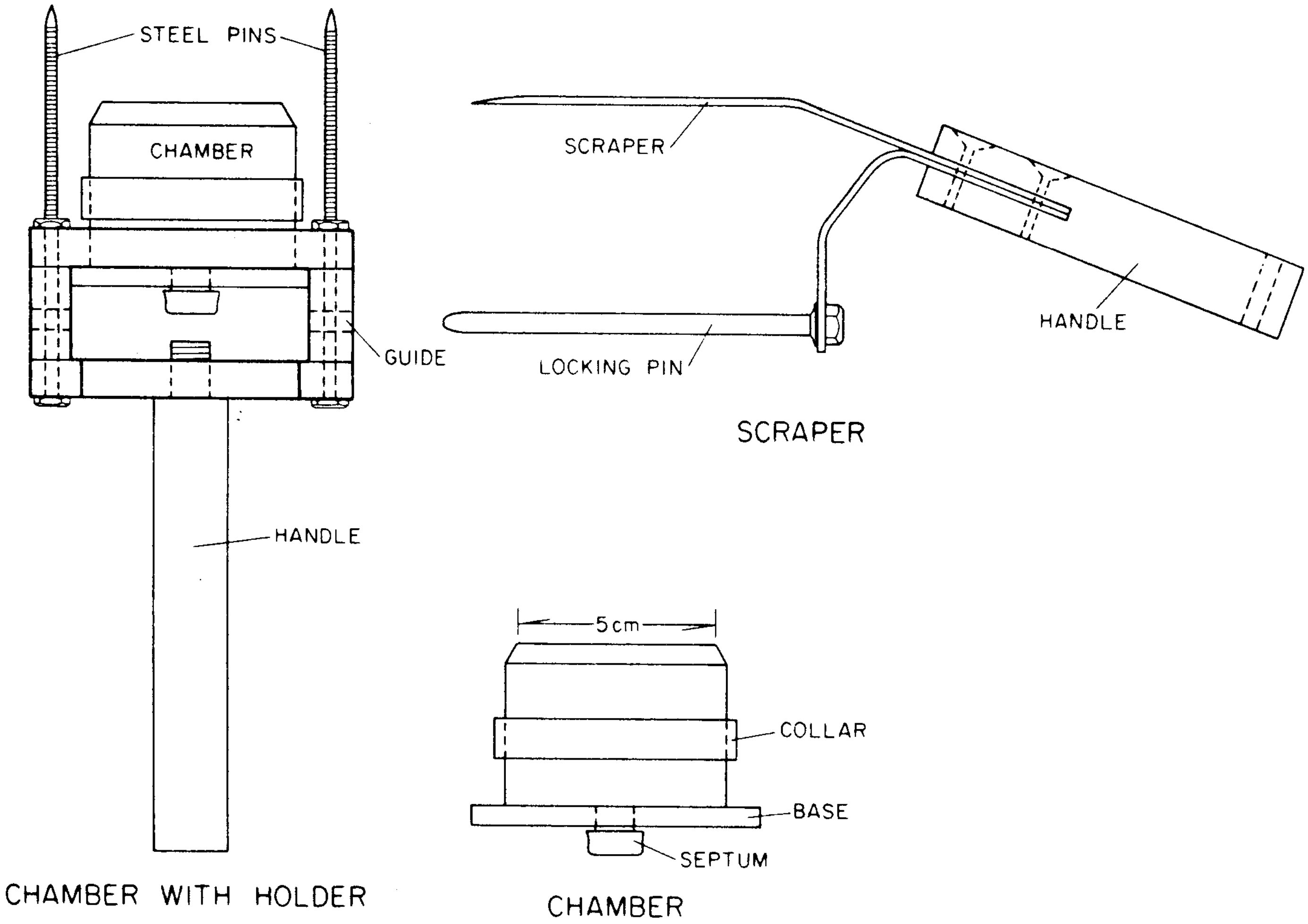
The need for a good *in situ* method for work in the Arctic prompted Clasby *et al*. (1973) to design a combined sampler-incubation chamber which could be operated by SCUBA divers. The chamber was constructed of 4.8 cm diameter plexiglass core tube lining 4 cm in length. One end was closed off with a plexiglass plate fitted with a rubber septum, and the top of the sampler was serrated to cut into the ice.

To place the chamber, a diver removed the septum, which allowed the water to evacuate, and screwed the sampler into the underside of the ice to a depth of 2 cm. The septum was then replaced and a syringe used to inoculate the chamber with ^{14}C-bicarbonate solution. After an appropriate incubation period a heavy metal spatula was used to chip away ice from around the chamber and then sever the top of the core. The sample was retained in the chamber by a core cap. Dark uptake rates were determined in a darkened chamber that was capped and suspended from ice pitons immediately following inoculation. The chamber was also used to collect samples for chlorophyll, standing stock, nutrient and other analyses.

Alexander _et al_. (1974) compared rates of primary productivity of Arctic ice algae determined by both the diver operated technique and surface core-culture chamber techniques, and found significantly higher apparent rates of carbon uptake with the _in situ_ method.

Although used successfully to measure primary productivity in sea ice near Point Barrow, Alaska (Clasby _et al_. 1973), we felt that the chamber should be redesigned to accomodate a greater range of ice conditions and to minimize sample loss during core extraction and capping.

Two new features were incorporated into the new chamber. The chamber was provided with a holder equipped with four threaded stainless steel pins adjusted to protrude approximately 2 cm from the chamber mouth (Fig. 1). The chamber could then be hammered into the ice where the pins would anchor it securely. In addition, a scraper was designed with a locking pin that fit into a guide in the holder. At the end of the incubation period, while the chamber is still anchored to the ice, the pin is started into the guide, and the core severed as the scraper is pushed into place, sealing the chamber mouth. The scraper is secured by a handle on the bottom of the holder which is screwed tightly against the pin. The chamber can then be returned to the surface with little sample loss. As an added precaution when



CHAMBER WITH HOLDER

SCRAPER

CHAMBER

Fig . 1. Ice algal incubation chamber.

returning the chambers to the surface, the scraper is held tightly over the chamber mouth to prevent leakage.

To measure dark uptake, a darkened chamber is hammered into the ice and the scraper inserted to enclose the ice sample prior to injecting the isotope. This allows the chamber to remain in place during the incubation period. As the added weight of the scraper has a tendency to pull the sampler from the ice, a donut-shaped float is placed over the handle of dark chambers to provide additional security.

The chamber is constructed of 5 cm inside diameter clear Lexan plastic tubing 4.5 cm high. The upper edge is beveled and the bottom glued to a square plastic base drilled to accept a serum bottle septum. The chamber is placed in its holder by dropping the base through a square opening and rotating 45 degrees. The holder provides support for the base of the chamber, and a tight fitting plastic collar is slipped over the outside of the chamber to keep it in place. The base of the holder is open to allow access to the septum for inoculation with a syringe. In practice, the chamber is rarely removed from the holder except for maintenance.

The scraper is constructed from stainless steel, with the blade sharpened and tempered to increase durability. A Lexan handle is attached at a 30 degree angle to provide clearance for the diver's hand when scraping the flat undersurface of the ice.

The new chambers were field tested in spring 1980 at a station approximately 25 km offshore from Prudhoe Bay, Alaska (ms in prep.). The ice was approximately 1.7 m thick. A variety of conditions were encountered on the underside of the ice during the two months the station was occupied. In April, when the ice was still rapidly accreting, the algae were associated with a layer of hard vertical platelets several centimeters deep. By early June, when the ice began to soften, the algae had formed a "slush layer" overlying harder ice. The new samplers performed satisfactorily under all conditions. They remained in place well and divers did not observe sample loss during extraction.

At intervals throughout the study we attempted to compare rates of primary production measured by both the older core liner type chambers (Clasby et al. 1973) and our new chambers. We were unsuccessful because the older style chambers would not remain in place in spite of numerous attempts by the divers. This clearly demonstrates the superiority of the new design, as the older chambers were totally ineffective in the ice conditions encountered during this study. The failure of the core liner type chambers to function during our study was surprising as they had been used successfully near Point Barrow, only a few hundred kilometers to the west. This suggests that there may be considerable year to year or regional variation in under-ice conditions in the Arctic.

Our sampler appears capable of accomodating a wide range of ice conditions, the major limitation being the depth of the layer of unconsolidated ice. The sampler will penetrate approximately 4.5 cm of unconsolidated ice, and is limited by the height of the chamber. By lengthening the chamber, pins, and scraper assembly, this design should work well in ice several times this depth. It is recognized however, that this chamber would have limited usefullness in the Antarctic, where the unconsolidated layer may be 1 m thick (Bunt 1963). Individual ice crystals are frequently very large and the introduction of a chamber would tend to interfere seriously with the integrity of the ice matrix.

Although we feel that our in situ chamber offers an improvement over previous methods, several problems have yet to be overcome before we feel that we can adequately assess rates of primary production in Arctic sea ice. As the ice algal layer is often formed of a matrix of ice crystals, it is difficult to insure adequate mixing of the isotope throughout the sample. The addition of a stirring apparatus to the chamber may prove worthwhile. However, artificial mixing would tend to destroy gradients which probably exist within the ice matrix and could affect carbon uptake rates. Also, due to the porous nature of the ice, an unknown amount of label may diffuse from the chamber during incubation. An estimate of this loss could be obtained by determining the total amount of isotope recovered at the end of the incubation period.

An additional problem is encountered when an area is sampled repeatedly by SCUBA divers. Exhaust air from the diver's breathing apparatus collects on the bottom of the ice leaving "pockmarks" or "craters", and divers have observed a reduction im algal growth in these craters. The use of a diving apparatus which would exhaust air directly to the surface would alleviate this problem.

These experimental problems lead to an underestimation of primary productivity of the ice algal community. It is therefore suggested that all such reported productivity data be considered as minimum values.

Acknowledgments

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APPENDIX II

Appendix Table II-1. Surface weather observations. All measurements were taken at *ca.* 1100. Where no number is present data were not available.

Date	Temp (°C) Air	Temp (°C) Water Sfc	Wind Speed (kt)	Wind Direction (° mag)	Weather	Cloud Type	Cloud Cover	Snow Depth (cm)	Ice Thickness (cm)
10 Apr	-22	-1.8	0		clear			5	
12	-19.5	-1.8	15	030	clear			5	
14	-18.2	-1.8	25	030	blowing snow			variable	
17	-15.2	-1.8	10-20	020	fog	broken		3	
19	-17.6	-1.8	20	020	clear			variable	
24	-14.7	-1.8	15-20	030	clear			5	169
28	- 9.4	-1.8	10-15	030	clear	stratus	10/10	2	
29	- 9.8	-1.8	10-15	040	clear	stratus	8/10	2-3	
2 May	- 8.5	-1.8	5	010	snow	stratus	10/10	6	
5	-11.0	-1.8	20	030	clear			3.5	
6	-11.5	-1.8	30	030	blowing snow			3	
8	-15.5	-1.8	20	030	clear	stratus/ cirrus	2/10	2	
15	- 6.0	-1.8	30	040	clear	stratus	10/10	3	
17	- 2.9	-1.8	20-30	050	clear	cirrus	3/10	2.5	176
19	- 7.5	-1.8	15	030	clear			2.5	
20	- 6.0	-1.8	5-10	030	snow	stratus	10/10	2	
22	- 6.2	-1.8	10-15	030	snow	stratus	10/10	variable	
24	- 2.0	-1.8	10-15	030	clear	stratus	10/10	2.5	
26	1.2	-1.8	20	035	clear	stratus	7/10	1	
29	0.0	-1.8	10-15	055	clear	stratus	5/10	0	
31	- 5.0	-1.8	15	030	clear	stratus	10/10	0	
2 Jun	1.0	-1.8	10	050	snow	stratus	6/10	0	178
3	- 0.5	-1.8	5	042	clear	stratus	6/10	0	
5	2.0	-1.8	0-5	090	rain	stratus	10/10	0	
7	2.0	-1.5	5	040	rain	stratus	10/10	0	
9	9.5	-1.5	0		clear		0/10	0	
11	9.5	0.0	0		clear	cirrus	3/10	0	

Appendix Table II-2. Concentration of microflagellates and diatoms in the ice and water column, Narwhal Island, spring 1980.

	0 m		7 m		Ice	
Date	Diatoms	Flagellates (Cells ℓ^{-1})	Diatoms	Flagellates	Diatoms	Flagellates (Cells m^{-2})
Apr 10	$3.4x10^4$	$2.0x10^5$	$2.5x10^3$	$6.0x10^4$	$1.7x10^8$	$5.8x10^7$
12		$1.9x10^5$		$1.3x10^5$		
14	$1.0x10^2$	$1.3x10^5$	$1.0x10^3$	$1.4x10^5$	$2.4x10^7$	$2.5x10^8$
17	$1.0x10^3$	$1.7x10^5$	$3.0x10^3$	$1.4x10^5$	$4.6x10^6$	$1.9x10^8$
19	$6.0x10^3$	$1.4x10^5$	$4.2x10^2$	$1.4x10^5$	$2.5x10^8$	$2.8x10^8$
24	$3.0x10^3$	$6.7x10^4$	$3.0x10^2$	$4.5x10^4$	$7.1x10^8$	$6.7x10^8$
29	$6.0x10^3$	$1.1x10^5$	$2.0x10^3$	$1.4x10^5$	$4.8x10^6$	$1.3x10^8$
May 2	$8.1x10^4$	$6.9x10^5$	$3.1x10^3$	$2.5x10^5$	$5.6x10^8$	$2.9x10^8$
5	$7.9x10^3$	$1.3x10^5$	$4.1x10^4$	$1.8x10^5$	$1.1x10^9$	$2.8x10^8$
8	$1.2x10^4$	$1.3x10^5$	$2.0x10^3$	$1.7x10^5$	$6.9x10^7$	$7.5x10^7$
15	$6.8x10^4$	$1.9x10^5$	$1.2x10^4$	$1.6x10^5$	$9.3x10^6$	$1.4x10^7$
17	$8.1x10^3$	$1.4x10^5$	$1.0x10^2$	$9.0x10^4$		
20	$2.5x10^4$	$1.5x10^5$	$3.0x10^3$	$1.9x10^4$	$1.6x10^8$	$7.9x10^7$
22	$3.3x10^4$	$1.2x10^5$	$1.9x10^4$	$4.8x10^4$	$7.9x10^8$	$5.8x10^8$
24	$1.7x10^4$	$1.5x10^5$	$6.0x10^3$	$7.4x10^4$	$8.2x10^8$	$5.0x10^8$
26	$1.4x10^4$	$1.1x10^5$	$1.0x10^3$	$2.9x10^4$	$1.0x10^9$	$7.9x10^8$
29	$1.8x10^4$	$1.0x10^5$	$2.0x10^3$	$1.0x10^4$	$8.5x10^8$	$7.5x10^8$
31	$8.0x10^3$	$6.0x10^4$	$1.0x10^4$	$1.3x10^4$	$1.2x10^9$	$2.0x10^9$
Jun 2	$1.5x10^4$	$9.0x10^4$	$3.0x10^3$	$2.7x10^4$	$8.5x10^8$	$9.2x10^8$
5	$3.6x10^4$	$2.3x10^4$	$6.0x10^3$	$2.3x10^3$	$6.7x10^8$	$9.9x10^8$
7	$5.9x10^4$	$1.3x10^5$	$8.0x10^3$	$7.0x10^3$	$6.6x10^8$	$1.6x10^9$
9	$2.4x10^4$	$6.6x10^4$	$3.0x10^3$	$7.0x10^3$	$1.1x10^9$	$1.0x10^9$
11	$1.6x10^5$	$1.5x10^5$	$3.0x10^4$	$6.8x10^4$	$7.0x10^6$	$8.7x10^6$

Appendix Table II-3. Concentrations of diatoms in the ice, water column, and benthos, Narwhal Island, spring 1980.

Date	Ice	Benthos	Water	0 m	7 m
		(Cells m^{-2})		(Cells ℓ^{-1})	
Apr 10	$1.7x10^8$		$1.2x10^8$	$3.4x10^4$	$2.5x10^3$
12					
14	$2.4x10^7$		$3.9x10^6$	$1.0x10^2$	$1.0x10^3$
17	$4.6x10^6$	$1.3x10^9$	$1.4x10^7$	$1.0x10^3$	$3.0x10^3$
19	$2.5x10^8$	$2.7x10^8$	$2.2x10^7$	$6.0x10^3$	$4.2x10^2$
24	$7.1x10^8$		$1.2x10^7$	$3.0x10^3$	$3.0x10^2$
29	$4.8x10^6$		$2.8x10^7$	$6.0x10^3$	$2.0x10^3$
May 2	$5.6x10^8$	$9.0x10^8$	$2.9x10^8$	$8.1x10^4$	$3.1x10^3$
5	$1.1x10^9$		$2.1x10^7$	$7.9x10^3$	$4.1x10^4$
8	$6.9x10^7$	$3.0x10^8$	$4.9x10^7$	$1.2x10^4$	$2.0x10^3$
15	$9.3x10^6$		$2.8x10^8$	$6.8x10^4$	$1.2x10^4$
17			$2.1x10^7$	$8.1x10^3$	$1.0x10^2$
20	$1.6x10^8$		$9.8x10^7$	$2.5x10^4$	$3.0x10^3$
22	$7.9x10^8$	$3.0x10^9$	$1.8x10^8$	$3.3x10^4$	$1.9x10^4$
24	$8.2x10^8$		$8.1x10^7$	$1.7x10^4$	$6.0x10^3$
26	$1.0x10^9$		$5.3x10^7$	$1.4x10^4$	$1.0x10^3$
29	$8.5x10^8$	$4.0x10^8$	$7.0x10^7$	$1.8x10^4$	$2.0x10^3$
31	$1.2x10^9$		$6.3x10^7$	$8.0x10^3$	$1.0x10^4$
Jun 2	$8.5x10^8$		$6.3x10^7$	$1.5x10^4$	$3.0x10^3$
5	$6.7x10^8$	$8.0x10^8$	$1.5x10^8$	$3.6x10^4$	$6.0x10^3$
7	$6.6x10^8$		$2.3x10^8$	$5.9x10^4$	$8.0x10^3$
9	$1.1x10^9$		$9.5x10^7$	$2.4x10^4$	$3.0x10^3$
11	$7.0x10^6$		$6.7x10^8$	$1.6x10^5$	$3.0x10^4$

Appendix Table II-4. Snow depth, percent surface light, and extinction coefficient (k) of ice determined from transects through snow drifts, Narwhal Island, spring 1980. The extinction coefficient (k) was determined after the ice algae layer was removed.

Snow Depth (cm)	Percent Surface Light		Extinction Coefficient k_{ice} (m^{-1})
	Ice	0 m	
Drift in lee of tent shelter; 28 Apr			
2.0	2.29	1.63	0.94
1.5	2.29	1.74	0.95
2.5	2.29	1.66	0.94
3.0	1.95	1.63	0.98
3.0	2.00	1.37	0.97
2.8	1.95	1.37	0.98
2.8	1.84	1.21	0.99
2.5	1.47	1.18	1.05
2.8	1.26	0.92	1.09
3.0	0.76	0.71	1.21
5.5	0.63	0.47	1.24
5.5	0.45	0.39	1.32
4.0	0.34	0.29	1.40
6.0	0.24	0.18	1.47
19.0	0.13	0.13	1.59
30.0	0.06	0.06	1.59
45.0	0.04	0.04	1.57
47.0	0.02	0.02	1.69
54.0	0.02	0.02	1.64
54.0	0.01	0.01	1.77
Drift in lee of tent shelter; 6 May			
2.0	0.88	0.69	1.18
1.0	1.20	0.76	1.11
2.0	1.20	0.92	1.10
2.0	0.92	0.74	1.17
2.0	1.27	0.64	1.09
2.0	1.43	0.69	1.06
2.0	1.29	0.74	1.09
2.0	1.09	0.70	1.13
2.0	0.58	0.22	1.29
2.0	0.66	0.37	1.25
3.0	0.50	0.28	1.31
4.5	0.41	0.23	1.35
6.0	0.18	0.14	1.54
8.0	0.10	0.09	1.67
18.0	0.07	0.06	1.66
24.0	0.03	0.03	1.80
32.0	0.02	0.02	1.81
36.0	0.01	0.01	1.92
44.0	0.01	0.01	1.85
46.0	< 0.01	< 0.01	

Appendix Table II-4. (cont.)

Snow Depth (cm)	Percent Surface Light Ice	0 m	Extinction Coefficient k_{ice} (m^{-1})
Drift in lee of tent shelter; 19 May			
0.5	1.27	0.55	1.10
0.5	1.59	0.64	1.04
1.5	1.40	0.64	1.07
1.5	1.37	0.66	1.07
2.0	0.92	0.57	1.17
2.0	1.05	0.54	1.14
2.0	1.11	0.45	1.12
1.5	1.30	0.55	1.09
2.0	0.93	0.51	1.17
2.0	0.85	0.39	1.19
3.0	0.50	0.26	1.31
4.0	0.35	0.24	1.40
5.5	0.23	0.17	1.49
12.5	0.15	0.12	1.53
20.0	0.10	0.09	1.56
26.0	0.05	0.05	1.92
28.0	0.03	0.03	1.76
39.0	0.02	0.02	1.75
36.0	0.01	0.01	1.92
37.0	0.01	0.01	1.91
Drift in lee of tent shelter; 3 Jun			
0.0	1.92	0.83	1.00
0.0	2.14	0.86	0.97
0.0	2.43	0.95	0.94
0.0	1.90	1.08	1.00
0.0	2.14	0.63	0.97
0.0	1.66	0.66	1.03
0.0	1.66	0.47	1.03
0.0	2.14	0.50	0.97
0.25	2.08	0.47	0.98
0.50	0.90	0.45	1.19
2.5	0.83	0.25	1.19
3.5	0.65	0.30	1.25
6.5	0.41	0.20	1.34
13.0	0.30	0.21	1.36
16.0	0.25	0.16	1.38
19.0	0.13	0.11	1.51
24.0	0.11	0.10	1.51
23.0	0.08	0.06	1.59
30.0	0.05	0.04	1.63
31.0	0.04	0.04	1.67

Appendix Table II-4. (cont.)

Snow Depth (cm)	Percent Surface Light		Extinction Coefficient k_{ice} (m^{-1})
	Ice	0 m	
Study area windward of tent shelter; 17 May			
2.0	2.30	1.22	0.92
2.0	2.10	1.30	0.94
2.0	2.10	1.08	0.94
2.0	1.65	0.85	1.00
2.0	2.04	0.82	0.95
2.0	1.81	1.05	0.98
2.0	1.40	0.74	1.04
2.0	0.94	0.64	1.14
2.0	0.82	0.47	1.17
2.0	0.77	0.45	1.19
2.5	1.05	0.60	1.11
2.5	0.94	0.48	1.14
3.0	0.78	0.53	1.18
7.0	0.60	0.30	1.21
3.0	0.51	0.26	1.28
3.0	0.68	0.34	1.21
3.0	0.57	0.27	1.25
5.5	0.52	0.24	1.26
10.0	0.23	0.14	1.42
20.0	0.10	0.07	1.53
Study area windward of tent shelter; 3 Jun			
0.0	3.11	1.87	0.88
0.0	3.14	1.43	0.87
0.0	2.67	1.90	0.91
0.0	2.43	1.48	0.95
0.0	2.44	0.92	0.95
0.0	2.64	1.54	0.92
0.0	2.25	0.80	0.96
0.0	1.58	0.47	1.06
0.0	1.52	0.30	1.05
0.0	1.84	0.50	1.02
0.0	1.60	0.38	1.06
0.0	1.60	0.56	1.06
0.0	1.28	0.51	1.11
0.5	0.86	0.29	1.22
5.0	0.83	0.21	1.20
3.0	0.50	0.21	1.18
4.0	0.62	0.26	1.25
7.0	0.60	0.18	1.29
13.0	0.47	0.17	1.26
20.0	0.15	0.09	1.47

FOODWEB AND NUTRIENT DYNAMICS IN NEARSHORE ALASKA BEAUFORT SEA WATERS

by

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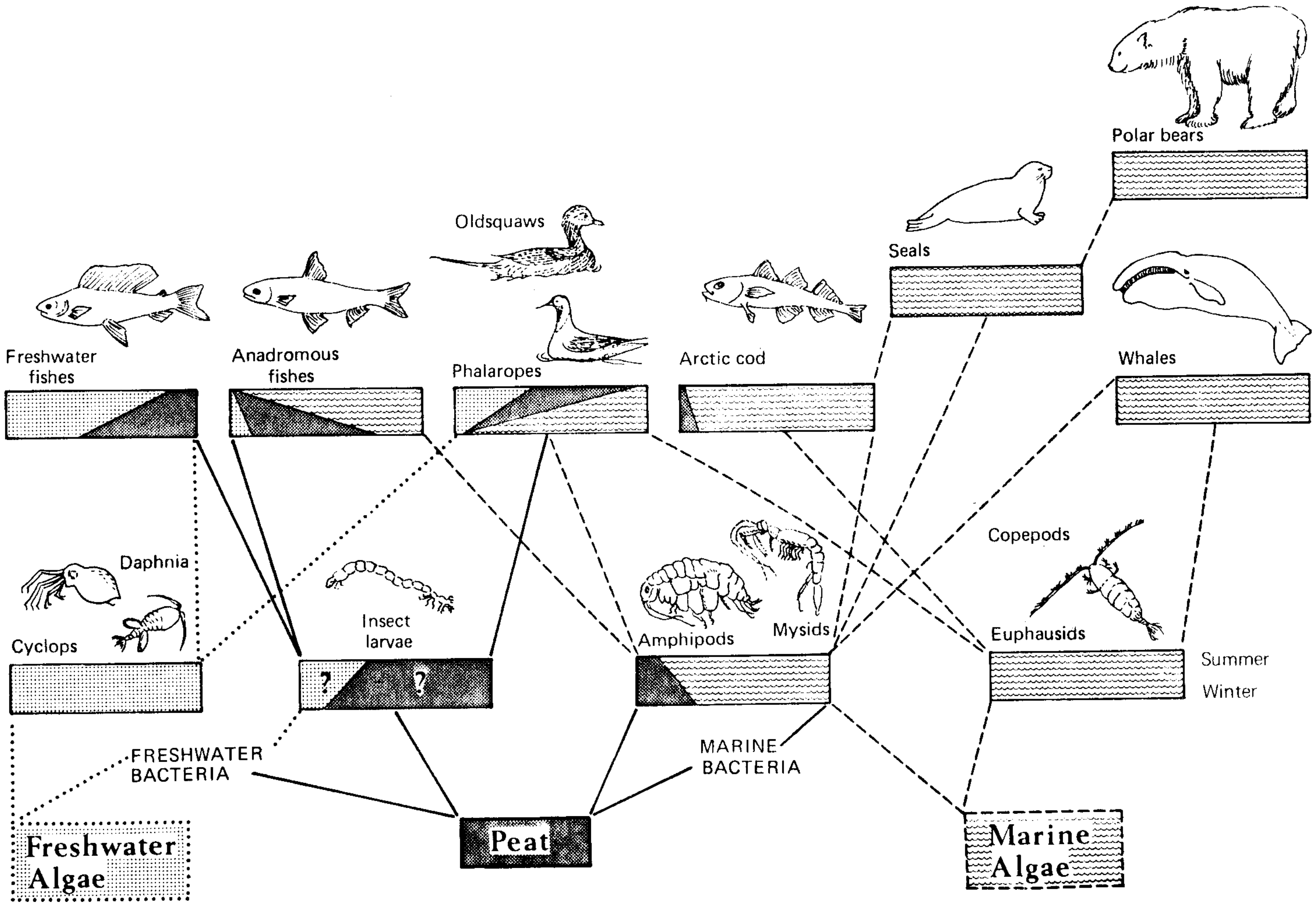

Frontispiece. Generalized foodweb structure and major seasonal energy dependencies in Alaska Beaufort Sea coastal ecosystems.

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I. SUMMARY OF OBJECTIVES, CONCLUSIONS AND IMPLICATIONS WITH RESPECT TO OIL AND GAS DEVELOPMENT

Objectives

The overall objective of RU 537 was to describe the principal processes supplying energy (i.e., fixed carbon) to the biota of the Beaufort Sea coastal zone and to estimate transfer efficiencies of this energy through the foodwebs of the nearshore zone. In addition, this research unit has investigated the nutrient dynamics of coastal waters and related the nutrient regimes to this production of energy. Both terrestrially derived and offshore derived nutrient sources are considered. The information obtained was initially for integration into the overall structure of the LGL Barrier Island study group, RU 467. Their efforts related this information to: 1) description of the overall ecosystem, 2) possible OCS direct impacts on the nearshore biota by offshore oil and gas development, and 3) possible impacts on the nearshore biota caused by "upstream effects" on land which would change the character of terrestrial input of nutrients and/or carbon to the marine ecosystem via erosional processes or runoff.

In addition, this research unit has cooperated with units 356 (Dr. Carter Broad) and 359 (Dr. Rita Horner) with the following objectives: 1) to seek information on the rates of macrofloral primary production in the "boulder patch" of Stefansson Sound (RU 356); 2) investigate the ability of indigenous species of amphipods to utilize peat carbon through symbiotic intestinal cellulose-degrading microfloral populations, (RU 356); and 3) cross calibrate estimation techniques for ice algal biomass and seasonal production (RU 359) with the goal of developing methods that would allow estimation of annual ice algal production based on observed standing stocks at particular intervals of the spring season.

Overview

The conclusions to date give evidence that trophic interdependencies of the nearshore Beaufort Sea are decidedly different from more temperate Alaska coastal zones with regard to the energy sources supporting the biota. Although the inputs of terrestrial peat to the marine waters do not contribute major amounts of energy to marine organisms, the peat is directly linked to the anadromous fishes and birds via the freshwater foodwebs. This is a most important point -- the reproductive success of oldsquaws and phalaropes and the overwintering success of anadromous fishes are established upon freshwater peat-based foodwebs. When these fishes enter the marine environment, their food shifts to marine invertebrates (mysids, amphipods, etc.) which derive their carbon from the phytoplankton, ice algae and benthic microalgae primary producers. The carbon isotope compositions of arctic marine and freshwater biota lead us to hypothesize that a major separation exists in the trophic system of the arctic coastal zone. Even though there is peat carbon available to organisms in the marine environment, due to the input from coastal erosion and the Colville River, utilization of this large reservoir of organic matter is limited by invertebrate assimilation capabilities. The strictly marine organisms, therefore, rely on the more variable supply of marine microalgal primary production. It may be significant that apical organisms of the pelagic foodweb (such as seals, whales and polar bears) are typified by large energy storage capacities which may assist in smoothing out the pronounced seasonal and, perhaps, annual variations in food supplies. The obligate freshwater fishes, on the other hand, have been shown to be heavily dependent on peat carbon which appears to be made available through the critical link of insect larvae (probably chironomids). Superimposed on these two schemes are the anadromous fishes, oldsquaws, and phalaropes. It is through the movement of these upper trophic level organisms that two energetically independent systems interact. Although this type of interaction certainly occurs elsewhere, the importance to both migrating species and prey organisms on which they feed cannot be underestimated in an environment where primary production is essentially nil for seven months of the year. It is reasonable to assume that the successful ecological adaptation of marine birds, such as the oldsquaws and phalaropes, to rearing their young on tundra ponds is in part in response to this reliable food source. Similarly, the anadromous fish populations overwintering in the arctic rivers can expect a relatively constant peat-based food supply independent of the variable seasonal microalgae production. The frontispiece shows the relationships of organisms to the energy sources supporting the nearshore and freshwater ecosystems.

The estimates of energy input to nearshore waters have been revised as new data obtained by this research unit and RU 530 are utilized to appraise the various input sources. These estimates show that over 50 percent of the carbon input to nearshore marine biota (within approximately 10 km of shore) is terrestrially derived from two primary processes, fluvial transport and coastline erosion. The rivers carry large quantities of organic matter during spring breakup and coastal erosion occurs during summer months, resulting in the deposition of large amounts of organic carbon along the shoreline. This carbon is composed primarily of peaty material that has been accumulating on land for up to 12,000 years. The freshwater and nearshore marine ecosystems are apparently "fossil fuel" subsidized, wherein the meager annual primary production by ice algae and phytoplankton is supplemented by organic carbon eroded from coastal peat bluffs and transported by river flow into the coastal zone. The distinctive carbon isotopic signatures of the materials from terrestrial and marine sources allow detection and quantitation of the source fractions in the tissues of the fauna comprising the foodwebs built upon these sources.

The input of allochthonous carbon to the Harrison Bay (Sale 71) area by the Colville River causes a disproportionate increase in terrestrial carbon relative to marine primary production. Over 85 percent of the fixed carbon budget is terrestrially derived, which readily accounts for the high percentages of peat carbon found in organisms collected from Harrison Bay in November 1979. If the detrital foodweb dependencies increase during winter in Harrison Bay (as has been found to occur in the freshwater habitats), the terrestrial carbon inputs may be even more critical than currently indicated.

Highlights and Conclusions

Since 1977, this research unit has sought to quantitate the energy inputs to the foodwebs of the nearshore Beaufort Sea and to determine the relative significance of peat detritus to higher trophic levels. Beginning with a limited investigation of the role of ice algal primary production and related nutrient cycling, this work expanded into a broad investigation of the major processes supplying energy to the ecosystem. The findings have been reported in past annual reports and have been modified as new data have been acquired.

An overall picture of nearshore arctic marine energy flow is emerging. The marine and freshwater ecosystems are remarkably different, but they are inseparably linked by the anadromous fishes and migratory birds that use both habitats and are apex organisms in arctic foodwebs. Arctic marine fauna are almost totally dependent upon marine primary production and have not adapted to direct utilization of the large inputs of terrestrial organic matter that enter nearshore waters via fluvial transport and coastline erosion. Presumably, this is because few of the indigenous invertebrates can utilize cellulosic matter as an energy source. An exception is the amphipod *Gammarus setosus* which has been shown to assimilate cellulose, but this organism is not a principal prey species of the fishes or birds that feed in the coastal Beaufort Sea.

In contrast, the freshwater aquatic fauna are heavily dependent upon detrital peat as a primary energy source, and the success of overwintering fish populations requires an almost complete shift to detrital foodwebs. The anadromous fishes which overwinter in the Colville River have been shown to continue feeding over the winter months and to rely almost entirely upon a food chain based on peat carbon. Similarly, oldsquaw ducks breeding on the coastal tundra in the small ponds and lakes have been found to contain as much as 20-60 percent peat carbon indicating that aquatic primary production is responsible for a variable fraction of their food requirements in summer months. Terrestrial carbon in the form of peat may, therefore, supply a significant fraction of the energy requirements of the freshwater ecosystem. Several highlights of the research results follow. For detailed descriptions of methods and results, the reader should seek the appropriate section in the report body.

The conclusions presented herein, especially with regard to the carbon isotope studies, are based upon samples analyzed to date. Some samples are still being processed, and our conclusions will be modified as new information is acquired.

Ice Algae

November 1980 sampling of sea ice cores north of Stefansson Sound yielded a surprisingly large population of ice algae at the ice-water interface. The ice algae layer was readily discernible to the eye, and chlorophyll-a concentrations averaged 87 mg/m^3 in the bottom 5 cm of ice. Integrating the bottom 10 cm of ice yielded a standing stock of 4.7 mg Chl-a/m^2 which translates into approximately 0.2 g C/m^2. No data are available as to year-to-year variation in arctic ice algal blooms during fall; indeed, to the author's knowledge, this is the first report of its occurrence. It is interesting that the documentation of Canadian arctic microalgae (Hsiao, 1980), which includes the Eskimo lakes area of the nearshore Beaufort Sea, makes no note of any bloom of ice algae in the fall, but instead found the minimum annual concentrations of ice algae during November. This marked contrast to our findings in November off Narwhal Island cannot be explained without better understanding of the environmental differences between the areas. Similar blooms have been reported in the Antarctic, and the author is indebted to Dr. Mitsuo Fukuchi of the Japan Polar Research Institute (with whom this was a joint effort) for the suggestion to look for their occurrence. Due to the low light intensities, short day length, and rapid rate of ice formation, it had been assumed that ice algae would not have time to grow before incorporation into congelation ice. The fall of 1980 was characterized by an unusually warm period in late October that may have contributed to favorable growth conditions.

The distribution and productivity of ice algae over much of the coastal zone between Cape Halkett and Stefansson Sound has been estimated from chlorophyll concentrations and from direct carbon measurements. Ice algal populations are highly variable as a result of sediment inclusion in the ice cover and other environmental variables such as hypersalinity, freshwater stress during runoff, and variable snow cover. Considerable effort has been directed toward obtaining a better estimate of the annual contribution of ice algae to the energy budget of the marine ecosystem. Based upon our efforts and the literature data, ice algae are believed to contribute 1-6 g C/m^2 to the nearshore Beaufort Sea, with the higher values occurring 20 or more kilometers offshore where the ice is free from sediment inclusions. In the nearshore areas, sediment-laden ice is very common and prevents light transmission through the ice cover over much of Harrison Bay and Stefansson Sound.

Although the area of sediment-laden ice varies greatly from year to year, and sampling density is insufficient to accurately quantify the total area covered, we feel that approximately one-third to two-thirds of the Stefansson Sound and Harrison Bay area are typically rendered unsuitable for ice algal growth. Progressing seaward, sediment in the ice diminishes and the increasing clarity of the ice and decreasing snow cover enhance growth conditions. At 160 km offshore (the farthest distance sampled), virtually all annual sea ice showed visible evidence of an ice algal layer on the bottom where pack ice motion had overturned pieces.

Estimation of annual production was accomplished using two methods. Observed standing stocks of chlorophyll-_a_ were halved to approximate a seasonal average density and the equivalent carbon fixation rates were integrated over a 60 day season using assimilation efficiencies obtained from literature data. The alternate technique involved converting observed chlorophyll concentrations to carbon by measuring carbon/chlorophyll ratios in ice algal samples. By multiplying the maximum standing stocks of ice algal carbon by a factor of 5, annual production was obtained. The factor 5 was an approximation derived from averaging several annual productivity/maximum standing stock values from the literature. We feel reasonably confident in these estimation techniques, since they agree with both our own and literature data. There are several pitfalls, however, that limit their usefulness. These are explained in detail in Section VI.

Chukchi Sea Ice Algae Studies, 1981

During trafficability studies in the Chukchi Sea during Spring 1981, the U.S. Coast Guard icebreaker Polar Sea sustained damage to the propeller shaft and became immobilized in the ice of Wainwright, Alaska. The termination of the trafficability studies afforded the opportunity to place graduate student Daniel Parrish on board to conduct ice algal studies over the course of the spring bloom. The situation did not prove very successful, however, due to severe fuel shortages on the vessel and the fact that whenever a lead opened, the vessel moved southward as rapidly as possible. As a result, only four ice stations were occupied yielding a very limited sampling density. Ice algal densities were variable reflecting ice rafting and snow depth, but were generally higher than observed in the Beaufort Sea. Maximum chlorophyll concentrations were found beneath smooth ice pans and ranged from 24.9 to 78.3 mg $\text{chl-}\underline{a}/m^2$, equivalent to 1.2 to 3.9 g C/m^2. Assuming an annual productivity equal to 5x the maximum standing stock, nearly 20 g C/m^2 were fixed under optimal conditions in the Chukchi Sea. This value agrees well with the 24 g C/m^2 estimated by McRoy and Goering (1976) for the Bering Sea, although their figure was listed as an average value. The overall trend, therefore, in ice algal productivity is a gradual decrease in annual production along a line northward from the Bering Sea into the Chukchi and then, presumably, north and eastward into the Beaufort Sea. This trend is due to the thicker ice, lower nutrient concentrations, deeper snow cover, and lower solar angles that prevail on a progression northward.

Phytoplankton Production

Field measurements of phytoplankton productivity under sea ice and during the open water months were undertaken on a limited scale by this research unit. Data have been obtained from Simpson Lagoon, Harrison Bay, Prudhoe Bay, Stefansson Sound, and offshore. Four sampling trips (17-18 June and 2 July, 1980; 24-28 May and 22-24 June, 1982) were specifically made to obtain chlorophyll fluorescence and primary production beneath melting sea ice late in the spring season.

All samples obtained confirm the hypothesis that primary production rates are low, but that shade adaptation allows active carbon fixation beneath the ice. Nevertheless, no evidence of a "spring bloom" was apparent during any sampling period, although fixation rates were highest in nearshore waters. This may mean that phytoplankton populations gradually increase during June and July as light intensities increase with the melting ice cover. The nutrients available for growth are also depleted during June and July, and thus prevent any major pulse of production as the ice cover disappears.

Estimates of total annual phytoplankton production were obtained by two techniques. The first method integrated average primary productivity rates over the summer season and adjusted the effective euphotic zone depths in response to the presence or absence of ice cover. The second method involved calculating a phytoplankton crop based upon maximum nutrient availability in the spring and then using approximations for turnover times based upon zooplankton standing stocks and estimated consumption rates. Both methods contain major uncertainties and the approximations obtained are most useful in a qualitative sense in determining which areas of the Beaufort Sea are most biologically productive.

Based upon the literature data available (Alexander, 1974; Horner, 1981) and our findings, we conclude that seasonal primary productivity in the coastal Beaufort Sea is typically between 0-2 g C/m^2-yr for ice algae and 5-20 g C/m^2-yr for phytoplankton for the nearshore areas such as Stefansson Sound, inner Harrison Bay, and Simpson Lagoon. Outside of the barrier islands and further offshore, ice algal productivity increases to 2-6 g C/m^2-yr and phytoplankton productivity increases to over 40 g C/m^2-yr. These increases reflect the clearer ice cover and the deeper water column which, when integrated over the euphotic zone, yield higher total primary productivity values. It is assumed that far offshore (beyond about 200 km) where pack ice is perennial, phytoplankton productivity decreases to very low annual totals of less than 1 g C/m^2-yr (Apollonio, 1959; English, 1959).

Erosional and Fluvial Inputs of Carbon to the Nearshore Marine Environment

Carbon, nitrogen, and phosphorus analyses on peat soil section samples have been completed for a large selection of sites along the Colville River, Simpson Lagoon, and the Beaufort Sea coastline west to the Cape Halkett area yielded a reasonably comprehensive picture of the nutrient content of the allochthonous matter entering the marine environment. In addition, S. Rawlinson of RU 530 has completed estimations of shoreline erosion rates for the entire coastline between Point Barrow and the Canadian border. Approximately 2.6 x 10^9 kg/year of peat soils erodes into the nearshore marine waters carrying 158 x 10^6 kg carbon, 10 x 10^6 kg nitrogen and 0.69 x 10^6 kg phosphorus. On an atom ratio basis, the C:N:P ratios are approximately 558:31:1. The peat soils have been shown to be readily oxidized microbiologically; thus mineralization of the incorporated nutrients would make them available for phytoplankton uptake.

Fluvial input of carbon and nitrogen has been determined for the Colville River discharge, and extrapolations were made to estimate total North Slope inputs to the Beaufort Sea. Annually, approximately 230 x 10^6 kg C and 15 x 10^6 kg N enter via river flow. Of this amount, about half is transported by the Colville River. This 115 x 10^6 kg C/year entering Harrison Bay compares with an estimated 20 x 10^6 kg C/year from ice algal and phytoplankton primary production. This high input of terrestrial carbon is reflected in ^{14}C content of the invertebrates sampled near Thetis Island which were found to contain over 25 percent peat carbon. The low efficiency of detrital foodwebs in the marine environment is probably responsible for the terrestrial carbon not comprising an even larger fraction.

Energy Flow and Trophic Relationships

Carbon isotope tracer techniques have revealed that the foodweb pathways of energy transfer into the fishes and birds of the nearshore Beaufort Sea are almost totally based upon marine primary production in spite of the large quantities of terrestrial carbon available to the nearshore ecosystem.

The organic matter transported by the Colville and Kuparuk Rivers was found to be strongly depleted in ^{14}C, and the depletion increased as breakup progressed. Thus, the major fraction of fluvially transported carbon is derived from eroded peat from river banks, and the input of surficial vegetative material is pronounced only during the initial stages of breakup in the rivers. The Kuparuk River contained the lowest quantity of ^{14}C in river particulate matter, approximately 71 percent of the 1950 standard radiocarbon activity compared to 65 percent for the mean radiocarbon content of Simpson Lagoon soil sections

Refined estimates of the mean ^{14}C content of the allochthonous carbon sources, and the determination of ^{14}C activity in several additional species of marine and freshwater fauna of the coastal zone and rivers, have revealed startling variations with regard to the utilization of eroded peat carbon. Anadromous fishes from the Colville River (arctic cisco, least cisco, humpback whitefish) are almost entirely dependent upon the marine ecosystem for their nutrition during summer as evidenced by $^{13}C/^{12}C$ isotope ratios of specimens collected from Simpson Lagoon and Harrison Bay in August and September.

After the anadromous fishes enter the Colville River during the fall, however, their food habits shift to a nearly complete dependence on detrital peat foodwebs. By the following June, the $^{13}C/^{12}C$ ratios of the fishes re-entering saltwater are typical of obligate freshwater fishes, and the ^{14}C content has fallen to concentrations equivalent to approximately 45-50 percent peat carbon. However, some samples of anadromous fishes obtained in June 1982 showed evidence of feeding in marine waters over the entire winter. Whether these fish wintered in saline delta channels or offshore is not known. This information is important in that it shows 1) the anadromous fishes are actively feeding during winter months, and 2) peat-based detrital foodwebs are the most important pathways of energy flow during winter in the freshwater aquatic ecosystem. Since fish can be presumed to be feeding on insect larvae and other invertebrates, the lower trophic levels must in turn be almost totally dependent upon peat carbon inputs.

Further evidence of the role of peat carbon in freshwater foodwebs came from an oldsquaw duck collected after nesting on the tundra for the summer. The $^{13}C/^{12}C$ ratio of this bird was typical of terrestrial carbon sources and the ^{14}C content ratio was equivalent to 60 percent peat carbon. Thus, some of the small ponds and lakes on which these birds live during the summer must be energetically supplied to a large extent by eroded peat carbon, and phytoplankton production inputs are exceeded by the vast quantities of peat. These tentative conclusions are supported by documented oldsquaw specimens collected from the Teshekpuk Lake area.

Marine Detrital-based Production

Laboratory experiments in cooperation with Dr. David Schneider (RU 356) were conducted at the Naval Arctic Research Laboratory in July 1979 to determine the cellulose oxidation capabilities of in situ populations of marine microflora and resident populations of amphipods. The experiments confirmed previous findings that active microbial oxidation occurs in the water column, but that *Onisimus* sp. amphipods do not have the ability to utilize cellulose (or peat) directly.

In contrast, experiments run with *Gammarus setosus* showed rapid cellulose uptake and metabolism. At 8°C, the average adult *Gammarus setosus* oxidized approximately 1.6 μg peat/hr to carbon dioxide. Microbial oxidation rates of peat in seawater yielded turnover times of about 1,050 days at 0°C and 640 days at 8°C. This turnover time implies that the fate of most eroded peat is microbial oxidation within the lagoon-nearshore system, since transportation offshore in this low energy environment is slow.

The collection problems associated with acquiring sufficient specimens of *Gammarus setosus* from the lagoon environment to perform radiocarbon activity determinations (for high precision, 5 g of carbon is required) have prevented the acquisition of isotopic data on these animals until recently. A sample collected by Dr. Schneider during July from the Chukchi Sea at Barrow showed a radiocarbon content of 96.6 percent modern, equivalent to approximately 30 percent peat carbon, the highest fraction in any marine organism analyzed to date. In addition, baited traps set in Simpson Lagoon during November 1979 yielded sufficient adult amphipods of *Atylus*, *Gammaracanthus*, and *Weyprechtia* spp. to obtain radiocarbon activities. These adult organisms also contained the low radiocarbon activities corresponding to body compositions of 16-23 percent peat carbon. These organisms are apparently partially dependent upon detrital peat and reflect the high inputs of terrestrial detritus to the nearshore environment.

Further work on measuring the rates of microbial oxidation of peat in offshore marine waters and in the freshwater environment confirmed that the oxidation of cellulose occurs in both marine and freshwater at temperatures down to freezing. Kuparuk River water collected in September 1980 oxidized cellulose at nearly twice the rate as marine water collected offshore of Reindeer Island and at approximately the same rate as marine waters from Simpson Lagoon. The addition to the water samples of small quantities of peat detritus collected from the shoreline increased oxidation rates, indicating active populations of bacteria associated with peat in seawater.

The Stefansson Sound Boulder Patch

The Boulder Patch is an area of pebbles, cobbles, and boulders in Stefansson Sound that provide a substratum for a diverse assortment of invertebrates and several species of algae. Linear growth in the kelp, *Laminaria solidungula*, is greatest in winter and early spring when nutrients are available for new tissue growth. The plant draws on stored food reserves to complete over 90% of its annual linear growth during the nine months of darkness under a turbid ice canopy. These reserves are accumulated by photosynthetic activity during the previous summer. The total carbon fixed by kelp in the Stefansson Sound "Boulder Patch" is approximately 146 x 16^6 g/yr (equivalent to 7 $g/m^2 \cdot yr$). This annual carbon input is roughly equivalent to that of phytoplankton in the overlying water column and provides a year-round energy source for consumers. Most of this carbon is released in dissolved or particulate form and appears to be a potential food source for filter-feeding animals and detritivores.

Stable carbon isotope ratios $^{13}C/^{12}C$) have provided evidence that kelp carbon ($\delta^{13}C$ = -14.8) is being utilized by many consumers in the Boulder Patch kelp community, including organisms that typically rely on phytoplankton ($\delta^{13}C$ = -24 to -26) as an ultimate food source. The ^{13}C:^{12}C ratios of organisms examined to date reflect their known diets from in situ behavioral observations, with a notable exception showing a higher than expected dependency on kelp carbon. *Mysis litoralis* ($\delta^{13}C$ = -19.1), an important crustacean in arctic foodwebs, is more enriched in ^{13}C than individuals collected some distance from the kelp community ($\delta^{13}C$ = -23.6) which may indicate a change in feeding strategy for this predominantly filter feeding organism. In general herbivores (chitons and snails) exhibited the highest carbon isotope ratios and filter feeders the lowest. The importance of kelp as a winter food souce may be seen in the shift of the carbon-isotope compostiion of mysids from summer to winter. The $^{13}C/^{12}C$ ratio in mysids is lowest in summer (most negative $\delta^{13}C$ values) when phytoplankton productivity is greatest, but this ratio increases during the winter as phytoplankton production ceases and the available food contains a greater proportion of kelp carbon relative to phytoplankton carbon. In respect to its carbon inputs, the relative simplicity of this community makes it an ideal system in which to examine foodweb structure and the importance of kelp carbon in trophic dynamics, a role that is not well understood.

Implications with Respect to Oil and Gas Development in the Coastal Beaufort Sea

Detrimental impacts on the primary producers and detritivores within the lease area could result from either spills of hydrocarbons or petroleum-related development. Since the range of specific insults to the environment is extreme, we will deal with the direct and indirect effects of developmental activities in a general sense. The research results of this RU have shown that: 1) most of the higher organisms including the larger invertebrates are dependent primarily upon marine primary production for their food during summer; 2) primary production in the nearshore zone is very low by most coastal standards; 3) extreme variability exists in the nearshore aquatic environment due to such natural phenomena as river breakup, daylight extremes, ice turbidity, solute exclusion during ice formation, and strong winds. It is reasonable to expect, therefore, that the microflora and fauna living in this environment are some of the most opportunistic and resilient organisms extent, for their living conditions demand flexibility. There are probably exceptions. The Boulder Patch floral and faunal densities and assemblages are anomalous and very likely unique due to the protected environment they enjoy and the paucity of similar areas free of ice gouging in deep (6 m) water with rocky substrate along the Alaska Beaufort coast. These same rigorous environmental conditions also imply, however, that the organisms living therein are periodically stressed. The fact that this coastline is a range limit for several species also implies that the stresses can be severe, and in come cases, limiting. In this context, the implications of petroleum development acquire a greater potential for impact. If the environmental stresses are increased through the addition of man-produced insults such as might result from toxic waste inputs, increased turbidity, radical changes in circulation patterns, or oil spills, the impacts on some species could be direct, with foodweb dependencies passing on the interspecific change. For example, an impact such as shoreline stabilization along the lease area would radically change the gross energetic input to the nearshore ecosystem by eliminating erosion of the peat bluff shorelines.

This impact might not become apparent in the higher organisms such as fishes due to their almost exclusive dependency upon marine primary production foodwebs. Some invertebrates, however, could be adversely impacted insofar as terrestrial peat has been found to supply over 20 percent of the energy requirements of some amphipods taken from Harrison Bay.

Major impacts would result from perturbations that altered the summer primary productivity of phytoplankton and ice algae. Oil spills, phytotoxic chemical discharges, or other impacts that decreased primary production in a significant fraction of the coastal zone would be felt by the entire foodweb, including all the anadromous fishes. Other direct effects on primary producers, such as uptake of toxic substances from low ambient concentrations, could indirectly produce severe impact at the higher trophic levels due to the biomagnification of toxicants during foodweb transfers. Toxic heavy metals or halogenated organic compounds are potential problems given the limited circulation that occurs during winter months in the lease area.

Long-range environmental impacts resulting from energy development in arctic Alaska may directly perturb the anadromous fishes and detritivores of the coastal zone through disturbances in freshwater habitats. Deep pools in the larger rivers and lakes are critical overwintering areas for the anadromous fishes which use the marine environment for feeding in summer months. River channel disturbances, increased organic loading in tributaries, nutrient loading from sewage effluents, etc., can all impact overwintering populations through oxygen depletion in under-ice waters. These potential impacts have been identified previously (Schell, 1974, p. 662-663). As, for example, dredging operations begin in the Colville Delta near Nuiqsut, the biological hazards associated with these activities will require continued monitoring.

In the more distant future, the vast arctic reserves of peat may be used as feedstock for synthetic natural gas production to replace declining production of North Slope fossil gas supplies. This will present a direct conflict through the appropriation for man's usage of an energy source now important to freshwater foodwebs and indirectly to marine foodwebs as a nutrient source. As our understanding of the interactions between terrestrial and marine ecosystems clarifies, further areas of potential developmental impacts will surely become evident.

II. INTRODUCTION

General Nature and Scope of Study

This research unit originally proposed to look at a very specific aspect of the nearshore primary production regime, namely the contributions of ice algae and the effects of thermohaline convection in supplying nutrients to ice algal populations. At that time, the importance of terrestrial detritus as an energy source became more evident, and this research unit began to consider the possible magnitude of its significance through the use of data collected previously by the author. These results, which have been refined and presented below (see Fig. 2), show the approximate magnitudes of carbon inputs to the Simpson Lagoon ecosystem and set forth an outline of isotopic techniques that allow determination of the relative inputs of peat carbon versus modern primary production carbon (Figs. 3 A, B). Using carbon isotope techniques, this research unit has undertaken the task of determining the significance of each of the carbon sources to the fauna of the coastal Beaufort Sea.

Specific Objectives

The specific objectives of this research unit included:

1. Determine the role of terrestrial allochthonous carbon versus marine primary production in the trophic energetics of marine

organisms in the nearshore Beaufort Sea through use of carbon isotopic tracer techniques.

2. Determine the total inputs of energy to the coastal ecosystem, including allochthonous carbon and nitrogen entering the system via terrestrial runoff and coastline erosion.

3. Compare standing stocks of epontic algae in relation to under-ice nutrient concentrations and ice turbidity.

4. Collect data delineating temporal and spatial variability in ice algal blooms in the nearshore Beaufort Sea.

5. Relate the observed patterns in nutrient availability over the annual cycle to the heterotrophic utilization of detrital carbon within the coastal ecosystem.

Relevance to Problems of Petroleum Development

An ecosystem with a substantial detrital component along large portions of the Beaufort Sea could be readily altered directly or indirectly through OCS-related petroleum development. A summary of the specific impacts that might affect the various sources of energy into the ecosystem includes:

Ice algal productivity:

1. Oil spills on or under the spring ice cover would diminish primary production through either phytotoxic effects or by attenuation of light passing through the ice sheet.

2. Alteration of bottom topography by dredging channels or constructing causeways could alter ice algal production by changing patterns of thermohaline convective flow beneath the

ice cover. Prevention of brine drainage by closing off deeper channels would lead to brine accumulation on the bottom which could seriously impact both fauna and flora.

Phytoplankton production: Open water primary production would be most sensitive to such impacts as phytotoxicity resulting from oil spills. The rapid lateral transport of water along the Beaufort Sea coast may, however, serve to minimize this aspect of potential impact. Potential impacts could also result from the input of nutrients, particularly nitrogen, as a result of secondary sewage effluent discharge. The increased nutrients would stimulate plant growth in summer and could have localized impact on primary and secondary production with possible alternation of the species composition in the area. These effects would not necessarily be classified as detrimental to the marine ecosystem.

Detrital-based production and heterotrophic productivity: Impacts upon the heterotrophic organisms that depend upon eroded and transported peat materials as their energy source would occur primarily through OCS-related developments that impinged upon the sources of detritus. Such procedures as shoreline stabilization could alter the food base by eliminating eroded materials. Causeway construction could change wave energy regimes and thus decrease shoreline erosion. Stabilization or channelizing of streambeds might add to or subtract from the total organic load carried by runoff waters.

Chronic toxicity and increased stress on microbial populations: An indirect impact due to developmental activity effects on the nearshore biota may arise through the physico-chemical interactions of peat detritus and pollutants in under ice waters. The high cation exchange capacity and the hydrophobic nature of the lignins and humic acids associated with peat make it act as an effective scavenger for multivalent cations, chlorinated hydrocarbons, and other polar and hydrophobic molecules. Chronic discharges of toxic or mutagenic substances into the shallow water column may lead to rapid scavenging of these substances by the detritus. During winter, the limited circulation beneath the ice may result in accumulation through chemical and physical processes to levels toxic to the microbial component. We have not addressed this potential problem in this study beyond showing that the peat supports an active microbial population throughout winter and summer. Although peat appears to be a minor input to total energy requirements of nearshore higher trophic level organisms, we do not know what effects may arise from alteration or inhibition of microbial populations in this component of the energy supply.

The Boulder Patch

A distinctive feature of the Alaska Beaufort Sea shelf biota is the absence of kelp and other species of benthic macroalgae. Pieces of kelp and red algae have been found only as drift on beaches between Pt. Barrow and the United States--Canadian border, and entire plants are seldom observed in significant numbers in driftlines. Collins (1927), in the last major account of benthic algae of the Alaska Beaufort Sea, indicated that no extensive stands of laminarioids were found between Pt. Barrow and the MacKenzie River, NWT. In contrast, many species of sublittoral benthic algae grow in the Canadian Arctic (Lee, 1973; Wilce, 1964).

The ecology of arctic kelp communities has not been studied, mainly due to the large amount of logistic support needed for a diving operation in the Arctic. Therefore, we know little about the energetic contribution made by sublittoral benthic algal communities to the arctic nearshore environment and the fauna associated with large stands of macroalgae. Lee (1973) postulated that colonization of submerged rocks in the Canadian Arctic by fast-growing ephemeral plants takes place after they are no longer icebound, but this hypothesis has not been tested. In temperate regions, subtidal field studies have addressed the temporal and spatial aspects of recolonization, the interaction among organisms, the importance of physical parameters, and the productivity of the algae in respect to its carbon or energetic input (Foster, 1975; Hatcher et al., 1977; Vadas, 1977).

In August 1971, Erk Reimnitz discovered abundant kelp and a diverse invertebrate fauna attached to cobbles and boulders near Prudhoe Bay in Stefansson Sound, Alaska, in an area now designated the "Boulder Patch" (by the U.S. Board of Geographic Names). The Boulder Patch has been the subject of cooperative geological (RU 205, E. Reimnitz and P. Barnes, principal investigators) and biological studies (RU 356, C. Broad, principal investigator) since 1978. These studies resulted from the need to provide adequate protection to sensitive biologically productive regions, while allowing simultaneous exploration of oil reserves in the immediate area. The Boulder Patch lies on top of promising offshore oil reserves, as evidenced by some tracts in this area receiving the highest bids in the joint State-Federal Beaufort Sea lease sale in December 1979 (Wilson, 1979).

The Boulder Patch is a rare feature of the Alaska Beaufort Sea shelf, which is blanketed predominantly by silty sands and mud (Barnes and Reimnitz, 1974). Most macroalgae depend on hard rock substrates for attachment, since they require a stable base for successful colonization, growth and reproduction. This fundamental need for a hard substratum was recognized by Kjellman (1883), in his classic treatise on arctic algae.

Mohr et al. (1957) first reported the existence of a kelp bed in Arctic Alaskan waters. Using a dredge, they collected a large amount of seaweeds, fishes and invertebrates at 13 meters depth about 50 miles southwest of Pt. Barrow in the Chukchi Sea. Collection of algae elsewhere in the Alaska Arctic has been limited to drift material picked up by various Canadian and American arctic expeditions during the late 19th and early 20th centuries (for complete review, see Mohr et al., 1957).

III. CURRENT STATE OF KNOWLEDGE

Primary Production

In comparison to the warmer waters along the more southern Alaska coastlines, the Beaufort Sea supports a relatively sparse biota. No appreciable harvests of renewable marine resources are made, with the exception of small commercial fisheries operated principally by residents in the estuaries along the coast, and seasonal harvesting of bowhead whales and seals. The zone of maximum biological productivity is confined to a relatively narrow strip along the coast wherein the interaction of terrestrial influences ameliorates and somewhat enhances the sparse oceanic regime.

The primary production supporting the pelagic community occurs in two distinct phases in the Beaufort Sea (and other polar waters). The initial algal bloom in the spring occurs well before the ~ 2 m ice cover has begun to melt, and after the returning daylight reaches crucial intensities sufficient to supply the necessary energy beneath the ice (Bunt, 1963; Apollonio, 1965). Epontic attached algal populations grow on the ice-water interface and thrive until the melt begins around the beginning of June. Literature estimates of the carbon fixed during this period range from about 1 g/m^2-yr in the shallow Prudhoe Bay area (Horner et al., 1974) to 5 g/m^2-yr Point Barrow (Alexander et al., 1974). Little is known about spatial variability in ice algal production along the Beaufort Sea coast.

Ice algal production has been assumed to be a strictly spring phenomenon in arctic waters (Alexander, 1974) in contrast to the Antarctic, where the onset of freeze-up occurs a full month earlier in the solar year, and thus considerably more light is available for epontic algal production. The conditions of the freeze-up algal bloom in the Antarctic are well documented (Hoshiai, 1969a, b, 1977), but no reports of a similar bloom in arctic waters has been reported. In November 1980, sampling of sea ice north of Narwhal Island near Prudhoe Bay yielded ice cores visibly laden with ice algae, the first evidence of an arctic freeze-up bloom. These samples are described in detail in the Results section of this report.

As the ice cover melts following the spring ice algal bloom, phytoplankton production assumes the major role in energetic input, although the stability of the water column caused by the melting of the nutrient-poor ice hinders the advection of deep-water nutrients to the photic zone. Only in limited areas near Barter Island has Hufford (1974) identified possible upwelling of deep waters. As a result, primary productivity of phytoplankton is low. Estimates range from less than 1 g C/m^2-yr in the central Arctic Ocean (Apollonio, 1959; English, 1959; Melnikov, 1980) to about 20 g C/m^2-yr on the coastal zone near Barrow (Alexander et al., 1974).

Input of Terrestrial Carbon to the Nearshore Coastal Zone

The enhancement of biological activity in the proximity of land has been long attributed to various factors among which are the provision of suitable habitat for both benthic flora and fauna, substrate for macrophytes and input of terrigenous nitrogen, phosphorus, and carbon via runoff from land. The arctic coastline provides very limited habitat for macrophytes or benthic infauna due to the 2 m freeze depth, which effectively eliminates the shallow nearshore zone as a year-round environment for marine organisms. In the deeper water, ice scouring creates sufficient habitat disturbance to account for the paucity of observed infauna. The exception to this generalization is the area of dense macrophytic algae that has been described by RU 356 in the central region of Stefansson Sound. This area has relatively deep lagoon waters (6 m) with protection from ice scouring afforded by the offshore barrier islands. In addition, a rocky substrate is available on the sea bottom in the form of relict cobbles and boulders. Dense stands of *Laminaria* are present, and this research unit has participated with RU 356 in assessing the contributions of this biologically rich community to the surrounding coastal waters.

The shallow lagoon areas with mud bottoms are characterized by low infaunal densities and a dearth of macroflora. Below the 2 m contour in the bays and lagoons, however, large standing stocks of invertebrates (amphipods, mysids, and isopods) are common and the LGL-Barrier Island Study (RU 467) personnel have documented the biomass in Simpson Lagoon. These invertebrates are commonly found in close association with eroded organic material from the shoreline. Studies by Broad (RU 356) have shown that certain gammarid amphipods and isopods do ingest and degrade the peat. This ingestion is probably accompanied by the removal and digestion of heterotrophic microflora and microfauna that are attached to the peat particles.

Using data obtained by Lewellen (1973) and the first author during an earlier study of the Simpson Lagoon shoreline (Schell, 1975), erosion rates and the resulting quantities of carbon and nitrogen washed into the lagoon were estimated for the shoreline between Oliktok Point and Beechey Point. These estimates have been expanded by Cannon and Rawlinson (RU 530) to include all of Simpson Lagoon and are presented in Section VI. Further estimates of the total input of allochthonous carbon to the Beaufort Sea have been made by the first author and S. Rawlinson (RU 530), showing that much of the total carbon input is terrestrially derived. Additional information on the coastal erosion rates in the Elson Lagoon area near Pt. Barrow are available from Lewellen (1970), and average coastal erosion rates are presented in Lewellen (1977). Hopkins and Hartz (1978) prepared a map of mean erosion rates along the boundaries of the National Petroleum Reserve - Alaska. All of these data are derived from the comparison of aerial photo profiles of beaches made in 1949, 1955, and within the last few years.

The other data required for accurate estimates of erosional inputs of carbon are the stratigraphic section compositions of the eroding bluffs. We have obtained eight profiles of eroding bluffs along the coast between Cape Halkett and Simpson Lagoon, including two from the Colville River at Ocean Point and Sentinel Hill. S. Rawlinson (unpublished data) has approximately 100 vertical bluff sections obtained between the Colville River and Flaxman Island, and has found the peat layer thickness to range between 10 and 220 cm and average about 50 cm. The thickness of the peat layer is highly variable along a small length of beach due to ice wedges and surficial relief of the polygons. Yet for the purpose of calculating gross peat inputs, the usage of this mean thickness of 0.5 m seems reasonable based upon the stratigraphic data. The implications of this compartmentalization of the energy input to the marine ecosystem are discussed in Section VI.

Natural Carbon Isotope Abundances

The usage of natural carbon isotope abundances to trace foodwebs is a relatively recent development, and this study is the first to successfully use both $^{13}C/^{12}C$ and $^{14}C/^{12}C$ ratios simultaneously. The rapid expansion of the literature on isotopic fractionation in foodwebs during the past few years is testimony to the desirability of new techniques in this field, although there have been conflicting interpretations in some of the studies (see, for example, Peterson et al., 1980). Most of the work to date has arisen from the usefulness of $^{13}C/^{12}C$ ratios separating vegetative carbon arising from C-3 and C-4 plants (Haines, 1976a, b; DeNiro and Epstein, 1978; Teeri and Schoeller, 1979). Where the inputs of terrestrial carbon constitute a significant fraction of the energy supporting nearshore marine ecosystems, such as in estuaries, stable carbon isotopes have proven somewhat useful in delineating probable energy sources to higher organisms (Haines and Montague, 1979). But as Peterson et al. (1980) pointed out, there is considerable ambiguity arising from the usage of a single isotopic marker in environments where a wide range of natural abundances may be found due to biochemical fractionation in foodwebs and differing photosynthetic pathways.

Within the marine environment, fractionation of stable carbon isotopes due to temperature effects has been documented (Sackett et al., 1965), and the contribution of terrestrial carbon to marine sediments was demonstrated by Gearing, et al. (1977). McConnaughey and McRoy (1979a, b) used $^{13}C/^{12}C$ isotope ratios to trace the importance of eelgrass (*Zostera marina*) to Bering Sea foodwebs and documented the natural isotopic abundances for many Bering Sea organisms. Carbon isotope ratios in deep sea hydrothermal vent mussels have been used to imply chemosynthetic food sources for organisms in this unusual environment (Rau and Hedges, 1979).

Although the preceding samples of studies using stable carbon isotope ratios demonstrate a growing interest in this technique, the carbon storage pools of the arctic environment have allowed us to take advantage of a second natural isotopic marker to determine foodweb pathways and to quantitate inputs with much greater precision. The great chronological age of the peat deposits has resulted in a marked ^{14}C depletion in this carbon source that is easily distinguished from modern sources. This radioactive marker, when used in conjunction with the stable isotope abundances of the various primary producers, has offered considerable insight into the interdependencies of nearshore arctic foodwebs.

IV. STUDY AREA: BEAUFORT SEA (90 PERCENT)
CHUKCHI SEA (10 PERCENT)

The study area for this project has been shifted from the originally proposed Elson Lagoon-Dease Inlet area near Point Barrow to the Stefansson Sound-Simpson Lagoon area approximately 60 km west of Prudhoe Bay, and then to the Sale 71 area in Harrison Bay. This shift in siting was made to allow integration with the tasks being undertaken by other OCSEAP investigators. The principal data collection and detailed analyses on primary production and heterotrophic production have now been made along most of this coastline. However, in conjunction with RU 530, estimates of terrestrial input of carbon along the entire Beaufort Sea coast via runoff and erosion have been undertaken in a much less detailed program west of Cape Halkett.

Laboratory experiments to determine the mechanisms by which trophic movement of peat carbon occurs were conducted at the Naval Arctic

Research Laboratory at Point Barrow. The ready availability of amphipods and isopods in Elson Lagoon allowed controlled laboratory experiments on cellulose biooxidation with freshly collected animals.

Stefansson Sound

Stefansson Sound extends from the Midway Islands in the west to Tigvariak Island in the east, and is enclosed by the protecting barrier island chain that consists of the McClure Island, Dinkum Sands, Cross Island, and the Midway Islands (Fig. 1k). Water depths in Stefansson Sound do not exceed 10 meters, and range from three to nine meters within the Boulder Patch. Waves have a short period because of shallow depth and limited fetch. Even during storms, waves rarely exceed 1.5 meters. Currents are predominantly wind driven during the open-water period, when easterly winds dominate. Therefore, the net drift is westward during the summer (Barnes et al., 1977; Matthews, 1981a, b). The rivers discharging into the sound supply only sand-size and finer materials. Peak discharge occurs in June following the river breakup, but very little sediment accumulates within the sound (Reimnitz and Ross, 1979). Currents are very weak to undetectable during the period of total ice cover (from mid-October through June). Bottom water temperatures in the vicinity of the Boulder Patch range from a nearly constant -1.9°C under the sea ice to 7°C during the open-water period. Salinity varies from 14 to 35 $^{o}/oo$ (Barnes et al., 1977). With the exception of the Boulder Patch, the bottom is characterized by silty sands and mud, and an infaunal assemblage dominated by polychaete worms, small molluscs and crustaceans (Feder and Schamel, 1976; Broad et al., 1978).

Freeze-up is usually complete by mid-October, and breakup begins in late June or early July. The benthic environment is largely protected by the offshore islands and shoals from gouging by deep draft ice. The winter ice field within Stefansson Sound is shorefast (i.e., attached to the shore), with minimal movement from early November through June. Ice thickness reaches a maximum of 2 m in early May before deterioration of the ice canopy begins.

V. SOURCES, METHODS, AND RATIONALE OF DATA COLLECTION

Primary Production by Epontic (Ice) Algae

The sampling program for ice algal production and spatial distribution occurred during the spring months and involved sampling the ice-water interface before and after the ice algal bloom. The first sampling period was during early April and yielded water chemistry data representing the maximum nutrient concentrations and salinities of the annual cycle. Fall 1980 saw the first ice algae sampling during freeze-up.

The second sampling trip of the spring, in late May, coincided with the maximum standing stocks of ice algae. Ice cores, water samples, and nutrient samples were taken at this time to estimate ice algal and phytoplankton biomasses in the water column. In order to expedite sampling and handling of collected ice cores, the ice algal biomasses were estimated via indirect techniques. Total in vivo fluorescence measurements were made on the melted core samples (or on diluted aliquots) and converted to dry weight by cross calibration with laboratory cultures of known algal populations. Since fluorescence is dependent upon many factors (among which physiological state, algal morphology, and past light history are very important), the algal biomasses shown are primarily for comparison and secondarily for quantification. These data are useful in projecting primary productivity estimates for the lease area.

Annual primary productivity by ice algae was also estimated using indirect methods based upon algal biomass and short-term primary productivity measurements. Our summarized results are semiquantitative at best (see Table 5 in Results and Discussion section). The estimates by Horner et al. (1974); McRoy and Goering (1976); Horner (1980), and this study are all based upon the extrapolation of standing stock data and short-term primary productivity experiments. Errors due to grazing, diurnal variations in light, loss of standing stock during sampling, etc., were approximated, but the paucity of data does not allow meaningful confidence levels. Station maps and sample locations are shown in Figure 1.

Analytical methods employed for nitrate, ammonia, and phosphate analyses are similar to those utilized by Alexander et al. (1974) for their ice algal studies. Particulate nitrogen analyses were run on glass fiber filters containing particulate material from melted ice cores or underlying water. The filters were burned, and the evolved nitrogen gas was measured using a Coleman Nitrogen Analyzer.

Phytoplankton Primary Productivity

Primary productivity measurements were made by filling three 150 ml glass bottles with water from each sample depth. A dark bottle blank (non-photosynthetic uptake correction) and two clear bottles were injected with 5.0 μCi of ^{14}C-labelled sodium bicarbonate, placed in a plastic basin under 5-10 cm of cold (<10°C) water, and incubated in sunlight. In June and July 1980, the samples were incubated for 24 hours with enough window screening covering the basin to set the light intensity at 425 microeinsteins at 1400 hours local time. The August 1980 samples were also incubated for 24 hours, but no screening was used since the skies were heavily overcast. In August 1981, the incubation period was reduced to 5 hours and the light intensities were adjusted to simulate in situ conditions by adding layers of screening until the same percentage of surface light (measured just below the water surface) was removed by the screens as was removed by the column of water above the sample depth. The light intensities in the tubs were 60 percent, 20 percent, 10 percent, 1 percent and 0.1 percent of surface light, and corresponded well with the light intensities measured in situ. In May and June 1982, the incubation period was 18 and 24 hours at simulated in situ light intensities.

At the end of an incubation, samples were filtered through 0.45 μm Millipore filters using weak suction, fumed with HCℓ vapors, and the filters were placed in scintillation vials. In Fairbanks, scintillation cocktail was added to the vials and the samples were counted in a Beckman LS-100 Liquid Scintillation System. Sample counting rates were

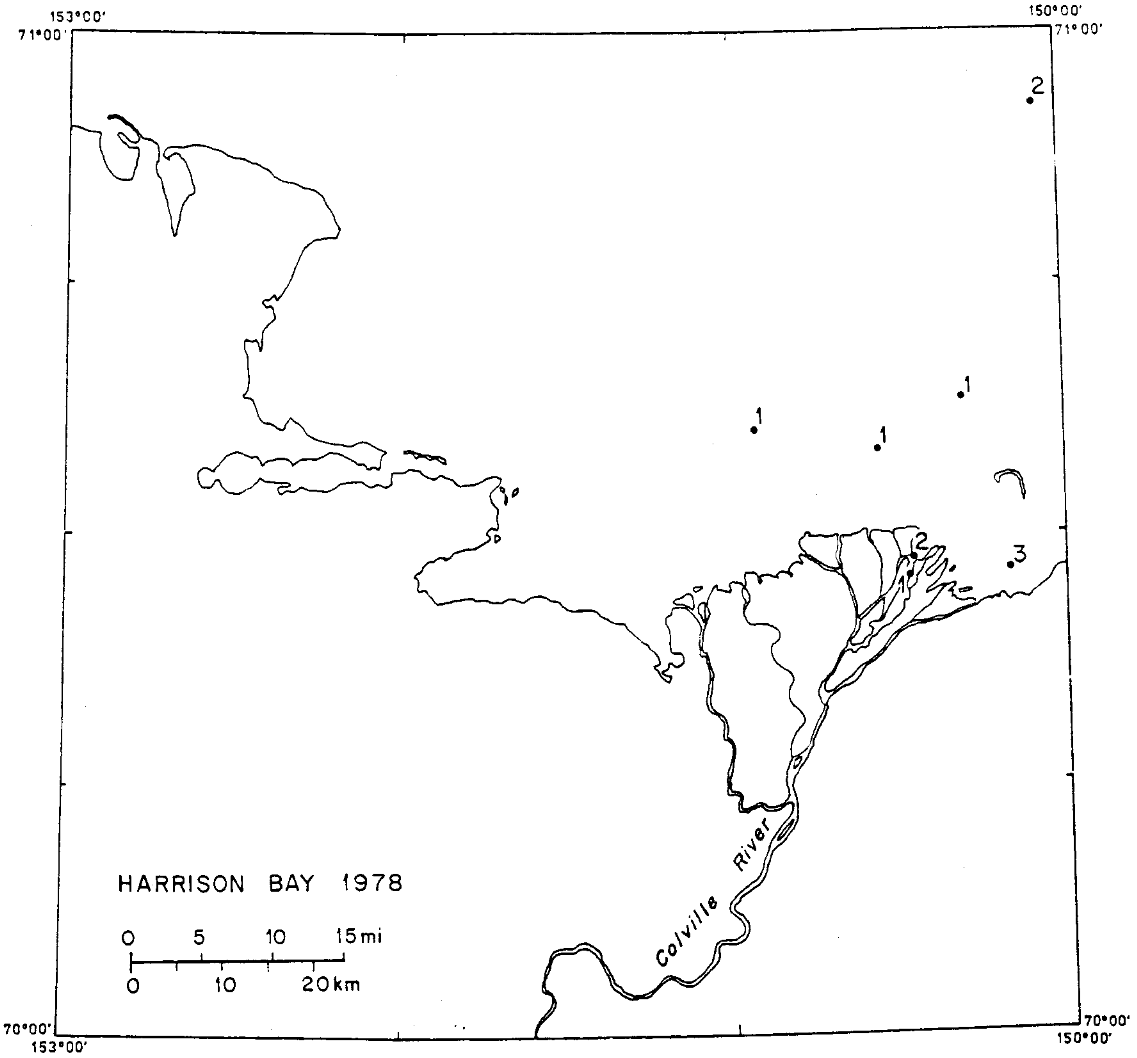

Figure 1A. Station locations and number of times occupied, 1978

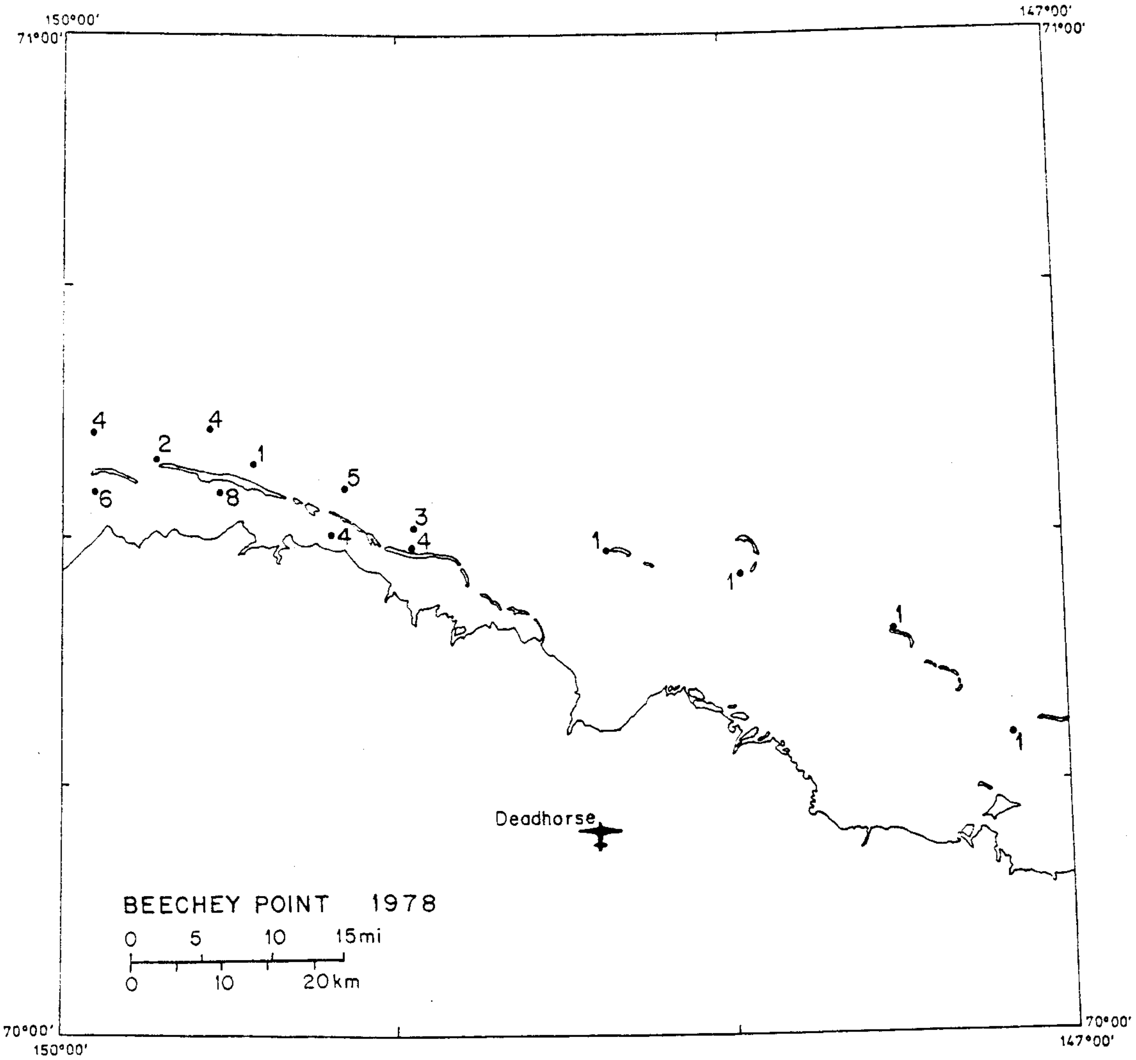

Figure 1B. Station locations and number of times occupied, 1978.

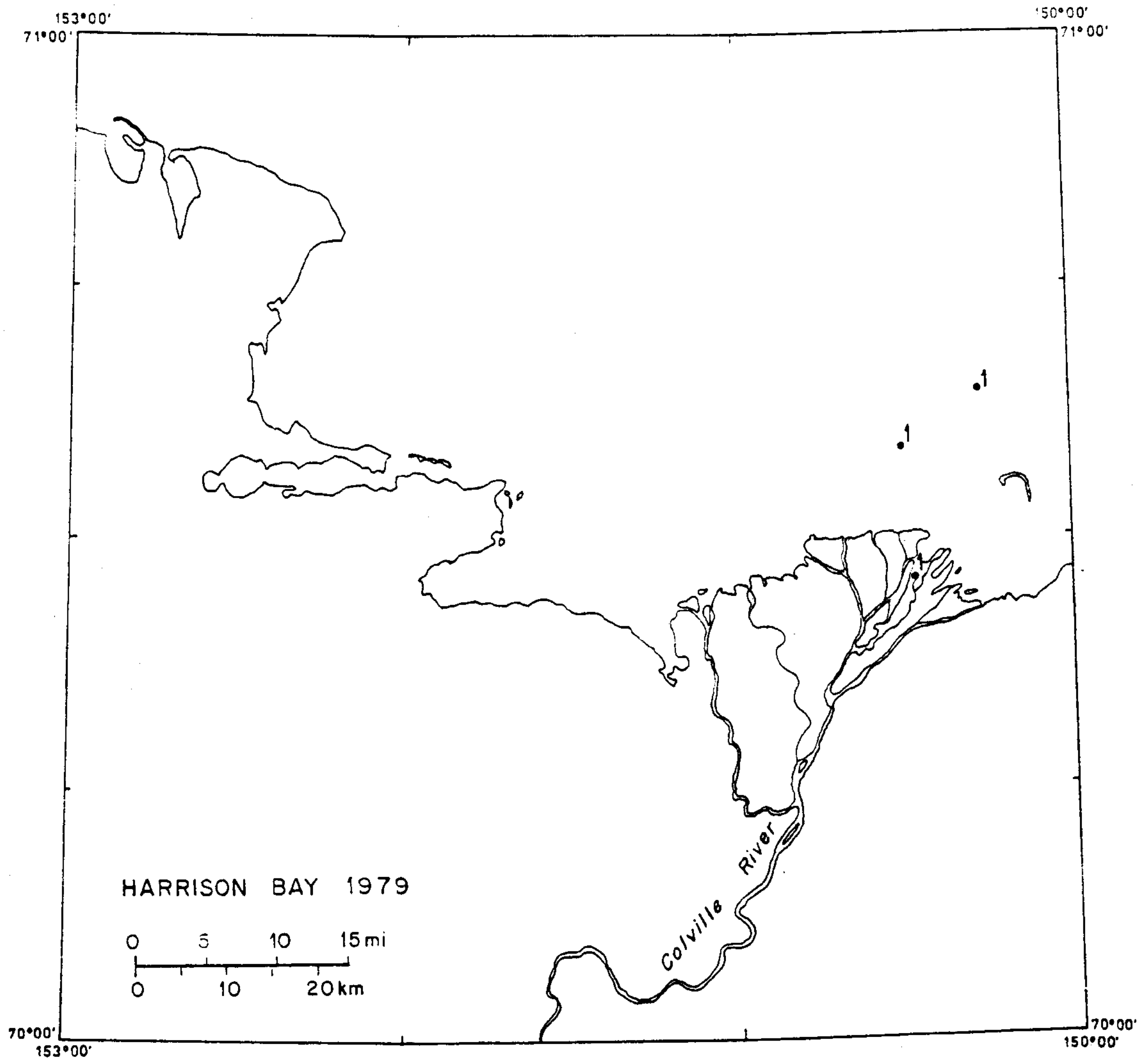

Figure 1C. Station locations and number of times occupied, 1979.

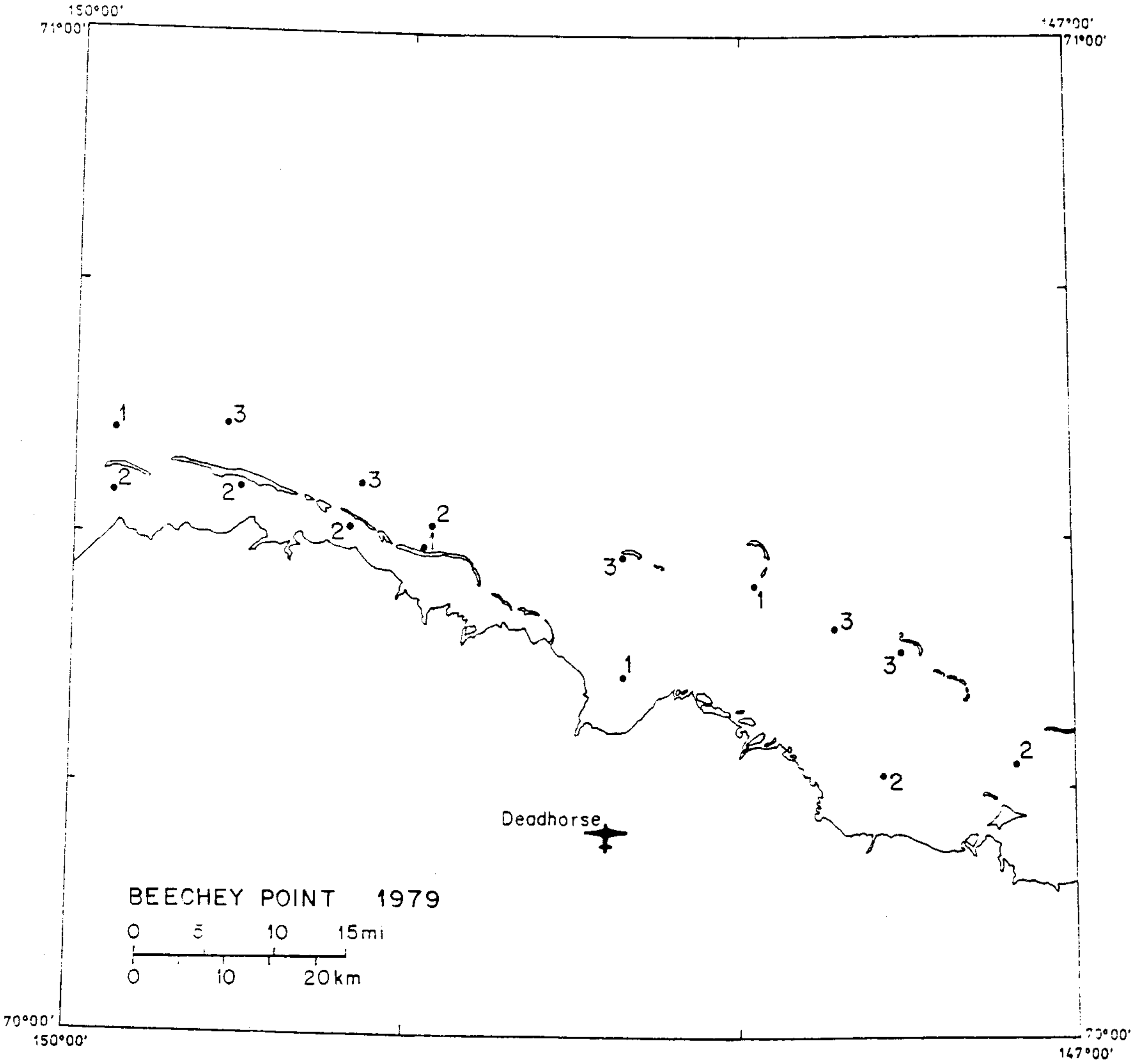

Figure 1D. Station locations and number of times occupied, 1979.

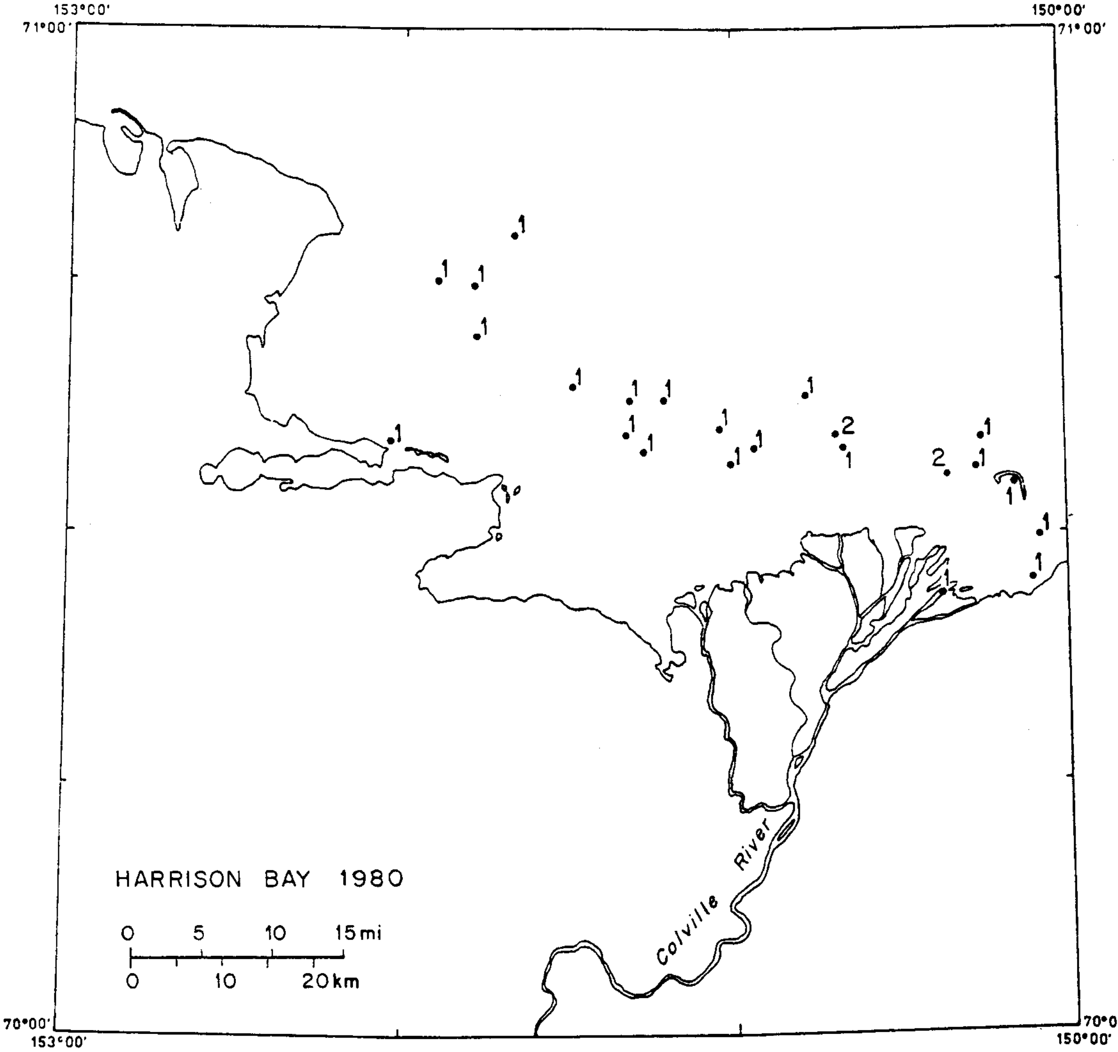

Figure 1E. Station locations and number of times occupied, 1980.

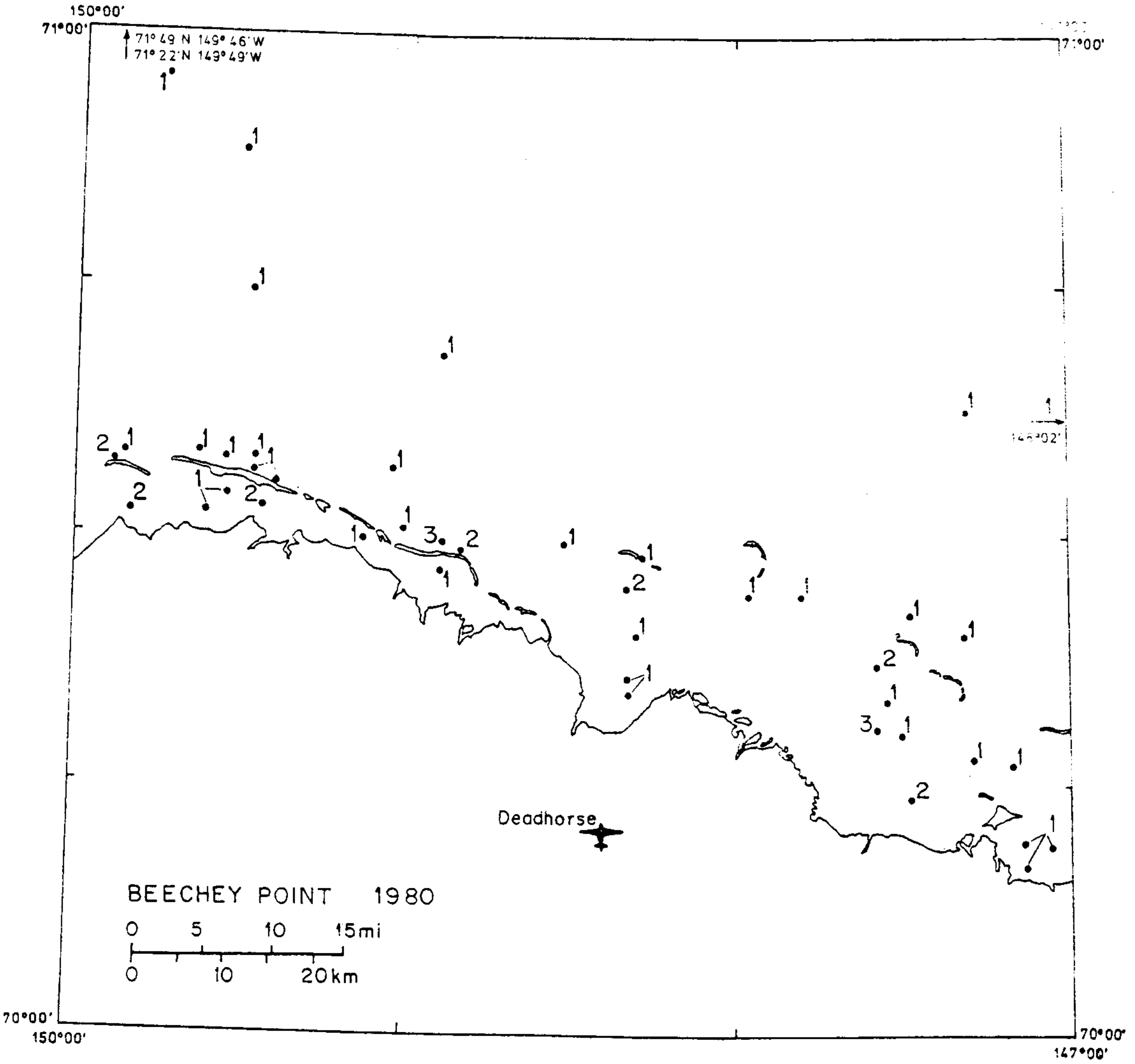

Figure 1F. Station locations and number of times occupied, 1980.

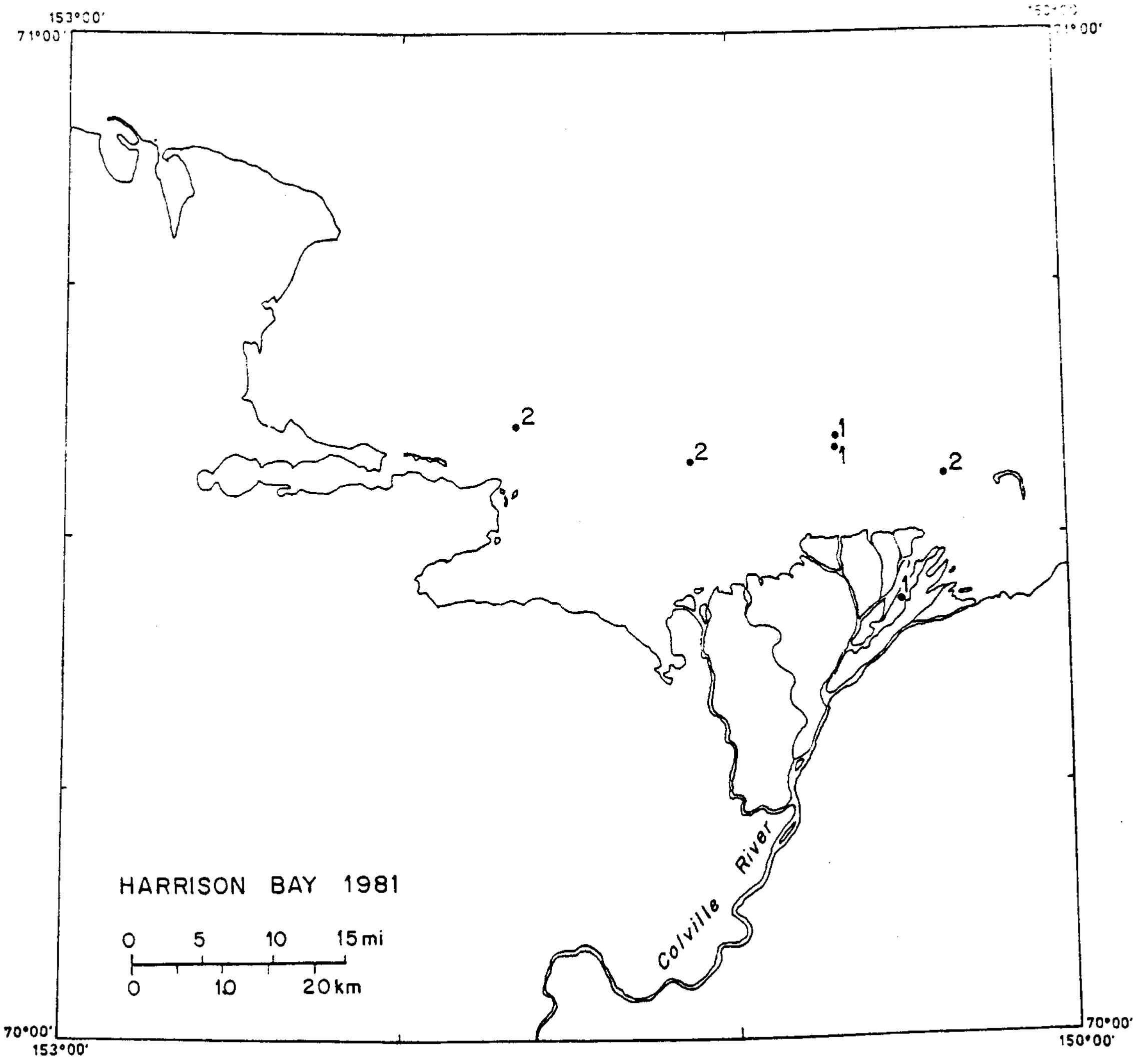

Figure 1G. Station locations and number of times occupied, 1981.

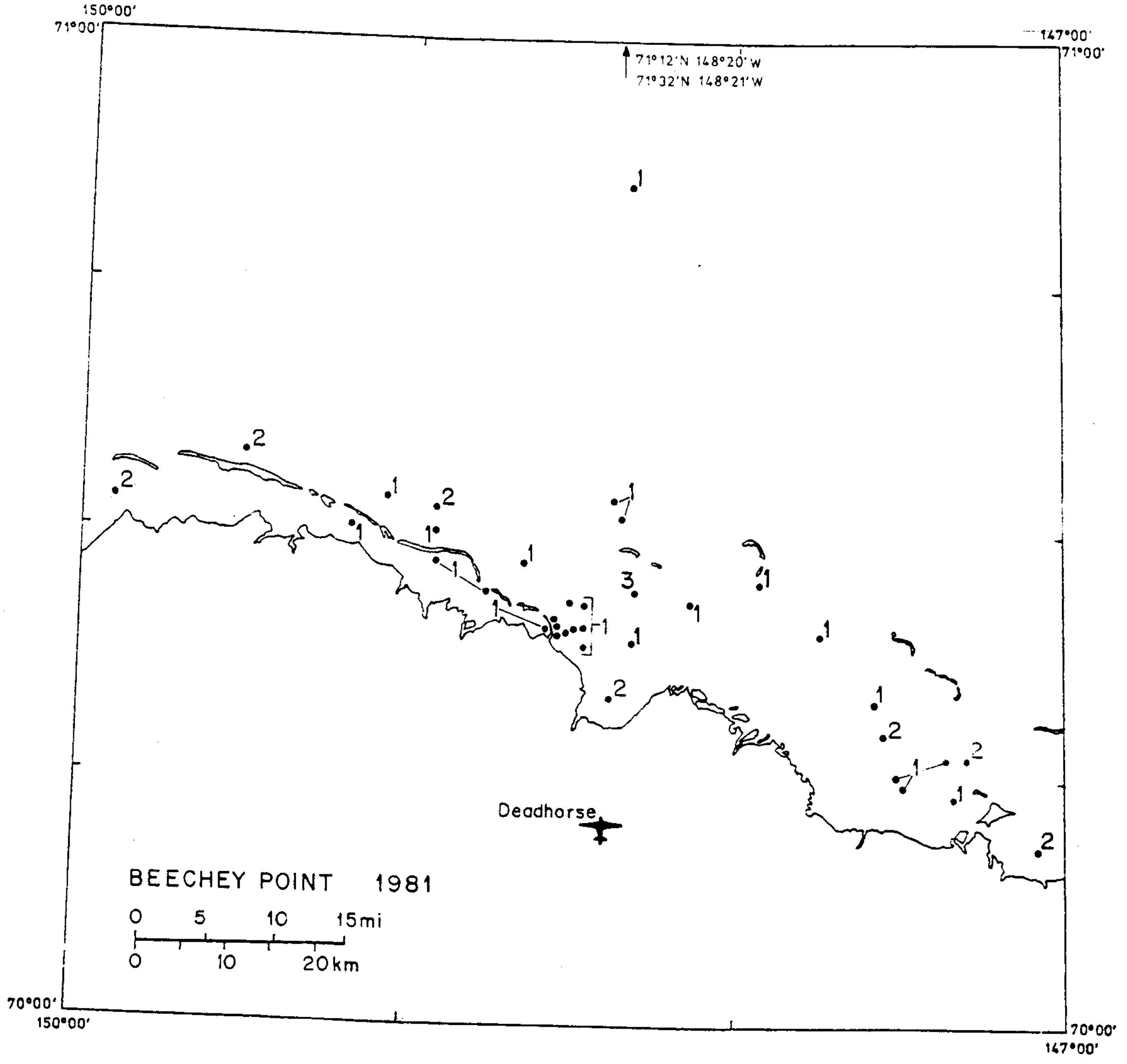

Figure 1H. Station locations and number of times occupied, 1981.

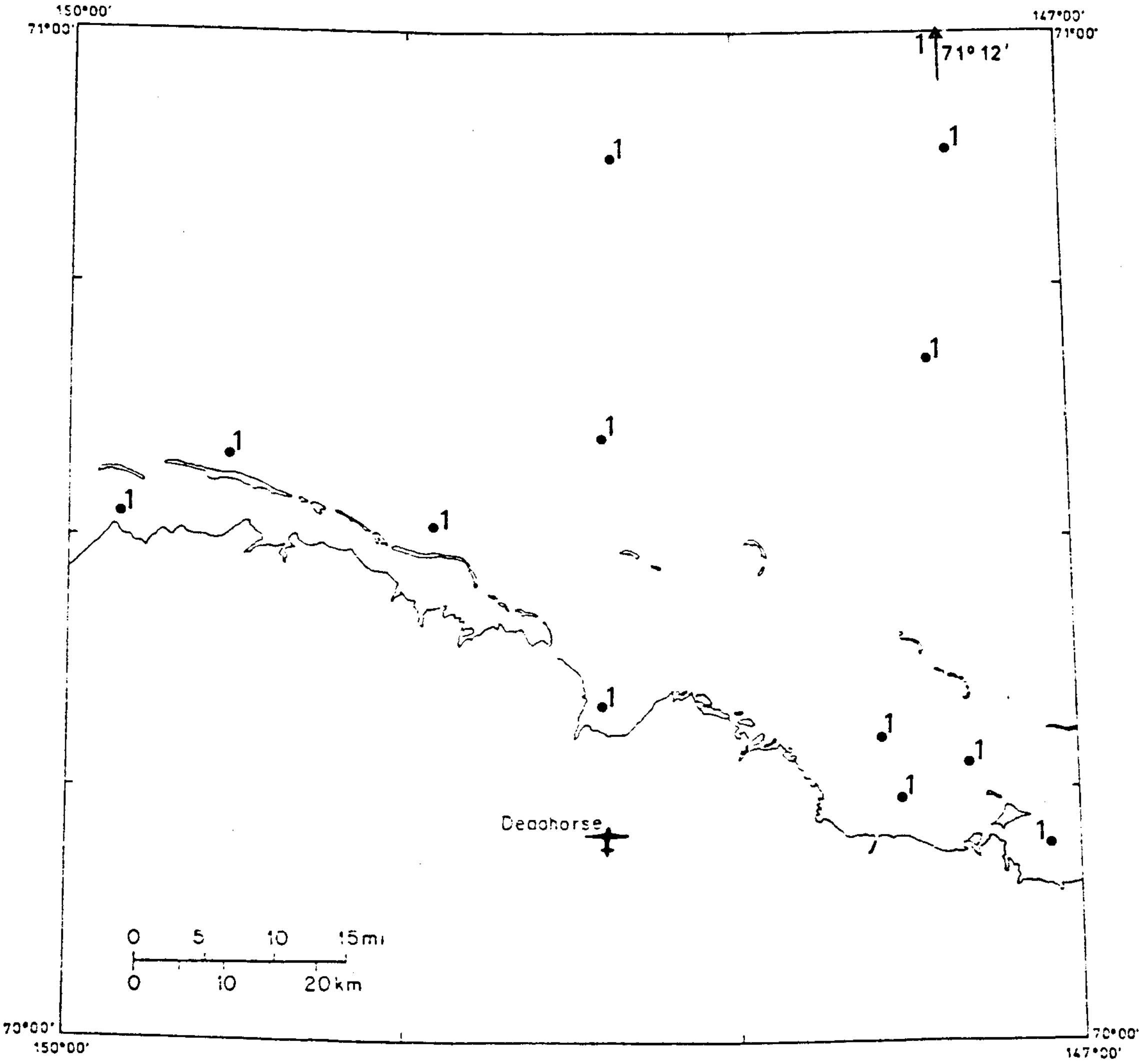

Figure 11. Station locations and number of times occupied, 1982.

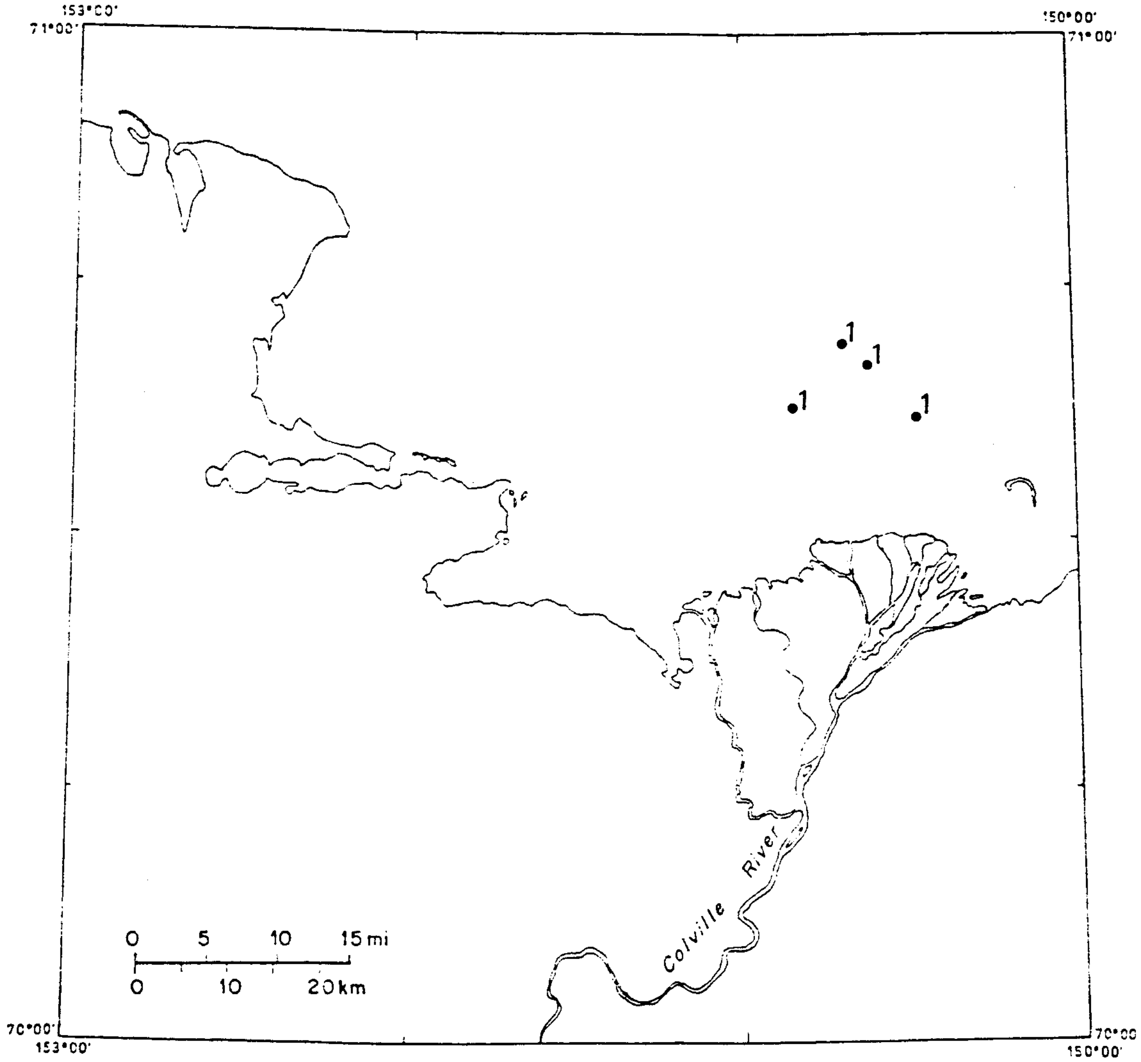

Figure 1J. Station locations and number of times occupied, 1982.

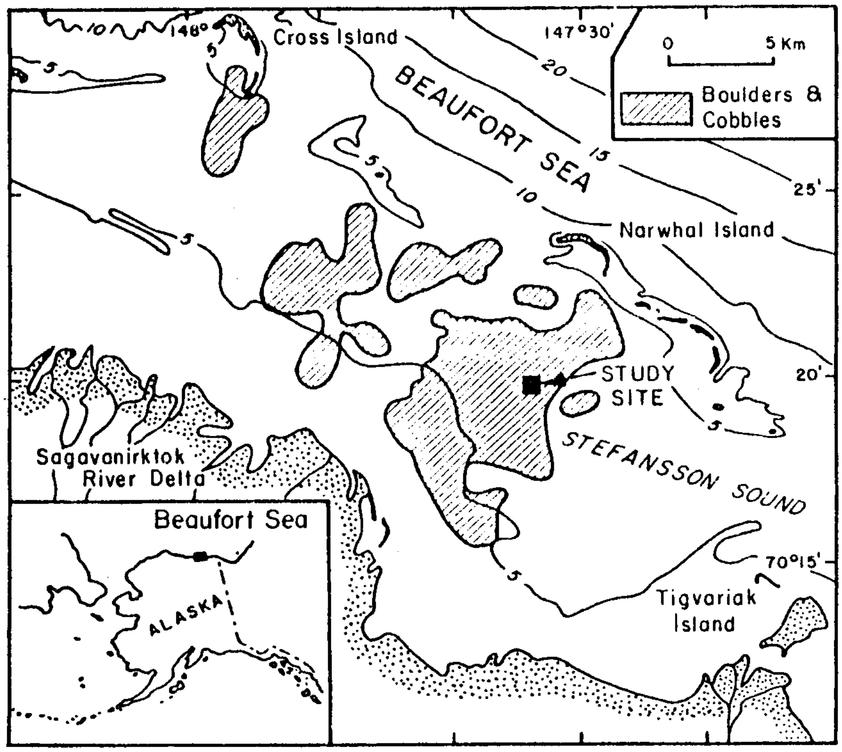

Figure 1K. Location of the Boulder Patch in Stefansson Sound (from Reimnitz and Ross, 1979). Depths in meters.

corrected for quench using a regression equation (r = 0.98) developed from the external standard channels ratios and the counting rates of standards of known quench. The photosynthetic rate was then calculated according to Strickland and Parsons (1972).

Annual Primary Production Estimates

Seasonal production was estimated by two methods: 1) integration of ^{14}C uptake rates over monthly intervals with a correction for ice cover; and 2) by calculating the biomass that could be supported through uptake of the available inorganic nitrogen. Since late-winter water column samples were characterized by high nitrate concentrations relative to ammonia, nitrate depletion was used as the principal indicator of uptake. Although there appears to be considerable variation in maximum nitrate concentrations in late winter from year to year, concentrations were sufficiently uniform spatially and with depth to allow area-wide extrapolation of uptake rates.

The ^{14}C uptake data used to calculate seasonal production have been summarized in Table 4. The major task in the extrapolation of integrated uptake rates over a wide area was to account for the variable ice cover and low solar angles over the summer. We used the data compiled by W. Stringer et al. (1981) to obtain average and dominant ice concentration data in the Harrison Bay-Prudhoe Bay area, and large-scale satellite imagery (Defense Meteorological Satellite Program)(see below) from the period 1978-1980 to establish ice-cover patterns over the entire Beaufort Sea region. Although cloudy weather prevented data acquisition over much of the summer, the generalized patterns of ice retreat were readily evident. Based upon these images, average ice retreat curves were drawn over a contour chart of the area. Integrated daily primary productivity rates were then multiplied by the period of open water available. Beneath ice cover, the light intensity was assigned a value of 10 percent of open water values based upon measurements made through offshore sea ice north of Narwhal Island in June and early June, 1980. An additional problem in calculating euphotic zone depths arises from the high incidence of cloudy, dark weather and the effects of low solar angles on light transmission to deep water.

Instantaneous ^{14}C data were obtained by "correcting" the rates given by Horner, 1980. We assumed that the methodology employed, in which the filtered cells were rinsed with 0.01 HCℓ, resulted in a loss of about 25 percent of the photosynthate (Allen, 1971).

Nimbus-7 Coastal Zone Color Scanner (CZCS) and Defense Meteorological Satellite Program (DMSP)

The possibility of obtaining wide scale estimates of phytoplankton standing stocks in the Beaufort Sea through use of the CZCS led us to attempt to acquire imagery from the Beaufort Sea in 1981 and 1982. Beginning on 26 July 1981, weekly pictures were taken from north of Alaska and accumulated at the Scripps Remote Sensing Facility at the University of California. Unfortunately, very poor weather conditions prevented the acquisition of even one image of wide scale usefulness. Furthermore, ground haze and the extreme variations in reflectivity between ice cover and the sea surface complicated the areas which were relatively clear in the images. Although one of us (DP) has been trained in CZCS data processing, the very poor image quality obtained and sharp increase in computer facility costs at Scripps caused us to drop this approach in favor of using information from large scale imagery.

We were fortunate to have access to a comprehensive selection of Defense Meteorological Satellite Program (DMSP) imagery in the library of the Geophysical Institute, University of Alaska. By reviewing the images available over the period 1978-1980 we were able to estimate the "average" position of the ice edge during the summer months. We then used this information to calculate ice-free days for projecting euphotic zone depths.

Utilization of Detrital Carbon and Transfer Efficiency Determination

The magnitude of detrital carbon input to the nearshore zone of Simpson Lagoon (Figure 2) required that the effects of this energy source be evaluated with respect to the inputs of primary production. Detrital input occurs through essentially two sources -- coastal erosion and runoff from the tundra. Thus, assessment of these inputs becomes a geomorphological problem for the former source and a hydrological problem for the latter. Chemical data on the eroded tundra have been previously obtained by Schell (1975) and have been refined through additional work since beginning this study. Vertical profiles of newly exposed permafrost shoreline bluffs at Milne Point and Pingok island were obtained in August 1978. Additional profiles of carbon content in eroding peat were obtained along the Colville River and western Harrison Bay during summer 1980.

Refinements in shoreline erosion rates along the Beaufort coast were determined by Cannon and Rawlinson (RU 530). Total organic carbon data for the Colville River waters have been kindly provided by the U.S. Geological Survey (Charles Sloan, personal communication) and flow data are available from the literature (Arnborg et al., 1967; Walker, 1974).

The utilization of detrital organic carbon by heterotrophs and the further transfer of this carbon into the foodweb has been investigated through the use of carbon isotope ratios in the various coastal marine living and nonliving organic materials. Figure 3A shows the three fractions that can comprise the organic carbon of a detritivore or their predators. The analytical techniques employed to identify these fractions are shown in Figure 3B. If the carbon in the eroded peat materials of the shoreline is incorporated to a significant extent into heterotrophic microorganisms, and these are then consumed and assimilated by benthic invertebrates such as amphipods, isopods, and mysid shrimp, then isotopic abundances in the higher organisms should reflect this food source with some variation ($\pm 1^{o}/oo$) due to biochemical fractionation. The data described below support this premise.

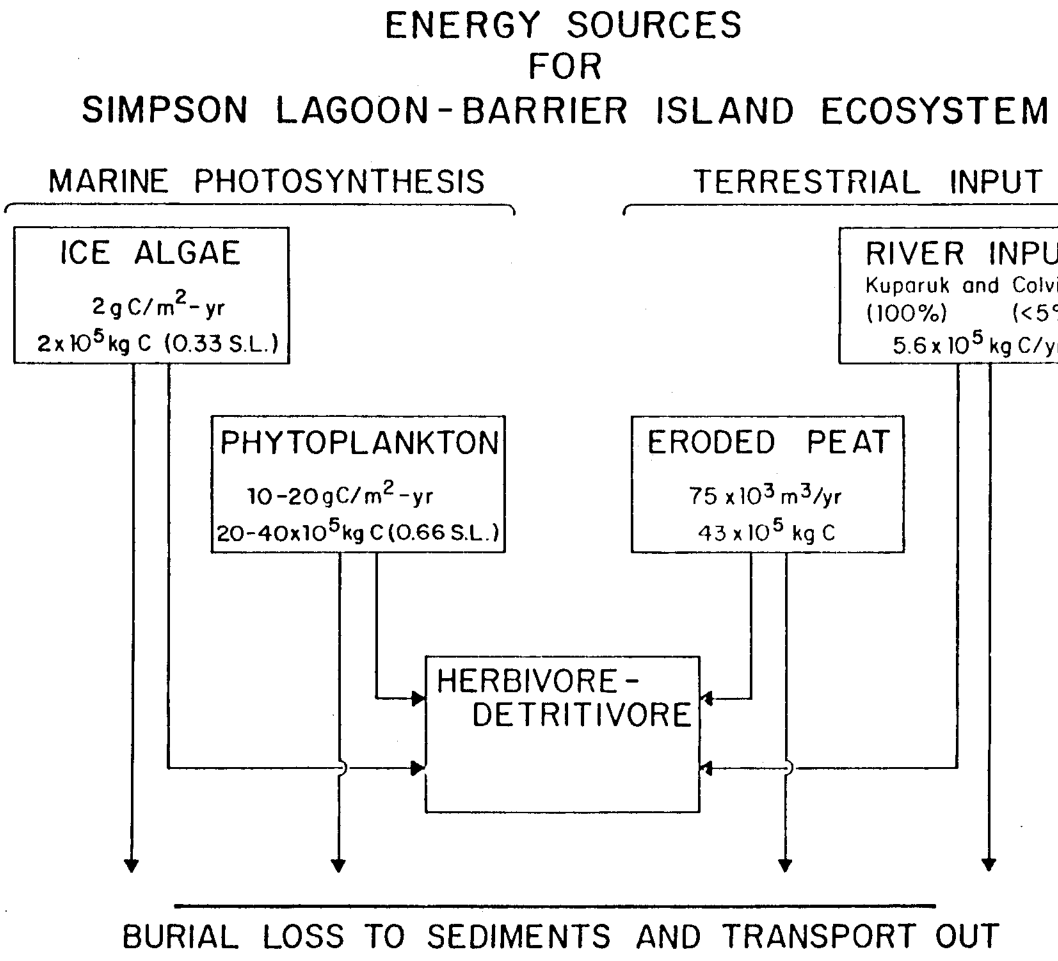

Figure 2. Box model of annual energy inputs to the Simpson Lagoon-Barrier Island ecosystem.

Stable isotope techniques allow the discrimination of food sources in ecosystems where the source materials (primary producers) have significantly different $^{13}C/^{12}C$ ratios. By comparing $^{13}C/^{12}C$

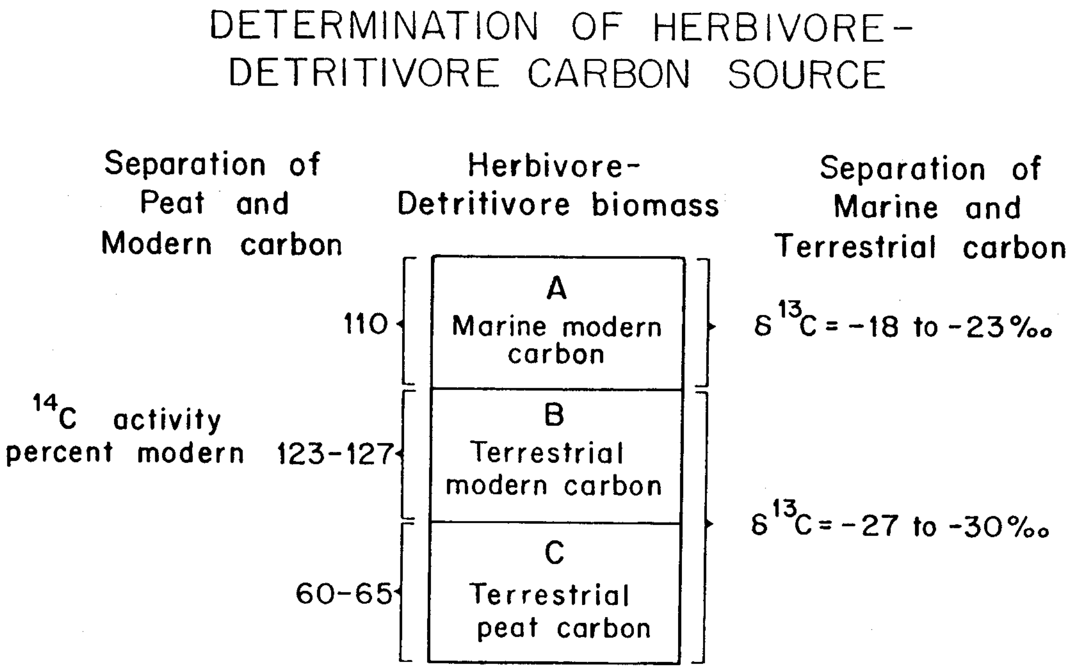

Figure 3A. Isotopic techniques for allocation of energy sources to consumers.

RADIOCARBON DATING

$$\%C = \left[\frac{\text{Mean peat age} - \text{Sample age}}{\text{Mean peat age}}\right] \times 100$$

$$\%\,A+B = 100 - C$$

= percent modern carbon (marine and terrestrial)

STABLE ISOTOPE RATIOS

$$\%A = \frac{{}^{12}C/{}^{13}C(\text{terr.}) - {}^{12}C/{}^{13}C(\text{sample})}{{}^{12}C/{}^{13}C(\text{terr.}) - {}^{12}C/{}^{13}C(\text{marine})} \times 100$$

$$\%B = 100 - (A+C)$$

= carbon derived from modern terrestrial sources.

Figure 3B. Allocation of carbon fractions in Figure 3A.

ratios of organisms at different trophic levels, the food sources of the higher organisms can be apportioned. This technique has been used by McConnaughey (1978) to study the detrital input of eelgrass beds in Izembek Lagoon to the fauna of the lagoon and nearshore Bering Sea. Although the method is acknowledged to be less sensitive than ^{14}C dating, the applicability to modern carbon sources increases its desirability and analytical cost is low compared to ^{14}C dating.

Samples for stable carbon isotope and radiocarbon analyses were treated as follows.

Lake sediments: Samples were collected either by Ekman dredge or by cores pushed by hand into the bottom. Samples were sectioned horizontally in sufficient size to yield at least 5 g of carbon. After suspension in dilute hydrochloric acid to remove carbonates, samples were settled, decanted, rinsed with distilled water, and dried (70°C) in a vacuum oven.

Peat soils: Sample sites were chosen where erosion had exposed a fresh break in the permafrost. Pick and shovel were used to dig to undisturbed permafrost and a vertical section was made at 10 cm intervals from beneath the vegetation surface mat to basal mineral soils. In some cases, layers of mineral soils were interposed between peat layers, and the gradation into basal mineral soils was indefinite. Samples were kept frozen until returned to the laboratory where they were thawed and the moisture contents were determined. A subsample of the dry peat was ground to a powder for carbon, nitrogen, and phosphorus determination, and further subsamples were used for loss-on-ignition, radiocarbon content, and stable carbon isotope ratios.

Animal tissues: Organisms collected for isotopic analysis were kept frozen in sealed polyethylene bags until returned to the laboratory. After thawing, small organisms such as mysids, amphipods, isopods, lemmings, and *Daphnia* were dried whole in a vacuum oven (70°C). Since these animals were not acidified prior to combustion an error in $\delta^{13}C$ due to carbonate inclusions may have occurred in amphipod samples. Subsequent analyses have shown this error to be +1.58. Larger organisms such as fishes and birds were skinned, and the muscle tissue dried for analysis. Large animals such as caribou, bowhead whales, and seals were subsampled for muscle and fat tissue. The whale and seal oil was rendered by heating to 80°C in a vacuum oven, and the oil poured off into a vial.

Vegetation: Fresh samples of aquatic and terrestrial plants were collected from the tundra at Milne Point and at Colville Village in the Colville River Delta. Samples were cleaned of foreign matter and dried.

Particulate matter: Samples of riverborne detritus were collected by suspending a 120 micrometer mesh plankton net in the Colville and Kuparuk rivers until sufficient material had been collected to assure 5 grams of carbon. No attempt was made to isolate any insect larvae or other living organisms from the collected material, since inspection did not reveal significant quantities present. Samples were dried in vacuo prior to analysis.

Carbon Isotope Analyses

All samples were sent to commercial laboratories specializing in radiocarbon analyses. Stable carbon isotope ratios were run on the same samples. Laboratory identification in the table of carbon isotope data (see Section VI) can be made from the second identification number with each sample: GX = Geochron Laboratories Division, Kreuger Enterprises, Cambridge Massachusetts; UM = University of Miami, Department of Geology, Miami, Florida; I = Teledyne Isotopes, Westwood, New Jersey; Beta = Beta-Analytic, Inc., Coral Gables, Florida. Radiocarbon activity was reported as percent modern normalized to $\delta^{13}C = -25\ ^{o}/oo$ to allow direct comparison among samples. Where the analytical precision was reported by the company, it is included in the data listing.

Cellulose Biodegradation Studies

Process studies to measure the rate of cellulose biodegradation in the under-ice waters of the Beaufort Sea were undertaken at the Naval Arctic Research Laboratory at Barrow. Water samples were collected at stations in Elson Lagoon, Smith Bay, and Dease Inlet. A big-tired truck was used for transportation on Elson Lagoon ice and a Cessna 180 ski-equipped aircraft was used to sample the latter two locations. In July 1979, hand netting of amphipods was employed to collect specimens of *Gammarus setosus*.

A baited trap was set overnight in Elson Lagoon. Upon retrieval, approximately 200 *Onisimus* and *Boeckosimus* amphipods were captured. These animals were used to investigate their ability to digest cellulose through a series of experiments employing ^{14}C-labeled cellulose mixed with peat samples obtained from Simpson Lagoon. Similarly, the microbial activity in the detrital peat was studied by measuring the production of radiolabeled CO_2 from added ^{14}C-labeled cellulose. Samples of seawater were incubated with ^{14}C-labeled cellulose, and aliquots were taken at approximately 12-hour intervals. These aliquots were acidified and stripped with nitrogen to remove the carbon dioxide fraction, which was subsequently absorbed in phenethylamine liquid scintillation cocktail. These experiments, conducted at 0° and 20°C, showed active microbial decomposition and oxidation of the labeled cellulose, with the fastest rates occurring at 20°C.

To test the hypothesis that *Onisimus* and *Boeckosimus* spp. possessed intestinal microflora which were active cellulose degraders (and thus were able to symbiotically contribute to the nutrition of the amphipods), an experiment was conducted using freshly captured animals fed on radiolabeled cellulose. Animals were offered both carrier-free and a mix of labeled cellulose and peat aged in seawater. A control of peat plus labeled cellulose without amphipods was used to determine the oxidation rate due to microflora alone. At 12 hour intervals, animals were sampled, and aliquots of seawater were stripped for radiolabeled carbon dioxide as described above.

Similar experiments were repeated in July 1979 at the Naval Arctic Research Laboratory in cooperation with Dr. David Schneider (RU 356) to test if the known detritivorous amphipod, *Gammarus setosus* could utilize cellulose. Experiments were conducted as described above using both *G. setosus* and *Onisimus* spp. at 0° and 8°C. The intestinal tracts of the *G. setosus* amphipods were surgically removed and the radioactivity of the guts and bodies determined separately. Each sample of tissue was

TABLE 1: Percent moisture, loss-on-ignition, carbon, nitrogen, and phosphorus in Beaufort Sea coastline and Colville riverbank soils.

STATION	LOCATION	DATE	DEPTH INTERVAL (cm)	SOIL MOISTURE	LOSS ON IGNITION	CARBON	NITROGEN	PHOSPHORUS
				(--------------------Percent of dry weight				------------------)
OCEAN POINT	70°4.3'N 151°22.5'W	5 AUG 80	0-10	35	8.7	3.0	0.14	0.09
			20-30	61	15.4	6.8	0.37	0.08
			40-50	118	26.5	15.7	0.69	0.07
			60-70	171	26.0	10.9	0.74	0.08
			110-110	148	15.5	6.2	0.39	0.08
			130-140	44	6.2	2.1	0.15	0.09
ATIGARU POINT	70°333'N 151°42.1'W	6 AUG 80	0-10	71	26.1	9.9	0.89	0.04
			20-30	23	8.9	6.1	0.24	0.03
			40-50	6	1.6	0.7	0.17	0.04
CAPE HALKETT	70°48.0'N 152°10.0'W	6 AUG 80	0-10	393	50.0	33.3	2.24	0.18
			10-20	66	16.2	4.5	0.51	0.06
SENTINEL HILL	69°51.0'N 151°36.0'W	5 AUG 80	0-10	30	38.7	17.9	1.03	0.07
			50-60	166	74.0	31.1	2.00	0.04
			180-190	424	56.0	31.2	2.24	0.05
ESOOK	70°08.1'N 152°33.8'W	5 AUG 80	0-10	57	3.5	5.1	0.49	0.07
			20-30	167	8.5	22.2	1.80	0.06
			50-60	26	2.3	1.6	0.04	0.07
MILNE	70°31.0'N 149°27.6'W	9 AUG 78	0-10	71	35.6	19.6	1.13	0.03
			30-40	57	38.6	20.8	1.15	0.03
			60-70	320	55.1	25.2	1.46	0.03
			90-100	436	84.5	37.8	2.33	0.02
			120-130	216	42.6	19.5	1.12	0.03
			150-160	258	57.7	28.2	1.59	0.02
			*160-170	135	35.8	18.1	0.88	0.02
PEAT ISLAND	70°34.2'N 149°34.4'W	9 AUG 78	0-10	40	15.1	5.1	0.57	0.02
			30-40	250	71.4	34.5	2.07	0.01
			50-70	373	33.3	15.5	0.85	0.03
			90-100	350	33.2	16.0	0.83	0.03
			120-130	148	19.6	9.0	0.47	0.03
			*150-160 (BASAL PEAT)	279	64.3	32.4	1.82	0.03
			170-180 (BASEMENT MINERAL)	256	4.0	3.4	0.06	0.04
SAGAVANIRKTOK RIVER	70°04.'N 149°38.0'W		*BASAL PEAT	104	20.1	13.1	0.77	0.02

*Radiocarbon dates determined.

oxidized with a Harvey Biological Oxidizer to carbon dioxide. The labeled gas was collected quantitatively in phenethylamine cocktail for scintillation counting.

Composition of Peat Soils

Peat soil samples were oven dried at 105°C for 8-10 hours to determine moisture content. Subsamples of 2-6 g were weighed in tarred crucibles, and combusted in a muffle furnace for 3 hours at 550°C, and reweighed to determine the loss-on-ignition. A longer combustion time was found to have no effect on the loss of weight. Subsamples of 10-100 mg were also combusted in a LECO TC-12 Automatic Carbon Determinator to measure the percent carbon content. Total nitrogen and total phosphorus in peat samples were determined on a Technicon II Autoanalyzer following Kjeldahl digestion.

The results of the carbon, nitrogen, phosphorus, and organic matter (as loss-on-ignition) analyses are listed in Table 1. The average for 33 peat soil samples is 16.0 ± 11.1(±1) percent carbon. A plot of percent carbon vs. percent loss-on-ignition fits the regression equation

$$y = 0.475x + 0.14 \qquad (r = 0.97)$$

where y is the percent carbon, and x is the loss-on-ignition. This yields an ash=free dry weight (AFDW) carbon content of 47.5 percent. although the temperature is high enough (~400°C) to remove CO_2 from some carbonates and water from clays, the y-intercept of almost zero and the excellent fit of the equation imply that these effects on the loss-on-ignition are small in these peaty soils. It is reasonable then that our equation should be similar to that of Ball (1964)

$$y = 0.458x - 0.4$$

in which the loss-on-ignition was determined by combusting a variety of soils at 375°C for 16 hours. This relationship will allow the estimation of carbon content in our future soil samples by measuring the

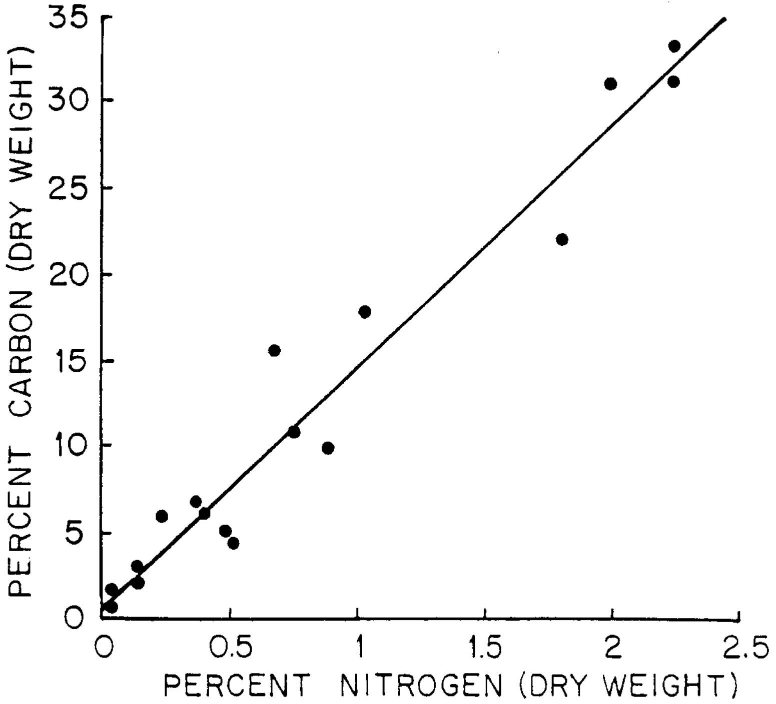

Figure 4. Carbon-nitrogen relationships in coastal and riverbank soils.

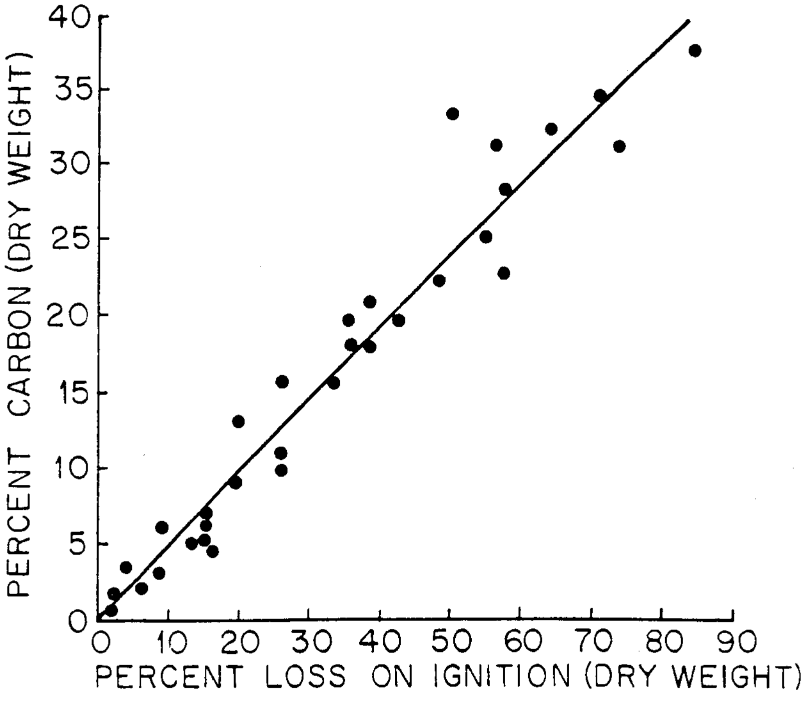

Figure 5. Loss-on-ignition and percent carbon in peat soils.

loss-on-ignition. A plot of the percent carbon vs. percent nitrogen yields the regression equation

$$y = 14.0x - 0.75 \qquad (r = 0.98)$$

where y is the percent carbon, and x is the percent nitrogen. The organic matter of these samples is, therefore, 3.4 percent nitrogen with a C:N atomic ratio of 16.3:1. The data on C:N relationships and loss-on-ignition versus carbon content are shown in Figures 4 and 5.

Chemical Analyses for Total Dissolved Phosphorus and Total and Dissolved Phosphate

A limited study of phosphate uptake kinetics was performed in 1978 in Simpson Lagoon to test if peat detritus was actively taking up phosphate from the overlying water column. Portions of bottom and surface water were analyzed for total and dissolved inorganic phosphate by the colorimetric method of Murphy and Riley (1962). The total phosphorus procedure involved a persulfate oxidation step to convert all of the phosphorus present to phosphate prior to colorimetric analysis (Gales et al., 1966). Total (persulfate labile) phosphorus was also determined on weighed portions of oven-dried peat.

Radiophosphate Uptake Measurement

For analysis of radiophosphate (^{32}Pi) uptake rates in seawater, samples of water from Simpson Lagoon (9 August 1978), and peat-amended seawater in duplicate 250 ml subsamples were removed from five gallon carboys and placed into glass bottles which had been carefully washed and pre-rinsed with the appropriate water.

To the duplicate 250 ml subsamples, amounts to equal final concentrations of 0.2 μM phosphate (^{31}Pi) plus 0.05-0.1 microcuries of ^{32}Pi were added (Rigler, 1966). Controls were poisoned with three drops of 10^{-2} M mercuric chloride, and all were incubated under constant illumination. At intervals (from 10 minutes to one day after the addition of ^{32}Pi and ^{31}Pi), 10 ml aliquots were removed and passed through 0.45 micrometer membrane filters using a constant suction of 400 mm Hg. The filters were placed in 10 ml of toluene-Triton X-100 counting cocktail, and the radioactivity was measured in a liquid scintillation counter to give (after correction for background radiophosphorus on the filter and subtraction from the total ^{32}Pi added), the amount of radiophosphorus in solution at different times after the addition.

Phosphate Uptake Rate Determinations

The rate of ^{32}Pi uptake (v*) was determined as a function of either exponential (first order) or linear (zero order) ^{32}Pi removal from solution according to Brown et al. (1978). The rate of ^{31}Pi uptake (v) was then calculated from

$$v = v^* \frac{Sn + A}{C},$$

where Sn was the indigenous ^{31}Pi level, A was the added ^{31}Pi level at time zero, and C was the total added ^{32}Pi at time zero.

Salinity Determination

Salinities were determined using a Grundy Model 6230 N salinometer to measure the conductivity ratios.

Light and Ice Sediment Load

Light measurements were made above an beneath the ice using a Photomatic light meter. Ice cores were collected with a 75 mm SIPRE corer and water samples were taken with a Van Dorn sampler. Sediment and ice algal layers observed in cores were sectioned, melted, and filtered onto precombusted, preweighed, Whatman 47 mm, glass fiber filters. When sediment content was high, the sample was well stirred to suspend the sediment, and an aliquot was removed for filtration. Filters were dried at 105°C for 8 hours and weighed to determine the amount of sediment. They were then placed in a dessicator with concentrated $HC\ell$ and fumed for 4 hours to remove carbonates, reweighed, and combusted in the LECO Carbon Determinator to measure the carbon content. The change in weight caused by fuming was negligible.

Chlorophyll-a and Phaeopigments

A Turner Designs Fluorometer (Model 10-005) was used to measure the in vivo fluorescence in sectioned and melted cores. The melt water was then filtered on Gelman Type A/E 47 mm glass fiber filters with a few drops of $MgCO_3$ suspension added as a preservative. The filters were folded in half, placed in glassine envelopes, and frozen for subsequent pigment extraction.

The extraction procedure and equation for calculation of chlorophyll-a were those of Strickland and Parsons (1972), and the calculation for phaeopigment was that of Lorenzen (1966).

Chlorophyll-a concentration was determined with the Turner Designs fluorometer that was cross calibrated against a Beckman DB and later a Bausch and Lomb Spectronic 2000 spectrophotometer. The equation used to determine chlorophyll-a spectrophotometrically was

$$C = 11.6\ E_{665} - 1.31\ E_{645} - 0.14\ E_{630}$$

where C is the chlorophyll-a in micrograms and E is the extinction at the indicated wavelengths.

The equation used to determine phaeopigments was

$$\mathrm{mgP/m^3} = \frac{\dfrac{F_o/F_a\mathrm{max}}{F_o/F_a\mathrm{max}-1}\ (K_x)\ [F_o/F_a\mathrm{max}(F_a) - F_o]}{V}$$

where F_0/F_A max is the maximum chlorophyll-a:phaeopigment fluorescence ratio (2.0), F_0 is the fluorometer reading before acidification, F_A is the fluorometer reading after acidification, K_x is the calibration constant, and V is the volume of water filtered in liters (Lorenzen, 1966). K_x was calculated from the chlorophyll data.

Field Logistics for Boulder Patch Studies

During the open-water period, sample was carried out from a 6 m Boston Whaler (the R.V. Arctic Char; National Oceanic and Atmospheric Administration). During ice covered periods most of the diving occurred at an acoustically marked study site, Dive Site 11 (DS-11; 70°19.25'N, 147°35.1'W; Figure 1k), where divers entered the water through holes cut in the ice using augers and ice chisels. Ice blocks were removed by helicopter or multiterrain vehicle (Rolligon). A heated insulated hut (Parcoll, Panebec Ltd., Montreal) placed over the dive hole functioned as a dive shelter and laboratory. Each diver wore a dry suit, a primary and backup breathing system, and headphones for wireless underwater communication with the surface (UDI-SUBCOM, Aberdeen, Scotland). Liquid silicone injected into the barrel of the first stage of the regulator prevented freezeups in the breathing system, especially when diving without a shelter. Divers were tethered to the surface and usually limited to a 25 m radius of the hole, although occasional ventures were made up to 50 m distant for short periods under special circumstances.

Primary Production in *Laminaria solidungula*

Linear growth of *Laminaria solidungula*, the predominant kelp, was followed by punching holes in the base of the blade, above the meristematic region (Chapman and Craigie, 1977). Production-to-biomass ratios were calculated to determine the total carbon input made by the brown algae to the marine environment. Since *L. solidungula* constitutes over 90% of the brown algal biomass, we focused on the productivity of this plant. The blade of *L. solidungula* is divided into distinct ovate segments of different sizes by constrictions that form annually. The growth of a new basal blade segment starts in November and continues until the following November. Since attrition occurs at the distal portion of the blade, the biomass of the basal segment is an accurate measurement of the plant's annual production. Seventeen plants, weighing between 1.5 and 33 grams, were carefully detached from their substratum in November 1979, and banded to a large plastic Vexar cage anchored to the seafloor for one year. Following retrieval of the cage in November 1980, the new basal segments of the plants were individually removed and weighed. These wet weights represented the annual production of the plant. The average annual production-to-biomass (P:B) ratio was obtained by dividing the biomass of the first blade segment by the initial plant weight. The percentage of dry weight to wet weight was determined by drying algal tissue in an oven at 30°C for 48 hours. The plants used for wet weight to dry weight determinations were collected haphazardly by divers at DS-11.

VI. RESULTS AND DISCUSSION

Ice Algae Distribution and Production

Prior to last year, it had been assumed that the low light intensities and rapid rate of ice accretion in the nearshore Arctic effectively prevented the appearance of a fall ice algal bloom, although freeze-up blooms were known to be an annual occurrence in the Antarctic. The Southern Ocean begins to freeze over a month earlier in the solar year, and the higher light intensities and very light snow cover readily account for the bloom. Logistically, the later freeze-up in the Arctic and thin ice cover prevented access to offshore ice and hindered ice algae research during this period of the year.

In cooperation with Dr. Mitsuo Fukuchi of the Japan Polar Research Institute, we were able to core new sea ice north of Narwhal Island and discovered a pronounced ice algal bloom on 9 November 1980. Vertical chlorophyll-a concentrations and associated nutrient concentrations in the underlying water are given in Table 2. The appearance of this bloom

TABLE 2. Fall ice algae samples, 9 November 1980.
Station Location: Narwhal Island, 70°25.3'N, 147°27.6'W

	Core NI-1			Core NI-2	
Ice Depth (cm)	Chlorophyll-a (mg/m^3)	Phaeopigments (mg/m^3)	Ice Depth (cm)	Chlorophyll-a (mg/m^3)	Phaeopigments (mg/m^3)
1-7	0.9	0.5	0-8	0.8	0.5
7-14	0.1	0.1	8-16	1.1	0.5
14-20	2.0	0.4	16-23	2.2	0.4
20-25.5	7.4	2.3	23-30	20.5	5.0
25.5-31	87.7	1.9	30-34	7.1	1.2
20-31	3.9(1)	0.2(1)	23-34	1.4(1)	0.3(1)
20-31	195.0(2)		23-34	70.0(2)	
	Core NI-3			Core NI-4	
0-7	1.2	0.4	0-10	1.0	0.3
7-13.5	2.4	0.1	10-20	1.4	0.2
13.5-20.5	3.5	1.5	20-27	2.6	0.6
20.5-27	3.2	0.1	33-38	101.9	4.9
13.5-27	0.4(1)	0.1(1)	27-38	4.7(1)	0.4(1)
13.5-27	20.0(2)		27-38	235.0(2)	

(1) Sum of bottom two intervals experssed as mg/m^2.

(2) Biomass (mg C/m^2) calculated as 50 x chl-a.

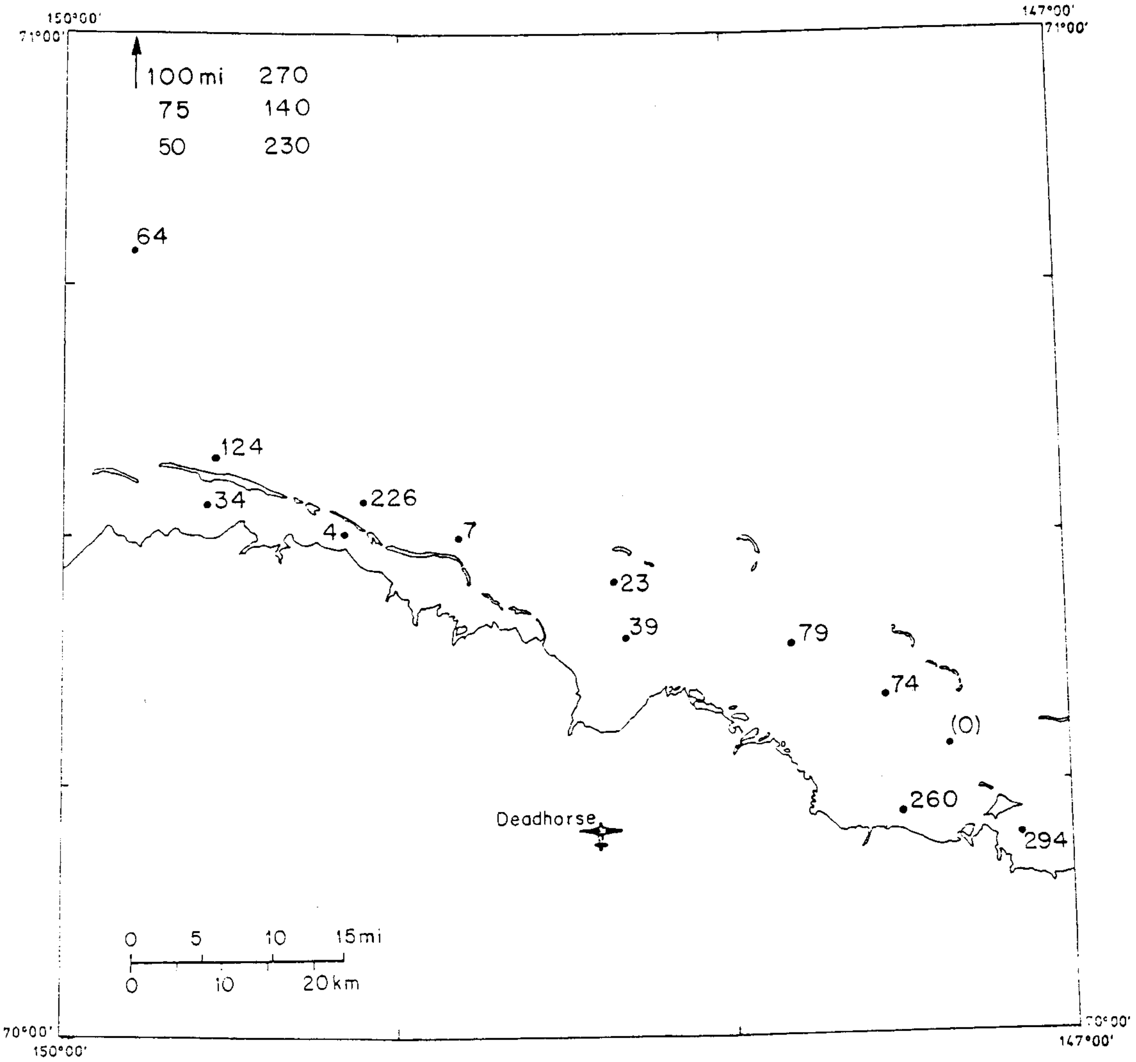

Figure 6. Ice algae standing stocks, May 1979. Values shown are estimates of plant carbon (mgC/m^2) determined from chlorophyll concentrations. Offshore stations (upper left) are measured from the shoreline.

may not be an annual occurrence in that an unusually warm spell of weather had preceded the sampling date and may have retarded ice growth sufficiently to allow development of the bloom. Normal ice accretion rates are on the order of 1 cm/day and it is hard to conceive of a dense algal bloom having time enough to form under these conditions. This bloom (fall 1980) was not as large as the spring ice algal bloom, and the observed chlorophyll-a concentrations were about 10 percent of maximum concentrations in May, corresponding to about 0.2 g C/m^2 standing stock. No data are yet available as to spatial or annual variability in the fall bloom, and further investigation of this phenomenon is a high priority for future studies. Lack of logistic support prevented any sampling in November 1981.

The major field effort in spring 1979 was directed toward obtaining a representative number of ice algal samples such that standing crop estimates could be projected for the lease area. Sixteen stations were occupied with triplicate cores obtained from each site. One transect was run approximately 100 miles north of the lease area to attempt to delineate trends in distribution with distance from shore. In addition, visual observations were made along lead and pressure ridge systems to obtain qualitative information regarding ice conditions and ice algae presence. The cores obtained were used to estimate standing stocks as described above and the data obtained are shown in Figure 6. The Stefansson Sound area showed the greatest variability in standing crops as might be expected from the large patches of turbid ice.

Offshore, the ice algae generally increased although patches of turbid ice were visible as far as 25 miles offshore. Along lead systems, overturned pieces of annual sea ice were often heavily discolored by algal populations. A general observation was that algae were present on ice of sufficient thickness (>1.0 m) such that the sheet represented all or most of the winter freezing season. No ice algae were visible on thin sheets which represented ice less than 2 months old. Cores cut from the fast-ice sheet near the open leads off Harrison Bay had dense populations and may represent a large area of uniformly high populations.

Closer to shore, the variability in algal biomass sharply increases. Simpson Lagoon was sampled at only two locations, but in

TABLE 3. Carbon content, sediment load, and light penetration in coastal Beaufort Sea ice. Intervals are for visible sediment bands.

Station	Date	Location	Ice depth (cm)	Snow depth (cm)	Integrated ice sediment load (g/m^2)	Percent surface light	Ice depth interval (cm)	Sediment load* (g/m^3 of ice)	Percent carbon in sediment (dry weight)
PB	12 APR 81	70°19.7'N 148°22.4'W	150	20	42	0.001	0-27	99	4.0
HB1	12 APR 81	70°36.0'N 151°38.0'W	170	20	145	0.0001	0-20 32-34, 53-57, 59-68, 97-102	390 125	5.8 3.2
HB2	12 APR 81	70°33.9'N 151°08.0'W	150	20	104	0.003	27-31 12-14, 20-22, 33-36	1660 325	3.2 4.1
8	14 APR 81	70°31.0'N 148°55.0'W	160	20	21	0.200	19-21	247	4.6
15	14 APR 81	70°26.4'N 148°19.0'W	160	20	51	0.084	22-88	53	7.0
18	13 APR 81	70°16.7'N 147°17.3'W	160	30	53	0.001	17-28 28-40	64 250	7.0 3.1
BP	13 APR 81	70°18.0'N 147°32.3'W	160	25	86	0.001	10-100	77	7.4
2	14 APR 81	70°35.1'N 149°28.6'W	160	20	26	0.290	15-20	196	3.7
3	14 APR 81	70°32.0'N 149°51.7'W	130	25	13	0.110	----	----	----
19	13 APR 81	70°11.0'N 147°03.0'W	150	15	15	0.067	----	----	----
20	13 APR 81	70°14.2'N 147°29.8'W	150	25	15	0.021	----	----	----
12	14 APR 81	70°33.3'N 150°21.6'W	160	10	16	0.150	----	----	----
13	12 APR 81	70°34.9'N 151°41.4'W	170	20	17	0.270	----	----	----

* Clear ice, not listed, averaged less than 10 g/m^3.

TABLE 4. Carbon content and particulate load in coastal Beaufort Sea ice. Intervals are for visible sediment bands.

Station	Date	Location	Ice Depth Interval (cm)	Particulate load (g/m^3 of ice)	Percent carbon in particulate matter (dry weight)
19-2	30 MAY 81	70°11.1'N 147°03.0'W	154-160 (bottom of ice)	41*	14.6
HB1-3	31 MAY 81	70°36.2'N 151°38.4'W	166-170	150*	18.7
HB2-1	31 MAY 81	70°34.2'N 151°08.3'W	164.5-170 (bottom of ice)	64*	11.8
TR1	2 JUNE 81	70°32.1'N	148-155	110	2.4
TR1-2		148°23.3'W	107-110	122	3.9
TR2-3B	2 JUNE 81	70°52.6'N 148°22.2'W	143.5-150 (bottom of ice)	48*	16.6
TR2-5B			142.5-150 (bottom of ice)	77*	13.8
3-2	31 MAY 81	70°32.1'N 149°52.0'W	165.5-170 (bottom of ice)	66*	10.4
12-2	31 MAY 81	70°33.4'N 150°21.5'W	135-140 (bottom of ice)	55*	8.2

*Predominantly ice algae. Clear ice (not listed) averaged less than 10 g/m^3.

both cases, algal populations were much lower than immediately outside of the barrier islands (see Figure 6). The ice in the lagoon was clear, but salinities in the underlying water were over $40^{0}/oo$ and may have been partially responsible for the low plant densities. Assuming that the water was at or near the freezing temperature, this would indicate ambient temperatures of about -2°C which may also inhibit growth.

Stefansson Sound yielded cores with plant biomasses ranging from nearly undetectable to almost 0.3 g C/m^2 in Mikkelsen Bay beneath clear ice. Most of the central area of Stefansson Sound and Prudhoe Bay had less than 0.1 g C/m^2 beneath the ice.

The light measurements listed in Table 3 were taken at the same stations as the ice algal samples, but a month earlier and not at identical locations. They do not, therefore, describe light conditions at the place or time of ice algal sampling, but serve to illustrate the range of variability in light penetration through the ice. The presence of winter snow cover is sufficient to decrease incident light to about 0.5-1.0 percent of that striking the snow surface, but the presence of even small amounts of particulate matter in the ice causes the rapid extinction of light to intensities approaching the limit of detection. Since the particulate matter is often dispersed over much of the upper ice column, the associated drastic light attenuation can be expected to persist almost as long as the ice cover lasts. Thus, primary production by ice algae in April and May, and by phytoplankton in June and even early July is effectively prevented in areas of sediment-laden ice in the Stefansson Sound-Simpson Lagoon area. Estimating a 50-75 percent areal extent of turbid ice, this condition probably reduced the 1979 ice algal productivity and possibly phytoplankton productivity to as low as 25-30 percent of the maximum possible if snow cover alone were attenuating light penetration. At this time, very little data exist on year-to-year variability of sediment-laden ice and on the length of persistence of the opaque ice into the summer season. Duration estimates based on satellite imagery indicate that approximately 40-50 percent of the Stefansson Sound area is ice free by the first week of July, followed by rapid dispersal of the remaining ice during the month. Thus, sediment-laden ice could potentially prevent light penetration into the water column for two or more weeks past the solar solstice, causing a large decrease in annual primary production. More detailed documentation on the ice retreat characteristics in relation to light penetration has been assembled using satellite imagery and field observation, and sediment-laden ice has been addressed as a topic in a previous workshop (Larsen, 1980). Although the mechanisms of incorporation are still unclear, turbid ice forms in the fall and is apparently related to the rate of freeze-up. Figure 7 shows a qualitative relationship between ice thickness and turbidity following fall freeze-up of 1978. The thicker ice is believed to have originated during super-cooling by fall storms over open water wherein rapid ice formation and sediment suspension occurred simultaneously.

The sediment loads listed in Tables 3 and 4 were calculated by multiplying the concentrations in each band by its volume. A sediment concentration determined to be 10 g/m^3 was used for clear ice and the total sediment in the core was found by summation of the individual bands. The load was placed on an areal basis by dividing this total by the area of the core barrel. The light and sediment data show that light penetration is strongly attenuated by the presence of sediment in the ice. The low extinction coefficients are for essentially clear ice and are comparable to those found by Horner and Schrader (1981) for ice of similar depth, but with twice as much snow cover (20-50 cm), whereas the high extinction coefficients are caused by the increased sediment load. Some of the higher percent carbon values from core sections arise from differences in the organic content of ice algae and sediment. The particulate matter in the bottom of the ice cores contained algae ranging from 8.2-18.7 percent carbon, while the upper core contained sediment of 2.3-7.4 percent carbon. These samples are shown in Table 4.

Ice algal primary production in the nearshore Beaufort Sea is a small fraction of the total annual primary production and is small relative to epontic algal production in the Bering and Chukchi seas, although very little data are available on the latter region. Table 5 compares the estimates of total annual production of epontic ice algae in other continental shelf waters of Alaska and the Antarctic with data obtained in the Beaufort Sea. Only the study by Alexander et al. (1974) represents integrated ^{14}C uptake measurements determined over the spring season. The remaining estimates are extrapolations made on

TABLE 5. Ice algae standing stock and primary productivity data.

	Maximum Chlorophyll-a (mg Chl-a/m^2)	Estimated standing stock (50 x Col. 1) (g C/m^2)	Estimated annual primary production (g C/m^2)	Ratio of annual production to standing stocks (Col. 3 divided by Col. 2)
Bering Sea				
McRoy and Goering (1974)	3.0	0.2	0.3(1)	2
McRoy and Goering (1975, 1976, and personal communication+)	50.0 - 100.0+	2.5 - 5.0	24.0(2)*	9.6 - 4.8
Chukchi Sea				
Alexander et al. (1974)	23.0	1.2	5.0	4.2
Schell (this study)	78.3	3.9	19.5**	-
Beaufort Sea/Canadian Arctic				
Anderson (1977)	0.5	<0.1	0.2*	5.0
Horner (1980)	3.0	0.2	0.9*	6.0
Horner and Schrader (1981)	26.5	1.3	0.7	0.5
Schell, (this study) Harrison Bay,	12.3	0.6	3.0**	-
Outside the barrier island,	10.7	0.5	2.5**	-
Stefansson Sound	6.4	0.3	1.5**	-
Hsiao (1980) Eskimo Lakes	5.7	0.3	1.5**	-
Frobisher Bay	25.3	1.3	6.5**	-
Grainger (1979) Frobisher Bay	4.6	0.2	1.0**	
Dunbar and Acreman (1980) Robeson Channel	10.3	0.5	2.5**	-
Barrow Strait/Austin Channel	13.8	0.7	3.5**	-
Hudson Bay	25.3	1.3	6.5**	-
Gulf of St. Lawrence	3.0	0.2	1.0**	-
Antarctic				
Burkholder and Mendelli (1965)(3)	123.0	6.2	6.2+	-
Meguro (1962)(3)	97.0	4.9	4.9+	-
Bunt (1963, 1964)	0.1	0.7	2.3*	3.5
Whitaker (1974)	1478.0	40.0(4)	40.0+	-
Whitaker and Richardson (1980)	244.0	9.1(5)	45.5**	-

(1) Calculated by Horner and Schrader (1981) from data of McRoy and Goering (1974).

(2) Calculated from total shelf ice algae productivity (24 x 10^6 metric tons C) divided by the shelf area (1,000 x 10^3 km^2).

(3) Samples collected from "snow" communities.

(4) Value reported by Whitaker (1974) for shelf on an ice berg.

(5) Estimated using carbon-chlorophyll-a ratio of 37.1, from Whitaker and Richardson (1980).

* ^{14}C incubated primary productivity.

** 5 x estimated standing stock.

\+ Grazing assumed negligible.

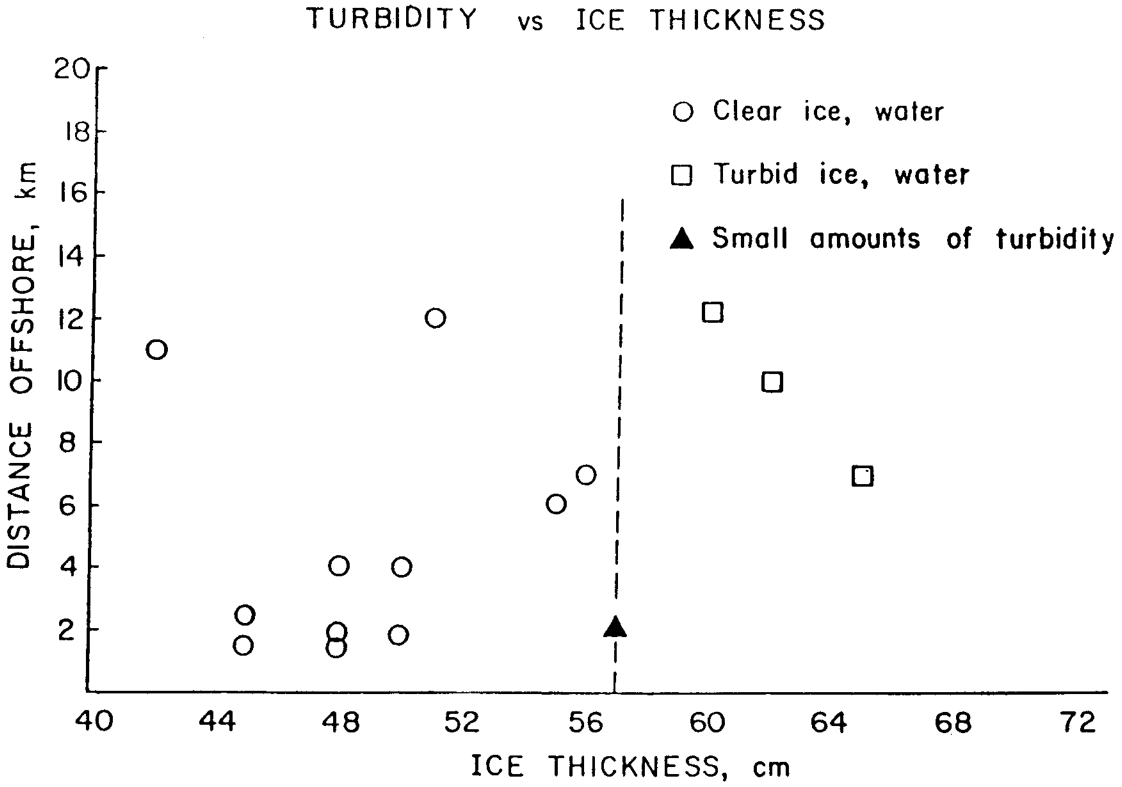

Figure 7. Fall 1978, ice turbidity and thickness in the Prudhoe Bay-Simpson Lagoon-Harrison Bay area.

either limited ^{14}C-uptake measurements or on standing stock measurements converted to productivity numbers by cross calibration with instantaneous productivity measurements and standing stocks estimated from chlorophyll concentrations.

The estimates of ice algal production for this study in Table 5 which are based in part on data from Table 6 are probably high since sampling is unavoidably biased by the choice of helicopter landing spots which are flat. Due to the roughness of pressure fields and the inaccessability of the bottom surface of pressure ridges, there are no data on ice algae from these areas. Light attenuation would be greater in pressure fields due to the increased snow cover, and/or thicker ice would be expected to preclude ice algal growth. However, the estimates of annual production in Table 5 do not take ice morphology into account, but are based on the actual samples taken and may result in a systematic error. In the context of total annual primary production and the effects of sediment-laden ice, this error would probably have little effect.

Coastal Beaufort Sea Ice Algae Studies

Coring of ice algae samples in 1981 was accomplished on 30-31 May and 2 June. Logistic delays prevented sampling at the typical spring bloom optimum period of 7-10 days previous to these dates and several cores, especially those near shore, showed evidence of algal loss through melting and from river runoff. Further offshore, we are more confident that the observed populations are at or near annual maxima, and this is corroborated by the simultaneous studies by Horner and Schrader (1981) who observed the maximum standing stocks of ice algae of Narwhal Island at this time. Because of the uncertainties in nearshore samples, however, we are not attempting to use 1981 samples to establish distributional trends in maximum annual standing stocks. Previous estimates of standing stocks based on cores obtained in May 1979 and May 1980 showed an increase in biomass progressing offshore -- except in areas of moving ice, algal populations ranged from very low densities in new ice to high concentrations in areas of stable annual sea ice.

TABLE 6. Chlorophyll-a and phaeopigment data from Beaufort Sea ice cores collected May 30, 31 and June 2, 1981.

Prudhoe Bay Site 70°19.9'N 148°22.7'W

Core	Snow cover (cm)	Ice depth interval (cm)	Chlorophyll-a (mg/m^3)	Phaeopigments (mg/m^3)	Estimated standing stock (mg C/m^2)
	5	164-170	2.0	1.7	
		Total (mg/m^2)	0.1	0.08	5.0
PB 2	14	162-165	0.3	0.2	
PB 2	14	165-170	1.2	0.9	
		Total (mg/m^2)	0.06	0.05	3.0
Station 20 70°14.4'N 147°29.5'W					
20-2	35	158-166	1.0	0.2	
20-2	35	166-170	3.0	0.6	
		Total (mg/m^2)	0.2	0.03	10.0
Station 19 70°11.1'N 147°03.0'W					
19-1	21	1535-160	14.6	1.5	
		Total (mg/m^2)	0.8	0.008	40
19-3	3	150-155	4.1	1.0	
19-3	3	155-160	46.1	10.2	
		Total (mg/m^2)	2.3	0.5	115
Station 18 70°16.6'N 147°17.2'W					
18-1	4	1365-145	6.1	1.9	
18-1	4	145-150	38.4	0.9	
		Total (mg/m^2)	2.2	0.2	110
18-2	11	137-144	3.8	0.3	
18-2	11	144-150	3.7	0.7	
		Total (mg/m^2)	0.4	0.05	20
Station BP 70°17.9'N 147°31.9'W					
BP-2	8	165-170	0.05	0.4	
		Total (mg/m^2)	0.02	0.02	1.0

TABLE 6. (Continued)

Core	Snow cover (cm)	Ice depth interval (cm)	Chlorophyll-a (mg/m^3)	Phaeopigments (mg/m^3)	Estimated standing stock (mg C/m^2)
		Station 8 70°31.0'N 148°56.2'W			
8-2	1	149-156.5	2.7	0.9	
8-2	1	1565-164	7.1	1.6	
8-2	1	164-170	24.3	3.6	
		Total (mg/m^2)	1.7	0.3	85
8-3	1	161-166	13.2	1.8	
8-3	1	166-170	227.8	18.7	
		Total (mg/m^2)	9.9	0.8	495
		Station 3 70°32.1'N 149°52.0'W			
3-1	10	159-165	12.4	1.5	
3-1	10	165-170	68.8	6.2	
		Total (mg/m^2)	3.9	0.4	195
3-3	13	157-164	11.0	1.1	
3-3	13	164-170	37.1	4.7	
		Total (mg/m^2)	2.8	0.3	140
3-4	7	158-165	14.4	3.9	
3-4	7	165-170	109.5	17.1	
		Total (mg/m^2)	6.4	1.1	320
		Station 12 70°33.4'N 150°21.5'W			
12-1	3	125.5-133	2.7	0.4	
12-1	3	133-138	4.0	0.6	
12-1	3	138-140	107.7	20.5	
		Total (mg/m^2)	2.8	0.5	140
12-3A	7	124-130	2.8	0.7	
12-3A	7	130-136.5	3.4	0.8	
12-3A	7	136.5-140	12.3	5.5	
		Total (mg/m^2)	0.8	0.3	40

TABLE 6. (Continued)

Core	Snow cover (cm)	Ice depth interval (cm)	Chlorophyll-*a* (mg/m^3)	Phaeopigments (mg/m^3)	Estimated standing stock (mg C/m^2)
		Station 13	70°35.1'N	150°41.1'W	
13-1	2	130-138	4.1	0.2	
13-1	2	138-144	1.5	0.3	
13-1	2	144-150	51.2	7.0	
		Total (mg/m^2)	2.1	0.3	105
13-2	2	138-146	8.4	0.0	
13-2	2	146-150	99.3	23.2	
		Total (mg/m^2)	4.2	0.8	210
13-3	20	139.5-145.5	3.1	0.6	
13-3	20	145.5-150	5.1	1.4	
		Total (mg/m^2)	0.4	0.1	20
13-4	30	138-144	1.5	0.4	
13-4	30	144-150	3.4	0.9	
		Total (mg/m^2)	0.2	0.06	10
13-5	2.5	142-147.5	8.8	1.1	
13-5	2.5	147.5-150	196.4	42.3	
		Total (mg/m^2)	53.	.1	265
		Station HB2	70°34.2'N	151°08.3'W	
HB2-2	3	163-166	4.6	0.8	
HB2-2	3	166-170	182.4	50.0	
		Total (mg/m^2)	7.2	1.9	360
HB2-3	2	161-165	5.5	1.2	
HB2-3	2	165-170	108.6	26.3	
		Total (mg/m^2)	5.6	1.4	280
		Station HB1	70°36.2'N	151°38.4'W	
HB1-1	2	152-159	12.6	1.5	
HB1-1	2	159-165	19.6	1.8	
HB1-1	2	165-170	206.1	34.0	
		Total (mg/m^2)	11.0	1.7	550

TABLE 6. (Continued)

Core	Snow cover (cm)	Ice depth interval (cm)	Chlorophyll-a (mg/m^3)	Phaeopigments (mg/m^3)	Estimated standing stock (mg C/m^2)
Station HB1 (Continued)					
HB1-2	3	155-161.5	5.3	0.4	
HB1-2	3	161.5-167	15.0	-	
HB1-2	3	167-170	466.7	10.48	
		Total (mg/m^2)	12.3	2.6	615
Station TR1 70°32.1'N 148°23.3'W					
TR1-1	4	185-190	1.0	0.2	
TR1-1	4	190-194.5	3.1	1.5	
TR1-1	4	194.5-198.5	25.0	1.0	
TR1-1	4	198.5-200	333.8	57.1	
	Total (mg/m^2; 194.5-200 cm)		0.2	0.03	10
TR1-2	4	184.5-192.5	2.9	2.4	
TR1-2	4	192.5-197.5	6.2	2.1	
TR1-2	4	197.5-200	125.0	34.3	
	Total (mg/m^2; 192.5-200 cm)		3.1	0.8	155
TR1-3	4	187-191.5	4.5	1.1	
TR1-3	4	191.5-196	6.8	1.0	
TR1-3	4	196-200	19.8	3.4	
	Total (mg/m^2; 191.5-200 cm)		0.8	0.1	40
TR1-4	4	186-191	1.2	0.7	
TR1-4	4	191-196	0.5	0.4	
TR1-4	4	196-200	1.1	.4	
		Total (mg/m^2)	0.1	0.01	5
TR1-5	4	187-193	1.9	0.4	
TR1-5	4	193-198	4.3	1.4	
TR1-5	4	198-200	93.4	20.4	
	Total (mg/m^2; 193-200 cm)		2.8	0.6	140
Station TR2					
TR2-1	3	147-150	95.5	29.6	
		Total (mg/m^2)	4.1	1.3	205

TABLE 6. (Continued)

Core	Snow cover (cm)	Ice depth interval (cm)	Chlorophyll-a (mg/m^3)	Phaeopigments (mg/m^3)	Estimated standing stock (mg C/m^2)
		Station TR2 (Continued)			
TR2-2	3	148-150	8.50	25.3	
		Total (mg/m^2)	10.7	3.2	535
TR2-3	3	132.5-139.5	2.2	-	
TR2-3	3	139.5-146.5	4.7	1.0	
TR2-3	3	146.5-150	98.9	16.7	
		Total (mg/m^2)	3.1	0.5	155
TR2-4	1	148-150	352.5	67.6	
		Total (mg/m^2)	4.4	0.8	220
TR2-5	1	135-141	2.1	0.4	
TR2-5	1	141-147	5.9	1.7	
TR2-5	1	147-150	332.7	65.4	
		Total (mg/m^2)	10.1	2.0	505
TR2-6	3	1-20	0.2	0.1	
TR2-6	3	10-20	0.4	0.3	
TR2-6	3	20-30	0.1	0.2	
TR2-6	3	30-40	0.2	0.1	
TR2-6	3	40-50	0.2	0.1	
TR2-6	3	50-60	0.1	0.1	
TR2-6	3	60-70	0.3	0.1	
TR2-6	3	70-80	0.8	0.4	
TR2-6	3	80-90	0.2	0.1	
TR2-6	3	90-100	1.3	0.3	
TR2-6	3	100-110	0.2	0.1	
TR2-6	3	110-120	0.1	0.0	
TR2-6	3	120-130	0.1	0.0	
TR2-6	3	130-140	0.3	0.0	
TR2-6	3	140-150	0.6	0.6	
TR2-6	3	150-163	1.8	0.2	
TR2-6	3	163-165	99.0	20.7	
	Total (mg/m^2; 150-165 cm)		3.6	0.7	180
		Station TR3 71°12.0'N 148°20.8'W			
TR3-2	3	140-147	1.5	0.2	
TR3-2	3	147-150	10.4	1.6	
		Total (mg/m^2)	0.4	0.07	20

Chlorophyll concentrations in the ice-water interface varied as widely in 1981 as has been observed in previous years. Average values in the inshore area of Harrison Bay and on a transect seaward of the barrier island were 4.7 and 4.4 mg Chl-a/m^2 with a range of 0.1-12 mg Chl-a/m^2. Concentrations often varied within stations in response to snow cover and sediment inclusions in the ice. Translating the chlorophyll concentrations to carbon, as explained below, yields estimates ranging from 5 to 600 mg C/m^2. Estimates for other areas are included in Table 5.

The carbon to chlorophyll ratio was determined from ice cores collected by this research unit and by RU 359, from their Narwhal Island ice station. A least squares regression applied to the data (Figure 8) gave a slope of 50.0 ± 8.9 (r = 0.86). For comparison, Whitaker and Richardson (1980) determined a carbon to chlorophyll-a ratio of 37.1 ± 3.8 for ice algae from a tide crack community of predominantly *Navicula glaciei* in the South Orkney Islands. The larger relative standard deviation of our data (18 percent) compared to Whitaker and Richardson's values (10 percent) is probably due to at least four factors. Our samples were collected over a two-year time period, our stations were spread over a wider area, there is a wide and variable input of terrestrial detritus into the nearshore zone, and species composition probably varied between stations.

An assimilation efficiency (carbon fixation rate/chlorophyll-a concentration) of 0.10 mg C/mg Chl-a-hr was calculated from the primary productivity and chlorophyll-a standing stock measurements of Horner and Schrader (1981). If the seasonal mean Chl-a concentration is multiplied by the assimilation efficiency, the average day length of 21 hours, and the 60 day growing season, the annual productivity can be estimated. Using the mean seasonal Chl-a concentration found at Narwhal Island of 8.2 mg Chl-a/m^2, the estimated productivity by this method is 1.0 g C/m^2-yr, which is slightly higher than the integrated value of 0.7 g C/m^2-yr reported by Horner and Schrader (1981).

We also calculated an assimilation efficiency of 0.39 mg C/mg Chl-a-hr from the data collected in 1973 by Alexander et al. (1974). To check this method of estimating primary productivity with the experimentally determined value, the assimilation efficiency was applied to the average chlorophyll-a concentration off Pt. Barrow of 10.9 mg Chl-a/m^2. The estimated productivity of 5.4 g C/m^2-yr is close to the integrated ^{14}C-uptake value of 5 g C/m^2-yr that they reported.

The estimate of annual primary production of 0.7 g C/m^2-yr due to ice algae off Narwhal Island made by Horner and Schrader (1981) may be too low. When the maximum chlorophyll-a standing stock is multiplied by the carbon to chlorophyll-a ratio of 50, which was determined on samples of algae provided by those investigators, the standing stock is 1.3 g C/m^2. Using their reported chlorophyll-a data, we constructed a best-fit exponential growth curve (Figure 9). The growth was bimodal and from this theoretical curve, total chlorophyll-a production is estimated at 34 mg Chl-a/m^2 (assuming no grazing or loss due to other factors). Carbon productivity from the exponential growth curve would be 1.7 g C/m^2-yr.

The data in Table 5 indicate estimated annual primary productivity is 2 to 9.6 ($\bar{x}$ = 5) times higher than the reported maximum standing stock. The data from Horner and Schrader (1981) shows estimated primary productivity that is 0.5 times the estimated standing stock. If we multiply the observed maximum standing stock (1.3 g C/m^2) by 5, estimated productivity of 6.5 g C/m^2-yr, approximately 10 times their estimated primary productivity, is obtained. Conceivably only about 10 percent of the algae were fixing carbon during the uptake experiments. However, this is inconsistent with data from previous investigators and inconsistent with the fact that the algae were growing exponentially.

When the assimilation efficiency of 0.39 mg C/mg Chl-a-hr calculated from Alexander et al. (1974) is applied to the average chlorophyll-a standing stock (8.2 mg Chl-a/m^2), the estimated primary productivity is 4 g C/m^2-yr. Ice algae productivity of 4 g C/m^2-yr off Narwhal Island is similar to ice algae productivity off Pt. Barrow. Maximum standing stocks were higher at Narwhal Island, but the bloom lasted longer off Pt. Barrow due to the absence of freshwater input from rivers.

Banse (1977) has described in detail the many pitfalls in attempting to use carbon to chlorophyll ratios as a general technique to obtain cell carbon. The principal causes of high variability are 1) changes in carbon to chlorophyll ratios within the cell during various

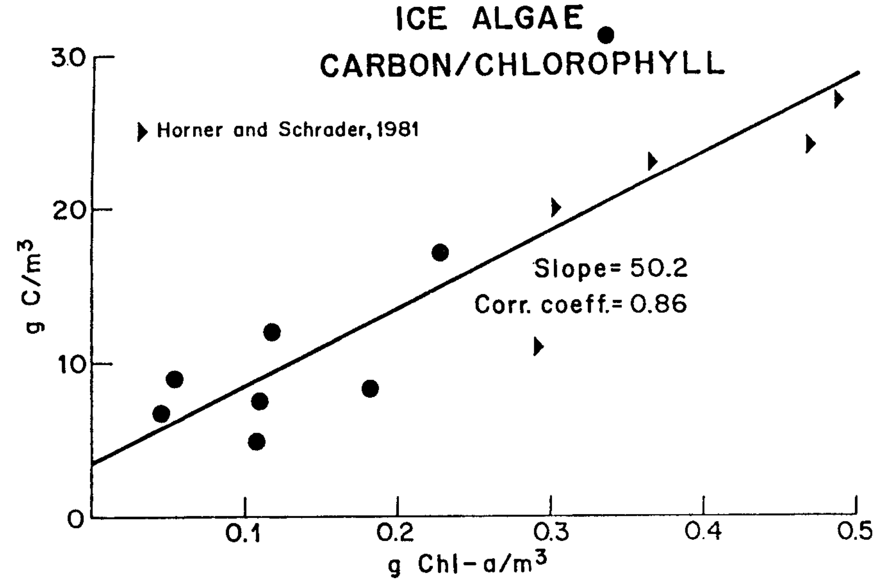

Figure 8. Carbon to chlorophyll relationship in samples of ice algae taken from the Beaufort Sea in the spring of 1980 and in the spring of 1981.

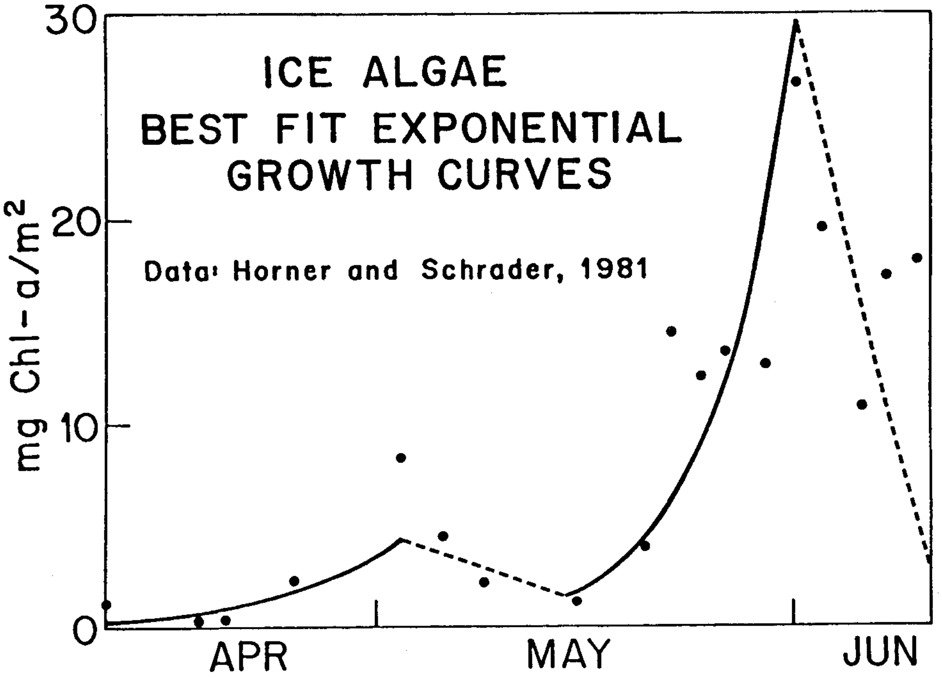

Figure 9. Computer generated best fit growth curve for spring, 1980, ice algae.

growth stages, 2) variation in the C/Chl-a ratio among species of phytoplankton, and 3) varying ratios of grazers to plants. We are fairly confident that the first two sources of error are small with regard to ice algae. Although Horner and Schrader (1981) have shown that a wide variety of species may be present in the algal populations, the heterogeneity does not appear to cause excess scatter in the points used to determine our C/Chl-a ratio. Also, there is no indication that cells are in other than rapid growth phases as shown from the adequate nutrient concentrations and increasing light over the course of the bloom. Although bimodality in the bloom would imply loss of cells and/or chlorophyll at the period of senescence in the first peak, once again our limited samples did not show this. We suspect that if an appreciable error in the C/Chl-a ratio exists, it would most likely arise from an increasing biomass of grazers in response to increasing chlorophyll (plants). We do not have the data yet to test this possibility and can only note that if this were a serious source of error, it should be reflected in a non-linearity of the plot with rapidly increasing C/Chl-a ratios at the higher chlorophyll-a concentrations.

Chukchi Sea Ice Algae Studies, Spring 1981

Ice cores were collected from four locations, designated I (67°59.0'N 167°28.0'W), II (68°22.9'N 167°44.3'W), III (68°22.5'N 167°53.2'W) and IV (68°54.9'N 166°28.0'W) during April and May, 1981 (Table 7). Water samples were also collected at these locations for nutrient and salinity determinations, and at other locations from the ship when ice conditions allowed.

In the cores collected from medium -sized (15-100 m) and small pans (less than 15 m) the chlorophyll-a concentrations were found to be fairly uniform within the different sampling groups. One core collected from a large pan (greater than 100 m diameter) (Station II), contained 78.3 mg Chl-a/m^2. Cores from medium-sized pans (from Stations I, III and IV) averaged 37.3 mg Chl-a/m^2, with a range of 24.9 to 56.9. Cores from small pans (Stations II and IV) averaged 3.5 mg Chl-a/m^2, with a range of 3.1 to 4.3 and a core collected from a submerged block contained 5 mg Chl-a/m^2. Chlorophyll-a in the water column ranged from 0.02 to 0.05 mg Chl-a/m^3. Phaeopigment concentrations typically equaled or exceeded the corresponding chlorophyll-a concentrations.

Standing stocks of the ice algae were estimated by multiplying the carbon-chlorophyll-a ratio of 50 to the chlorophyll-a values from the ice cores. The core from the large pan contained 3.9 g C/m^2. The cores from the medium pans had an average of 1.9 g C/m^2 with a range of 1.2 to 2.8 g C/m^2. The small pans had an average of 0.18 g C/m^2 with a range of 0.16 to 0.22 g C/m^2.

Estimates of annual primary productivity were made by using the 0.39 mg C/mg Chl-a-hr average assimilation efficiency derived from data reported by Alexander et al. (1974). This was multiplied by the averaged chlorophyll-a values to estimate average primary productivity, and then by an average day length of 20 hours and a 60 day growing season. The estimated productivity was calculated to be 18.3 g C/m^2 for the large ice pan, 8.7 g C/m^2 for the medium pans, and 0.8 g C/m^2 for the small pans.

Core III B had a higher chlorophyll-a content than any other core from medium-sized pans and had two distinct bands of algae, located approximately 45 cm from the top of the ice and at the bottom. The upper band accounted for 40 percent of the total 56 mg Chl-a/m^2. Occasionally during ice breaking operations, ice was observed containing two or sometimes three very distinct bands. If these bands contain large numbers of viable algae, then the carbon produced in these ice pieces could be significantly greater than would be expected from interface production only. Estimating that 80 percent of the ice cover was composed of large and medium-sized pans, an overall productivity for a 60 day season would be 11 g C/m^2. This estimate of ice algae productivity is approximately twice that of Alexander et al. (1974) for the Chukchi Sea, near Point Barrow.

Ice algae productivity in the Bering Sea has been estimated at 24 x 10^6 metric tons of carbon for the entire shelf area or 24 g C/m^2 (McRoy and Goering, 1976). Chlorophyll-a values in cores collected from the Bering Sea in 1972 were typically 5 to 50 mg Chl-a/m^2, similar to our cores collected from the Chukchi Sea (3 to 78 mg Chl-a/m^2). If the ice cores from the Chukchi Sea and Bering Sea were collected during the height of the spring bloom, and if the rates of primary productivity are comparable, then ice algae productivity in the southern Chukchi Sea may be only slightly less than that of the Bering Sea.

Phytoplankton Production in the Beaufort Sea

Phytoplankton photosynthesis provides the bulk of fixed carbon in the Beaufort Sea. Initial algal production in the spring occurs as ice algae, and phytoplankton production does not become a significant fraction of carbon input until the ice begins to melt, and the ice algae are dispersed into the underlying water column. Although Alexander and Niebauer (1981) and Horner and Schrader (1981) believe that the predominant ice algae species are not the initial phytoplankton species, Hameedi (1978) concludes that the ice algae are a major source of the initial phytoplankton populations. Our work in the Beaufort Sea has been limited to the nearshore zone (usually less than 10 m depth) due to logistic constraints and the emphasis on studying the projected lease areas. Nevertheless, we have attempted to integrate our data into the overall productivity regimes of the coastal Alaska Beaufort Sea. To accomplish this integration, we have relied heavily upon the past work of R. Horner (accomplished from icebreakers and reported in Horner, 1981), the limited data available from Alexander et al. (1975), and our own studies.

Our overall perspective is that phytoplankton primary production is low in the Beaufort Sea and ranges from <10-50 g C/m^2-yr. The lowest values are found in the nearshore waters less than 2 m deep where turbidity, salinity stress, and the shallow euphotic zone limit productivity and far offshore occur where perennial ice cover limits light, and low nutrient concentrations limit standing stocks and growth rates. In the intermediate area, the retreat of the pack ice northward in summer, nutrients supplied by terrestrial runoff, and the maximum euphotic zone depths lead to the maximum productivities observed. We have no data from the Arctic Ocean far offshore (>200 miles), and the low estimate is projected as a result of ice cover, which is assumed to

TABLE 7. Chukchi Sea ice algae data, 1981

Station I 67°59.0'N 167°22.1'W 27-IV-81

Core I Ice thickness: 1 m Snow: 12 cm

Depth Interval (cm)	Chlorophyll-a (mg/m^3)	Phaeopigment (mg/m^3)
75-82	26.2	0.3
82-87	25.6	2.6
87-92	39.5	2.3
92-96	67.9	7.3
96-100	516.7	47.4
Totals mg/m^2 (Bottom 8 cm)	30.3	2.2
Totals mg/m^2 Whole Core	34.6	2.4

Station II 68°22.9'N 167°44.3'W 3-IV-82

Core II A Ice thickness: 1 m Snow: 10 cm

Depth Interval (cm)	Chlorophyll-a (mg/m^3)	Phaeopigment (mg/m^3)
19.5-26.5	1.4	0.7
26.5-36.5	1.5	0.7
36.5-43.5	1.0	0.5
43.5-49.5	0.8	0.5
49.5-56.5	2.1	0.6
56.5-65.5	11.7	4.0
56.5-65.5	11.7	4.0
65.5-70	7.9	1.9
70-76	10.6	1.7
76-83	12.9	5.1
83-90	3.2	1.1
Totals (mg/m^2)	3.1	1.0

Station III 68°22.5'N 167°53.2'W 5-IV-81

Core II B Ice thickness: 2m Snow: 19 cm

Depth Interval (cm)	Chlorophyll-a (mg/m^3)	Phaeopigment (mg/m^3)
167-174	23.3	24.4
174-182	12.9	1.4
182-190	3.3	0.8
190-200	11.9	10.4
Totals mg/m^2	3.3	1.1

Core II C Ice thickness: 0.8 m Snow: 20.5 cm

Depth Interval (cm)	Chlorophyll-a (mg/m^3)	Phaeopigment (mg/m^3)
58-62	10.3	1.6
62-68	19.1	1.9
68-73	16.0	1.7
73-80	1460.9	162.9
Bottom 7 cm (mg/m^2)	76.1	8.5
Total (mg/m^2)	78.3	8.7

Core III A Ice thickness: 3 m Core length: 2.9 m Snow: 41 cm

Depth Interval (cm)	Chlorophyll-a (mg/m^3)	Phaeopigment (mg/m^3)
0-9.5	1.44	0.57
9.5-17.5	1.26	0.52
17.5-26	1.63	0.39
26-35.5	0.85	0.36
35.5-44	0.53	-
44-52	0.40	0.11
52-61	2.86	0.19
61-69	2.30	0.26
69-78	1.12	0.15
78-88	0.67	0.01
88-97	2.17	0.38
97-107	2.86	0.37
107-115	0.16	-
115-124	0.46	0.25
124-135	0.11	0.05
135-144	0.58	0.67
144=155	0.34	0.24
155-165	1.42	1.17
165-174	2.03	0.43
174-182	1.22	0.36
182-191	1.79	0.46
191-199	0.48	0.23
199-207.5	1.01	0.31
207.5-215.5	3.06	0.88
215.5-222.5	3.26	0.95
222.5-230	2.50	0.97
230-237.5	5.33	0.95
237.5-244.5	13.93	1.51
244.5-252.5	2.66	-
252.5-262	2.00	-
262-271	1.66	0.43
271-285	0.97	0.25
Totals (mg/m^2)	3.96	0.93

Core III B Ice thickness: 1.75 m Snow: 12 cm
Core contained visible layers.

Depth Interval (cm)	Chlorophyll-a (mg/m^3)	Phaeopigment (mg/m^3)
18-25	20.0	1.8
25-33	83.0	8.3
33-42	193.4	32.5
42-48	44.0	5.5
48-55	22.8	4.7
102-110	37.3	2.3
110-117.5	26.6	3.2
153.5-162.5	148.6	14.7
162.5-172.5	208.1	15.7
Totals of bottom two sections (mg/m^2)	27.3	2.3
Totals of whole core (mg/m^2)	56.4	6.2

Station IV 68°54.7'N 166°28.0'W 8-IV-81

Core IV A Ice thickness: 0.9 m Snow: 10.5 cm

Depth Interval (cm)	Chlorophyll-a (mg/m^3)	Phaeopigment (mg/m^3)
77.5-84	15.8	1.8
84-90	557.9	81.0
Totals (mg/m^2)	24.9	3.6

Core IV B Ice thickness: 1.0 m Snow: 7 cm
Layer present at 11-22 cm from top of ice.

Depth Interval (cm)	Chlorophyll-a (mg/m^3)	Phaeopigment (mg/m^3)
11-22	1.3	0.2
94-97	26.8	-
97-100	1595.6	195.6
Totals (mg/m^2)	33.3	4.0

Core IV C Ice thickness: 0.4 m Snow: 0 cm

Depth Interval (cm)	Chlorophyll-a (mg/m^3)	Phaeopigment mg/m^3)
23-30	14.0	-
30-40	49.7	-
Totals (mg/m^2)	4.3	-

Core IV D Ice thickness: 0.8 m Snow: 6-7 cm

Depth Interval (cm)	Chlorophyll-a (mg/m^3)	Phaeopigment (mg/m^3)
62.5-70	39.2	8.2
70-77	25.7	3.2
Totals (mg/m^2)	3.4	0.6

reduce light intensities on top of the water column to less than 10 percent of surface irradiance and create a substantially shallower euphotic zone. Data used for areal projections of primary production are listed in Tables 8 and 9.

The area of seasonally open water typically contains 4-10 μg-atoms nitrate N/ℓ at the onset of plant growth, and data from Hufford (1974) show that depletion occurs to at least 50-60 m in much of the nearshore area. If uptake by plants is the primary removal mechanism, minimum annual production can be estimated by assuming unidirectional movement into the particulate fraction and a C:N atom ratio of 7.5. For a mean depth from shore to the 50 m contour of 25 m, and an average of 7 mg-atoms N/m^3 nitrogen taken up, fixation equals 175 mg-atoms N/m^2 which should correspond to 1312 mg-atoms C/m^2 (= 15.7 g C/m^2).

Offshore phytoplankton production is assumed to be limited by ice, and the extent of ice cover therefore governs the areas available for a deep euphotic zone. Satellite imagery provides the most effective means of assessing the temporal and spatial extent of ice-free areas. Research Unit 267 (W. Stringer) has compiled ice extent data for the Harrison Bay-Prudhoe Bay vicinities based on imagery from 1972-1980. These data were used to project probable integrated primary productivity rates and seasonal totals in this area. We then used larger scale satellite imagery (Defense Meteorological Satellite Program) of the entire Beaufort Sea to estimate the extent of ice retreat over the summer and projected the annual productivity at points shown in Figure 10 to reflect these values. The estimated annual primary production values are shown in Figure 11 for the Harrison Bay-Prudhoe Bay area. Figure 12 shows the average seasonal ice retreat for 1978-1980 and Figure 13 shows contoured estimates of primary production in g C/m^2-yr for the Beaufort Sea projected through the ice retreat data and average ^{14}C uptake data.

Problems in extrapolating annual primary productivity rates in the high Arctic arise from two environmental conditions: low solar angles and ice cover. The low solar angles limit the light entering the water column through increased reflectance in water, but no data were obtained on diurnal variability in reflectance of snow and ice surfaces. Melnikov (1980), however, found that snow melt and thinning of the ice

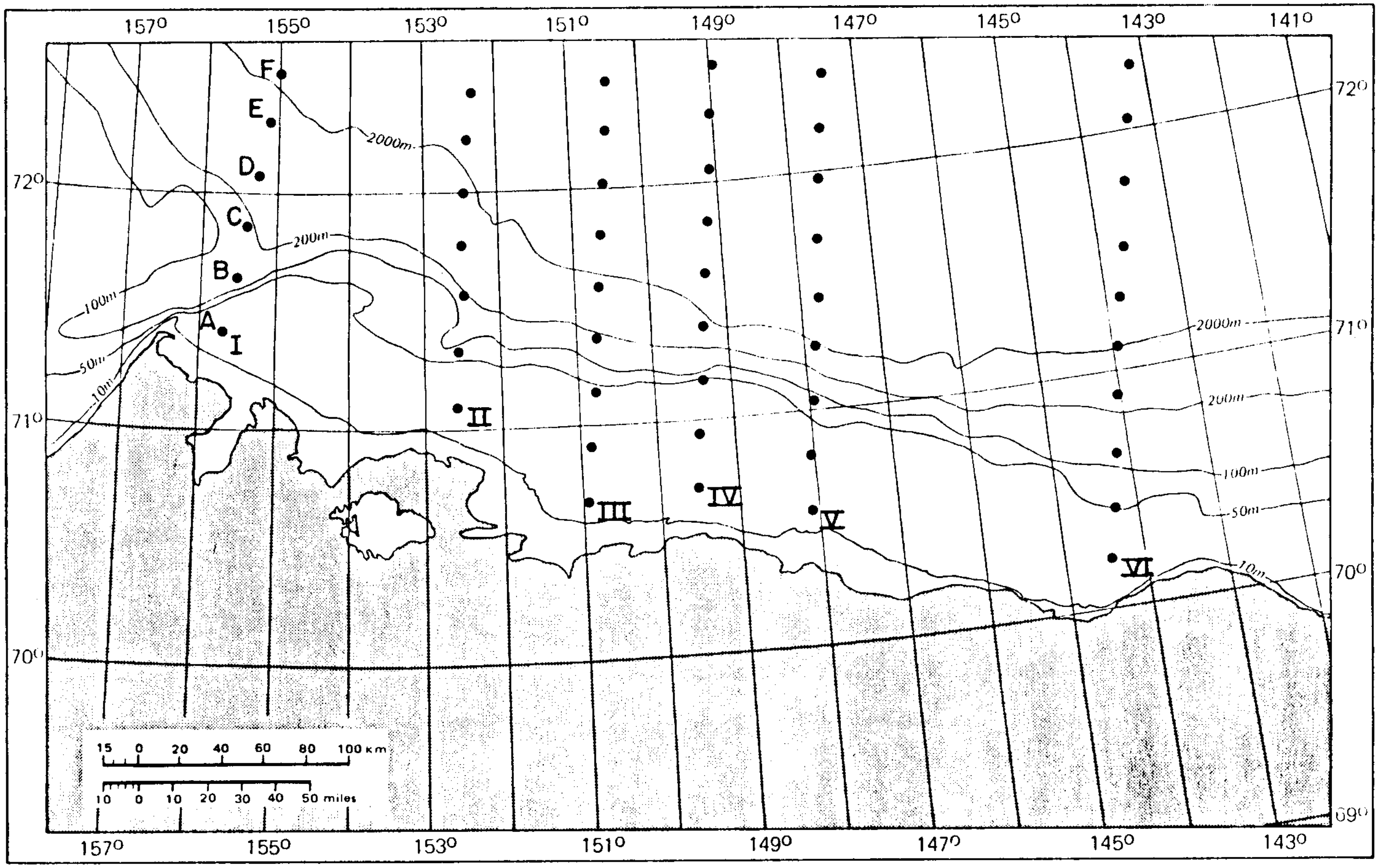

Figure 10. Transect points used for projecting annual primary productivity. Calculated annual productivities are listed in Table 10.

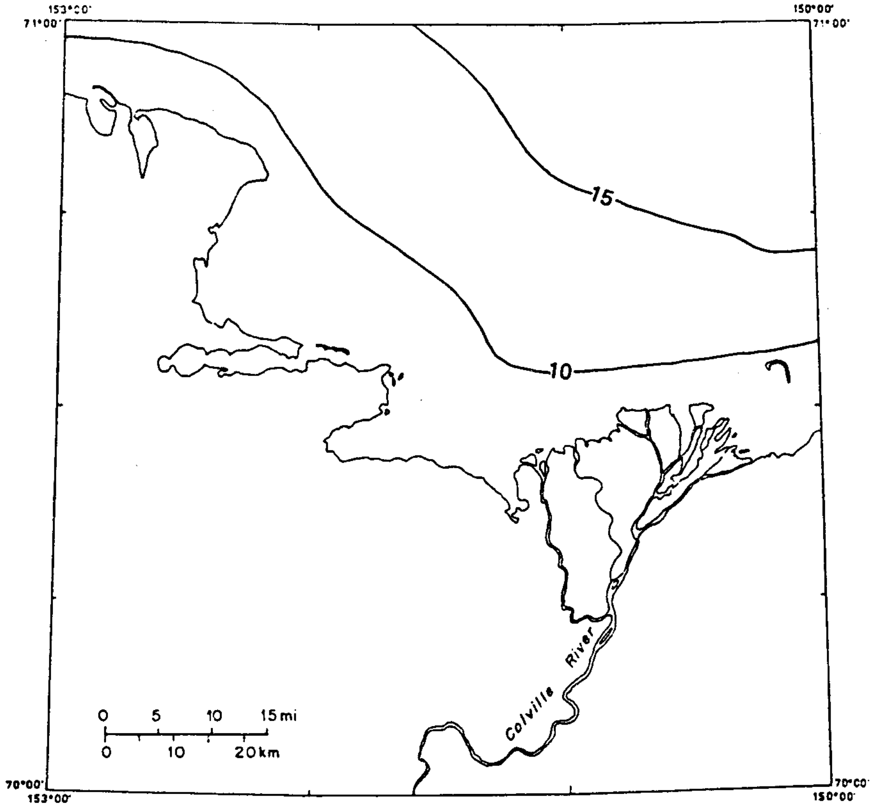

Figure 11A. Phytoplankton annual primary production (g C/m^2) projected from euphotic zone depths, ice retreat data, and ^{14}C uptake measurements. Contours do not match those of Figure 12 because ice data span a longer interval (1972-1980).

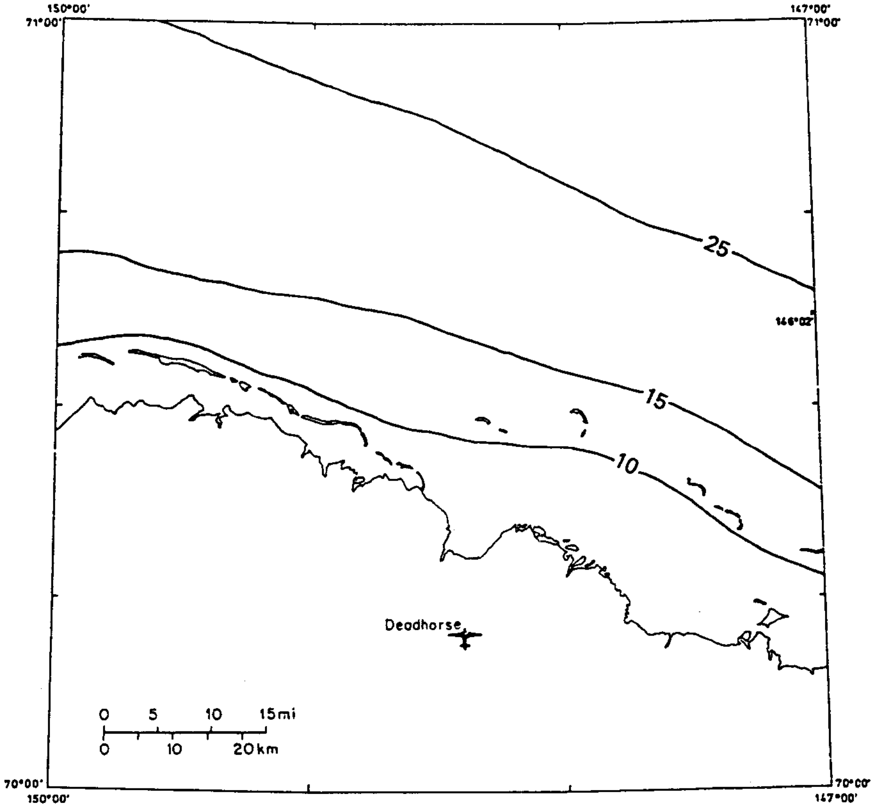

Figure 11B. Phytoplankton annual primary production (g C/m^2) projected from euphotic zone depths, ice retreat data, and ^{14}C uptake measurements. Contours do not match those of Figure 12 because ice data span a longer interval (1972-1980).

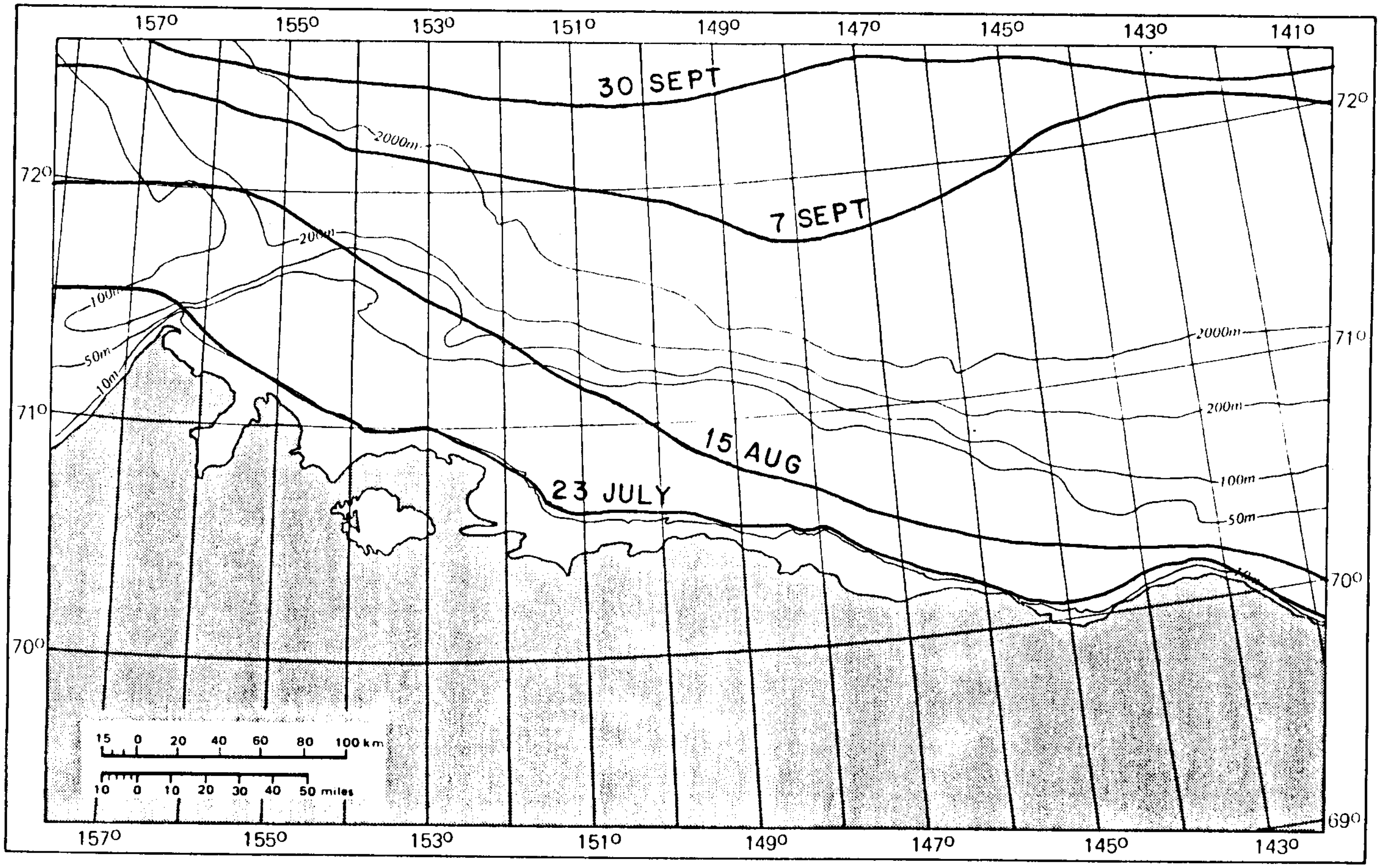

Figure 12. Average seasonal ice retreat 1978-1980, based upon DMSP imagery.

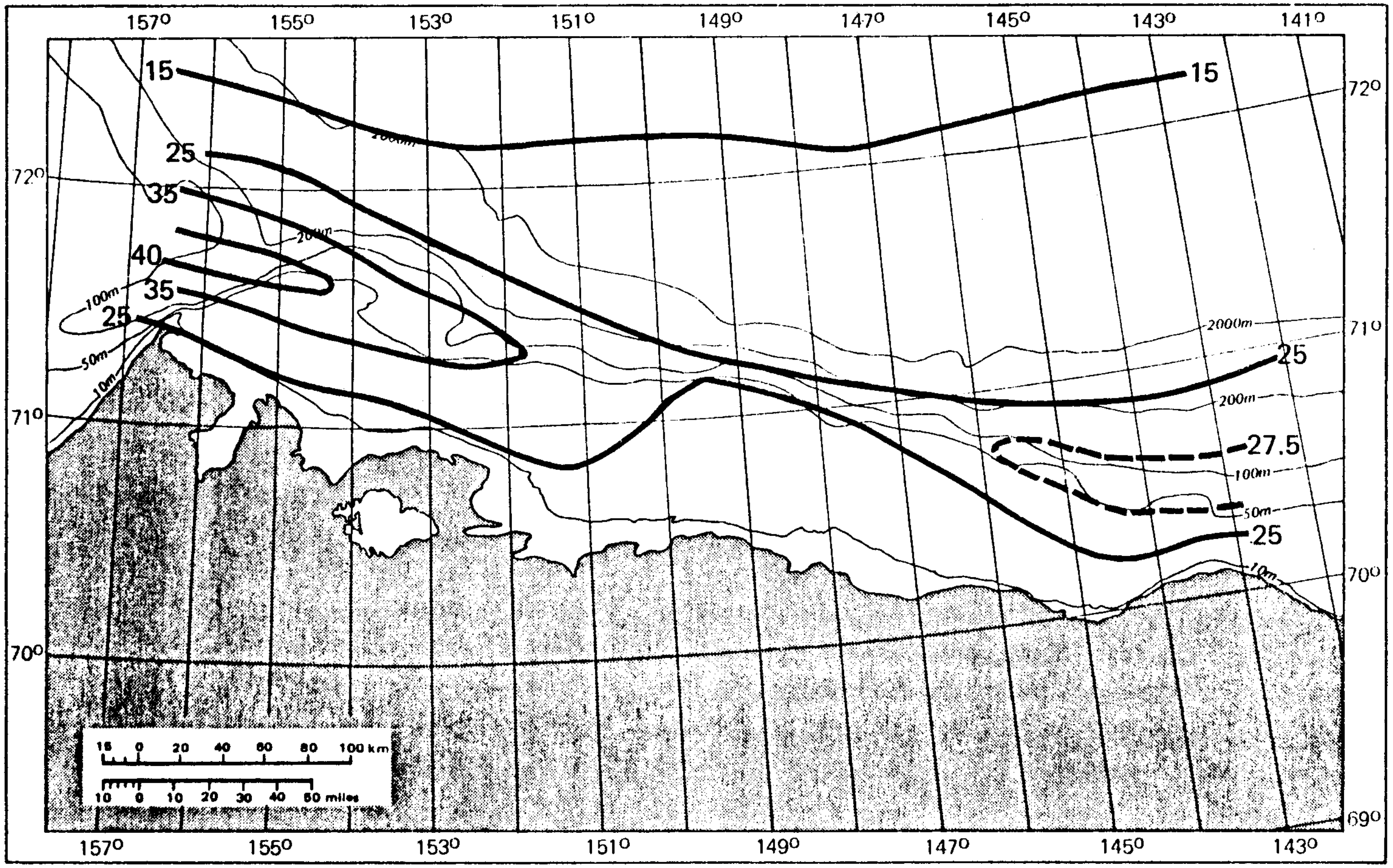

Figure 13. Average annual primary production (g C/m^2-yr) in the Alaska Beaufort Sea, 1978-1980. Contours are based upon satellite imagery of ice distribution, ^{14}C uptake measurements and nitrogenous nutrient concentrations.

TABLE 8. Primary production rate data - Beaufort Sea (mg C/m^3-hr)

	May	June	July	August	September
Offshore(1)					
SOURCE					
This study	--	0.2	1.2	--(2)	--(2)
Horner (1980)	--	--	0.9*	0.9(2)	0.5(2)
Alexander (1975)	--	--	--	2.4	--
Rates used to estimate productivity	(0.07)	(0.2)	0.9 (0.35)	0.9 (0.35)	0.5 (0.4)
Nearshore(3)					
Coyle (1974)	--	--	5.1	1.0	--
Horner and Schrader (1981)	0.07	0.09	--	--	--
Alexander (1975)	--	--	--	1.5	--
This study:					
Prudhoe Bay	--	--	--	0.5	--
Harrison Bay	--	--	--	0.3	--
Foggy Island Bay	--	--	--	0.7	--
Simpson Lagoon	--	--	--	0.5	--
Rates used to estimate productivity	(0.07)	(0.09)	1.1+ (0.35)	1.0 (0.35)	1.0**(0.4)

(1) Data from stations outside the 10 m depth contour. Values in parentheses are for under-ice water.

(2) Average of primary productivity measurements from 1976-77.

(3) Averages of data from stations within the 10 m depth contour.

* Assumed to be the same as the August value.

\+ Estimated from nutrient (nitrogen) availability.

** Assumed to be the same as the averaged August value.

TABLE 9. Monthly primary production in the Alaska Beaufort Sea.

	June 30 days x 24 hrs	July 31 days x 24 hrs	August 31 days x 20 hrs	September 15 days x 12 hrs	Totals
Offshore (50 m)					
Euphotic zone depth (m)(1)	50	50	50	50	
Average primary productivity (mgC/m^3-hr)(2)	0.2	0.9	0.8	0.4	
Monthly production (g C/m^2)					
a) Beneath ice	3.6	16.7	12.4	1.8	34.5
b) Open water	7.2	33.5	24.8	3.6	69.1
Mid-depth (10-50 m)					
Average euphotic zone depth (m)	30	30	30	30	
Monthly production (g C/m^2)					
a) Beneath ice	3.2	14.8	11.0	1.6	30.6
b) Open water	4.4	20.1	14.9	2.1	41.5
Nearshore (1-10 m)					
Average euphotic zone depth (m)	4	5	5	5	
Average primary production (mgC/m^3-hr)(2)	0.1	1.1(3)	1.0	1.0	
Monthly production (g C/m^2)					
a) Beneath ice	0.3	4.0	3.1	0.9	8.3
b) Open water	0.3	4.0	3.1	0.9	8.3

(1) Open water euphotic zone; under ice euphotic zone is assigned equivalent to 10 percent surface light intensity; 50 m depth is assigned from observed nutrient depletions (Hufford, 1974).

(2) Values from Table 8.

(3) Values based on nitrate-N availability.

cover compensates to a large extent for the decreasing solar angles over the course of the summer. The experiment of Steeman Nielsen (1975) which investigated productivity at 55°N during April was felt to be somewhat appropriate for open water conditions since the solar angle at that time approximates that at 70°N in June. He found that during dark, cloudy days, net productivity was reduced by up to 50 percent and the euphotic zone was effectively shallowed by insufficient light.

The assumptions made in the construction of the contours of primary production (Figure 13) require that this map be used as a qualitative guide to regional productivity. We have not included estimates of ranges or errors and do not have sufficient data on offshore productivity to predict accurately the effects of ice cover on nutrient supply, phytoplankton growth or light attenuation. We have employed approximations based on what we believe are reasonable assumptions. The assumptions and data include:

1) The ^{14}C uptake rates applied to under-ice areas were taken from Horner (1980) in areas greater than 6 oktas of ice and from our June 1982 measurements. All rates from Horner (1980) were adjusted upward by 25 percent to compensate for assumed loss of photosynthetic products during acid rinsing of filters. Her light intensities used for incubation (ca. 44 $\mu E/m^2$-sec) were similar to under-ice natural intensity.

2) Ice cover is assumed to melt at a constant rate over the summer. Although Melnikov (1980) has shown that melt rates vary widely during the season and from year to year, this approximation was used for simplicity. The under-ice euphotic zone is predicted to increase from 9 to 23.5 m during the summer assuming the extinction coefficient of ice remains constant.

3) The data of Hufford (1974) show nutrient depletion to over 60 m in nearshore areas of ice-free water. We, therefore, use 50 m as a conservative maximum euphotic zone depth.

4) Average ice-free days were calculated from Figure 12.

5) Algal growth rates were calculated from ^{14}C-uptake rates and standing stocks estimated from chlorophyll concentration (Table 10). These rates are shown in Figure 14.

6) Standing stocks and growth rates were assumed uniform during each month.

Table 11 summarizes the number of ice-free days along each transect of Figure 11. These estimates were derived from the average ice retreat curves shown in Figure 12. Since the cloud cover was often continuous for over a week at a time, there are probably considerable inaccuracies in our estimates of the "ice edge" position at a given date but we had little alternative to using an average rate of retreat. For the purpose of assessing regional productivity, however, we feel this technique presents the best approximation.

We also list in Table 12 our estimates of primary productivity in nearshore waters taking into account ice cover and subsequent open water season.

Offshore nutrient data are available for late summer from Hufford (1974) for the Beaufort Sea and from Kinney et al. (1970) for the Chukchi Sea. Both sources show that nutrient depletion occurs in the upper 35-50 m over most of this area. The deep Chukchi Sea water is richer than the Beaufort Sea due to additions of Bering Sea winter water, and we assumed 12 μg-atoms nitrate -N/liter available at the onset of primary production based upon data from Alexander et al. (1975) and Schell (unpublished data). This quantity of inorganic nitrogen would yield (at C:N ratio = 7.5) approximately 54 g C/m^2-yr with a 50 m euphotic zone. If the phytoplankton standing stocks cause a reduction in the euphotic zone, then overall productivity may be less. We feel, however, that the sinking of cells and the earlier open water may result in maximum annual production near 50 g C/m^2.

Although the above calculations are based upon the uptake of nitrate-N into the particulate fraction, it is certainly true that some regeneration of ammonia and mineralization of organic nitrogen must occur. When considering the Beaufort Sea out to a distance of 200 km from land, the inputs of terrestrial nitrogen shrink to insignificance.

TABLE 10. Estimates of annual production (g C/m^2-yr) derived from adjusted ^{14}C primary productivity rates and from measured algal growth rates (AGR).

Transect:	I		II		III		IV		V		VI	
Station	^{14}C	AGR	^{14}C	AGR	^{14}C	AGR	^{14}C	AGR	^{14}C	AGR	^{14}C	AGR
A	34	34	30	30	21	20	22	24	18	20	26	30
B	44	49	38	44	29	33	23	31	22	30	30	38
C	35	42	29	37	29	37	26	35	26	36	27	36
D	25	35	22	33	26	36	21	32	31	32	25	35
E	17	28	18	29	20	31	18	30	18	30	22	33
F	13	23	14	25	18	30	17	29	17	28	21	32
G			13	23	17	28	16	27	15	27	18	30
H					14	25	13	24	14	25	17	29
I					13	23	13	23	13	24	17	28
J											13	23

TABLE 11. Estimated number of ice free days for stations shown in Figure 11 based on DMSP Imagery, 1978-1980.*

Transects:	I			II			III			IV			V			VI		
Station	Jul	Aug	Sep	Jul	Aug	Sep	Jul	Aug	Sep	Jul	Aug	Sep	Jul	Aug	Sep	Jul	Aug	Sep
A	12	31	30	9	31	30	16	31	30	1	31	30	1	31	30	0	25	30
B	1	31	30	0	24	30	0	30	30	0	14	30	0	13	30	0	14	30
C	0	21	30	0	13	30	0	16	30	0	9	30	0	10	30	0	11	30
D	0	9	30	0	5	30	0	10	30	0	3	30	0	4	30	0	8	30
E	0	7	30	0	2	30	0	2	30	0	0	30	0	0	30	0	5	30
F	0	0	30	0	0	10	0	0	29	0	0	24	0	0	23	0	3	30
G				0	0	0	0	0	22	0	0	16	0	0	15	0	0	30
H							0	0	7	0	0	5	0	0	7	0	0	26
I							0	0	0	0	0	0	0	0	2	0	0	24
J																0	0	0

* June was ice covered for all stations and is not included in the table.

TABLE 12. Phytoplankton production estimates (g C/m^2-yr) from ^{14}C uptake rates and algal growth rates (AGR) for depth intervals in the nearshore Beaufort Sea (<20 m).

Depth interval (m)	June		July		August		September	
	^{14}C	AGR	^{14}C	AGR	^{14}C	AGR	^{14}C	AGR
0-5	0.3	1.4	3.1	3.4	3.1	2.3	1.8	1.4
5-10	0.2	1.8	2.0	3.4	3.1	2.2	1.8	1.3
10-15	0.0	1.8	0.4	3.3	3.1	2.3	1.8	1.4
15-20	0.0	1.8	0.0	3.4	3.1	2.2	1.8	1.3
Total	0.5	6.8	5.5	13.5	12.4	9.0	7.2	5.4

However, the regeneration of nitrogen assimilated by phytoplankton through grazing and excretion by zooplankton becomes the variable which could alter annual production estimates by a large fraction. If, for example, phytoplankton populations were capable of using the very low light levels efficiently and the particulate nitrogen pool was turned over just one time during the summer, our estimates of primary production based upon N uptake would be low by a factor of 2. As pointed out earlier in discussing terrestrial inputs, this almost certainly occurs in the shallow brackish warm waters next to the coastline.

Another approach toward estimating annual production was the application of the equation of Eppley and Peterson (1979). In seeking to relate the productivity arising from "new" nitrogen advected or diffused into the euphotic zone (Dugdale and Goering, 1967) with the productivity resulting from nitrogen (primarily ammonia) regenerated in situ, they established the relationship.

New production/total production = 0.0025 (total production). Harrison, et al. (1982) applied this equation to Baffin Bay waters and calculated total annual production of 188 g C/m^2-yr, about double previous estimates from the game area. They derived their estimate from measured nitrate and ammonia uptake rates. They did not, however, adjust this estimate downward to compensate for the period of winter darkness when growth would be solely light limited.

When we assume an assimilation of 4 μg-atoms NO_3-N/liter and a 35-50 m euphotic zone we obtain a "new carbon" production between 12.6 and 18 g/m^2. Inserting these values into the equation, our total annual production would equal 71-85 g C/m^2-yr. If we apply a reduction factor based on the fact that light is severely limiting between mid-October and mid-April, the range of annual production is 35-42 g C/m^2-yr. These values are in good agreement with the annual productivities we predict from ^{14}C-uptake data alone. It should be noted the Eppley-Peterson equation was intended for offshore, oligotrophic waters. The pronounced stratification, ice cover and low nutrient concentrations in the Beaufort Sea produce conditions very similar to offshore oceanic waters of lower latitudes.

Truett (1981), in his synthesis of the Simpson Lagoon ecosystem study notes the importance of the wind-driven longshore transport in

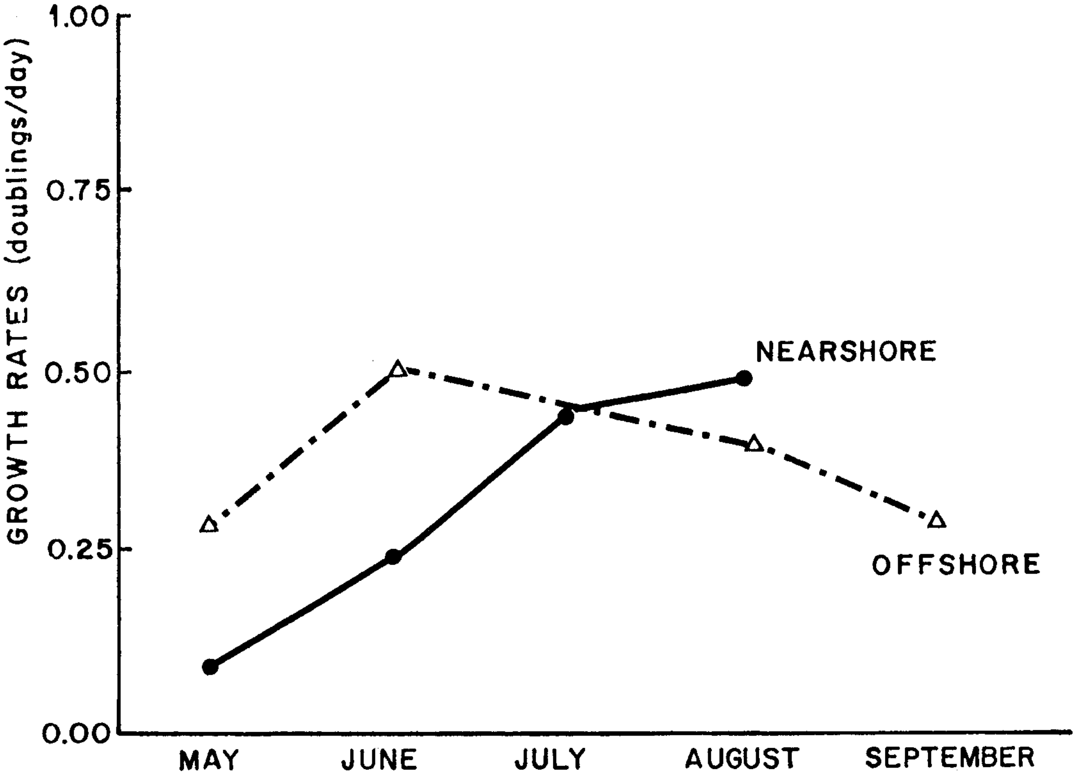

Figure 14. Phytoplankton growth rates in offshore and nearshore Beaufort Sea waters.

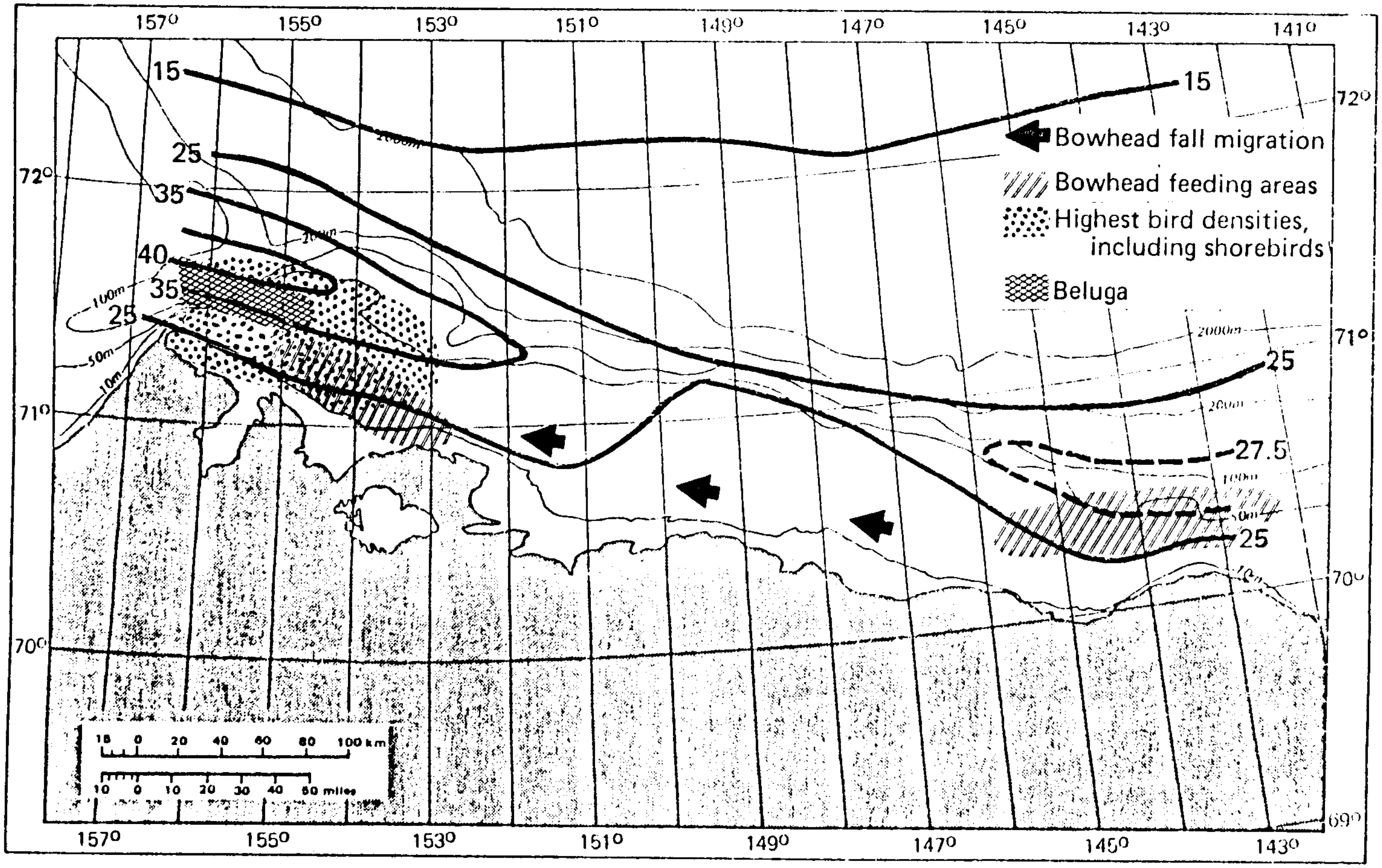

Figure 15. Observed concentrations of marine mammals and birds in relation to areas of projected primary production.

determining the water characteristics along the shoreline. This brackish warm water is a mix of river water and marine water which is transported by prevailing easterly winds to the west. Satellite imagery shows evidence of this transport along the entire shoreline. We hypothesize that the continual addition of freshwater laden with inorganic and organic nitrogen should result in a progressive nutrient enrichment in coastal waters as the longshore transport approaches Point Barrow. At Point Barrow, the Bering-Chukchi water moving northward intersects this flow and induces eddy formation in the area northeast of the Plover islands. The enhanced production anticipated from mixing the more nutrient-rich Bering-Chukchi waters and the enriched brackish coastal water should be evident as increased primary and secondary production in this area.

Chlorophyll concentration data from Horner (1981) support this premise and we estimate that annual production may approach 50 g C/m^2 which makes this area one of the most productive of the Alaskan Beaufort Sea. Braham and Krogman (1977) identify this area as a fall concentration locality for bowhead whales during the westward migration which may be a result of increased concentrations of prey organisms.

Other investigators have identified areas near Barrow and Barter Island as being important habitat for mammals and birds. Figure 15 shows composited information from Braham and Krogman (1977), Divoky (personal communication), Frost and Lowry (1981), and Burns et al. (in preparation) regarding observed concentrations of birds and marine mammals in the Beaufort Sea. The short food webs with vertebrate consumers relying on herbivorous mysids, amphipods, euphausids and copepods lends credence to the apparent correlation between areas of high primary production and faunal density.

Cellulose Biodegradation in Marine Waters

Oxidation of cellulose in the waters of Elson Lagoon by microbial populations was demonstrated in 1978 in a series of laboratory experiments performed at the Naval Arctic Research Laboratory at Barrow. During 1979, in cooperation with D. Schneider (RU 356), these experiments were expanded to test the ability of the amphipods *Gammarus* *setosus* and *Onisimus* sp. to utilize peat detritus as a food source and to acquire additional data on microbial oxidation by in situ populations at temperatures typical of summer and winter environments. The 1978 experiments had revealed active microbial oxidation in peat exposed to seawater and in the water column. Figure 16 shows the temperature effects on cellulose oxidation using water from two stations in Elson Lagoon. The cellulose was suspended in the seawater, and subsamples were stripped for radiolabeled carbon dioxide to yield the plot shown. The active degradation of cellulose at 0°C indicates that the microbial populations have adapted to the cold environment. It is reasonable to assume that the influx of eroded peat contributes to the active populations of microorganisms in the water column.

The ability of amphipods to feed upon and digest detrital material directly would be an obvious adaptive advantage in arctic waters where photosynthesis is highly seasonal. Work by RU 356 on feeding preferences of the common amphipods of Elson Lagoon has shown that some amphipods ingest and appear to assimilate peat detritus. The amphipod *Gammarus setosus* was the most active peat consumer, but unfortunately this species was not present among the animals trapped during the December 1978 experiments. Instead, a mix of small amphipods, primarily the predatory amphipods *Boeckosimus* sp. and *Onisimus* sp. were tested for peat ingestion and cellulose biodegradation. Neither species was found to release radiolabeled carbon dioxide into solution, indicating there was no assimilation of the cellulose. The presence of amphipods in samples of seawater and peat yielded lower oxidation rates than peat plus seawater alone. Possible grazing of meiofauna and bacteria may have caused this depression in the rate of carbon dioxide evolution, but the lack of label appearing in the amphipods did not lend support to this concept.

Although these initial experiments did not support the hypothesis that amphipods were directly utilizing detrital peat, the high rates of microbial biooxidation in the water column and associated with the peat detritus were felt to warrant further investigation to help establish mean lifetimes for peat particles in the nearshore waters. During July 18-20, 1979, the microbial oxidation rates of peat were again measured and compared with the oxidation rates due to the ingestion of the peat by the amphipods *Onisimus* sp. and *Gammarus setosus* at typical summer

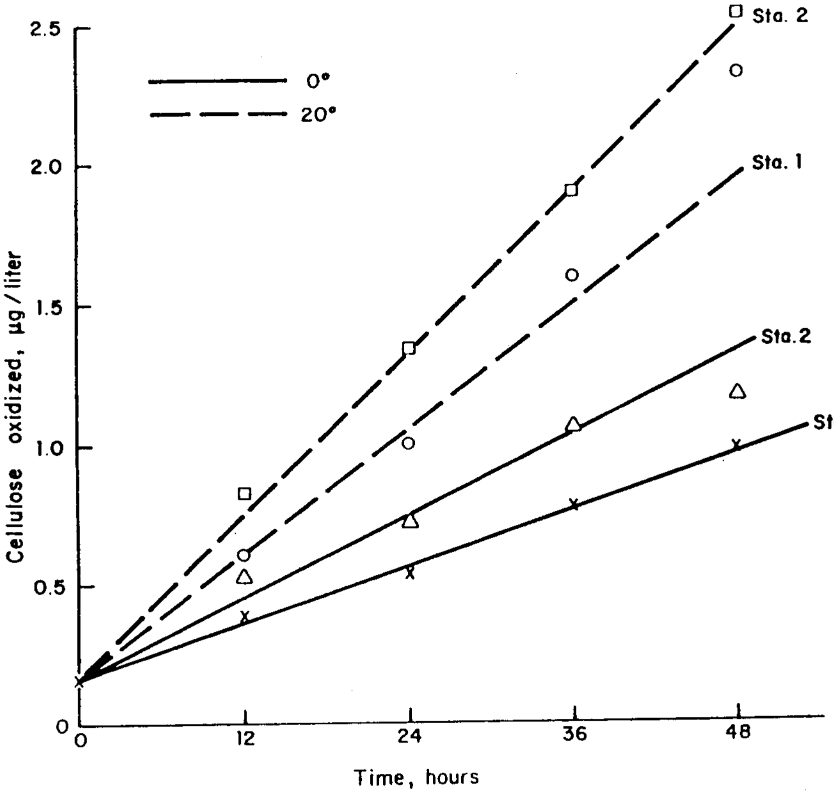

Figure 16. Carbon dioxide evolution from ^{14}C-labeled cellulose in Elson Lagoon water.

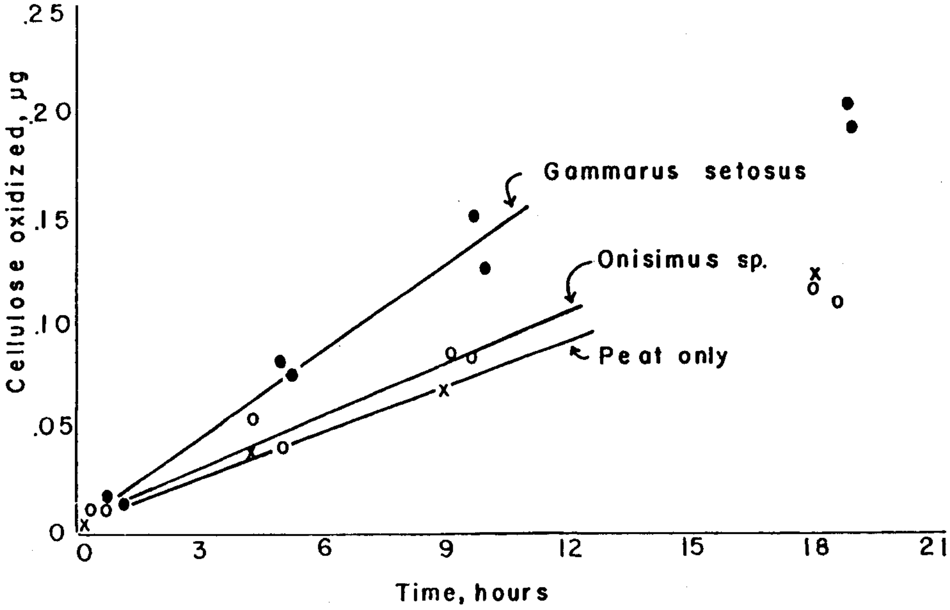

Figure 17. Carbon dioxide evolution from ^{14}C-labeled cellulose mixed with seawater-wet peat and fed to amphipods.

lagoon temperatures. The results of these experiments, which are summarized in Figure 17, show a remarkable contrast between the two amphipods in cellulose oxidation rates. The sample with *Onisimus* amphipods showed a carbon dioxide evolution rate that closely approximated the background rate due to microflora in the detritus and water, confirming the apparent inability of this genus to assimilate peat detritus. In contrast, the sample with *G. setosus* yielded a much higher rate of oxidation. Dissection of the animals showed that radioactivity from the cellulose had been incorporated into body tissue, although considerable variability occurred among animals, preventing a meaningful estimate of assimilation efficiency. Nevertheless, after mixing with 9 mg peat (dry weight), an average of 0.3 percent of the radiolabeled cellulose had been oxidized to carbon dioxide over the 18 hour experiment. Dividing this oxidation rate into the total weight of peat, a mean assimilation rate of 1.5 μg peat/amphipod-hr is obtained, assuming the peat is assimilated at rates near those of the labeled cellulose. Incorporation of metabolized ^{14}C-cellulose into body tissue, as measured in the dissected animals, was approximately as great as oxidation to carbon dioxide, indicating utilization of the cellulose for growth. These invertebrates represent the most efficient pathway we have found by which peat carbon can be transferred to higher organisms in marine foodwebs.

The rate of peat oxidation by microfloral and meiofaunal populations was estimated in a similar fashion. During the 18 hour experiment, 8°C, 0.13 percent of the label was released as carbon dioxide which translates to a turnover time of 6×10^2 days. At 0°C, the turnover time was 4×10^2 days. This is somewhat surprising, but it may only reflect increased populations of microorganisms in the sample of peat which had been held for a day in the laboratory prior to the experiment. These data compare well with data from the 1978 experiments on peat oxidation, which gave a turnover time of 6×10^2 days at 0°C using a sample of seawater-saturated peat from Milne Point. We suspect the agreement is more coincidental than indicative of similarity in oxidation rates, since it would be more reasonable to expect wide variations due to differing populations of bacteria, nutrient concentrations, temperature, oxygen concentrations and response to fresh versus degraded peat materials. The turnover times do indicate, however, that the peat is readily oxidized by microorganisms and contributes to ecosystem energetics in the nearshore zone.

Nutrient Dynamics and Under-ice Circulation

Nutrient concentrations rise steadily in the under-ice waters of the nearshore Beaufort Sea following the cessation of plant uptake in the fall. The increase is due to three additive factors -- regeneration in situ by microbial activity, advective transport, and freeze concentration of the solutes in underlying water as the ice thickens. By November, samples taken in the nearshore area showed nitrate concentrations of approximately 1-2 μg-atoms NO_3-N/liter, although the phosphate concentrations remained very low in Simpson Lagoon. The low phosphate concentrations in the presence of nitrate may indicate that bacterial nitrification is active in these waters following mineralization of organic N in eroded peat. Microbial uptake of phosphate has been demonstrated in eroded peat samples from Simpson Lagoon, and high nitrification rates were evident in the Colville Delta channels in earlier studies (Schell, 1974).

By spring, tidal and surge-pumped currents and thermohaline convection have replaced nearshore waters from all areas where offshore exchange is possible. The generalized movement of the under-ice water as shown in Figure 17 was hypothesized as a possible supply of nutrients to ice algae by this research unit in 1977. The combination of nutrient data, ice algal biomass in Stefansson Sound, and the current data obtained by Brian Matthews (RU526) now strongly support this concept.

In order to determine the residence time of water in Stefansson Sound during the winter we have developed a two-layer model based on conservation of salt and volume. It describes the under-ice salinity changes inside the barrier islands as a function of brine exclusion during ice formation and flushing by less saline offshore water. Figure 18 shows the model in box form with all the necessary parameters. The mathematics of the model are as follows:

$$\frac{dS}{dt} = \left(V \frac{ds}{dt} - s \frac{dV}{dt}\right)/V^2$$

where

$\frac{dS}{dt}$ = change in salinity inside Stefansson Sound with time

$\frac{ds}{dt}$ = change in total salt content of Stefansson Sound with time

= $RF(S-a)A_s + US_iA_p - USA_p$

$\frac{dV}{dt}$ = change in volume of water in Stefansson Sound with time

= $-RA_s$

V = volume of Stefansson Sound at any time (t)

= $(Z_o - Rt)\ A_s$

s = Total salt content of Stefansson Sound at any time (t)

= $(Z_o - Rt)(S - ab)\ A_s$

This yields the equation:

$$\frac{dS}{dt} = \frac{S(A_sR(F + 1) - A_pU) + A_pS_i\ U - A_sRa(F+b)}{A_s(Z_o - Rt)}$$

which can be solved for U:

$$U = \frac{A_sR[Rta(F + b) - Z_o(F + 1)\ (S_o(1 - \frac{Rt}{Z_o}) - S_t)]}{A_pZ_o[S_o - S_t + \frac{Rt}{Z_o}\ (S_o - S_i)]}$$

where:

S_i = offshore salinity

S_t = Stefansson Sound salinity at any time (t)

S_o = Stefansson Sound salinity at time (t=o)

F = fraction of salt excluded during ice formation

R = rate of ice formation

Z = depth of Stefansson Sound at any time (t)

Z_o = depth of Stefansson Sound at time (t=o)

a = salinity of lower layer minus salinity of upper layer
b = fraction of water column which is the upper layer
A_s = area of Stefansson Sound
A_p = Mean cross-sectional area of passes between barrier islands which define Stefansson Sound for the time period considered
U = velocity of currents through passes of cross-sectional area equal to A_p

The velocity in the upper layer (U_u) = U/b, while the velocity in the lower layer (U_l) = $U/1-b$.

Table 13 lists the salinity data for three winter seasons accumulated from Matthews (1981), Toimil and England (1982), and this report, and the current velocities and residence times calculated from the model. In order to compare our velocities with those measured by Matthews (1981), we have also considered the upper layer thickness to be equal to one-third of the water column.

Our calculated currents are quite consistent from one year to the next, but for the same 49 day period in 1978, Matthews (1981) measured currents about three times higher than our values. Given the frequent surges induced by barometric changes during the winter, periodic high current velocities are to be expected. It seems most reasonable to conclude then, that the residence time for water in Stefansson Sound during the winter is about 20-60 days, with an average of near 40 days in the spring season. From nutrient data acquired offshore, we can calculate the uptake efficiency of the epontic algae as the water moves shoreward at the ice-water interface. Table 14 lists the environmental conditions in Stefansson Sound at the peak of the ice algal bloom in late May. Note that there is no indication of nutrient limitation at this late stage in the development of the epontic algal community. Instead, as described above, light is the predominant factor restraining primary production. Limited data are available on the rate of nutrient utilization in June, but this may be the time of increasing productivity beneath areas of leads or clear ice. Melting and sloughing off of the ice algal layer should result in greatly increased light penetration which, when coupled with 24 hour sunlight, should provide favorable conditions for phytoplankton photosynthesis.

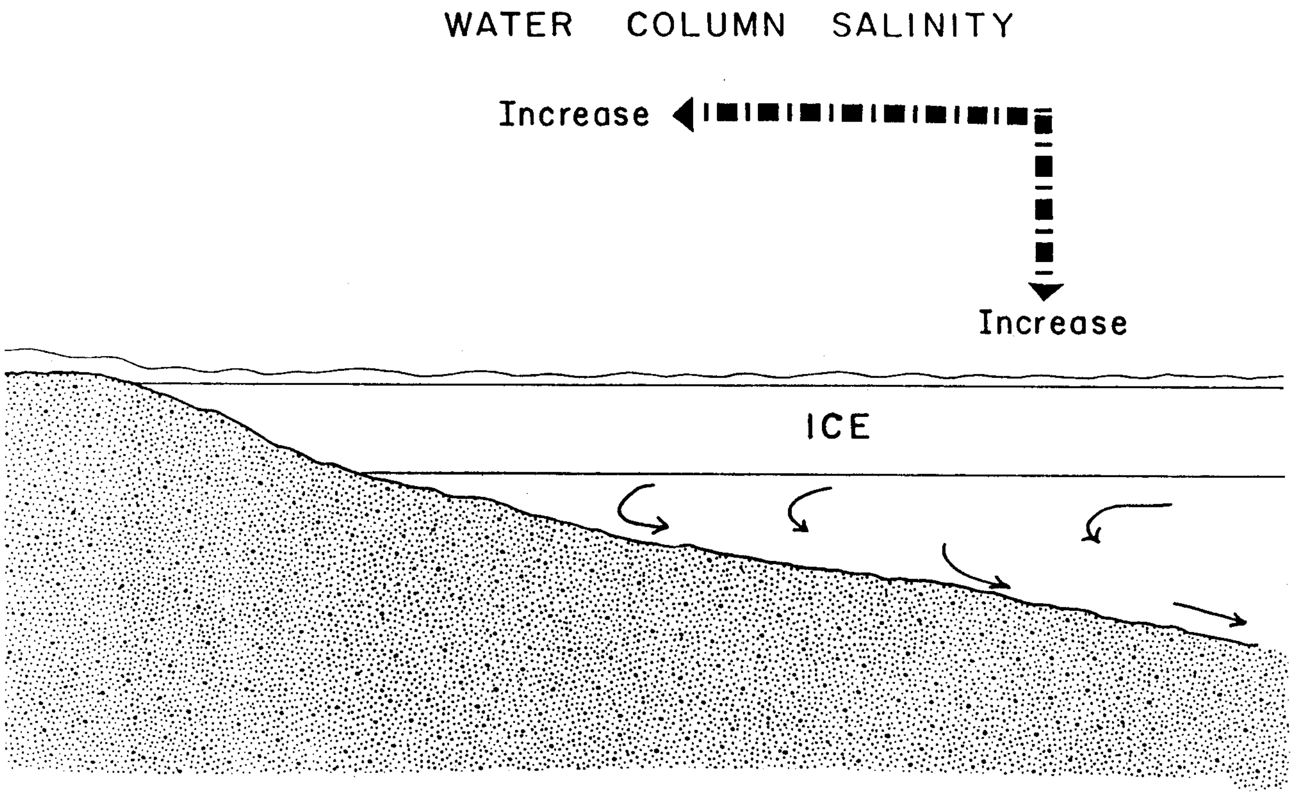

Figure 18. Generalized thermohaline convection pattern induced by brine exclusion during ice formation.

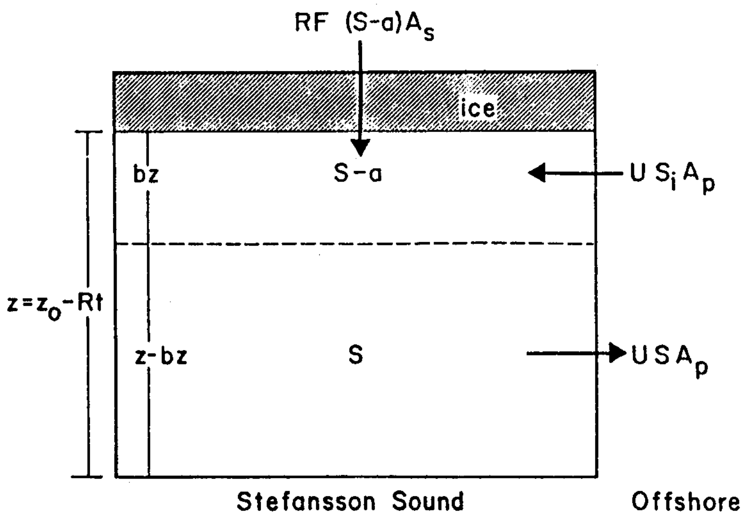

Figure 19. Water exchange model for Stefansson Sound. (See text for explanation of terms.)

TABLE 13. Water exchange model data and results.

Year	Period	t (days)	Z_o (m)	S_o (ppt)	S_t (ppt)	U_u (cm/sec)	U_l (cm/sec)	Residence Time (days)
1978 - 79	12 Nov - 31 Dec	49	3.6	32.5	34.3	1.1	0.5	50
	12 Nov - 12 Feb	92	3.6	32.5	34.8	1.5	0.7	36
	24 Jan - 31 March	66	2.9	33.4	34.0	0.7	0.3	49
	12 Nov - 31 March	139	3.6	32.5	38.0	0.8	0.4	46
1980 - 81	9 Nov - 7 May	180	3.6	28.8	33.1	0.8	0.4	45
1981 - 82	1 Oct - 25 May	237	4.0	27.8	34.4	0.6	0.3	60

a = 1.0 ppt
b = 0.33
F = 0.83 (Schell 1975)
S_i = 31.5 ppt
R^1 = 0.01 m/day (Schell 1975)
A_s = 8.8×10^8 m^2
A_p^s* = $(252 - 0.5t) \times 10^3$ m^2

* In this equation, t is the time since the start of freeze-up.

Table 14. Under-ice conditions in late spring, Stefansson Sound Beaufort Sea.

ENVIRONMENTAL CONDITIONS
STEFANSSON SOUND - MAY 1979

SALINITY	32 - 50 ‰	ICE	1.6 - 2.0m
WATER TEMP.	-1.8 to -2.9°	AIR TEMP.	-30 to 0°
SNOW COVER	10 - 50cm	DAYLIGHT	> 20 hrs

LIGHT PENETRATION, UNDER-ICE - 0.0 - 0.90 % surface
MAXIMUM LIGHT INTENSITY, UNDER-ICE ~1000 lux
~20 μE m^{-2} s^{-1}

NUTRIENT CONCENTRATIONS

NITRATE + AMMONIA - N	4 - 10 μg - at/l
PHOSPHATE - P	0.5 - 1.1 "
SILICATE - Si	20 - 50 "

Since nutrient concentrations provide little insight into the dynamics of nitrogen and phosphorus cycling and limiting elements, we have attempted to assess the relative magnitudes of the major factors governing the availability of nutrients in nearshore waters.

Allochthonous inputs of terrestrial nitrogen occur during the summer months and offer several reasons for probable importance to the marine ecosystem:

1. Peak input occurs during breakup flooding and injects both inorganic and organic nitrogen into the nearshore marine waters early in the primary production season.

2. Water temperatures of the river water are usually much higher than the marine waters, and microbial processes should be accelerated.

3. River water contains several times greater concentrations of dissolved and particulate organic nitrogen than marine waters. Marine water, however, is relatively rich in phosphate and may accelerate microbial growth through synergistic effects. High nitrification rates observed in delta channels with mixed marine and freshwater (Schell, 1975) tend to support this hypothesis.

To assess the role of terrestrial nutrients in marine phytoplankton production, a mass balance calculation made on nitrogen inputs can be compared to nitrogen requirements by phytoplankton in the nearshore zone. Assumptions and determinations include:

1. Late winter inorganic nitrogen concentrations in marine waters averaged 4 μg-atoms/liter in the 1.8 m ice cover (this study; Schell and Hall, 1972).

2. Planimetry of the nearshore zone of the Alaskan Beaufort Sea out to the 10 m contour defines an area of 8.7×10^9 m^2. For estimation of water volume in this area, a uniform slope offshore

is assumed and an average distance offshore of 10 km to the 10 m depth contour.

3. Annual ice thickness is 1.8 m, and 20 percent of solutes in the water is included in the ice during freezing.

4. Total river runoff into the Beaufort Sea from commencement of spring flow until July 1 is 16.8 x 10^9 m^3. Average nitrate-N concentration in the river water is 4 µg-atoms/liter.

5. Organic nitrogen input from the rivers is 840 x 10^3 kg-atoms. Inorganic nitrogen input is 70 x 10^3 kg-atoms.

The formation of the winter ice cover reduces the underlying water volume from 44 x 10^9 m^3 to about 30 x 10^9 m^3. At 4 mg-atoms N/m^3, a total standing stock of 120 x 10^3 kg-atoms of inorganic nitrogen is present in the water at the onset of algal growth in spring. Another 11 x 10^3 kg-atoms are present in the ice cover and are released during brine drainage and melting, yielding a total in situ standing stock of 131 x 10^3 kg-atoms of inorganic nitrogen (mostly nitrate-N).

As breakup progresses, river runoff adds an additional 70 x 10^3 kg-atoms inorganic nitrogen and 840 x 10^3 kg-atoms dissolved and particulate organic nitrogen. Data from the Colville Delta saline waters indicate in situ nitrification rates of 0.23 µg-atoms N/liter-day. Mineralization rates of dissolved organic nitrogen in Elson Lagoon during late spring occurred at 0.13 µg-atoms N/liter-day (Schell, 1974). Since these rates were observed at temperatures near -2°C, the warmer runoff water of Colville River flow in June may result in faster rates of mineralization.

It is interesting to compare the primary productivity rates measured in the Beaufort Sea with the nitrogen available for growth. Using a carbon:nitrogen atom ratio of 7.5, the inorganic nitrogen entering the nearshore zone is sufficient for the fixation of 1.5 x 10^6 kg-atoms carbon. If mineralization were sufficiently fast to make available most of the dissolved organic nitrogen, the total nitrogen standing stock would be sufficient to produce 7.8 x 10^6 kg-atoms C on a once-through uptake. Our estimate of annual carbon fixation for this same area (via ^{14}C-uptake data) is about 10-15 x 10^6 kg-atoms for the May-July period. Since grazing and regeneration would turn over much of the nitrogen in situ, the amounts present at the start of the season and transported into the coastal zone must account for the observed productivity. Since nitrogen is the limiting nutrient for marine primary production, we can also estimate that turnover of the nitrogen pool must occur 7-10 times during this period if the terrestrial organic nitrogen does not mineralize at an appreciable rate. If, however, the major fraction of the organic nitrogen is mineralized and enters the marine nitrogen cycle, then the necessary turnovers drop to only two or three times during the fixation of the 10-15 x 10^6 kg C. The data from Hufford (1974) indicate that deeper (75 m) offshore concentrations of nitrate are higher (10-15 μg-atoms N/liter), and it is possible that wind mixing in summer may advect larger quantities of nitrogen to the euphotic zone. This source is probably much more important further offshore.

These estimates are not intended to represent the quantitative movements among compartments of the coastal nitrogen cycle, but to describe the probable major role of allochthonous nitrogen to coastal productivity. The observed rates of carbon fixation coincide well with the conceptual model of nitrogen supply. Although loss from the nearshore zone through sedimentation and transport offshore beyond the 10 m contour must account for a fraction of the inputs, uptake rates are rapid, as evidenced by the depletion of nitrate concentrations in Harrison Bay off the mouth of the Colville River.

The uptake of dissolved nitrogen into the particulate fraction progresses until the cessation of primary productivity in the fall. Soon thereafter, decomposition and regeneration of inorganic nitrogen result in the accumulation of nitrate and ammonia in the water column. The large quantities of organic nitrogen accumulated through uptake and fluvial transport over the summer should be reflected in high standing stocks of nitrate and ammonia, but this condition is not observed except in localized areas of restricted circulation. Instead, tidal and surge-pumped currents coupled with thermohaline convection transport more saline, denser waters containing the regenerated nutrients offshore. As mentioned above, the currents measured by Matthews (1981) and calculated from our water exchange model yield residence times for Stefansson Sound water during winter of 20-60 days. Schell (1975) has made a similar estimation for Dease Inlet and concluded that thermohaline convection and surge and tidal flushing could replace the under-ice waters as often as every 7-10 days. The significance these currents add to nutrient budgets is pronounced.

Data obtained from a transect offshore in spring 1982 support our model. Figures 20 and 21 show the salinity and nutrient concentrations northward across Stefansson Sound and approximately 50 km beyond Narwhal Island. Salinities within the lagoon system and in downslope bottom water offshore are higher than in the overlying water column by 3-10 percent. Nitrate concentrations are about doubled, however, indicating that the mineralization of organic nitrogen and nitrification processes continue throughout the winter. By dividing the increase of 3 μg-atoms NO_3 - N/liter by the calculated residence times of 20-60 days in the lagoon, we estimate the input rate due to in situ regeneration of nitrate at 0.05-0.15 μg-atom N/liter-day. This estimate compares favorably with previous estimates of 0.13 μg-atom N/liter-day in Elson Lagoon near Barrow and 0.07 μg-atoms N/liter-day in saline channels of the Colville delta (Schell, 1974).

Instead of accumulating high concentrations of inorganic nitrogenous nutrients in the nearshore under-ice waters over the winter season, this nitrogen is largely transported to offshore deep water. The ambient concentrations in early spring are derived from the offshore surface water advected toward the coast. Since these waters are relatively low in nitrogenous nutrients, the role of allochthonous inputs during breakup and river flow over the summer season are accentuated.

Phosphate Uptake Experiments -- August 1978

The results in Table 15 show the concentrations of dissolved inorganic phosphate (DIP) and total organic phosphorus (TOP) in Milne

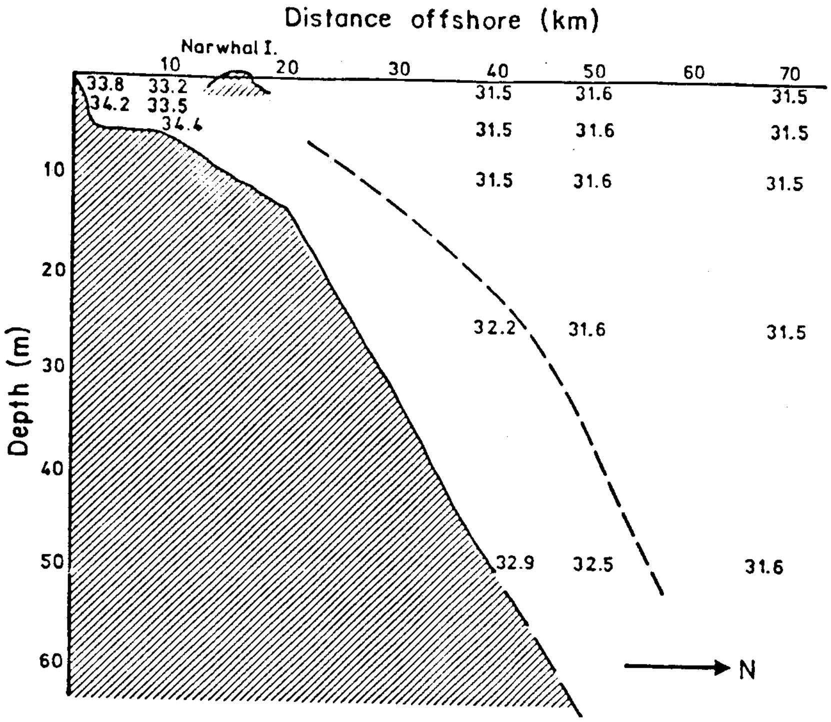

Figure 20. Salinities (ppt) north of Prudhoe Bay, Alaska, 28 May 1982.

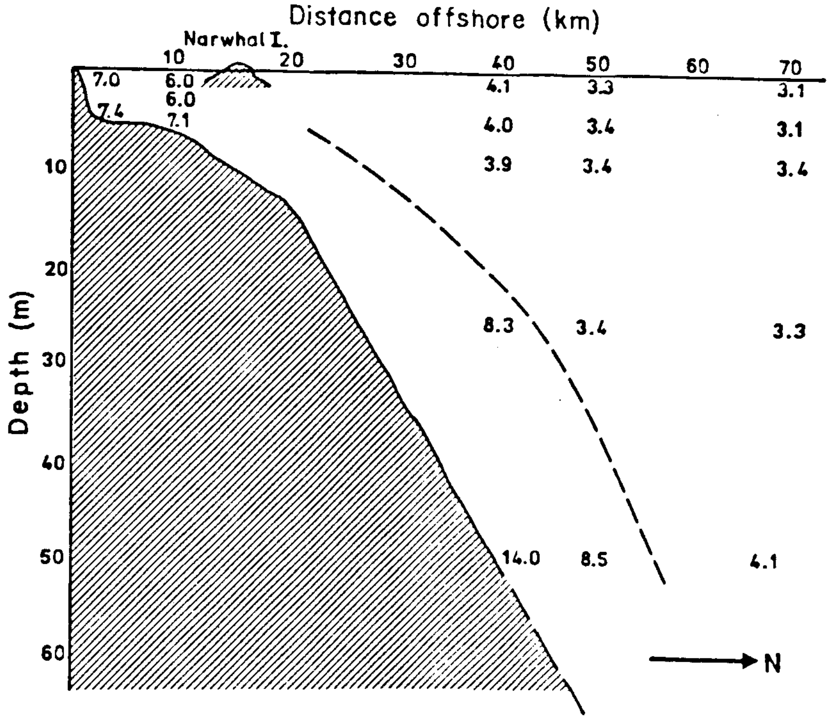

Figure 21. Nitrate concentrations (μg-atoms N/liter) north of Prudhoe Bay, Alaska, 28 May 1982.

Point seawater. The phosphate uptake rates of Milne Point seawater samples and peat-amended Milne Point seawater samples are shown in Tables 16 and 17. The peat-amended seawater took up phosphate at a significantly higher rate than the $HgC\ell_2$ poisoned control and the autoclaved control, indicating that the uptake was predominantly biological in nature versus a nonbiological sorption (Table 17). Since the phosphate uptake rates in seawater did not increase significantly with concentration up to additions of 0.50 μg atom P/liter, and the indigenous concentration was 0.20 μg atom P/liter, the mechanisms responsible for uptake and release of phosphorus at these lower concentrations were most likely in steady state (Table 16). The increased uptake response to additions of higher concentrations of phosphate (1.0 and 2.0 μg atom P/liter) probably indicates a stimulation of biological phosphate incorporation above steady state levels. A physical sorption study might test this interpretation.

Carbon Isotope Studies of Nearshore Foodwebs

The intricacies of nearshore and estuarine marine foodwebs present formidable obstacles to assigning significances to various energy source materials supporting resident fauna. Primary production from phytoplankton, benthic microalgae, macrophytes, and allochthonous terrigenous vegetation can all contribute with varying efficacy, and the quantification of inputs is often difficult or impossible. Recent studies have sought to bypass the various foodweb steps between source and consumer of interest by making use of natural $^{13}C/^{12}C$ isotope ratios to estimate source allocations. If a moderately large difference in the $^{13}C/^{12}C$ isotope ratios of the source materials occurs, then relative significances can be ascribed to these sources upon determination of carbon isotopic abundances in the organisms of interest. The marked difference in $\delta^{13}C$ resulting from C-3 and C-4 photosynthetic pathways yields a natural signal easily traced in herbivores grazing on these plants (DeNiro and Epstein, 1978). As long as the source materials and dietary preferences have a relatively large separation in isotopic signature and are limited to two or three in

TABLE 15. Phosphorus analyses - Milne Point water.

Station	Date	DIP* µg-atom P/liter	TOP** µg-atom P/liter
1 (surface)	27 Jul 78	0.36	0.72
4 (bottom)	27 Jul 78	2.07	1.55
1 (surface)	7 Aug 78	0.20	0.49
4 (bottom)	7 Aug 78	0.15	0.24
1 & 4 (pooled)	8 Aug 78	0.12	

*DIP = dissolved inorganic phosphate
**TOP = total organic phosphorus

TABLE 16. Phosphate uptake by Milne Point seawater.

Phosphate Added* (µg-atom P/liter-hr)	Uptake Rate (ng-atom P/liter-hr)
Carrier free ^{32}Pi	5.6
0.05	5.5
0.10	4.8
0.50	6.9
1.0	18.0
2.0	52.0

*Ambient dissolved inorganic phosphate - 0.20 µg-atom P/liter.

TABLE 17. Phosphate uptake by peat amended seawater.

Sample	Total Inorganic Phosphate (µg-atoms P/g peat)	Uptake Rate (µg-atoms P/g peat-hr)
Peat and filtered Milne Point water	3.12	1.08
$HgCl_2$ poisoned	3.12	0.17
Autoclaved	3.12	0.03

number, the allocation of the source material can often be accomplished. Nature is rarely so cooperative. In estuarine situations where several of these studies have been performed, flora are varied in species and isotopic composition. Studies by Haines and colleagues (Haines, 1976a, b; Haines and Montague, 1979; Hackney and Haines, 1980) using the ^{13}C differences between C-3 and C-4 plants in Georgia and Mississippi estuaries, attempted to quantitate the dependencies of marsh fauna on the marsh grasses *Spartina* spp. and *Juncus* spp. with moderate success. Major difficulties arose however, due to natural variability in the $\delta^{13}C$ within a given species and due to contributions of heterogeneous populations of epiphytic algae, photosynthetic bacteria, and numerically minor species of vascular plants occurring within the environment with overlapping $^{13}C/^{12}C$ abundances. The possibility of chemosynthetic fixation as a major pathway of carbon input has been proposed by Peterson et al. (1980) to alternatively account for some of the conclusions reached by Haines (1977) regarding the role of *Spartina*-derived detritus in supporting Georgia estuarine ecosystems. The ambiguous conclusions arise from the overlap in the $\delta^{13}C$ signal and the use of a single isotopic label to trace foodweb pathways.

We present here a study on arctic Alaska estuarine foodwebs using both ^{13}C and ^{14}C natural abundances, and describe an ecosystem having a large dependency on allochthonous carbon with a delay of up to several thousand years occurring between primary production and its utilization by consumer organisms. Nearshore carbon inputs consist of primary production by ice algae and phytoplankton, supplemented by peat and vegetative detritus transported by the rivers or added directly by shoreline erosion. Within the shallow nearshore zone (out to the 10 m depth contour, approximately 10 km), allochthonous carbon inputs are about equal to annual primary production (see Figure 22). Since radiocarbon dating of soil sections showed that the peat has been accumulating for 8,000-12,000 years B.P., large depletions in ^{14}C abundances would be found in a foodweb based on peat carbon. $^{13}C/^{12}C$ abundances typical of coldwater marine algae were anticipated in pelagic organisms offshore (McConnaughey and McRoy, 1979a) and a uniform C-3 isotopic signature typical of peat and tundra vegetation represent the terrigenous organic matter. The typically

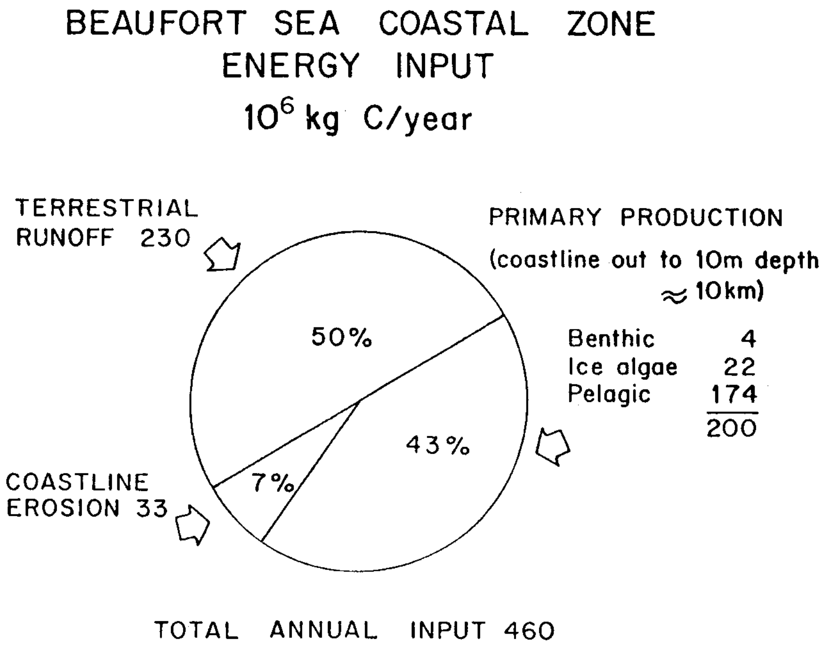

Figure 22. Annual inputs of carbon to the nearshore waters of the Beaufort Sea.

short food chains of the Arctic also indicated minimal problems with biochemical fractionation effects (DeNiro and Epstein, 1978). Organisms consuming these sources either directly or indirectly should yield an isotopic distribution based on source materials as shown in **Figure 23.**

Preliminary sampling of the particulate organic matter transported by the Colville River over the breakup flood season indicated that the bulk of the fluvial particulate carbon was peat and not modern vegetative detritus carried by surficial runoff. In contrast, the large mysid and gammarid amphipod populations in the receiving marine waters showed only minor depressions in ^{14}C content and had $\delta^{13}C$ values indicative of predominantly marine carbon. Radiotracer experiments with ^{14}C-labeled cellulose indicated active microbial degradation of the peat when exposed to marine waters but the foodweb linkages necessary for efficient transfer to higher trophic levels are apparently lacking. Apical marine organisms from Simpson Lagoon such as four-horn sculpins (*Myoxocephalus quadicornus*) and arctic cod (*Boreogadus saida*) also contained carbon isotope abundances typical of pelagic primary producers, confirming their dependency upon marine carbon fixation.

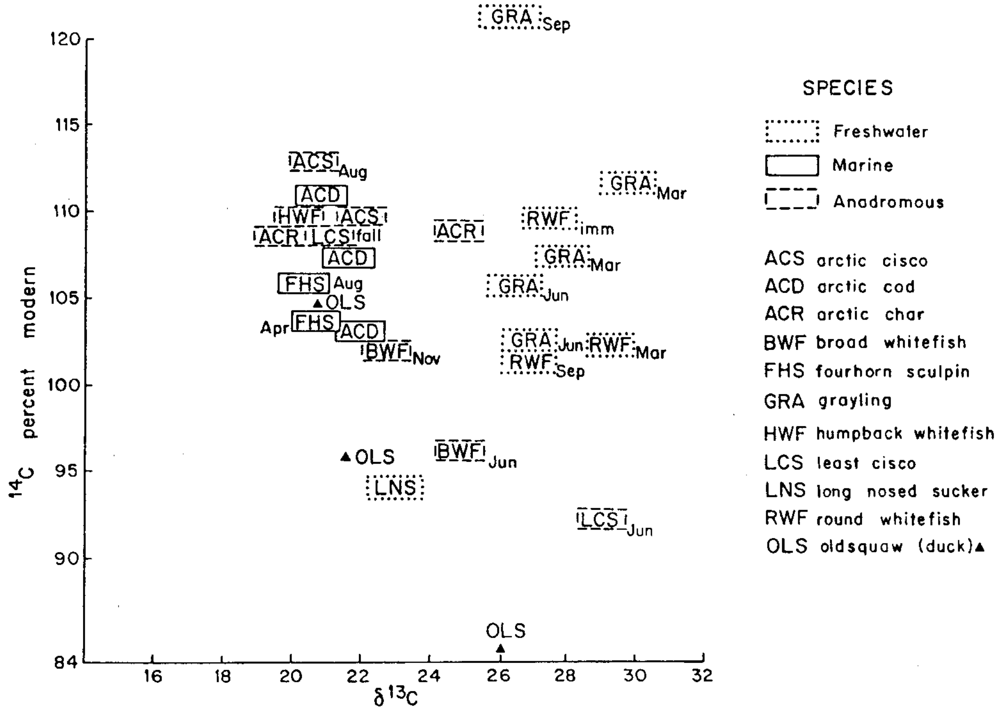

Figure 23. Carbon isotope distribution in coastal Beaufort Sea organisms.

Seasonal residents of the nearshore Beaufort Sea marine waters are typified by avifauna such as migratory oldsquaw ducks (*Clangula hyemalis*) and several species of anadromous fishes, principally ciscoes (whitefish), which enter the marine environment after overwintering in the rivers. The oldsquaw ducks of breeding age migrate north to the tundra lakes and ponds where they nest, molt, and feed upon freshwater invertebrates. Non-breeders and some of the pre-molting birds (males), however, summer on the nearshore lagoons and feed upon the marine invertebrates, thereby splitting the species into segments dependent upon freshwater or marine foodwebs. A detailed description of avifauna is given by Johnson and Richardson (1981). Similarly, the whitefish do not re-enter the rivers until freeze-up and ascend the rivers to overwinter in deep pools. Since Alaskan north slope rivers freeze to the bottom in shallow areas, and essentially cease flowing for most of the late winter (Arnborg et al., 1966), movement within the river system is very restricted for the obligate freshwater fish species and the overwintering anadromous fish. Samples of fish were collected prior to entering the Colville River, beneath the ice in March, and in the Colville Delta as they were re-entering the marine waters in June.

Figure 23 shows the isotopic composition of a cross-section of the fishes and oldsquaw ducks from freshwater and marine environments and a complete list of isotopic data is presented in Table 18. The marine fish are tightly grouped near $\delta^{13}C$ of -21 ppt and a ^{14}C content of 104-110 percent modern.[1] The anadromous species captured after feeding in the marine environment for the summer are isotopically indistinguishable from obligate marine species, indicating that peat is not a significant source of carbon to nearshore marine foodwebs. The principal prey species found in stomach contents were mysids (^{14}C = 106 percent modern) and gammarid amphipods (^{14}C = 104 percent modern), indicating that very little of the peat carbon is passed up the food chains to the larger marine invertebrate populations. One species of amphipod, *Gammarus setosus* was anomalously low in ^{14}C abundance (96.6 percent modern) and has been shown by Schneider (1980) to be an avid consumer of peat detritus, and Schell (1980) has shown that ^{14}C-labeled cellulose is readily consumed and respired by the

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[1] Carbon-13/12 ratios are expressed as $\delta^{13}C_{PDB}$, where $\delta^{13}C_{PDB} = [(R_{sample} - R_{std})/R_{std}] \times 1{,}000$, where R is the ratio $^{13}C/^{12}C$ and $\delta^{13}C$ is reported in parts per thousand relative to the PDB standard. The carbon-14 activity of a 1950 AD sample is expressed as 100 percent modern, normalized to $\delta^{13}C$ of -25 ppt to correct for fractionation effects. Modern tundra vegetation is 122-140 percent with lower values in annual grasses, leaves and aquatic algae. Higher values are found in woody plants, standing dead grasses, and sedges. Marine macroalgae samples (*Laminaria* spp.) are 103-107 percent (n = 4). "Average peat" was taken to be the mean activity of a uniform layer of peat accumulating at constant rate for 8,142 years. Actual basal peats along shorelines and rivers ranged from 3,400 to 12,600 years B.P. The mean was 36.3 percent modern (n = 6, S.D. = ± 15.3 percent modern), yielding an average activity of 62.9 + 10.2, -11.3 percent modern. This average peat activity is probably lower than the overall activity of peat entering the aquatic systems. An actual particulate sample from the Colville River was 74.4 percent modern. Since no quantitation of modern material in these samples was attempted, the more conservative value of 62.9 percent was used to determine peat carbon content in organisms. Isotopic analyses were performed by Beta Analytic, Inc., Geochron Division of Krueger Industries, and Teledyne Isotopes. Precision in ^{14}C analyses was typically ± 1 percent and $\delta^{13}C$ analyses were ± 0.05-0.1 ppt. Analyses costs limited replication of samples. *Laminaria* from one collection site were sent to each laboratory and yielded the following activities: 105.7 (GD, KI); 105.0, 107.1 (BAI); and 102.8 (Teledyne).

organism. It does not, however, comprise a large fraction of the prey invertebrates consumed by the anadromous fishes and oldsquaws (Griffiths and Dillinger, 1981). Apparently the microbial-meiofaunal-invertebrate foodweb pathways in the marine waters are inefficient to the point that apical foodweb organisms receive very little direct benefit from detrital inputs.

Arctic freshwater organisms contrast markedly with marine organisms in their variability in ^{14}C content. Although modern aquatic primary production centers at about 123 percent modern, as evidenced by both submerged algal mats (122.2) and emergent macrophytes (123.9, n = 3), the ^{14}C content of the fauna varies from 120.9 to 93.5 percent modern. The seasonal variation of ^{14}C content in Colville River grayling (*Thymallus arcticus*) suggests a major alteration of food dependencies over the hydrologic year (Figure 24). Grayling are known to feed heavily upon surface drift insects (Morrow, 1980) in headwaters during summer when benthic primary production is rapid, and the ^{14}C content of fish taken in September is in agreement. With the appearance of ice cover in September, the available food becomes the benthic and epibenthic insect larvae in the rivers in overwintering areas. Two fish sampled in March had ^{14}C contents of 108 and 111 percent modern, and by June, when breakup of the nearly 2 m thick ice cover occurred, two fish yielded values of 102 and 106 percent modern. Since under-ice primary production is nil during the arctic winter darkness, this shift in ^{14}C content must represent an increasing reliance on peat carbon to replace recent primary production. By using the value of 123 percent modern as that of modern freshwater energy sources and 63 percent modern as average peat activity, the peat carbon content in grayling can be estimated to range from less than 4 percent in summer to a maximum of near 37 percent by the end of the winter season.

Some of the anadromous fish sampled follow a similar pattern. Least ciscoes (*Coregonus sardinella*) and arctic ciscoes (*Coregonus autumnalis*) caught in October and November entering the Colville River Delta were isotopically marine modern fish ($\delta^{13}C$ = -17.5 to -22.9, 102.9 to 109.2 percent modern). In June, a least cisco netted during breakup flooding and out-migration contained stable carbon isotope ratios typical of freshwater fish ($\delta^{13}C$ = -29.1) and a large

TABLE 18. Summary of Carbon Isotope Data - Beaufort Sea - November, 1981

Sample Identification	$\delta^{13}C$	^{14}C activity	
		Years B.P.	% Modern (corr. to $\delta^{13}C = -25^{o}/oo$)
VEGETATIVE			
MIL 78-3; GX5822, Sagavanirktok River basal peat	-28.5	3,400	65.5
MIL 78-2; GX5821, Pingok Is. basal peat	-28.3	8,432	35.0
MIL 78-4; GX5824, Tundra plants, modern	-28.2		141.1 ± .5
MIL 78-1; GX 5820, Milne basal peat	-28.7	9,052	32.4
I-6838 Oliktok basal peat	--	8,550	34.5
I-6839 Kavearak Pt. basal peat	--	12,660	20.8
81-8; Beta 2918, *Nostoc* mats, 27 Jun 81	-20.24		122.2 ± 0.9
81-9; Beta 2919, *Arctophila fulva*	-19.51		123.6 ± 0.6
81-12; Beta 3530, *Arctophila fulva*	-26.85		121.1 ° 0.8
81-13; Beta 3531, *Carex aquatilis*	-30.49		127.1 ± 0.6
81-15; Beta 3533, Basal peat, Lake 3, USFWS camp	-27.24	9,805	29.5 ± 1.3
81-19; Beta 3537, *Salix* spp.	-28.14		138.1 ± 0.6
79-5; GX 6274, *Laminaria*, whole plants	-15.4		105.7
79-7; UM-1738, *Laminaria* stipes	-17.47		105.0 ± .8
79-8; UM-1739, *Laminaria* blades	-15.04		107.1 ± 1.4
79-23; I-II, 354, *Laminaria* blades	-18.2 ± .2		102.8 ± 0.8
79-12; UM-1803, Colville R. particulate C., 2 Jun 79	-26.39	900	89.4 ± 1.6
79-14; UM-1804, Kuparuk R. particulate C., 31 May 79	-26.89	2,683	71.6 ± 1.1
79-11; Beta 1027, Colville R. particulate C., 12-14 Jun 79	-27.01	2,375	74.4 ± .9
81-6; Beta 2650, Lake C-2, o-7.5 cm Seds.	-30.71	3,840	62.0 ± 0.9
81-7; Beta 2651, Lake C-2, 7.5-18 cm Seds.	-29.61	4,400	57.8 ± 0.7
81-16; Beta 3534, Gooseneck Lake sediments	-27.09	2,068	77.3 ± 0.7
INVERTEBRATES			
MIL 78-6; GX5825, Mysids Aug 78	-23.6		105.9
MIL 78-8; GX5827, *Saduria*, Aug 78	-18.5		103.1
MIL 78-9; GX5828, *Onisimus* amphipods, Aug 78	-18.3		103.7
79-18; Beta 1030, *Saduria*, S.L., Nov 79	-20.43		102.9 ± .9
79-19; Beta 1031, *Gammaracanthus* amphipods, Nov 79	-20.91		99.8 ± .8
79-20; Beta 1032, *Weyprechtia* amphipods, Nov 79	-20.71 ± .05		98.4 ± 1.5
79-21; Beta 1033, Arctic cisco *Coregonus autumnalis*, stomach contents, Nov 79	-22.70 ± .02		97.4 ± 0.6

TABLE 18. (Continued)

Sample Identification	$\delta^{13}C$	Years B.P.	^{14}C activity % Modern (corr. to $\delta^{13}C = -25^{0}/oo$)
82-12; Beta 5015, Arctic cisco stomach contents (amphipods), fall 81	-23.43		103.6 ± 0.9
80-10; Beta 1742, *Gammarus setosus*, Barrow, Jul 80	-19.92		96.6 ± 0.8
81-11; Beta 3529, *Daphnia*, cyclops, Helm. pond, 29 Aug 81	-16.41		119.8 ± 0.8
FISH Marine			
MIL 78-5; GX 5824, Four Horn sculpin, *Myoxocephalus quadricornis* (Aug 78)	-20.5		105.3
79-9; UM-1740, Four horn sculpin (Apr 79)	-20.82		104.4
79-2; GX 6271, Arctic cod, *Boreogadus saida*, (Aug 78)	-21.5		107.3
79-10; UM-1741, Arctic cod (Aug 78)	-21.6		103.7
80-13; Beta 1745, Arctic cod, offshore (May 80)	-20.89		109.8 ± 0.8
Anadromous			
MIL 78-7; GX5826, Humpback whitefish, *C. pidschian*, Colv. delta, fall 77	-20.4		109.5
MIL 78-10; GX5829, Least cisco, *C. sardinella*, Colv. delta, fall 77	-21.2		109.2
80-8; Beta 1741, Least cisco, Jun 80	-29.10	687	91.8 ± 0.8
80-21; Beta 1987, Least cisco, Colv. delta, Nov 80	-22.90		103.1 ± 1.2
81-18; Beta 3536, Least cisco, imm., Helm. pond, 29 Aug 81	-28.8		114.3 ± 0.8
82-1; Beta 5004, Least cisco, Colv. delta, 10 Oct 81	-20.58		105.6 ± 0.8
82-2; Beta 5005, Least cisco, Colv. delta, 17 Oct 81	-20.58		107.3 ± 0.8
82-3; Beta 5006, Least cisco, Colv. delta, 26 Oct 81	-21.33		108.3 ± 0.7
82-4; Beta 5007, Least cisco, Colv. delta, 4 Nov 81	-22.06		106.5 ± 0.7
82-5; Beta 5008, Least cisco, Colv. delta, 20 Jun 82	-21.22		106.8 ± 0.8
82-6; Beta 5009, Least cisco, Colv. delta, 20 Jun 82	-23.23		110.9 ± 0.8
GX5388; Arctic cisco, *C. autumnalis*, Colv. delta, fall 77	-21.8		109.6
79-6; GX6275, Arctic cisco, Aug 78	-20.7		112.7
82-7; Beta 5010, Arctic cisco, Colv. delta, 10 Oct 81	-17.50		106.4 ± 1.0
82-8; Beta 5011, Arctic cisco, Colv. delta, 4 Nov 81	-19.07		103.2 ± 0.7
82-9; Beta 5012, Arctic cisco, Colv. delta, 13 Nov 81	-20.50		102.9 ± 0.8
82-10; Beta 5013, Arctic cisco, Colv. delta, 20 Jun 82	-21.84		102.4 ± 0.9
82-11; Beta 5014, Arctic cisco, Colv. delta, 20 Jun 82	-21.33		104.3 ± 0.9

TABLE 18. (Continued)

Sample Identification	$\delta^{13}C$	^{14}C activity % Modern	(corr. to $\delta^{13}C$ = -25^{o}/oo)
		Years B.P.	
80-7; Beta 1740, Broad whitefish, *C. nasus*, 16 Jun 80	-24.86		94.8 ± 0.6
80-23; Beta 1989, Broad whitefish, 5 Nov 80	-22.26		102.0 ± 0.8
82-13; Beta 5016, Broad whitefish, Colv. delta, 20 Jun 82	-20.53		104.8 ± 1.0
79-15; Beta 1028, Round whitefish, *Prosopium cylindraceum*, Sep 79	-26.9 ± 0.9		101.4 ± 0.8
80-2; Beta 1267, Round whitefish, adult, Mar 80	-29.32 ± 0.1		101.8 ± 0.7
80-1; Beta 1075, Round whitefish, imm., Mar 80	-27.50 ± 0.5		109.0 ± 0.7
80-17; Bea 2005, Round whitefish, 22 Mar 80	-24.68		110.4 ± 0.8
80-19; Beta 1985, Arctic char., Oct 80	-24.56		106.8 ± 1.0
81-2; Beta 2375, Arctic char., Colv. delta, Nov 80	-20.04		107.6 ± 0.8
80-20; Beta 1986, Boreal smelt, *Osmerus mordax*, fall 80	-21.72		108.4 ± 1.1
Freshwater			
79-17; Beta 1029, Grayling, *Thymallus arcticus*, Colv. R., Sep 79	-26.4 ± .02		120.9 ± .7
80-3; Bea 1268, Grayling, 22 Mar 80 (21 cm)	-29.82 ± .03		111.1 ± 0.6
80-24; Beta 1990, Grayling, 22 Mar 80	-28.18		107.5 ± 0.9
80-4; Beta 1738, Grayling, Jun 80 (35 cm)	-26.68		105.5 ± 1.1.
80-5; Beta 1739, Grayling, Jun 80	-26.92		102.1 ± 1.0
80-11; Beta 1743, Long-nosed sucker, *Catoctomus catostomus*, Colv. R., Aug 80	-23.01		93.5 ± 0.8
81-1; Beta 2374, Burbot, Colv. R., Nov 80	-23.38		107.1 ± 0.8
BIRDS			
79-1; GX6270, Oldsquaw, *Clangula hyemalis*, adult female, Simpson Lagoon	-20.7		104.9
80-14; Beta 1746, Oldsquaw, adult female, Thetis Is., 2 Aug 80	-21.55		95.8 ± 2.0
80-15; Beta 1747, Oldsquaw, male, 2 Aug, Thetis Is.	-2606	1,305	85.0 ± 0.8
81-3; Beta 2555, Oldsquaw, male, 26 Jun 80 (#33-80)	-21.02		114.7 ± 0.7
81-4; Beta 2556, Oldsquaw, juv., 28 Aug 80 (124, 125-80)	-27.77		109.6 ± 0.7
81-5; Beta 2557, Oldsquaw, male, post-molt (#123-80)	-28.51		104.6 ± 0.7

TABLE 18. (Continued)

Sample Identification	$\delta^{13}C$	^{14}C activity % Modern	(corr. to $\delta^{13}C = -25^{0}/oo$)
			Years B.P.
MAMMALS			
Terrestrial			
81-10; Beta 2920, Lemming, *Lemmus sibericus*, female, 27 June 81	-26.09		127.4 ± 0.5
81-14; Beta 3532, Lemming, *L. sibericus*, 4 imm., 29 Aug 81	-26.75		126.1 ± 0.8
81-17; Beta 3535, Caribou, Aug 81	-28.68		130.6 ± 0.6
Marine			
81-B4-Mus; Beta 2921, Bowhead, male, 28.5 ft., Barrow, 30 May 81	-18.92		101.8 ± 0.9
81-B4-Oil; Beta 2922, Bowhead, *Balaena mysticetis*, male, 28.5 ft., Barrow, 30 May 81	-21.00		102.8 ± 1.0
81-WW2-Oil; Beta 2924, Bowhead, female, 58 ft., Wainwright, 18 May 81	-25.53		93.1 ± 0.8
81-WW3-Mus; Beta 2923, Bowhead, female, 54 ft., Wainwright, 27 May 81	-17.95		102.2 ± 0.8
81-WW3-Oil; Beta 2925, Bowhead, female, 54 ft.	-24.90		105.3 ± 0.7
81KK2-1-Oil; Beta 3538, Bowhead, male, 46 ft., 8 Sep 81	-25.20		104.9 ± 0.7
81KK2-2M-Mus; Beta 3545, Bowhead, male, 46 ft., 8 Sep 81	-18.65		102.7 ± 0.9
81KK3-1-Oil; Beta 3539, Bowhead, female, 53 ft., 22 Sep 81	-21.37		98.2 ± 0.8
81KK3-2M-Mus; Beta 3544, Bowhead, female, 53 ft., 22 Sep 81	-19.01		103.5 ± 0.9
81-21-Oil; Beta 3541, Ring seal, *Phoca hispida*, PPUP-11-81, female	-22.69		97.8 ± 0.8
81-22-Mus; Beta 3542, Ring seal, PPUP-11-81, female	-16.97		113.1 ± 0.7
81-23-Mus; Beta 3543, Bearded seal, *Erignathus barbatus*, PPUE-2-81	-18.10		104.8 ± 0.8

depression in ^{14}C (91.8 percent modern) equivalent to 55 percent peat carbon. The other least ciscoes and all arctic ciscoes caught in June were isotopically marine fish (^{13}C = -21.2 to -23.2, 102.4 to 110.9 percent modern). It is not known whether these fish overwintered in saline delta channels or offshore. The only other anadromous fish sampled in both fall and spring was the broad whitefish *C. nasus*, which showed an isotopic shift but did not lose its entire marine carbon content over the winter as indicated by δ^{13}C values. This may reflect wintering on the high fat content in the fish following summer feeding in the marine environment.

Some of freshwater fish sampled varied widely in ^{14}C content but did not show a seasonal trend. Round whitefish, *Prosopium cylindraceum*, a freshwater fish widely distributed in the Colville River system, showed a range in isotopic composition that is difficult to define given the lack of knowledge on the past life history of the fish sampled. Two of the four fish sampled, however, were depleted in ^{14}C to 101 and 102 percent modern which corresponds to approximately 35 percent peat carbon, whereas the other two fish at 110 percent modern were 21 percent peat carbon. One specimen of long-nosed sucker, *Catostomus catostomus* collected in the summer from the Colville River was 93.5 percent modern or equivalent to 49 percent peat, but had a δ^{13}C of -23.0 which is relatively enriched in ^{13}C for a freshwater fish. Although this fish is a detritivore and the apical organism in detrital foodwebs, this difference in δ^{13}C is difficult to ascribe solely to biochemical fractionation effects which occur between trophic levels and are typically less than one del unit (DeNiro and Epstein, 1978).

The three samples of oldsquaw ducks shown in Figure 23 represent close to the full spectrum of foodweb dependencies and isotopic variation found in resident fauna. Sample 79-1 (Table 18) was a non-breeding female taken from Simpson Lagoon after summering in marine waters. It is isotopically similar to obligate marine fish and reflects a diet of marine invertebrates. Sample 80-14 is a female that had recently returned to marine waters after nesting on the tundra and had been feeding in the marine habitat for several days. Sample 80-15 is a post-molt male which was taken very shortly after leaving the tundra lakes and reaching Harrison Bay. This bird has a δ^{13}C value near typical of freshwater organisms and shows a ^{14}C depression equivalent to 60 percent peat carbon. At 85 percent modern, this bird shows the lowest ^{14}C content of any organism we have sampled to date, and implies that the insect larvae and other prey organisms it had consumed must also have had the same cumulative ^{14}C depression. We have not yet been able to acquire enough insect larvae (especially chironomids, the favored prey organism) to perform precise radiocarbon content determinations but the availability of accelerator carbon dating instruments in the near future will enable us to analyze these small samples.

Three documented oldsquaw samples were acquired in 1980 from lakes (70°42'N, 152°40'W) near Cape Halkett west of Harrison Bay (E. Taylor, personal communication). These birds included a migrant newly arrived to the tundra in June (81-3), a juvenile taken in August (81-4), and a post-molt male (81-5). They clearly reflected the isotopic composition of their food. Bird 81-3 was marine-modern and the two birds from the tundra were isotopically terrestrial and ^{14}C depressed although only to a maximum peat equivalent of 31 percent peat carbon in the male. The higher ^{14}C content of the juvenile (81-4), which favored shallow areas for feeding, reflects a higher percentage of modern primary production supporting prey organisms. The considerable difference in peat content between bird 80-15 (60 percent) and 81-5 (30 percent) may indicate that considerable variation occurs in energy source dependencies among the lakes on the coastal plain.

The changes which occur in the carbon isotopic composition of birds and fishes upon changing their food source makes these organisms particularly amenable to in situ determinations of carbon metabolic rates. Until now, the use of isotopic tracers in measuring transfer rates of carbon in foodwebs has been limited to experiments performed in the laboratory. Whereas these experiments can yield useful information, their artificial nature and the problems associated with closed system tracer experiments (Conover and Francis, 1973) detract from their utility.

The model in Figure 25 allows a first attempt to be made at determining carbon turnover rates for organisms living in their natural environment. This technique eliminates container effects since the system is necessarily an open one. The model assumes a steady state condition for the predator (i.e., no growth), which should hold quite well for the adult specimens we have used in the calculations. The other assumption is that the carbon in the organism is instantaneously mixed so that respired carbon has the same isotopic composition as the organism. This assumption should also be reasonable since the rates are measured over long periods of time.

The model essentially results in an equation describing the exponential change in isotopic composition of the predator ($\delta^{13}C_t$, $^{14}C_t$) from its value at the time it changed its food source ($\delta^{13}C_{t=o}$, $^{14}Ct=o$) to that found after feeding for some period (t) on different food ($\delta^{13}C_F$, $^{14}C_F$). Table 18 provides the necessary information on the isotopic composition of predators at various times as well as that of their food sources. For all turnover rate calculations we have used the following values for food: $\delta^{13}C$ marine = -21.0, $\delta^{13}C$ terr = -28.5, ^{14}C marine = 110.0, ^{14}C terr. modern = 125.0, ^{14}C river = 92.0.

Least cisco $\delta^{13}C$ values (Figure 26) indicate that a ^{13}C isotopic equilibrium had been reached between fish and food by the end of the spring. Therefore, we expect that equilibrium has also been reached with respect to the ^{14}C isotope. This reasoning leads us to believe that until more data is available on the ^{14}C content of prey organisms, a ^{14}C activity of 92 percent modern should be used for the food of fish overwintering in the river. Sampling of the river for benthic invertebrates is planned and should allow us to refine this estimate.

The calculated turnover rate constants and turnover times ($^1/K$) for least ciscoes are given in Table 19. Because the June and September fish have an isotopic composition which is essentially the same as their food, we have estimated the turnover rate to be at least as great as that necessary for the fish to be within one $\delta^{13}C$ unit or two ^{14}C percent modern units of its food.

The results show that during the summer a least cisco assimilates an amount of carbon greater than 1.5 percent of its body carbon each day. This rate is comparable to that of 2.3 percent calculated from the results of a feeding experiment performed by Craig and Haldorson (1981)

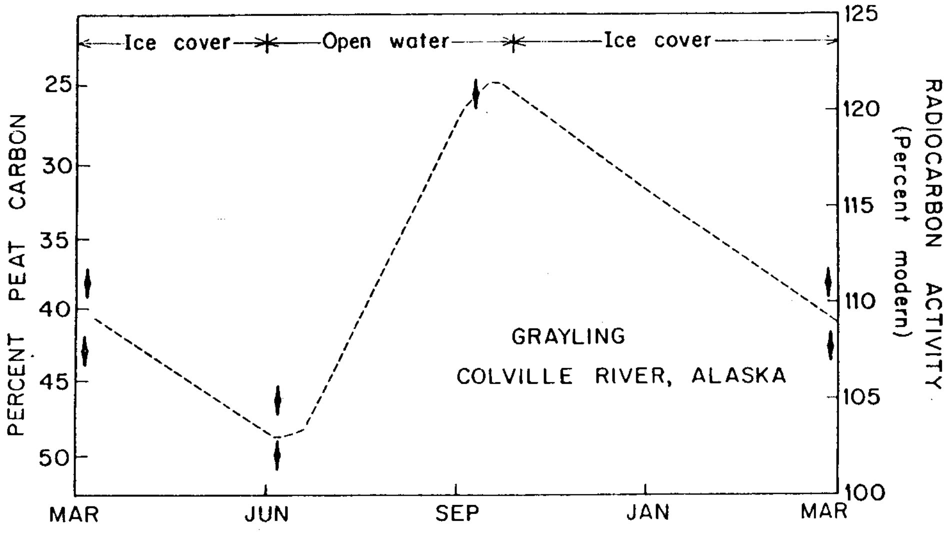
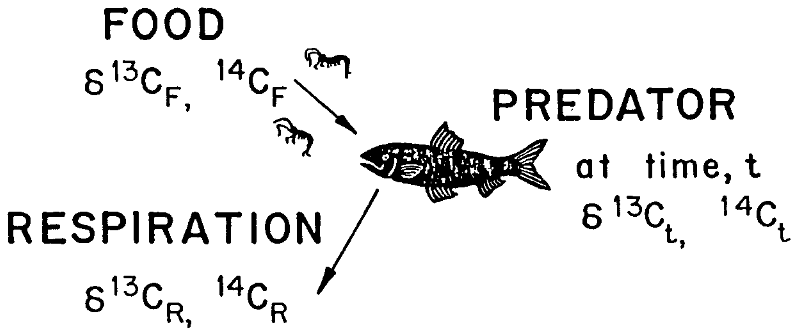


Figure 24. Seasonal variation in radiocarbon activity of Colville River grayling (*Thymallus arcticus*).



$$^{14}C_t = \left(^{14}C_{t=o} - {}^{14}C_F\right) e^{-kt} + {}^{14}C_F$$

$$\ln\left(^{14}C_{t=o} - {}^{14}C_F\right) \Big/ \left(^{14}C_t - {}^{14}C_F\right) = kt$$

k = Turnover rate

Figure 25. Model of carbon isotope turnover in consumer organisms.

TABLE 19. Turnover rate determination.

	Season interval	Isotope used	Turnover rate (${}^{o}/o$ day^{-1})	Turnover time (days)
Least cisco	SEP-JUN	Both	>0.7	<140
	JUN-SEP	Both	>1.5	<70
Arctic cod	JUN-SEP	Lit.	2.3	45
Grayling	SEP-JUN	^{14}C	0.3-0.4	250-330
	JUN-SEP	^{14}C	>1.2	<85
Broad Whitefish	NOV-JUN	^{13}C	0.2	500
		^{14}C	0.5	200
Oldsquaw	JUN-AUG	^{13}C	2.8	35
	JUN-SEP	^{13}C	2.7	35
	JUN-SEP	Lit.	10.0	10

on an arctic cod, using a carbon/wet weight conversion of 0.06 for food and 0.11 for fish, and an assimilation efficiency of 0.7. During the winter, however, we estimate that these fish reduce their turnover rates to about 25-50 percent of the summer rates.

The arctic grayling, an obligate freshwater fish, also switches its energy source from summer to winter (Figure 24). Since more data are available for the grayling, it was possible to perform a least squares linear regression on a plot of $\ln ({}^{14}C_{t=o} - {}^{14}C_{food}/{}^{14}C_t - {}^{14}C_{food})$ vs. time to determine the value of K (slope). The plot is shown in Figure 27 and is a good fit for field data ($r = 0.94$). Carbon turnover rates in grayling are slightly slower than those of the least cisco (Table 19), but are similarly reduced from summer to winter. These reductions in carbon metabolism by overwintering fishes may well be a response to colder water temperatures and a decreased availability of food in the overwintering areas of the river.

We have also compared seasonal isotopic shifts in samples of migratory birds. When oldsquaw ducks arrive at the tundra lakes and ponds after overwintering in a marine environment, their $\delta^{13}C$ values reflect their marine carbon composition. Through the course of the summer, however, their ^{13}C content decreases in response to the freshwater food (Figure 28). This change has been used to calculate the turnover rates for oldsquaw ducks (Table 19). It is not known when our

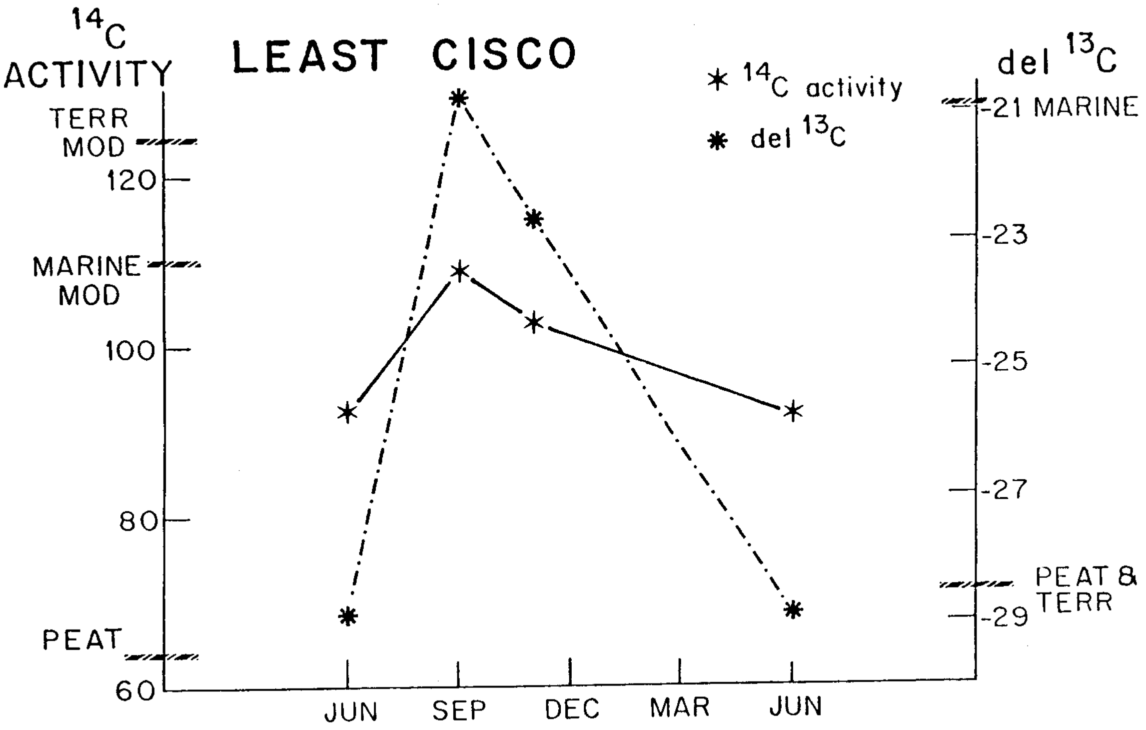


Figure 26. Seasonal variation in carbon isotopic composition of least cisco (*Coregonus sardinella*).

specimens arrived on the tundra, but by assuming that they arrived no earlier than mid-June (E. Taylor, personal communication) we can say that these birds turn over at least 2.7 percent of their body carbon each day. This rate is much slower than that of 10 percent calculated from the equation of Kendeigh et al. (1977) for bird energy requirements during the molting period, using a Kcal/wet weight conversion of 1.9 and an oldsquaw wet weight of 895 g. This may imply that these oldsquaws began feeding in freshwater much later than mid-June, either because they arrived later in the season, did not feed extensively during breeding activities and while setting up their territories or had a low availability of food in the early summer before the sediments thawed.

We believe that as more samples of predators and their food items are obtained, this method will allow us to gain valuable information on the energetics of consumer organisms and the ways in which they may alter their metabolism under changing environmental conditions.

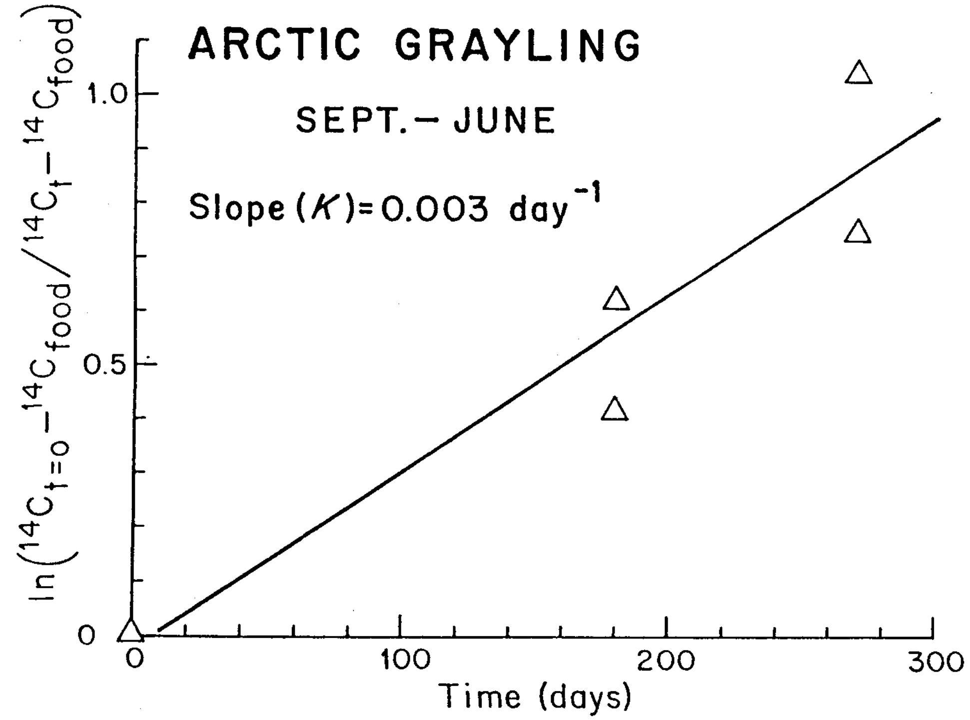


Figure 27. Least squares regression determination of carbon turnover rate constant in grayling (*Thymallus arcticus*).

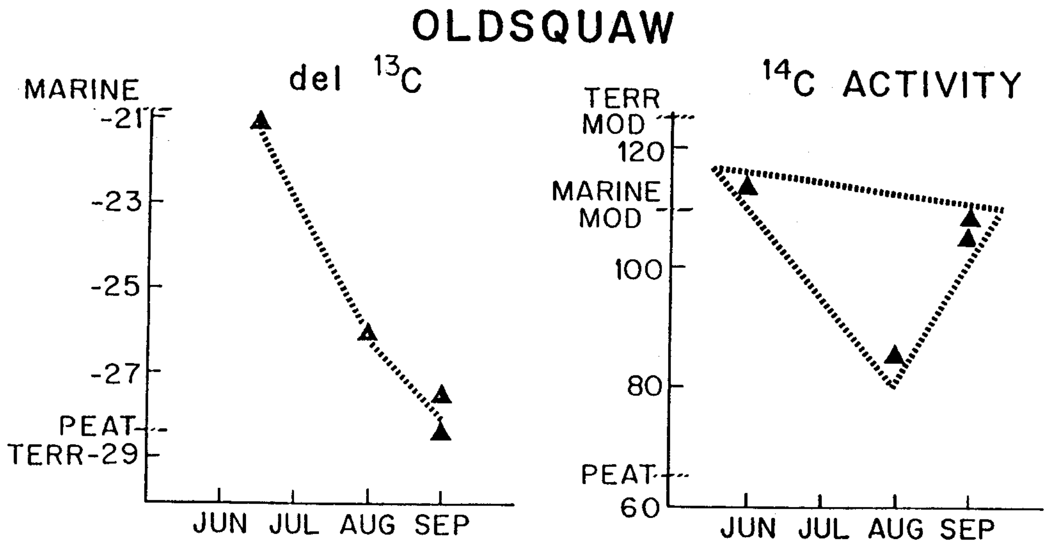


Figure 28. Seasonal variation in carbon isotopic composition of oldsquaw ducks.

The foodweb linkages represented in the utilization of peat carbon and transfer to higher organisms constitute a remarkable adaptation to a temporally independent carbon source in an area which is characterized by extremes in seasonal primary production. The success of the freshwater fishes and waterfowl in turn depends upon the prey organisms which use the peat carbon efficiently. To date, because of sampling difficulties and the unavailability of instrumentation capable of radiocarbon determination on small samples, we have been unable to directly measure the peat carbon content of the various insect larvae which constitute the prey organisms.

Of the most common freshwater prey organisms found in fish and bird stomachs, chironomid larvae constitute the most logical link between peat and higher trophic levels. Their abundance and ubiquity, coupled with a known ability to subsist in anaerobic organic sediments, makes these organisms the likely major efficient link in detrital foodwebs based on peat. We have collected several samples of these organisms and as accelerator ^{14}C-dating service becomes available at the University of Arizona, we will test this hypothesis. In addition, through a series of laboratory feeding experiments we hope to obtain peat assimilation efficiencies by chironomids at temperatures typical of arctic aquatic environments. This work is currently in progress.

Foodwebs in the arctic coastal zone interact strongly through the anadromous fish and waterfowl. The data presented herein show that the marine foodwebs can be significantly affected by terrestrial detritus only through indirect effects arising from nutrient additions to the phytoplankton nutritional requirements derived from mineralization of peat organic nitrogen. Developmental impacts on seals, polar bears, and arctic cod can be predicted to be minimal if the impacts affect only the input of allochthonous carbon.

In contrast, we have shown that onshore impacts which could alter food chain structure (e.g., indiscriminate use of insecticides, stream bed alternation, stripping of peat from shorelines) could in turn impact apical marine organisms such an anadromous fish and waterfowl populations which have aesthetic and subsistence value to humans. The same applies to the obligate freshwater organisms of high trophic levels.

(*Phoca hispida*) taken off Pingok Island. This sample, kindly supplied by K. Frost of Alaska Department of Fish and Game, also yielded a ^{14}C activity below 100 percent modern and is close to the activity shown by a fall whale taken at Barter Island (81KK3).

The initial samples of marine mammal tissues analyzed in 1981 show a wide variation in isotopic composition. Although we do not have sufficient samples to make any definitive statements about primary feeding and energy accumulation areas, we are looking forward to acquiring more data from the marine mammals and their prey from the Bering and Beaufort seas.

Linear Growth in *Laminaria solidungula* and *L. saccharina*

Figure 30 shows the results of growth measurements taken from November 1979 to July 1981. In *L. solidungula* in 1980 the lowest rate of linear growth (0.25 mm/day) occurred during the ice-free period, from July to November. Maximum growth rates in 1980 were recorded between February and April (1.41 mm/day). In *L. saccharina*, the lowest rate of linear growth occurred between November 1979 and February 1980 (0.12 mm/day) and the highest between late April and late July 1980 (4.69 mm/day). Similar results were obtained for 1981 but the periods of maximum and minimum growth are not as well defined because of one less visit to the study site. Since the turbid ice canopy in Stefansson Sound prevented penetration of light between October and early July, *L. solidungula* completed most of its annual linear growth in absolute darkness. In contrast, *L. saccharina* may have completed much of its growth during and immediately following breakup in late June and July when light penetration of the ice canopy is more likely to occur.

Concentrations of inorganic nitrogen in the form of NO_2^- and NO_3^- in the seawater are shown beneath the growth curves for both species of *Laminaria* in Figure 30. The concentrations of inorganic nitrogen follow an annual cycle typical of Arctic (Chapman and Lindley, 1980) and temperate waters (Chapman and Craigie, 1977; Wheeler and North, 1981) and are shown here for the period between November 1979 and

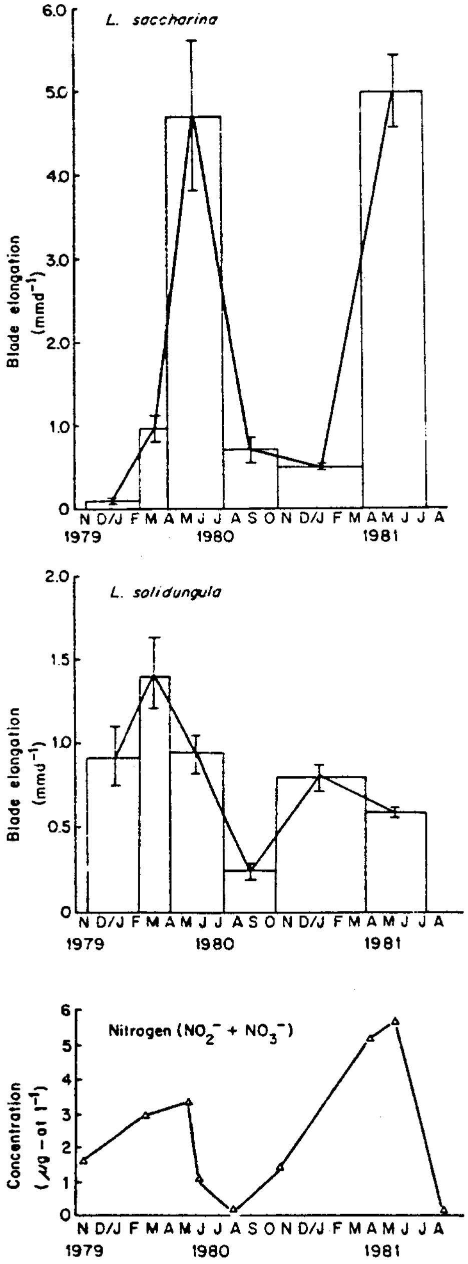


Figure 30. The pattern of blade growth (means ±95% confidence limits) in *Laminaria saccharina* and *L. solidungula* in relation to seasonal variations in inorganic nitrogen concentrations.

August 1981. Levels of inorganic-N are lowest in summer (less than 0.1 μg-at N/1), increase through the fall and winter months, and peak in late May (3.3 to 5.7 μg-at N/1). Periods of highest linear growth in both *L. solidungula* and *L. saccharina* occur during higher concentrations of inorganic nitrogen. A similar pattern between growth and nitrogen availability has also been documented for *L. solidungula* in the Canadian High Arctic by Chapman and Lindley (1980).

Growth in *L. solidungula* in the Boulder Patch is both energy and nitrogen limited, since neither resource is available in sufficient quantities simultaneously. During the summer open-water period when light is available, the plants must fix all the carbon necessary for their annual growth, reproduction, and metabolism. Little growth occurs during this period due to insufficient concentrations of inorganic-N needed for the synthesis of new tissue. Instead, the products of photosynthesis are stored and used during the winter when inorganic-N is available for the production of a new blade. Inorganic-N is depleted as a result of the annual spring bloom of microalgae and is slowly replenished through regeneration and exchange with ocean water. Our in situ growth studies of *L. solidungula* show that these plants can produce 95% of their original biomass as new plant tissue annually. Based on this, the net carbon contribution made by these plants to the ecosystem can be calculated from data on standing crop and carbon content.

An Annual Carbon Budget for the Boulder Patch

Figure 31 shows the annual net increase in biomass of 17 plants as a function of their initial weight. The average annual production-to-biomass ratio (P:B) was 0.95 ± 0.14 (mean ± 95% confidence limit), and the annual mean growth was 0.0022 g/g-day (grams of wet weight added per gram of plant per day). The standing crop of all three species of kelp (of which *L. solidungula* constituted over 95%) ranged from 67 g/m^2 in areas of 10 to 25% rock cover to 262 g/m^2 where rock cover exceeds 25%. Using the results of the geophysical surveys conducted by Toimil (1980), the area of 10 to 25% rock cover is about 13 x 10^6 m^2, and the area with cover greater than 25% is 7.3 x 10^6 m^2. Integrated over these areas, the standing crop of the kelp is estimated to be 2.8 x 10^9 g.

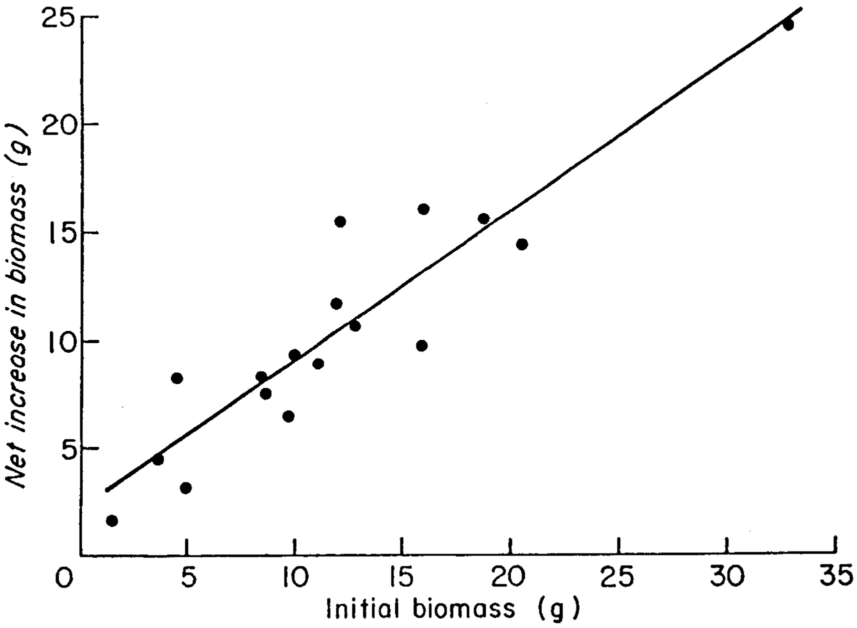


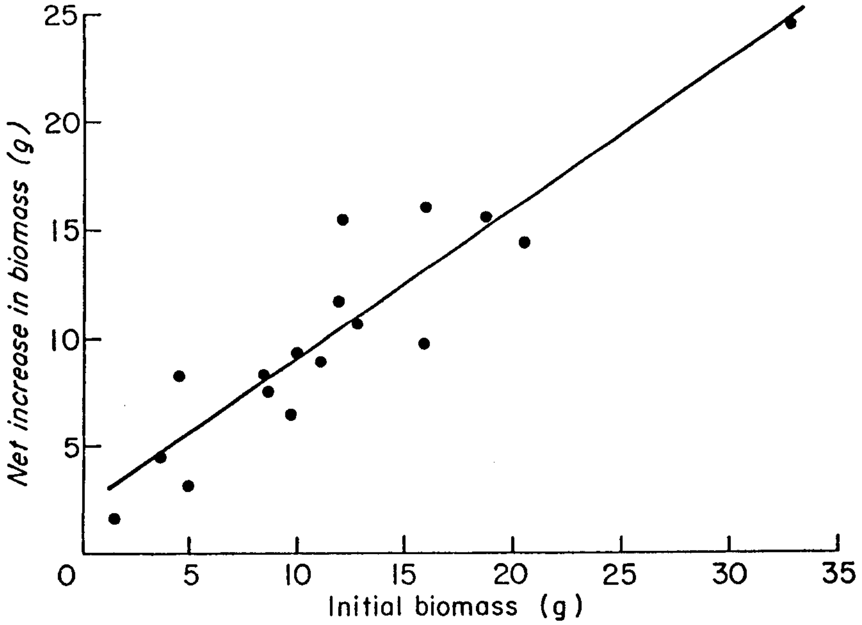
Figure 31. Annual net increase in biomass as a function of initial biomass in *L. solidungula* plants living under a turbid ice canopy.

The standing crop of kelp in Stefansson Sound is 0.48 x 10^9 g dry weight assuming that the standing crop is about 17% dry matter. Over 90% of the standing crop is *L. solidungula*. The carbon content of the dry matter in *L. solidungula* is approximately 32% (Chapman and Lindley, 1981) and varies little seasonally. On this basis, the annual energetic contribution made by the kelp in Stefansson Sound is 146 x 10^6 g C or about 7.2 g C/m^2 based on a P:B ratio of 0.95. This estimate does not take into account any patchiness in the turbid ice canopy or its complete absence in some years.

In years characterized by the presence of a turbid ice canopy, only three sources of marine carbon are available to consumers in the Boulder Patch - kelp, phytoplankton, and benthic microalgae. The spring bloom of ice microalgae, which is common in most arctic coastal areas (Alexander, 1975; Hsiao, 1980) does not occur in this area because of the lack of light caused by the presence of turbid ice. Assuming an annual P:B ratio of 7 for benthic microalgae (mean biomass 3.3 g/m^2), the net carbon production is 0.39 g/m^2-yr or 8 x 10^6 g/m^2-yr.

TABLE 20. (Continued)

ECHINODERMATA		
41-07	*Leptasterias graenlandica*	-21.7
CHORDATA		
41-21	*Boreogadus saida*	-21.2
41-38A	*Liparis herschelinus*	-21.3
41-38B	*Liparis herschelinus*	-20.1
41-75	*Myoxocephalus quadricornis*	-18.8
ALGAE		
41-26B2	*Laminaria solidungula*	-14.6
41-68	*Neodilsea integra*	-18.8
	EASTERN BEAUFORT SEA	
18-BDR-1	*Mysis litoralis* (3) (formally 8-81-BDR)	-21.0
81-SC-1A	Copepods (12) (formally 8-81-SC1)	-24.6
81-SC-1B	Copepods (14) (formally 8-81-SC2)	-23.2
81-SC-3	*Mysis litoralis* (formally 8-81-SC3)	-20.8
	FEEDING EXPERIMENTS	
32-TK-1	*Mysis relicta* (6)	-19.8
32-TP-2	*Mysis relicta* (2)	-20.2



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Phytoplankton productivity is estimated at 102 x 10^6 g C/yr, based on C-14 labeled uptake experiments at this site . The contribution made by the kelp is 146 x 10^6 g C/yr. Kelp thus contributes a major source of carbon to consumers in the Boulder Patch (Figure 32).

Carbon Isotope Studies in the Boulder Patch

In the Boulder Patch in Stefansson Sound, $^{13}C/^{12}C$ ratios indicate that kelp carbon is utilized and important to several organisms in the kelp bed itself (Table 20). Organisms observed directly feeding on or in contact with the kelp (chitons and snails, $\delta^{13}C$ from -17 to -17.5) exhibited ratios closest to that of kelp ($\delta^{13}C$ = -14.6). Mysids, which are known to be filter feeders, presented the greatest surprise. Mysids collected by Schell near the Colville River (80 km west of the Boulder Patch) had $\delta^{13}C$ values of -23.6, which indicates a microalgal food source as predicted by its feeding habit. In the kelp bed, mysids had $\delta^{13}C$ values of -18.9 and -19.4, indicating a dependence on macroalgal carbon. It is not apparent at this time how these animals incorproate macroalgal carbon into their tissue.

The $^{13}C/^{12}C$ ratio obtained thus far are also highly encouraging in that the carbon content of the organisms reflect their predicted food source. Obligate filter feeders (hydroids, $\delta^{13}C$ = -23.5) had ratios similar to that of phytoplankton ($\delta^{13}C$ = -23 to -25). The amphipod *Atylus* consumes a variety of food which was reflected in widely different $\delta^{13}C$ values between organisms (-19.5 and -22.3). In general, $^{13}C/^{12}C$ ratios reflect known diets of these organisms thus adding credibility to the use of stable carbon isotope ratios in this study.

The importance of kelp as a winter food source may be seen in the shift of the carbon-isotope composition of mysids from summer to winter (Figure 33). The $^{13}C/^{12}C$ ratio in mysids is lowest in the summer (most negative ^{13}C values) when phytoplankton productivity is greatest, but this ratio increases during the winter as phytoplankton production ceases and the available food contains a greater proportion of kelp carbon relative to phytoplankton carbon.

TABLE 20. Summary of Carbon Isotope Ratios of Biota Collected in the Boulder Patch.

Sample Number	Description	$\delta^{13}C$
	BOULDER PATCH	
PORIFERA		
41-04	*Choanites lutkenii*	-20.0
CNIDARIA		
41-59	*Sertularia cupressoides*	-23.5
41-20	*Gersemia rubiformis*	-22.0
ANNELIDA		
41-52	*Spinthera alaskensis*	-21.8
MOLLUSCA		
41-11	*Polinices* spp. (several)	-17.0
41-03	*Amicula vestita*	-17.5
ARTHROPODS		
	Amphipoda	
41-01A	*Atylus carinatus*	-19.5
41-01B	*Atylus carinatus*	-22.3
41-76	*Weyprechtia heuglini*	-21.0
41-77	*Gammarus setosus*	-20.5
41-42	*Gammarocanthus loricatus*	-20.2
	Crustacea	
41-44A	*Mysis litoralis* (3)	-19.4
41-44B	*Mysis litoralis* (3)	-18.9
111-01	*Mysis litoralis* (4) (formally 11-81-01)	-20.0
41-43J	*Mysis litoralis* (8)	-20.9
81-02	*Mysis litoralis* (3) (formally 8-18-02)	-21.2

TABLE 20. (Continued)

ECHINODERMATA		
41-07	*Leptasterias graenlandica*	-21.7
CHORDATA		
41-21	*Boreogadus saida*	-21.2
41-38A	*Liparis herschelinus*	-21.3
41-38B	*Liparis herschelinus*	-20.1
41-75	*Myoxocephalus quadricornis*	-18.8
ALGAE		
41-26B2	*Laminaria solidungula*	-14.6
41-68	*Neodilsea integra*	-18.8
	EASTERN BEAUFORT SEA	
18-BDR-1	*Mysis litoralis* (3) (formally 8-81-BDR)	-21.0
81-SC-1A	Copepods (12) (formally 8-81-SC1)	-24.6
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81-SC-3	*Mysis litoralis* (formally 8-81-SC3)	-20.8
	FEEDING EXPERIMENTS	
32-TK-1	*Mysis relicta* (6)	-19.8
32-TP-2	*Mysis relicta* (2)	-20.2

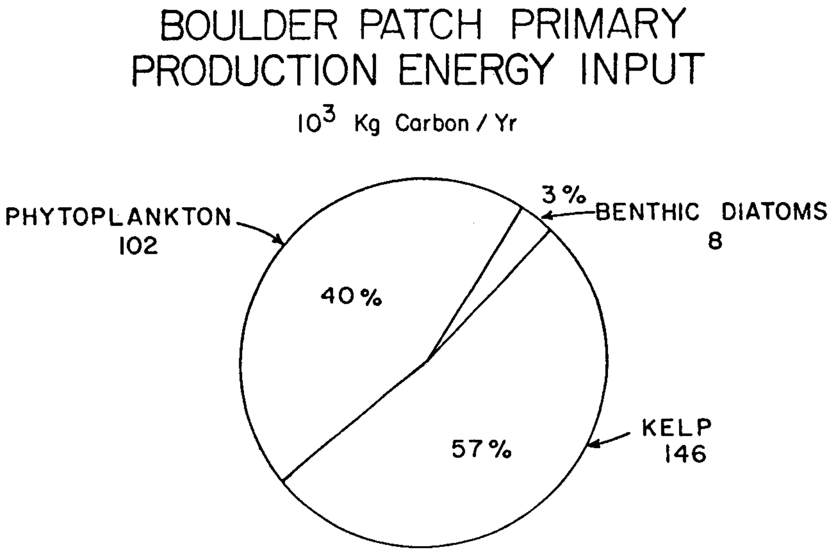

Figure 32. Carbon inputs to the Stefansson Sound Boulder Patch.

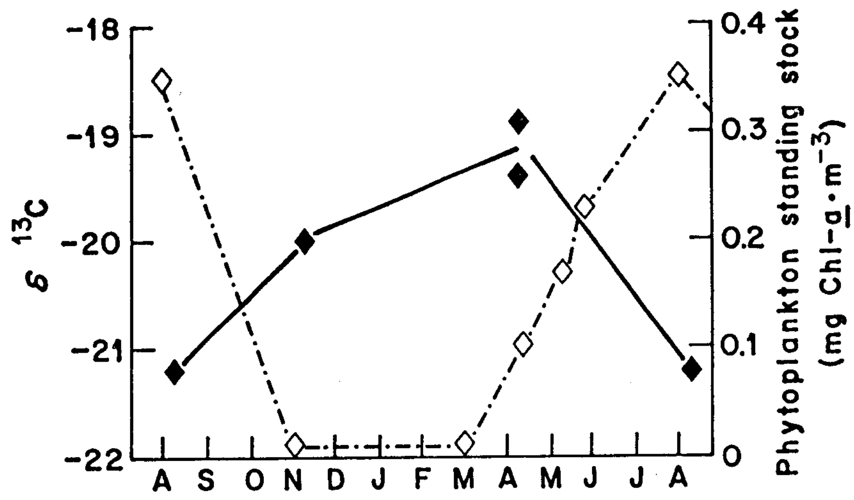

Figure 33. The relationship between mysid (*Mysis litoralis*) carbon isotope composition and phytoplankton standing stock in the Boulder Patch.

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Appendix 1. Nutrient and Salinity Data, 1980.

Date	Station	Location		Depth (m)		Salinity	Nitrate + Nitrite -N	Phosphate -P	Silicate -Si
				Bottom	Sample	$^0/oo$	(---------microgram-atoms/liter------------)		
5 Mar	Boulder Patch	70°19.6'N	147°34.5'W	5	0.0	35.88	2.93	0.55	18.0
					3.0	35.89	2.87	0.57	17.6
					5.0	35.93	2.87	0.51	17.6
6 Mar	Boulder Patch	70°19.6'N	147°34.5'W	5	0.0	35.95	2.88	0.48	18.3
					3.0	35.96	3.00	0.49	18.9
					5.0	36.01	2.98	0.58	18.1
3 Apr	15	70°26.5'N	148°19.7'W	4	0.0	36.20	3.43	0.57	18.2
					3.0	36.30	3.00	0.49	18.9
					4.0	35.80	2.98	0.58	18.1
3 Apr	16	70°26.1'N	147°55.9'W	6	0.0	36.30	2.82	0.65	14.2
					6.0	36.10	2.91	0.30	14.5
3 Apr	17	70°22.6'N	147°43.4'W	5	0.0	36.50	3.40	0.72	18.2
					5.0	36.80	3.52	1.34	17.7
3 Apr	18	70°16.7'N	147°17.3'W	6	0.0	36.40	3.68	0.90	20.6
					6.0	---	4.19	0.86	21.0
3 Apr	19	70°11.0'N	147°03.5'W	5	0.0	37.30	3.64	1.05	19.7
					4.5	---	3.64	0.77	19.6
3 Apr	20	70°14.2'N	147°29.8'W	3	0.0	37.80	3.60	0.56	19.6
					3.0	37.70	3.61	0.56	19.6
3 Apr	22	70°23.8'N	148°19.0'W	1	1.0	---	4.97	0.76	19.7
4 Apr	12	70°33.3'N	150°21.6'W	7	0.0	35.70	2.92	0.63	8.2
					3.0	35.80	2.99	0.63	13.2
					7.0	36.00	3.16	0.65	17.1

Appendix 1. (Continued)

Date	Station	Location		Depth (m) Bottom	Depth (m) Sample	Salinity ^{0}/oo	Nitrate + Nitrite -N	Phosphate -P	Silicate -Si
							(---------microgram-atoms/liter	------------	------------)
4 Apr	13	70°34.9'N	150°41.5'W	8	0.0	35.30	2.85	0.63	12.9
					4.0	35.45	2.96	0.71	--
					7.5	---	2.91	0.63	13.6
4 Apr	3	70°32.1'N	149°51.7'W	2	2.0	---	2.95	0.55	17.3
4 Apr	11	70°27.5'N	150°04.7'W	2	2.0	---	4.85	0.50	40.7
4 Apr	4	70°35.4'N	149°51.7'W	12	0.0	35.20	2.70	0.68	12.8
					5.0	34.90	2.85	0.61	14.6
					8.0	29.60	2.67	0.68	13.1
					11.5	36.90	3.01	0.59	15.6
5 Apr	9	70°32.8'N	149°42.9'W	2	2.0	---	3.73	0.62	25.1
5 Apr	10	70°35.6'N	149°42.9'W	14	0.0	34.90	2.65	0.71	13.1
					4.0	34.90	2.60	0.67	13.2
					9.0	34.81	2.53	0.69	12.5
					13.8	36.40	2.78	0.67	14.2
5 Apr	Colville River (Helmericks)	70°26.0'N	150°23.0'W	5	0.0	23.71	4.60	0.19	32.2
					5.0	31.00	5.84	0.27	45.7
6 Apr	1	70°33.6'N	149°25.2'W	2	2.0	61.49	3.30	--	26.5
6 Apr	2	70°35.3'N	149°27.0'W	11	0.0	35.29	3.26	0.54	17.0
					6.0	35.24	3.43	0.57	16.9
					10.5	35.60	3.29	0.55	17.1
6 Apr	6	70°32.3'N	149°02.6'W	8	0.0	35.17	3.15	--	17.4
					5.0	35.50	--	0.44	15.9
					8.0	32.60	3.72	0.61	20.3

Appendix 1. (Continued)

Date	Station	Location		Depth (m)		Salinity $^{0}/oo$	Nitrate + Nitrite -N	Phosphate -P	Silicate -Si
				Bottom	Sample		(---------microgram-atoms/liter		-----------)
6 Apr	8	70°31.1'N	148°54.0'W	7	4.0	35.55	3.32	0.49	17.2
					6.9	35.50	3.26	0.50	18.1
6 Apr	14	70°20.2'N	148°20.3'W	2	2.0	---	4.44	0.41	33.1
					2.5	---	4.39	0.35	33.1
6 Apr	17	70°29.2'N	148°50.1'W	2	2.0	59.02	4.47	0.59	26.5
6 Apr	21	70°28.7'N	148°33.0'W	7	0.0	35.70	3.33	0.56	17.2
					4.0	34.20	3.23	0.55	17.4
					6.5	36.00	3.28	0.57	17.3
25 May	4	70°34.6'N	149°50.4'W	9	0.0	35.1	3.31	0.67	16.5
					9.0	35.8	3.44	0.67	17.4
25 May	75	71°49.8'N	149°46.6'W	13	0.0	32.4	1.58	0.62	10.7
					5.0	32.4	1.54	0.51	10.5
					13.0	32.4	1.40	0.54	10.5
24 May	50	71°22.9'N	149°49.6'W	12	0.0	32.9	2.67	0.62	16.5
					7.0	32.8	2.78	0.60	19.4
					12.0	32.8	2.83	0.61	17.6
25 May	25	70°51.7'N	149°40.6'W	13	0.0	32.5	1.41	0.61	9.7
					7.0	32.5	1.42	0.61	9.3
					13.0	32.5	1.40	0.50	9.3
28 May	19	70°11.1'N	147°03.2'W	5	0.0	35.8	2.79	0.58	17.5
					5.0	37.6	3.36	0.47	19.4
28 May	18	70°16.4'N	147°12.2'W	5	0.0	35.9	3.11	0.57	18.1
					5.0	---	3.18	0.53	19.0

Appendix 1. (Continued)

Date	Station	Location		Depth (m) Bottom	Depth (m) Sample	Salinity $^{0}/oo$	Nitrate + Nitrite -N	Phosphate -P	Silicate -Si
							(---------microgram-atoms/liter	------------)	
28 May	20	70°14.2'N	147°29.3'W	5	0.0	9.3	1.85	0.15	27.6
					5.0	30.0	3.22	0.53	19.7
28 May	Boulder Patch	70°17.7'N	147°32.4'W	6	0.0	35.3	3.00	0.65	17.8
					6.0	35.9	3.31	0.55	20.2
28 May	17	70°22.4'N	147°33.8'W	7	0.0	33.8	2.84	0.55	18.1
					7.0	38.1	3.40	0.51	22.7
29 May	14	70°20.0'N	148°20.5'W	2	0.0	---	2.46	0.55	14.4
29 May	16	70°26.1'N	147°55.9'W	7	0.0	---	2.92	0.58	16.0
					7.0	35.0	3.07	0.56	17.6
29 May	22	70°23.8'N	148°19.0'W	2	0.0	35.3	3.05	0.61	16.9
29 May	15	70°26.5'N	148°19.7'W	7	0.0	---	3.94	0.53	20.6
					6.5	---	3.90	0.52	16.5
29 May	7	70°27.9'N	148°54.7'W	2	0.0	---	3.00	0.54	16.1
29 May	8	70°30.7'N	148°53.4'W	7	0.0	---	2.95	0.56	16.1
					7.0	34.9	3.11	0.40	24.9
29 May	6	70°31.5'N	149°01.2'W	10	0.0	---	2.95	0.55	15.4
					5.0	---	3.07	0.58	17.4
					10.0	35.3	2.90	0.53	16.6
29 May	2	70°34.8'N	149°27.1'W	12	0.0	35.3	3.48	0.57	17.9
					7.0	35.6	3.17	0.58	17.1
					12.0	35.6	3.18	0.53	17.5

Appendix 1. (Continued)

Date	Station	Location		Depth (m) Bottom	Depth (m) Sample	Salinity °/oo	Nitrate + Nitrite -N	Phosphate -P	Silicate -Si
							(---------microgram-atoms/liter-----------)		
29 May	10	70°35.5'N	149°37.0'W	10	0.0	35.3	3.48	0.57	16.8
					2.0	---	--	--	--
					5.0	35.5	3.21	0.53	17.6
					10.0	35.9	3.03	0.56	17.5
30 May	5	70°30.0'N	149°09.5'W	2	0.0	---	3.66	0.51	29.5
30 May	Harrison Bay	70°34.7'N	151°19.6'W	5	0.0	1.7	--	--	--
					5.0	34.9	--	--	--
30 May	Harrison Bay	70°33.7'N	150°57.0'W	7	0.0	34.8	--	--	--
					7.0	35.3	--	--	--
30 May	13	70°34.2'N	150°41.0'W	7	0.0	35.6	--	--	--
					7.0	35.8	--	--	--
30 May	12	70°33.1'N	150°21.0'W	8	0.0	36.4	3.57	0.53	18.1
					5.0	36.3	--	--	--
					8.0	36.2	3.31	0.48	17.6
30 May	11	70°29.3'N	150°07.3'W	--	0.0	2.3	--	--	--
30 May	3	70°31.7'N	149°50.4'W	--	0.0	15.7	3.12	0.18	23.9
17 Jun	4	70°35.4'N	149°51.7'W	9	0.0	1.10	0.34	0.29	8.2
					5.0	0.80	0.50	0.34	9.7
					9.0	33.00	2.34	0.71	14.1
17 Jun	1	70°33.6'N	149°25.2'W	2	0.0	0.80	0.23	0.20	5.8
					2.0	9.30	0.96	0.25	13.2

Appendix 1. (Continued)

Date	Station	Location		Depth (m)		Salinity ^{0}/oo	Nitrate + Nitrite -N	Phosphate -P	Silicate -Si
				Bottom	Sample		(---------microgram-atoms/liter------------)		
17 Jun	202	70°44.8'N	149°27.1'W	12	0.0	32.80	1.42	0.59	9.7
					6.0	33.20	1.52	0.72	9.9
					12.0	33.45	1.03	0.72	11.0
17 Jun	808	70°40.7'N	148°53.4'W	12	6.0	34.40	2.06	0.74	13.1
					12.0	33.80	2.05	0.71	12.1
18 Jun	Boulder Patch	70°20.5'N	147°33.8'W	7	0.0	0.20	0.61	0.16	13.1
					4.0	4.60	0.58	0.16	17.1
					7.0	---	1.14	0.35	16.3
18 Jun	Lead	70°38.3'N	147°20.3'W	12	0.0	31.6	1.15	0.68	10.0
					12.0	32.9	1.71	0.64	11.5
18 Jun	Seal hole	70°38.6'N	146°02.0'W	12	0.0	5.2	--	0.25	2.4
					12.0	31.6	2.11	0.92	13.5
18 Jun	19	70°10.5'N	147°07.0'W	5	0.0	27.3	0.23	0.21	3.4
					5.0	---	--	--	--
2 Jul	1	70°33.6'N	149°25.2'W	2	0.0	35.4	0.18	0.09	9.2
					2.0	39.9	0.10	0.23	7.0
2 Jul	220	70°54.8'N	149°27.1'W	12	0.0	0.8	--	0.03	0.4
					6.0	33.5	1.49	0.46	10.2
					12.0	33.5	1.84	0.51	12.4
2 Jul	880	70°50.7'N	148°53.4'W	12	0.0	0.8	--	0.21	0.6
					6.0	32.2	1.34	0.53	11.0
					12.0	---	--	--	--

Appendix 1. (Continued)

Date	Station	Location		Depth (m)		Salinity °/oo	Nitrate + Nitrite -N	Phosphate -P	Silicate -Si
				Bottom	Sample		(---------microgram-atoms/liter------------)		
2 Jul	8	70°30.7'N	148°53.4'W	12	0.0	1.6	0.10	0.37	32.9
					6.0	33.0	2.06	0.57	13.0
					12.0	34.5	2.61	0.56	15.5
2 Jul	Beach	70°30.4'N	148°55.0'W	0	0.0	2.9	0.20	0.05	9.0
8 Aug	28	70°44.0'N	151°53.0'W	6	0.0	21.11	0.10	0.00	6.9
					3.0	21.43	0.10	0.00	5.7
					6.0	27.00	0.50	0.35	8.7
8 Aug	27	70°40.0'N	151°46.0'W	6	0.0	22.74	0.10	0.14	8.5
					3.0	22.84	0.10	0.26	10.0
					6.0	25.95	0.10	0.28	9.0
8 Aug	26	70°37.3'N	151°28.7'W	7	0.0	24.57	0.10	0.21	16.7
					3.0	24.54	0.20	0.25	16.9
					6.0	26.82	0.50	0.30	12.3
13 Aug	25	70°34.1'N	151°15.6'W	7	0.0	27.49	0.50	0.50	13.8
					3.0	28.05	0.50	0.45	12.4
					6.0	30.26	0.20	0.44	9.1
13 Aug	24	70°33.5'N	151°00.0'W	7	0.0	20.30	2.33	0.22	30.3
					3.0	29.92	0.50	0.49	9.7
					6.0	30.76	0.50	0.60	9.4
13 Aug	23	70°35.0'N	150°42.6'W	7	0.0	29.25	0.10	0.25	9.1
					3.0	29.72	0.10	0.49	8.6
					6.0	31.89	0.50	0.55	8.3
13 Aug	34	70°33.5'N	150°17.1'W	6	0.0	28.70	0.10	0.16	9.9
					3.0	28.70	0.50	0.50	9.7
					6.0	31.22	0.50	0.54	7.0

Appendix 1. (Continued)

Date	Station	Location		Depth (m) Bottom	Depth (m) Sample	Salinity ^{0}/oo	Nitrate + Nitrite -N	Phosphate -P	Silicate -Si
							(---------microgram-atoms/liter------------)		
9 Aug	33	70°35.0'N	150°15.0'W	9	0.0	22.80	0.10	0.16	22.1
					5.0	28.27	0.10	0.50	10.2
					9.0	30.73	0.50	0.54	8.2
9 Aug	32	70°35.0'N	151°03.0'W	9	0.0	20.29	0.50	0.11	25.8
					9.0	21.57	1.00	0.12	19.8
9 Aug	31	70°36.3'N	151°13.9'W	9	0.0	19.50	0.10	0.14	16.4
					5.0	23.47	0.10	0.16	11.3
					9.0	30.87	0.50	0.51	7.6
9 Aug	30	70°36.3'N	151°17.5'W	9	0.0	24.37	0.10	0.20	8.3
					5.0	24.34	0.10	0.20	9.1
					9.0	30.59	0.20	0.40	6.0
9 Aug	29	70°43.0'N	151°47.0'W	9	0.0	23.19	0.10	0.08	7.0
					5.0	29.44	0.10	0.22	7.0
					9.0	27.36	0.10	0.31	6.3
14 Aug	37	70°47.2'N	151°40.0'W	13	0.0	23.73	0.10	0.26	10.5
					7.0	30.89	0.10	0.00	2.1
					13.0	31.77	0.20	0.80	4.0
14 Aug	38	70°37.4'N	150°49.0'W	13	0.0	26.13	0.10	0.61	9.0
					7.0	29.97	0.10	0.62	7.9
					13.0	32.10	0.10	0.66	9.1
7 Aug	35	70°32.8'N	150°09.5'W	3	0.0	25.19	0.10	0.28	8.8
					2.5	26.30	0.10	0.32	11.7
9 Aug	36	70°33.8'N	152°02.7'W	1	0.0	13.84	0.10	0.00	7.6
					1.0	13.90	0.50	0.11	8.3

Appendix 1. (Continued)

Date	Station	Location		Depth (m)		Salinity ^{0}/oo	Nitrate + Nitrite -N	Phosphate -P	Silicate -Si
				Bottom	Sample		(---------microgram-atoms/liter------------)		
4 Sep	Kuparuk River	70°15.0'N	148°59.5'W	--	0.0	---	0.50	0.00	60.5
4 Sep	Reindeer Island	70°28.9'N	148°20.9'W	--	0.0	23.46	0.10	0.31	13.2
4 Sep	Peat Island			--	0.0	---	1.00	0.12	26.2
9 Nov	Narwhal	70°25.3'N	147°29.6'W	10	0.0	28.20	1.25	0.54	19.5
					5.0	30.04	4.50	0.84	25.8
					10.0	31.07	4.59	0.91	30.8
9 Nov	Boulder Patch	70°19.3'N	147°35.1'W	5	0.0	28.16	1.17	0.14	20.8
					5.0	28.76	0.10	0.32	19.0

Appendix 2. Nutrient and Salinity Data, 1981.

Date	Station	Location		Depth (m) Bottom	Depth (m) Sample	Salinity $^{0}/oo$	Nitrate + Nitrite -N	Ammonia -N	Phosphate -P
							(---------microgram-atoms/liter----------)		
12 Apr	Prudhoe Bay	70°19.7'N	148°22.4'W	2	1.5	43.55	10.0	1.4	0.77
12 Apr	Harrison Bay 1	70°36.0'N	151°38.0'W	5	1.7	30.82	6.9	0.5	1.19
					5.0	34.41	6.1	0.5	1.15
12 Apr	Harrison Bay 2	70°33.9'N	151°08.0'W	7	1.5	31.78	5.0	0.3	1.25
					3.0	32.79	4.7	0.7	1.17
					6.5	32.92	5.3	0.2	1.19
12 Apr	13	70°34.9'N	150°41.4'W	7	1.7	33.03	5.5	0.0	1.27
					3.5	32.83	5.7	0.0	1.29
					7.0	32.67	5.7	0.2	1.29
12 Apr	Colville River	70°24.5'N	150°28.9'W	2	1.3	1.20	13.7	2.1	0.12
13 Apr	20	70°14.2'N	147°28.8'W	5	1.5	32.88	8.5	0.0	1.3
					5.0	33.98	5.4	0.1	1.29
13 Apr	19	70°11.0'N	147°03.5'W	4	1.5	33.45	6.0	0.1	1.27
					4.0	33.59	5.5	0.2	1.32
13 Apr	18	70°16.7'N	147°17.3'W	5	1.6	28.33	4.0	0.0	1.20
					5.0	32.98	5.8	0.1	1.22
13 Apr	Boulder Patch	70°18.0'N	147°32.3'W	7	1.6	32.92	4.6	1.1	1.15
					3.0	32.80	4.1	0.1	1.20
					6.5	31.52	5.3	0.2	1.30
14 Apr	12	70°33.3'N	150°21.6'W	7	1.6	32.88	5.6	2.2	1.44
					3.0	32.16	5.4	2.7	1.24
					6.5	32.71	7.2	0.1	1.28
14 Apr	3	70°32.0'N	149°51.7'W	2	1.3	39.76	6.6	0.7	0.83

Appendix 2. (Continued)

Date	Station	Location		Depth (m) Bottom	Sample	Salinity °/oo	Nitrate + Nitrite -N	Ammonia -N	Phosphate -P
							(---------microgram-atoms/liter----------)		
14 Apr	2	70°35.1'N	149°28.6'W	12	1.6	32.53	4.6	0.5	1.28
					6.0	32.45	4.8	0.2	1.32
					12.0	32.47	5.6	0.2	1.29
14 Apr	8	70°31.0'N	148°55.0'W	12	1.6	33.07	4.8	0.3	1.32
					6.0	32.93	4.7	0.0	1.32
					12.0	32.94	4.6	0.1	1.27
14 Apr	15	70°26.4'N	148°19.0'W	8	1.6	33.06	4.8	0.0	1.33
					4.0	32.15	4.2	0.0	1.27
					8.0	33.92	4.9	0.0	1.27

Appendix 3. Chlorophyll, Phaeopigments, ^{14}C Primary Productivity Rates and Light Data from 1982 Stations.

Date	Station	Location	Depth (m)	Chlorophyll	Phaeopigments	Primary Productivity (mg/m^{3}hr)	Light (ft candles)	% Surface
				(mg/m^3 for phytoplankton; mg/m^2 for ice algae)				
25 May	HB 1 A	70°38.2'N 150°28.2'W	ice core	76.1	3.5	N.D.	N.D.	N.D.
			1.5	0.07	0.08	N.D.	N.D.	N.D.
			6	0.05	0.04	N.D.	N.D.	N.D.
			12	0.01	0.03	N.D.	N.D.	N.D.
25 May	HB 2 A	70°40.5'N 150°36.4'W	ice core	0.1	<0.01	N.D.	N.D.	N.D.
	B		ice core	0.1	0.01	N.D.	N.D.	N.D.
			1.5	0.01	0.02	N.D.	N.D.	N.D.
			5	0.01	0.02	N.D.	N.D.	N.D.
			10	0.02	0.03	N.D.	N.D.	N.D.
25 May	HB 3	70°41.9'N 150°40.9'W	1.5	<0.01	0.02	N.D.	N.D.	N.D.
			6	0.02	0.03	N.D.	N.D.	N.D.
			12	<0.01	0.01	N.D.	N.D.	N.D.
25 May	HB 4 A	70°38.0'N 150°52.0'W	ice core	27.3	2.9	N.D.	N.D.	N.D.
	B		ice core	7.9	0.7	N.D.	N.D.	N.D.
			1.5	0.15	0.12	N.D.	N.D.	N.D.
25 May	20 A	70°14.2'N 147°29.8'W	ice core	2.9	0.2	N.D.	N.D.	N.D.
	B		ice core	2.7	0.3	N.D.	N.D.	N.D.
	C		ice core	7.4	0.5	N.D.	N.D.	N.D.
			12	0.08	0.06	0.02	3.0	0.05
25 May	BP A	70°19.6'N 147°34.5'W	ice core	19.9	0.9	N.D.	N.D.	N.D.
	B		ice core	22.0	1.0	N.D.	N.D.	N.D.
	C		ice core	20.0	0.2	N.D.	N.D.	N.D.
			2	0.49	0.04	0.03	5.0	0.1
			4	0.05	0.04	N.D.	N.D.	N.D.

Appendix 3. (Continued)

Date	Station	Location	Depth (m)	Chlorophyll	Phaeopigments	Primary Productivity (mg/m^3hr)	Light (ft candles)	Surface
				(mg/m^3 for phytoplankton; mg/m^2 for ice algae)				
26 May	8 A	70°30.4'N 148°55.0'W	ice core	<0.1	<0.1	N.D.	N.D.	N.D.
	B		ice core	<0.1	<0.1	N.D.	N.D.	N.D.
	C		ice core	<0.1	<0.1	N.D.	N.D.	N.D.
			2	0.03	0.05	0.00	N.D.	N.D.
			5.5	0.03	0.03	N.D.	N.D.	N.D.
			11	0.06	0.08	N.D.	N.D.	N.D.
26 May	2 A	70°34.9'N 149°27.5'W	ice core	8.5	1.2	N.D.	N.D.	N.D.
	B		ice core	3.4	0.1	N.D.	N.D.	N.D.
	C		ice core	11.5	0.4	N.D.	N.D.	N.D.
			2	0.35	0.30	0.00	N.D.	N.D.
			4	0.16	0.12	N.D.	N.D.	N.D.
26 May	3 A	70°32.1'N 149°51.7'W	ice core	0.3	<0.1	N.D.	N.D.	N.D.
	B		ice core	2.6	<0.1	N.D.	N.D.	N.D.
	C		ice core	0.1	<0.1	N.D.	N.D.	N.D.
			1.5	0.29	0.35	0.00	N.D.	N.D.
28 May	P. Bay A	70°20.0'N 148°20.5'W	ice core	2.3	0.3	N.D.	N.D.	N.D.
	B		ice core	7.4	0.9	N.D.	N.D.	N.D.
	C		ice core	0.9	<0.1	N.D.	N.D.	N.D.
			1.7	5.62	1.03	0.33	N.D.	N.D.
28 May	18 A	70°16.7'N 147°17.3'W	ice core	1.4	0.2	N.D.	N.D.	N.D.
	B		ice core	0.1	<0.1	N.D.	N.D.	N.D.
	C		ice core	0.3	0.0	N.D.	N.D.	N.D.
			1.7	0.08	0.06	0.03	N.D.	N.D.
			3.5	0.07	0.06	N.D.	N.D.	N.D.
			6.5	0.04	0.05	N.D.	N.D.	N.D.

Appendix 3. (Continued)

Date	Station	Location	Depth (m)	Chlorophyll	Phaeopigments	Primary Productivity (mg/m^{3}hr)	Light (ft candles)	% Surface
				(mg/m^3 for phytoplankton; mg/m^2 for ice algae)				
28 May	19 A	70°11.0'N 147°03'W	ice core	1.5	0.4	N.D.	N.D.	N.D.
	B		ice core	2.0	0.1	N.D.	N.D.	N.D.
				1.1	<0.1	N.D.	N.D.	N.D.
			1.7	0.19	0.11	0.13	N.D.	N.D.
			4.5	0.42	0.31	N.D.	N.D.	N.D.
28 May	NT 2 A	70°40.4'N 147°24.4'W	ice core	6.2	0.6	N.D.	N.D.	N.D.
	B		ice core	6.5	0.5	N.D.	N.D.	N.D.
	C		ice core	6.3	3.1	N.D.	N.D.	N.D.
	C'		ice core	15.7	1.8	N.D.	N.D.	N.D.
28 May	NT 2 (under ice)		1.5	0.04	0.02	0.09	110	1.2
			5	0.03	0.02	0.14	60	0.6
			10	0.42	0.01	N.D.	N.D.	N.D.
			25	<0.01	<0.01	N.D.	N.D.	N.D.
			50	0.24	0.02	N.D.	N.D.	N.D.
	NT 2 (lead)		0	0.07	0.03	0.05	2,800	62.2
			5	0.06	0.02	0.06	1,000	22.2
			10	0.05	0.06	0.03	500	11.1
			25	0.01	0.01	0.01	130	2.9
			50	0.31	0.64	N.D.	N.D.	N.D.
28 May	NT 3 A (under ice)	70°52.9'N 147°20.2'W		0.4	<0.1	N.D.	N.D.	N.D.
			1.5	0.07	0.04	0.04	10	0.1
			5	0.08	0.04	N.D.	N.D.	N.D.
			10	0.08	0.05	N.D.	N.D.	N.D.
			25	0.06	0.03	N.D.	N.D.	N.D.
			50		0.02	N.D.	N.D.	N.D.

Appendix 3. (Continued)

Date	Station	Location	Depth (m)	Chlorophyll	Phaeopigments	Primary Productivity (mg/m^{3}hr)	Light (ft candles)	% Surface
				(mg/m ^{3} for phytoplankton; mg/m^2 for ice algae)				
	(crack)		2	0.19	0.10	0.05	1,200	17.1
			6	0.12	0.08	0.04	500	7.1
28 May	NT 4 A	71°12'N 147°20.2'W		2.6	<0.1	N.D.	N.D.	N.D.
	B			4.3	0.2	N.D.	N.D.	N.D.
	(under ice)		1.5	0.65	0.09	0.25	190	2.6
			5	0.14	0.08	0.09	71	1.0
			10	0.17	0.10	N.D.	N.D.	N.D.
			25	0.13	0.08	N.D.	N.D.	N.D.
			50	0.07	0.05	N.D.	N.D.	N.D.
21 June	PBT 2	70°52'N 148°20.5'W	0	0.65	0.92	0.53	3,500	38.9
			5	0.20	0.05	0.47	700	7.8
			10	0.20	0.13		N.D.	N.D.
			15	0.19	0.05	0.28	N.D.	N.D.
			20	0.21	0.07	0.28	N.D.	N.D.
			25	0.12	0.05	0.10	87	1.0
			30	0.05	0.02	0.04	N.D.	N.D.
			35	0.04	0.02	<0.01	N.D.	N.D.
			40	0.04	0.02	0.01	N.D.	N.D.
			50	0.02	0.02	N.D.	N.D.	N.D.
			60	0.11	0.20	N.D.	N.D.	N.D.
23 June	PBT 1	70°35.5'N 148°20.5'W	1	0.16	0.03	0.86	600	7.1
			5	0.14	0.03	0.17	130	1.5
			10	0.16	0.02	0.06	31	0.4
			15	0.19	0.03	0.04	12	0.1
			20	0.19	0.02	<0.01	11	0.1
			23	1.22	0.99	N.D.	N.D.	N.D.

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