

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

by

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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 11 - 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 111 - April 13 - May 2, 1977
9. *Discoverer*, Leg IV - May 20 - June 11, 1977

In addition, a UH1H helicopter flight was conducted from Nome during the first week of April, 1977.

CHAPTER 11

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 analyze **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), Thorning-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 Ken, 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	<i>Chaetoceros debilis</i> , <i>C. scolopendra</i> , <i>Thalassiosira nordenskioldii</i>	May 1923	Surface water filtered through silk bolting cloth	
Allen (1929)	Unimak Island	<i>Chaetoceros debilis</i> , <i>Skeletonema costatum</i>	April 1924 August 1924		
Aikawa (1932)	Bering Sea	<i>Chaetoceros atlanticus</i> , <i>C. eriphilum</i> , <i>Corethron hystrix</i> , <i>Rhizosolenia alata</i> , <i>R. hebetata</i> f. <i>semispina</i> , <i>R. hebetata</i> f. <i>hiemalis</i> , <i>Thalassiothrix longissima</i>	July, August 1928		
Phifer (1934)	Bering Sea, Bering Strait	<i>Denticula seminae</i> , <i>Stephanopyxis nipponica</i>	July 26, Aug. 1934	centrifugation and settling	
Cupp (1937)	Scotch Cap, southern pt. of Unimak Island	<i>Biddulphia aurita</i> , <i>Thalassiosira</i> spp. especially <i>T. nordenskioldii</i> , <i>Chaetoceros socialis</i> , <i>C. debilis</i> , <i>Leptocy lindrus danicus</i> , <i>Asterionella japonica</i>	April Ap-May or June-July July, Sept. or early Nov.		
Motoda and Kawarada (1955)	Aleutian waters	<i>Chaetoceros</i> spp. <i>Corethronhystrix</i> , <i>Denticula</i> sp. <i>Nitzschia seriata</i> , <i>Rhizosolenia hebetata</i> f. <i>semispina</i>			1X10 ⁵ to 1X10 ⁷ cells/m ³
Marumo (1956)	S. of Kamchatka Peninsula	<i>Chaetoceros convolutes</i> , <i>C. debilis</i> , <i>Corethronhystrix</i> , <i>Denticula</i> sp. , <i>Nitzschia seriata</i>		centrifugation and settling	
Kawarada (1957)	Bering Sea	<i>Chaetoceros convolutes</i> , <i>C. compressus</i> , <i>C. debilis</i> , <i>C. radicans</i> , <i>C. constricts</i> , <i>Nitzschia closterium</i> , <i>N. delicatissima</i> , <i>N. longissima</i> , <i>N. seriata</i> , <i>Rhizosolenia hebetata</i> f. <i>semispina</i>		centrifugation and settling	10 ³ to 10 ⁴ min 10 ⁶ max cells /liter
Kawarada and	Bering Sea	<i>Thalassiosira</i> , some <i>Chaetoceros</i> , <i>Chaetoceros</i> spp. <i>Corethronhystrix</i> , <i>Coscinodiscus oculus-iridis</i> , <i>Denticula</i> sp. <i>Thalassiosira decipiens</i>	April, May	centrifugation and settling	
Karohji (1959)	Northern Bering Eastern Bering	<i>Chaetoceros</i> (subgenus <i>Hyalochaete</i>) , <i>Nitzschia seriata</i> , <i>Chaetoceros</i> (subgenus <i>Phaeoceros</i>), <i>Chaetoceros concavicornis</i> , <i>Coscinodiscus</i> sp. <i>Rhizosolenia hebetata</i> f. <i>semispina</i> , <i>C. atlanticus</i>		underway plankton recorder with silk bolting cloth net	
Ohwada and Kon	Bering Sea	<i>Chaetoceros atlanticus</i> , <i>C. concavicornis</i> , <i>C. convolutes</i> , <i>C. compressus</i> , <i>C. constricts</i> , <i>C. debilis</i> , <i>C. decipiens</i> , <i>Corethronhystrix</i> , <i>Denticula</i> sp. , <i>Fragilaria islandica</i> , <i>Rhizosolenia alata</i> , <i>R. hebetata</i> f. <i>hiemalis</i> , <i>R. hebetata</i> f. <i>semispina</i> , <i>Nitzschia seriata</i> , <i>N. closterium</i>		concentrating surface water	10 ⁴ to 10 ⁷ cells/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	<i>Chaetoceros</i> (subgenus <i>Hyalochaete</i>), predominantly <i>Chaetoceros furcellatus</i>		sedimented plankton samples	
Karohji (1972)	Bering Sea	<i>Denticula seminae</i> , <i>Thalassiothrix longissima</i> , <i>Chaetoceros atlanticus</i> , <i>C. convolutus</i> , <i>Coscinodiscus curvatulus</i> , <i>C. oculus-iridis</i> , <i>Nitzschia seriata</i> , <i>Rhizosolenia hebetata</i> f. <i>hiemalis</i>	June, July	net	Alaska Coastal area: 6800x10 ³ cells/m ³
Motoda and Minoda (1974)	off shore waters Bering Sea	<i>Chaetoceros convolutus</i> , <i>C. convavicornis</i> , <i>C. debilis</i> , <i>C. compressus</i> , <i>C. radicans</i> , <i>C. didymus</i> , <i>C. seiracanthus</i> , <i>C. furcellatus</i> , <i>C. constrictus</i> , <i>Rhizosolenia hebetata</i> f. <i>hiemalis</i> , <i>Denticula seminae</i> , <i>Nitzschia seriata</i> , <i>N. delicatissima</i> , <i>N. longissima</i> , <i>Fragilaria</i> spp., <i>Thalassiothrix longissima</i>	Early mid-summer	surface water and vertical net hauls	1X10 ⁵ to 1X10 ⁹ cells/m ³
Taniguchi et al. (1976)	Eastern Bering Sea	<i>Thalassiosira hyalina</i> , <i>T. nordenskioldii</i> , <i>Fragilaria</i> , <i>Navicula</i>	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., *Corethron 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: *Nitzschia 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 Flay 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.

Homer (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. Homer (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. <i>Discoverer 808 (leg one)</i> | May 15-May 30, 1975 |
| 2. <i>Discoverer 808 (leg two)</i> | June 2-June 19, 1975 |
| 3. <i>Discoverer 810</i> | August 9-August 28, 1975 |
| 4. <i>Miller Freeman 815</i> | November 10-November 26, 1975 |
| 5. <i>Surveyor 1</i> | March 14-April 2, 1976 |
| 6. <i>Surveyor 2</i> | April 12-April 30, 1976 |
| 7. <i>Surveyor 5</i> | March 16-April 4, 1977 |
| 8. <i>Surveyor 6</i> | April 14-May 1, 1977 |
| 9. <i>Discoverer 4</i> | 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., *Emiliana 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). *Emiliana huxleyi* and *Calciopappus 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 non-motile *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 $\frac{1}{2}$ 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 to calculate the similarity matrices used for cluster analysis routines:

Czekanowski

$$C_{s_{1,2}} = \frac{2W}{A+B} \text{ where } A = \text{the sum of the measures of attributes of entity 1}$$

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

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																															
		1					2					3					4					5											
		55	56	57	58	59	60	61	62	25	26	27	30	37	48	49	50	52	53	54	[23]	12	[3	4	5	6	7	8	9	10	11		
S P E C I E S	I	1	1	1	1		1	1		6	4				6	3	2	1	1	1	6	6	3	3	6	5	4	5	5	3	1		
		2								2	1											5	5	9	9	3	2	4	3	3	4	4	3
	II	a								5	1	5	2	5	2	5	2	5	2														
		3																								1	1	1	1	1	1	1	1
	III	13					1	1																									
		14																															
	IV	20																															
		15	1													1	2	2	1	2	1												
	V	5	6	8	8	15	16	15	10	10																							
		6									[2	2	4	4	4	3	3															
VI	11	2	2	2	2	2	2																										
	4														1	2	2	2			1	1	1										
VII	10																																
	12																																
VIII	16																																
	17																																
IX	18																																
	19																																
X	vu	7																															
	vii	9																															
XI	7																																
	9																																

		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	1	1	1	1	5	5	2	2	0	1	8	16	5	14	26	43	43	44	42	23	42	48	46	37	26	33	45	43	32	36	36	35	50
	2					1	1				8	6	6	17	21	30	23	23	21	15	14	15	15	4	3	4	7	3	6	3	3	4	4	
II	8					2	2			1	2	2																						
	3									2	2	2																						
III	13									1	1	1	1																					
	14					1																												
IV	15																																	
	5																																	
V	6																																	
	11																																	
VI	4	2	2			1	2			1	1																							
	10					1	1	1																										
VII	12	1	1			1				1	1																							
	16	1	1			1	1			1	1																							
VIII	17					2	2																											
	18					2	2	1		1	1																							
IX	19					1				1	1																							
	7																																	
X	9																																	

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 11-3). 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 laciniatus*, *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 vanhoeffeni*, *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.

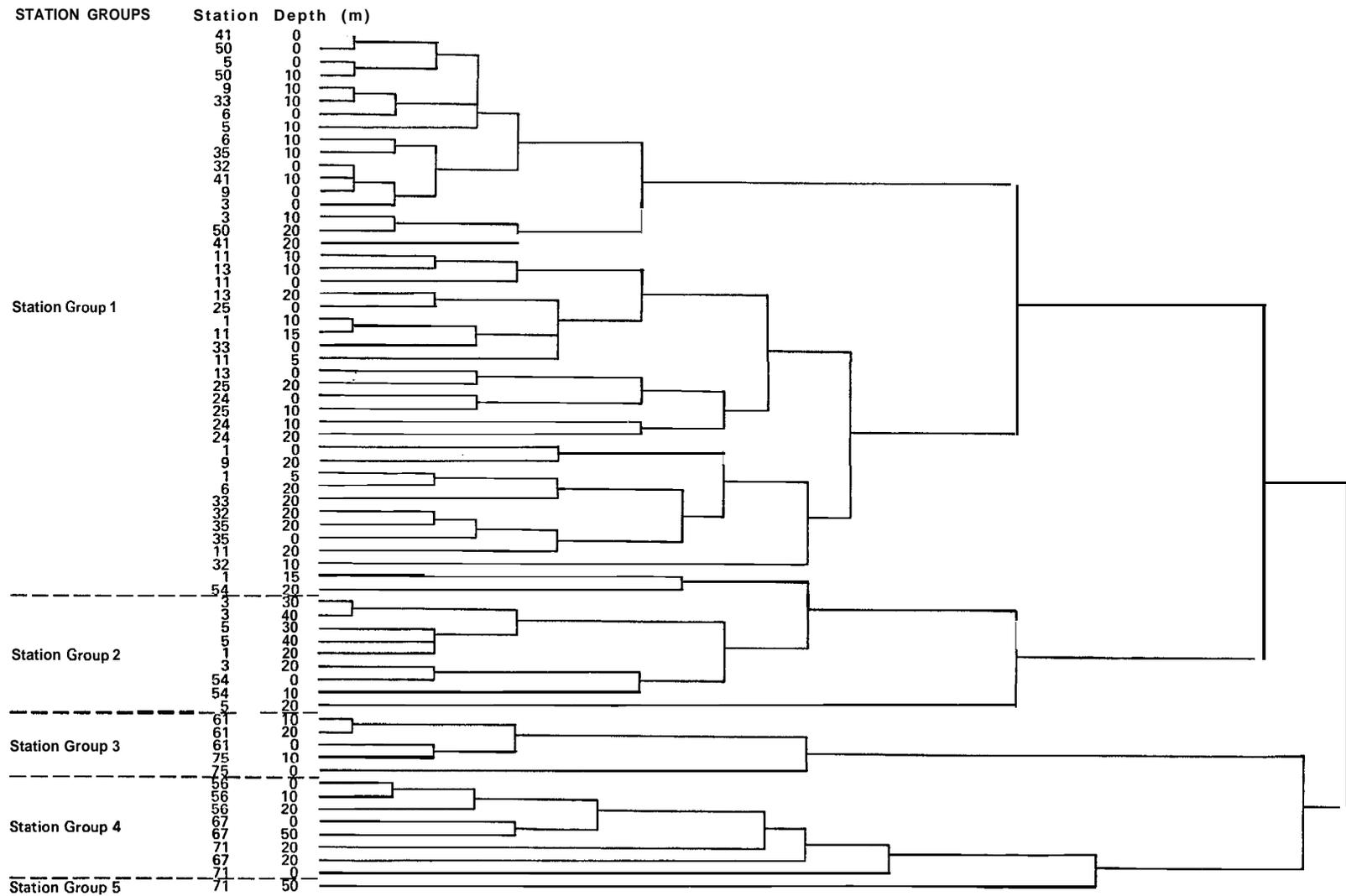
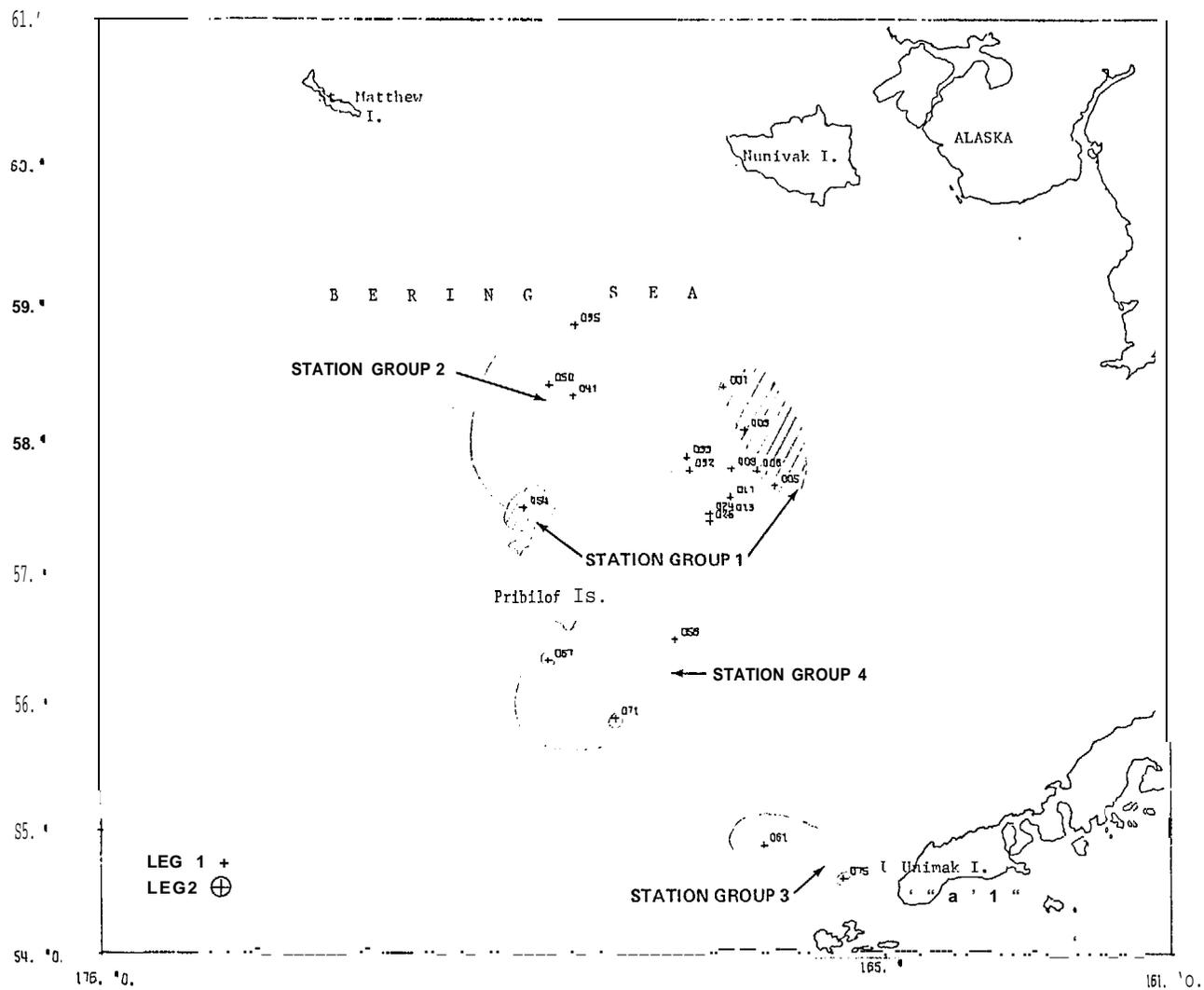


Figure II-1. Dendrogram of the station groups formed by cluster analysis using the Czekanowski similarity coefficient with untransformed data. *Discoverer* Cruise 808, May-June 1975.



PHYTOPLANKTON STATIONS, DISCOVERER CRUISE 808, 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 $\times 10^3$; 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		25t06				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

Station	Depth (m)							Location	Date Collected	Notes	
	O	5	10	15	20	30	40				50
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

Station	Depth (m)							Location	Date Collected	Notes	
	O	5	10	15	20	30	40				50
61	x 57.25		x 44.67						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

Station	Depth (m)							Location	Date Collected	Notes	
	O	5	10	15	20	30	40				50
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

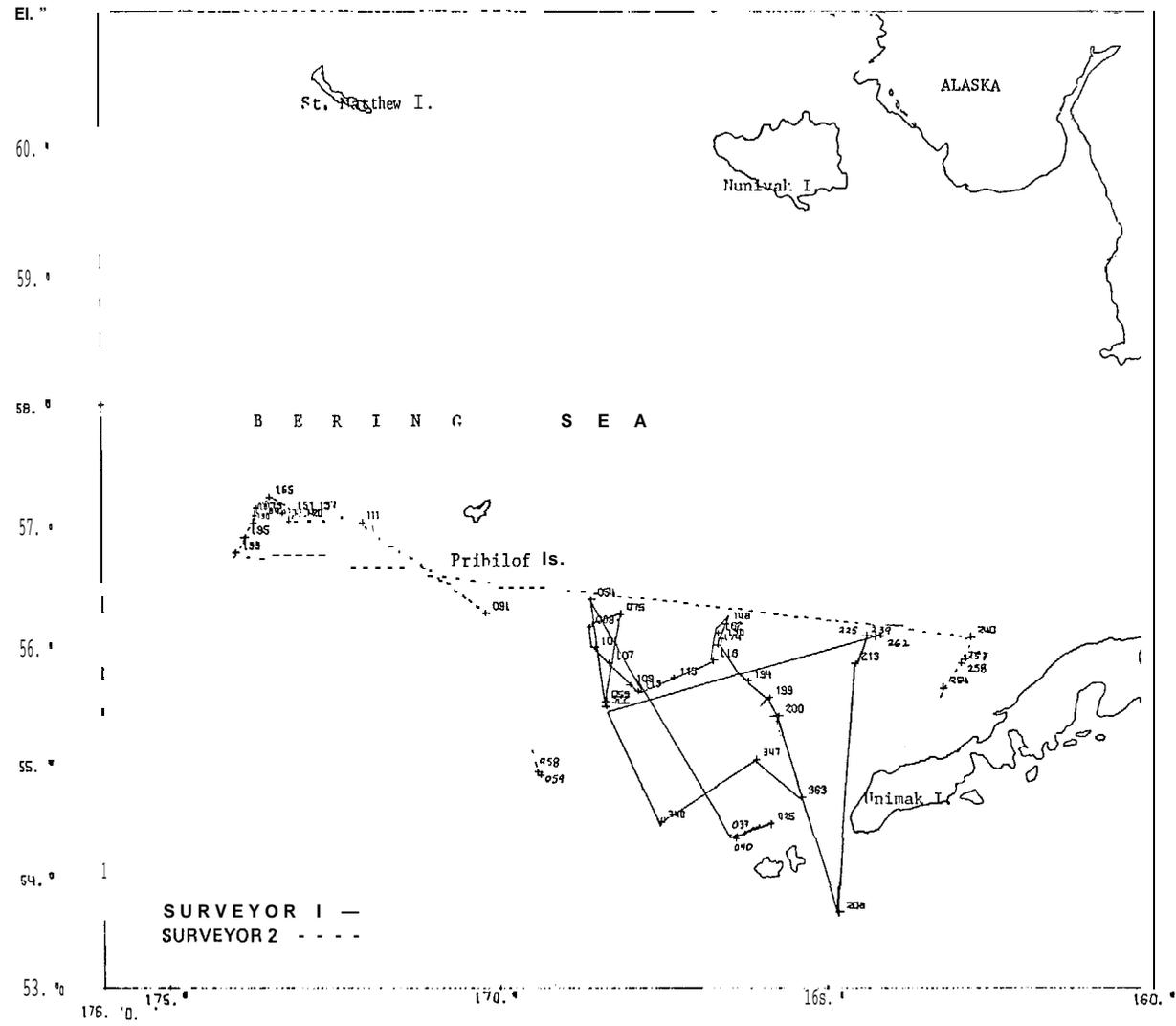
Station Group 3 which showed the influence of the Aleutian Pass water, was unique because it contained large quantities of *Nitzschia* spp. (*Pseudonitzschia* group). *Thalassiosira nordenskioldii* was also important. Other species, which occurred in Station Group 3, were *Chaetoceros* spp., *Nitzschia*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



SURVEYOR CRUISES 1 & 2, 1976

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 10⁵; x indicates the sample is a member of
the Station Group indicated

STATION GROUP 1

Station	Depth (m)										Location	Date Collected	Notes
	0	10	20	30	40	50	60	75	90	100			
25	x .356		x .408								54.4617 165.83	17 March 1976	N. of Unimak Paas
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

Station	Depth (m)										Location	Date Collected	Notes	
	0	10	20	30	40	50	60	75	90	100				
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

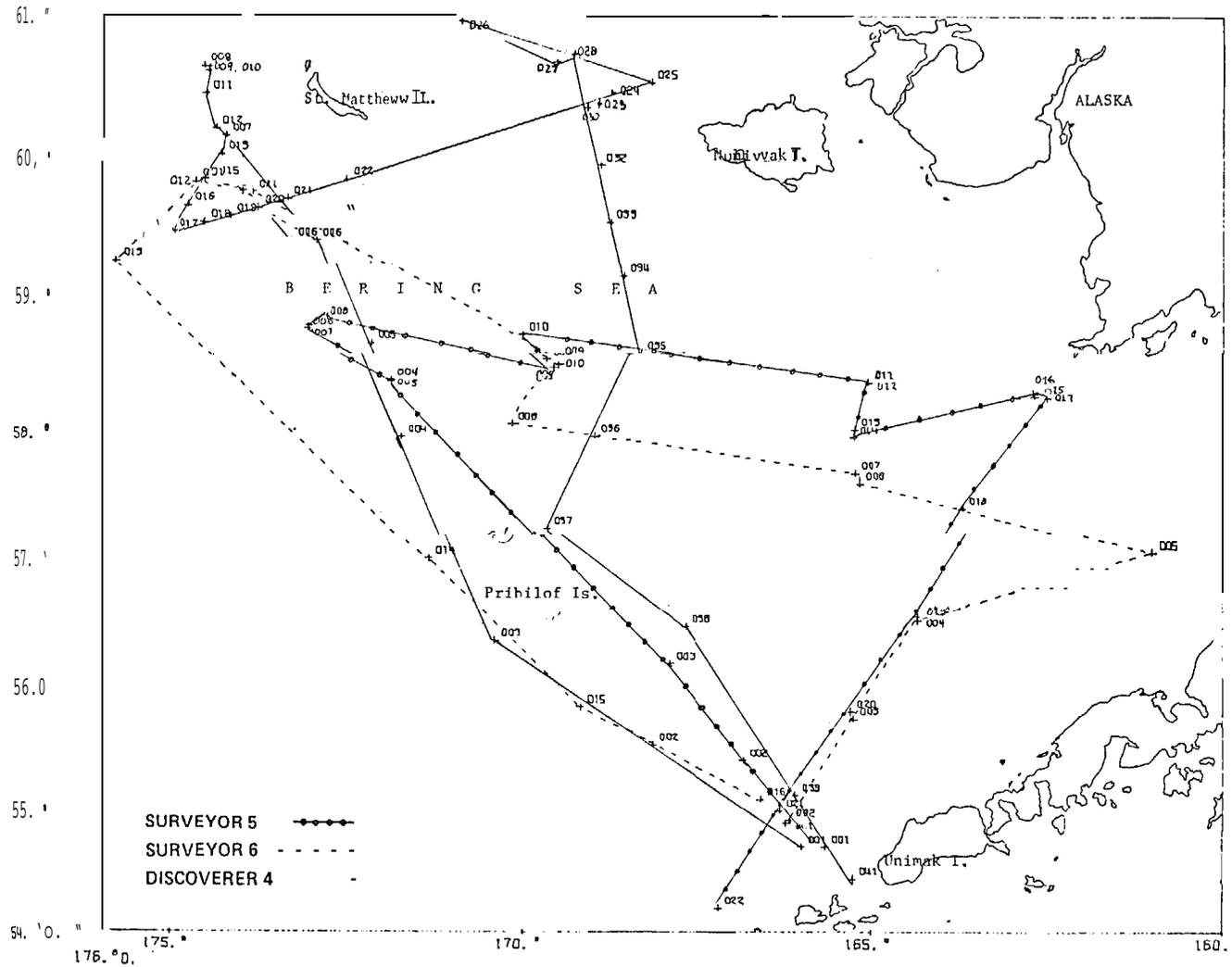
therefore designated "Pre-bloom Group 1". The major species in Pre-bloom Group 1 were microflagellates and members of the diatom genera *Nitzschia*, *Thalassiosira* and *Cylindrotheca*. Densities ranged from 3.6×10^3 - 1.6×10^5 cells/liter with microflagellates making up about 68 percent of all individuals 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. *gravidā*, *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. *gravidā*, *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 vanhoeffeni*, *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 (2×10^4 cells/liter) but, occasionally increased to 2×10^5 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.



1977 PHYTOPLANKTON STATIONS

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.

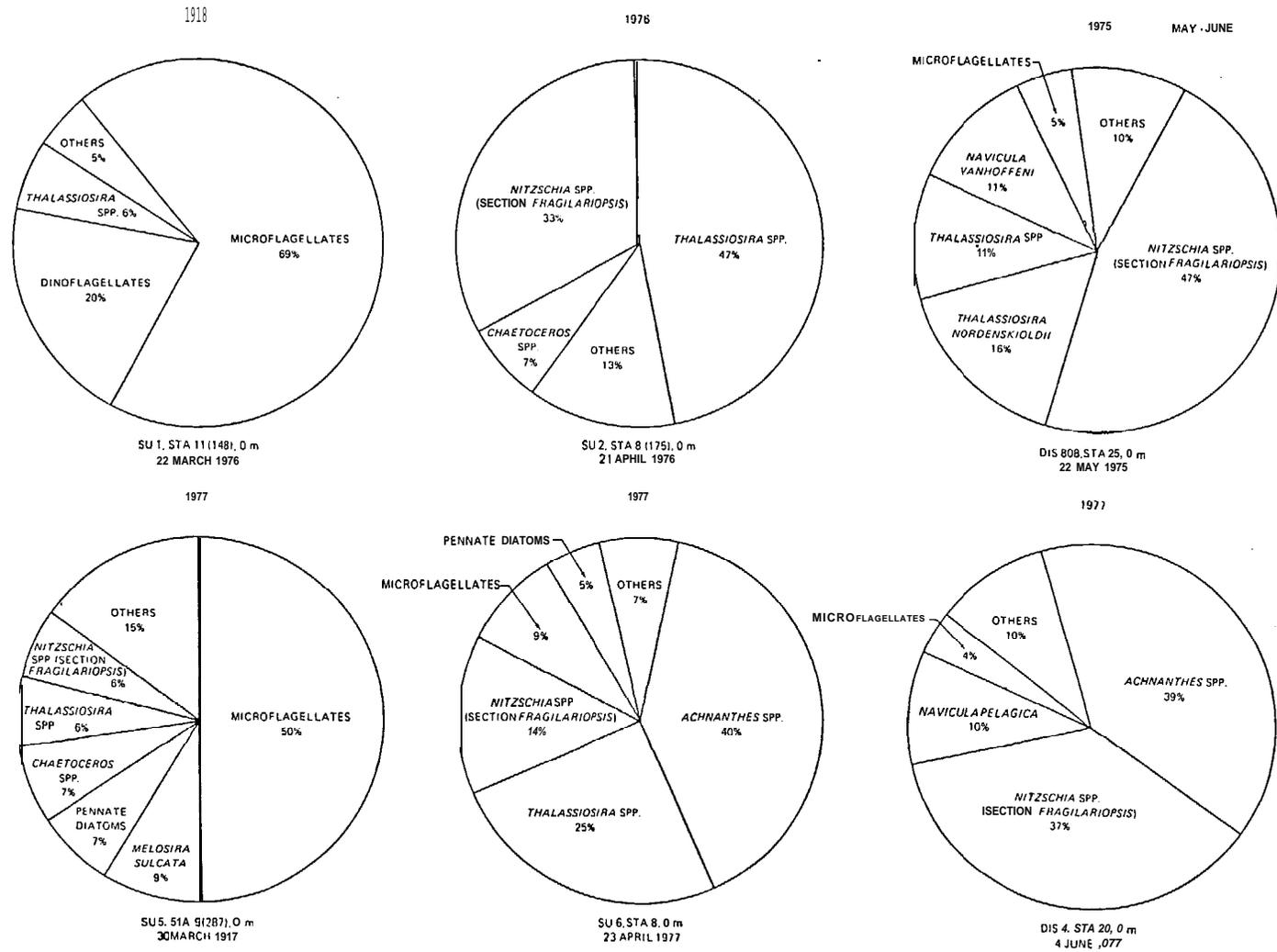


Figure II-5. Percentage composition of the phytoplankton at Bering Sea ice stations over different months, in 3 successive years. (On depth).

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 10⁵; x indicates the sample is a member of
the Station Group indicated

STATION GROUP 1								
Station	Depth (m)					Location	Date Collected	Notes
	0	10	20	30	50			
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 Out- side 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								
Station	Depth (m)					Location	Date Collected	Notes
	0	10	20	30	50			
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*. *Rhizosolenia alata*, *Eucampia zodiacus*, 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

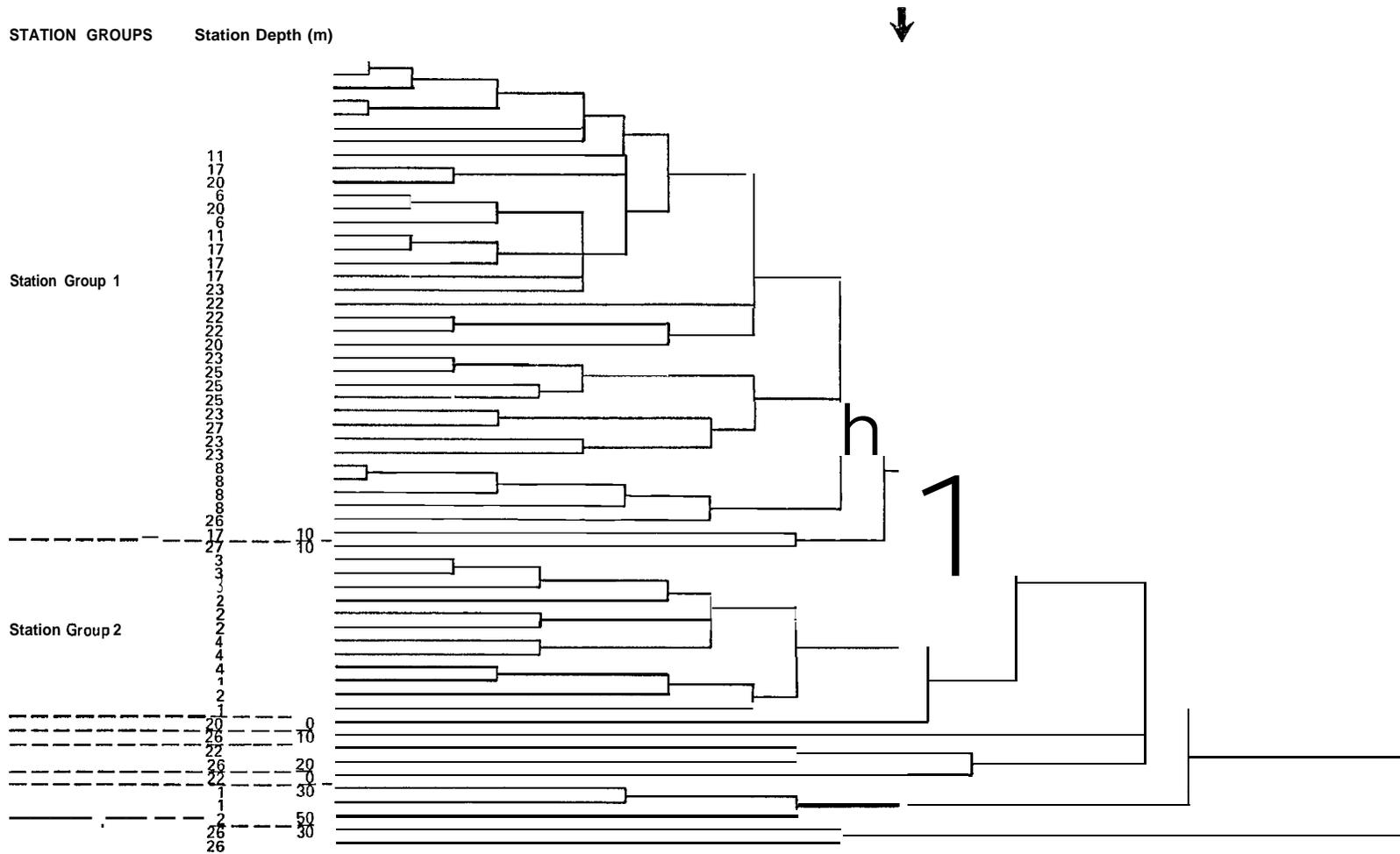


Figure II-6. Dendrogram of station groups formed by cluster analysis using the Czekanowski similarity coefficient with natural logarithm transformed data. *Discoverer* Cruise 4, May-June 1977.

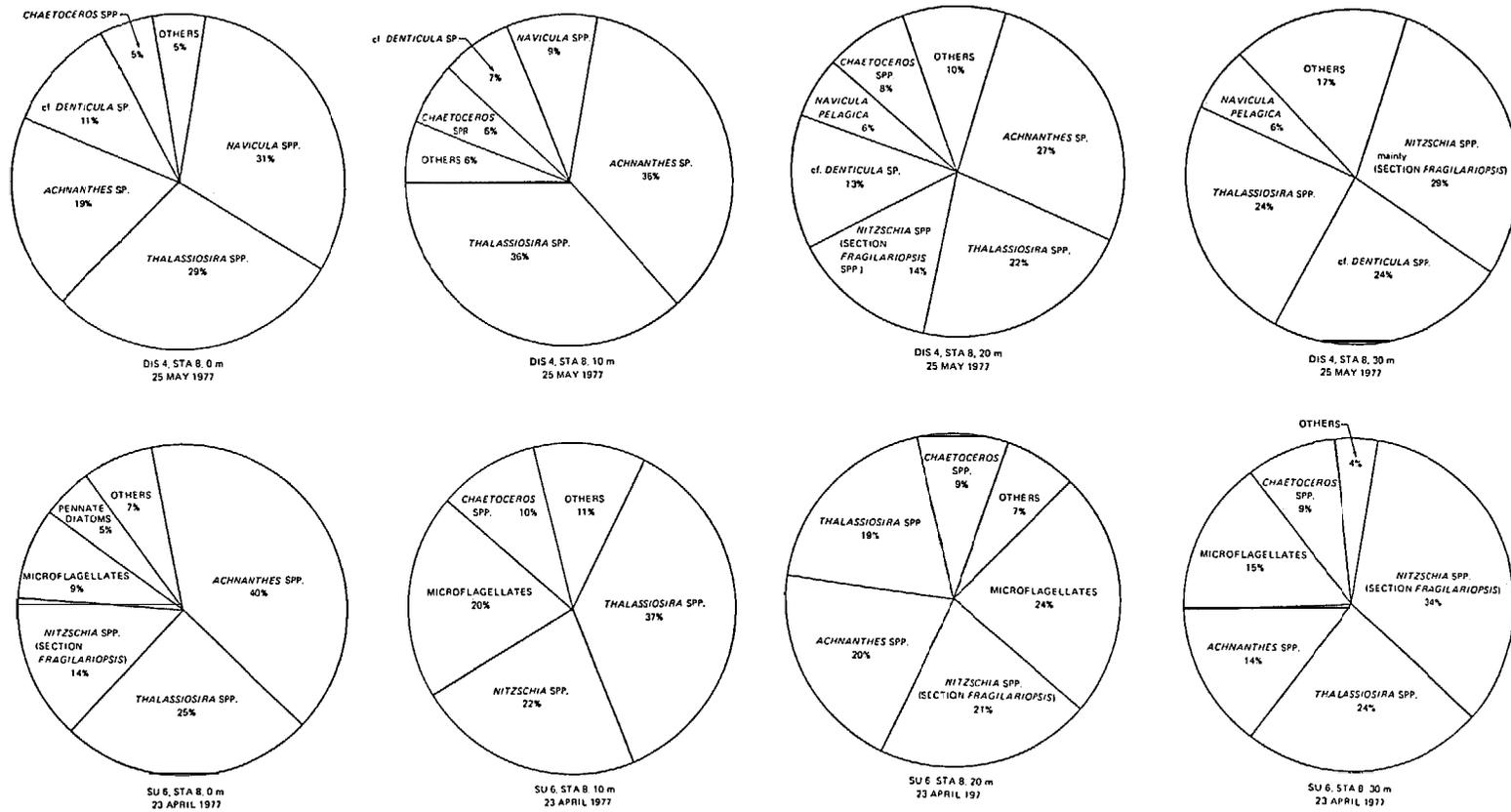


Figure II-7. Percentage composition of the phytoplankton at selected ice stations in the Bering Sea, *Discoverer* Cruise 4, May 1977, *Surveyor* Cruise 6, April 1977. Vertical distribution through the water column.

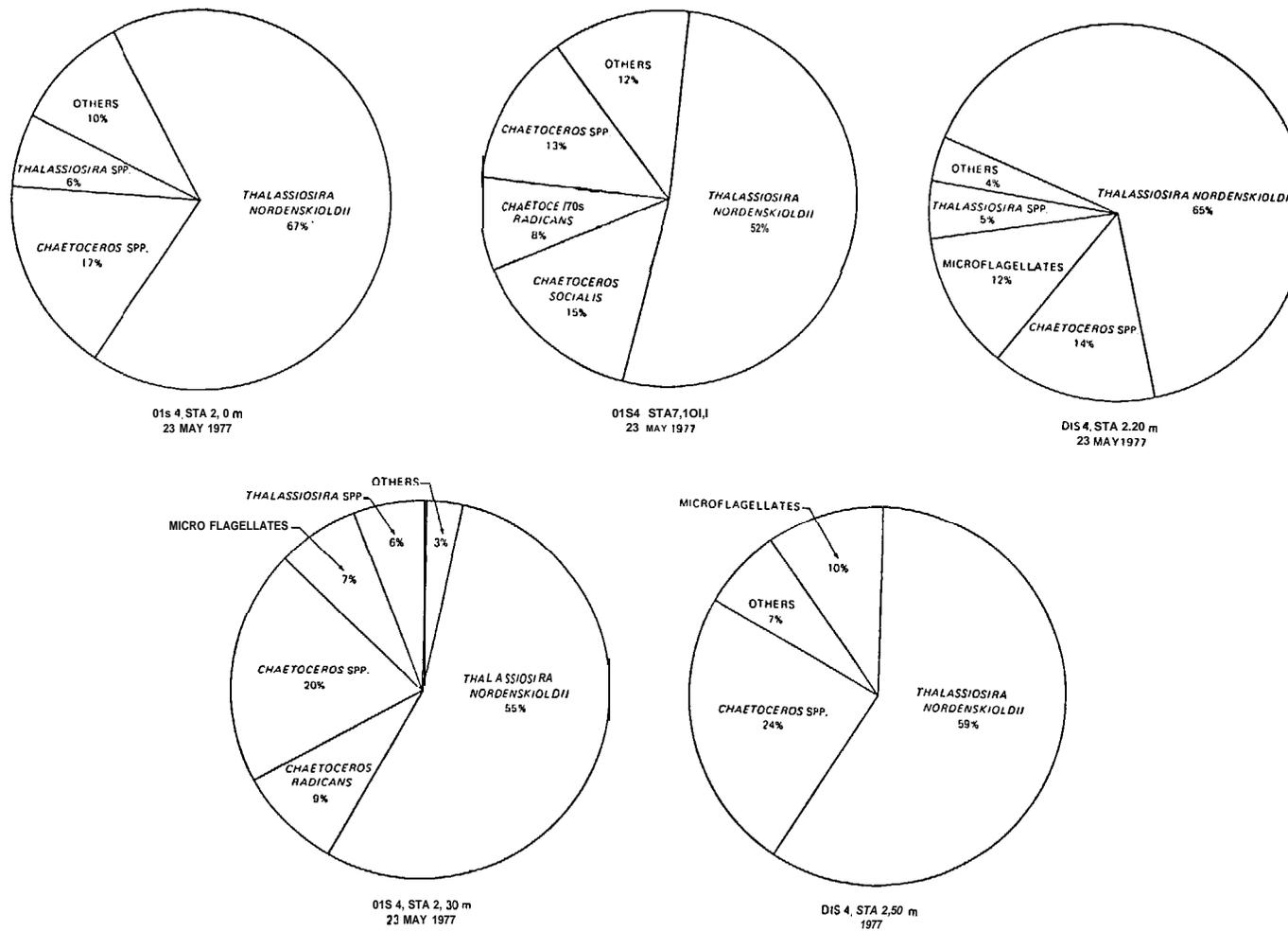
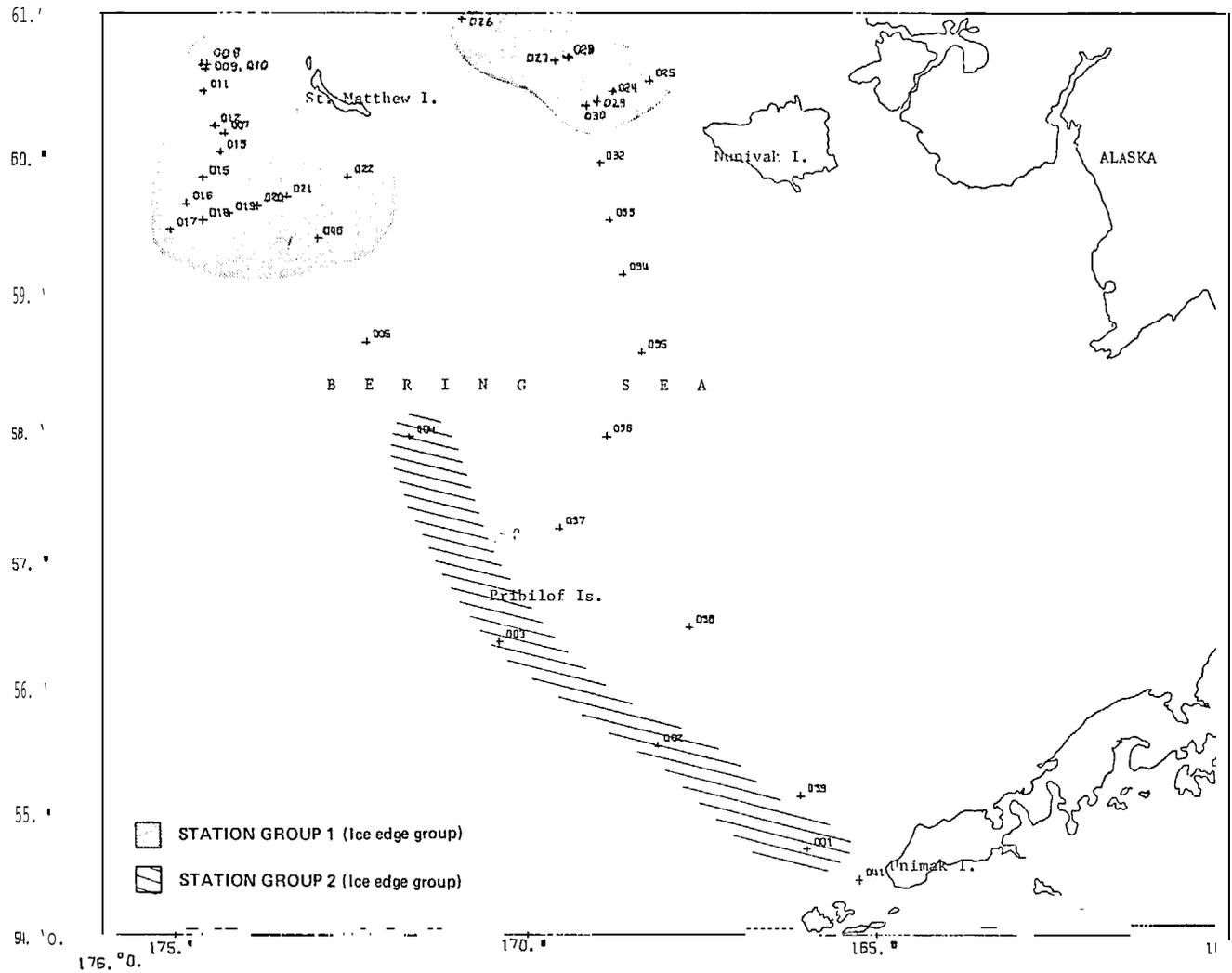


Figure II-8. Percentage composition of the phytoplankton at shelf break Station 2, in the Bering Sea, *Discoverer* Cruise 4, May 1977. Vertical distribution through the water column.



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. Similarity *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 *Proto-peridinium* 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; Tuimey-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 or 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, particularly 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 *Nitzschia 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, 11-10). 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

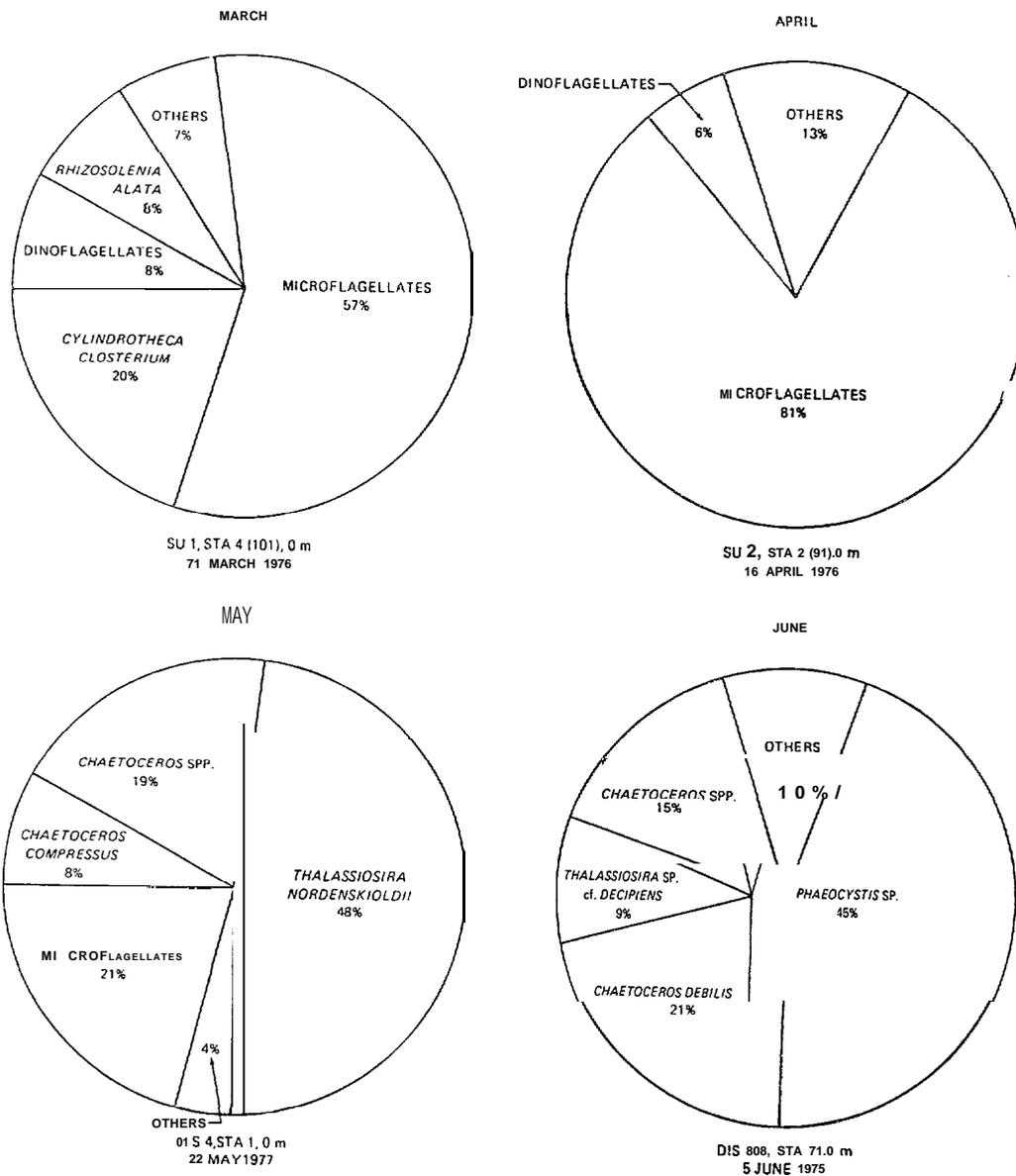


Figure 11-10. Percentage composition of the phytoplankton at shelf break stations in the Bering Sea in different months. (On depth).

(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 11-6

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

x indicates the taxon was found in that environment

Taxon	Slush ice	Water column
<i>Actinopterychus undulatus</i>	x	
<i>Amphiprora</i> sp.	x	
<i>Biddulphia aurita</i>	x	x
<i>Chaetoceros radicans</i>		x
<i>Chaetoceros</i> spp.	x	x
<i>Coscinodiscus radiatus</i>	x	
<i>Cylindrotheca closterium</i>	x	x
<i>Gyrosigma</i> or <i>Pleurosigma</i> spp.	x	x
<i>Melosira sulcata</i>	x	x
<i>Navicula</i> spp.	x	x
<i>Nitzschia</i> spp. (section <i>Fragilariopsis</i>)	x	x
<i>Pleurosigma</i> sp.	x	
<i>Porosira glacialis</i>	x	
<i>Rhizosolenia hebetata</i>		x
<i>Thalassionema nitzschioides</i>	x	x
<i>Thalassiosira polychorda</i>		x
<i>Thalassiosira</i> sp.	x	x
unidentified pennates	x	x
<i>Peridinium</i> spp.		x
dinoflagellates		x
<i>Halosphaera</i>		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
<i>Achnanthes</i> sp.	x		x
<i>Amphiprora</i> sp.			x
<i>Asterionella japonica</i>			x
<i>A. kariana</i>	x		x
<i>Bacteriosira fragilis</i>			x
<i>Biddulphia aurita</i>	x		x
<i>Chaetoceros</i> sp. cf. <i>cinctus</i>			x
<i>C. compressus</i>			x
<i>C. convolutus</i>			x
<i>C. debilis</i>			x
<i>c. decipiens</i>			x
<i>C. lacinosus</i>			x
<i>C. radicans</i>			x
<i>C. socialis</i>			x
<i>Chaetoceros</i> sp.			x
<i>Coscinodiscus</i> sp.			x
<i>Cylindrotheca closterium</i>			x
<i>Cylindrotheca</i> sp.			x
cf. <i>Denticula</i> sp.			x
cf. <i>Detonula</i> sp.			x
<i>Ditylum brightwellii</i>	x		
<i>Eucampia zoodiacus</i>			x
<i>Gyrosigma</i> or <i>Pleurosigma</i> sp.	xx		x
<i>Melosira sulcata</i>	x		
<i>Navicula pelagica</i>			x
<i>N. vanhoffeni</i>			x
<i>Navicula</i> sp.			x
<i>Nitzschia frigida</i>	x		x
<i>N. seriata</i>	x		x
<i>Nitzschia</i> sp. (section <i>Fragilariopsis</i>)	xx		x
<i>Porosira glacialis</i>			x
<i>Stephanopyxis nipponica</i>			x
cf. <i>Tabellaria</i> sp.			x
<i>Thelassionema nitzschiodes</i>	x		x
<i>Thalassiosira gravida</i>			x
<i>T. nordenskioldii</i>			x
<i>T. polychorda</i>			x
<i>T. rotula</i>			x
<i>Thalassiosira</i> sp.	xx		x
<i>Thalassiothrix frauenfeldii</i>			x
unidentified pennate diatoms	x		x
<i>Peridinium</i> 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 time 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

Chrysophyte

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.

co sp. cf. *curvisetus* Cl..

Co danicus Cl.

C. debilis Cl.

C. decipiens Cl.

C. furcellatus Bail.

C. sp. cf. *fragilis* Meun.

C. sp. cf. *holsaticus* Schutt

C. lacinosus Schutt

C. lorenzianus Grun.

C. radicans Schutt

C. seiracanthus Gran

C. septentrionalis Oestrup

Co *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 zodiacus 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) Meun.)
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. styliiformis Brightw.
 cf. *Rhabbonema* sp. Kuetzing

APPENDIX

CONTINUED

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

Dietyocha fibula Ehr.
Ebria tripartita (Schum.) Lemm.

Dinophyta

Ceratium fusus (Ehbg.) Clap. Lachm.
C. lineatum (Ehr.) Cleve
C. tripes (O.F. Muller) Nitzsch.
Dinophysis norvegica Clap. et. Lachm.
cf. Gymmodinium sp.
cf. Oxytoxum Sp.
Proto-peridinium minisculum (Pavil.) (ex. *Peridinium minisculum* Pavil.)
P. pallidum (Ostenf.) Balech (ex. *P. pallidum* Ostenf.)
P. depressum (Bail.) Balech (ex. *P. depressum* Bail..)
Proto-peridinium 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.

Gooney (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 synthesis 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 fluctuating 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 micro-nekton 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 from 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 surface or per unit volume were transformed to base ten **logarithms**, an acceptable technique that tends

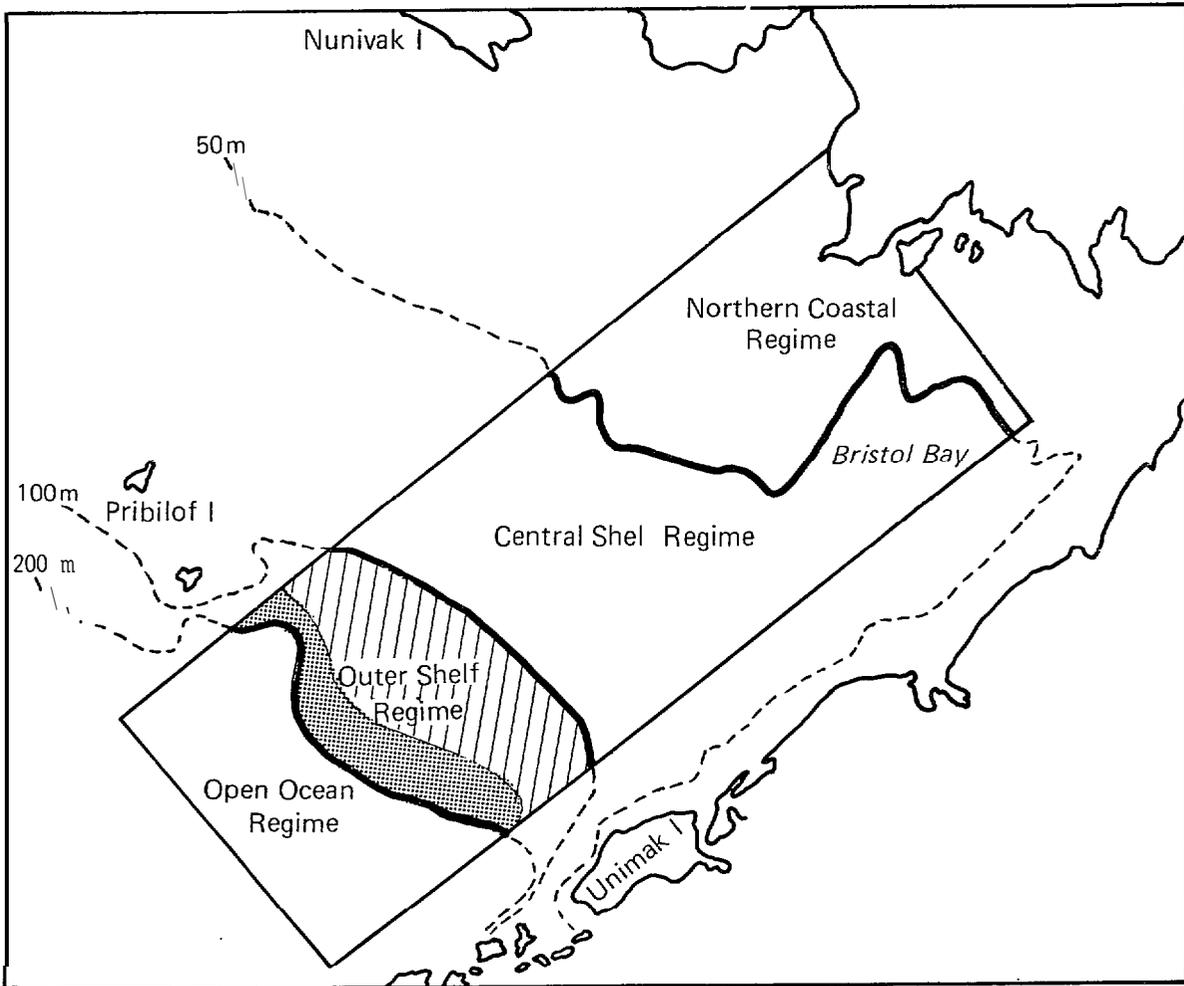


Figure III-1. Bathymetric regimes used as sampling areas in the southeast Bering Sea.

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 dielily 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 retrieval speed of the net (~ 1 m/sec). The amount of water filtered, 160 m³ per tow from 200 m to the surface, was adequate for the common species but exceedingly marginal or completely inappropriate 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 organisms, 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 consistently 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		
<i>Aequorea forskalea</i>		x
<i>Perigonimus yoldia-arcticae</i>		x
<i>P. multicirratu</i>		x
<i>P. brevicornis</i>		x
<i>Calycopsis nematophora</i>		x
<i>Bougainvillia superciliaris</i>		x
<i>Corymorpha flammea</i>		x
<i>Tubularia prolifer</i>		x
<i>Coryne tubulosa</i>		x
<i>C. principis</i>		
<i>Obelia longissima</i>		x
<i>Ptychogena lactea</i>		x
<i>Eirene indicans</i>		x
<i>Aglanthe digitale</i>		
<i>Aegina roses</i>		x
<i>Dimophyes arctica</i>		x
Scyphozoa		
<i>Periphylla hyacinthina</i>		x
<i>Chrysaora helova</i>		x
Ctenophora		
<i>Beroe</i> spp.		x
Annelida		
Polychaeta		
<i>Hesperone complanata</i>		x
<i>Eteone Longs</i>		x
<i>Lopadorrhynchus</i> sp.		x
<i>Pelagobia longicirrata</i>		x
<i>Typhloscolex muelleri</i>		
<i>Tomopteris septentrionalis</i>		x
<i>Laonice cirrata</i>		x
<i>Glycera capitata</i>		x
<i>Lumbrinereis</i> sp.		x
<i>Scoloplos armiger</i>		x
<i>Pelagobia longicirrata</i>		x
<i>Capitella capitata</i>		x
<i>Maldane sarsi</i>		x
<i>Terebellides stroemi</i>		x

TABLE III-1

CONTINUED

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

TABLE III-1

CONTINUED

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

TABLE III-1

CONTINUED

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

TABLE III-1

CONTINUED

Taxa	Common	Rare
Decapoda		
<i>Pandalus borealis</i>		x
<i>P. Sp.</i>		x
<i>Eualus macilenta</i>		x
<i>Paracrangon echinata</i>		x
<i>Paralithodes camtschatica</i>		x
<i>Chionoecetes spp.</i>		x
<i>Hyas spp.</i>		x
<i>Telmessus cheiragonus</i>		x
<i>Erimacrus isenbeckii</i>		x
Chaetognatha		
<i>Eukrohnia hamata</i>	x	
<i>E. bathypelagica</i>		x
<i>Sagitta elegans</i>	x	
Chordata		
Larvacea		
<i>Fritillaria borealis</i>		x
<i>Oikopleura spp.</i>	x	
Teleostei		
<i>Clupea harengus pallasii</i>		x
<i>Mallotus villosus</i>		x
<i>Bathylagus pacificus</i>		x
<i>B. stilbius schmidti</i>		x
<i>Stenobranchius leucopsarus</i>		x
<i>Theragra chalcogramma</i>		x
<i>Sebastes spp.</i>		x
<i>Liparis spp.</i>		x
<i>Nectoliparis pelagicus</i>		x
<i>Atheresthes stomias</i>		x
<i>Hippoglossoides elassodon</i>		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		
<i>Aglantha digitale</i>	x	
<i>Perigonimus brevirostris</i>		x
<i>Perigonimus</i> c.f. <i>P. yoldia arctica</i>		X
<i>Perigonimus multicirratu</i>		x
<i>Calycopsis nematophora</i>		x
<i>Bougainvillea superciliaris</i>		x
<i>Rathkea jaschnowi</i>		x
<i>Corymorpha flammea</i>		x
<i>Coryne principis</i>	x	
<i>Ptychogena lactea</i>		x
<i>Eirene indicans</i>		x
<i>Aegina roses</i>		X
<i>Aequorea forskalea</i>		x
<i>Pantachogan haeckeli</i>		x
<i>Melicertum campanula</i>		x
<i>Botrynema burcei</i>		x
<i>Halicreas minimum</i>		x
<i>Crossota brunnea</i>		x
Scyphozoa		
<i>Periphylla hyacinthina</i>		x
<i>Atolla wyvillei</i>		x
<i>Chrysaora melanaster</i>	x	
<i>Chrysaora helvola</i>		x
<i>Cyanea capillata</i>	x	
<i>Phacellophora camtschatica</i>		x
<i>Aurelia limbata</i>		x
Siphonophora		
<i>Dimophyes arctica</i>		x
<i>Vogtia serrata</i>		x
<i>Ramosia vitiazi</i>		x
<i>Rosacea plicata</i>		x
Chaetognatha		
<i>Sagitta elegans</i>		x
<i>Eukrohnia</i> spp.		x
<i>Sagitta scrippsae</i>		x
Mollusca		
<i>Galiteuthis armata</i>		x
<i>Chiroteuthis veranyi</i>		x
<i>Gonatus fabricii</i>		x
<i>Gonatus magister</i>		x
<i>Gonatopsis</i> sp.		x

TABLE III-2

CONTINUED

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

TABLE III-2

CONTINUED

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

TABLE III-2

CONTINUED

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

TABLE III-2

CONTINUED

Taxa	Common	Rare
Teleostei (cent'd)		
<i>Clupea harengus pallasii</i>		x
<i>Lumpenus medius</i>		X
<i>Artediellus pacificus</i>		x
<i>Stenobranchius leucopsarus</i>	x	
<i>Bathylagus pacificus</i>		x
<i>Bathylagus alascanus</i>		X
<i>Ptilichthys goodei</i>		x
<i>Stenobranchius nannochir</i>		x
<i>Nectoliparis pelagicus</i>		x
<i>Bathylagus stilbius schmidti</i>	x	
<i>Hippoglossus stenolepis</i>		x
<i>Malacocottus zonurus</i>		x
<i>Hemilepidotus</i> sp.		x
<i>Chauliodus macouni</i>		x
<i>Bathymaster signatus</i>		x
<i>Triglops pingeli</i>		x
<i>Ammodytes hexapterus</i>		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 discernible 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 111-3

DISTRIBUTION PATTERNS BY REGIME FOR NUMERICALLY DOMINANT ZOOPLANKTON
AND MICRONEKTON GROUPS IN THE SOUTHEAST BERING SEAA. Usually Most Abundant in the Open Ocean

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

B. Usually Most Abundant in the Outer Shelf

Oithona spinirostris
Thysanoessa inermis
 Majiidae (larvae)

C. Usually Most Abundant in the Central Shelf

<i>Calanus glacialis</i>	<i>Parathemisto libellula</i>
<i>C. marshallae</i>	<i>Thysanoessa raschii</i>
<i>Pseudocalanus</i> spp.	<i>Sagitta elegans</i>

D. Usually Most Abundant in the Northern Coastal Area

Acartia longiremis

E. No Consistent Regime Affinity

<i>Aglantha digitale</i>	<i>Thysanoessa</i> spp. (juveniles)
<i>Calanus</i> spp. (juveniles)	<i>T. spinifera</i>
Copepod nauplii	<i>Oithona similis</i>

F. Absent in the Northern Coastal Regime

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

The copepod *Oithona spirostris*, the euphausiid *Thysanoessa inermis*, and spider crab (Majidae) 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 prefer 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/m² 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/m³) 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/m²) 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 components 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.

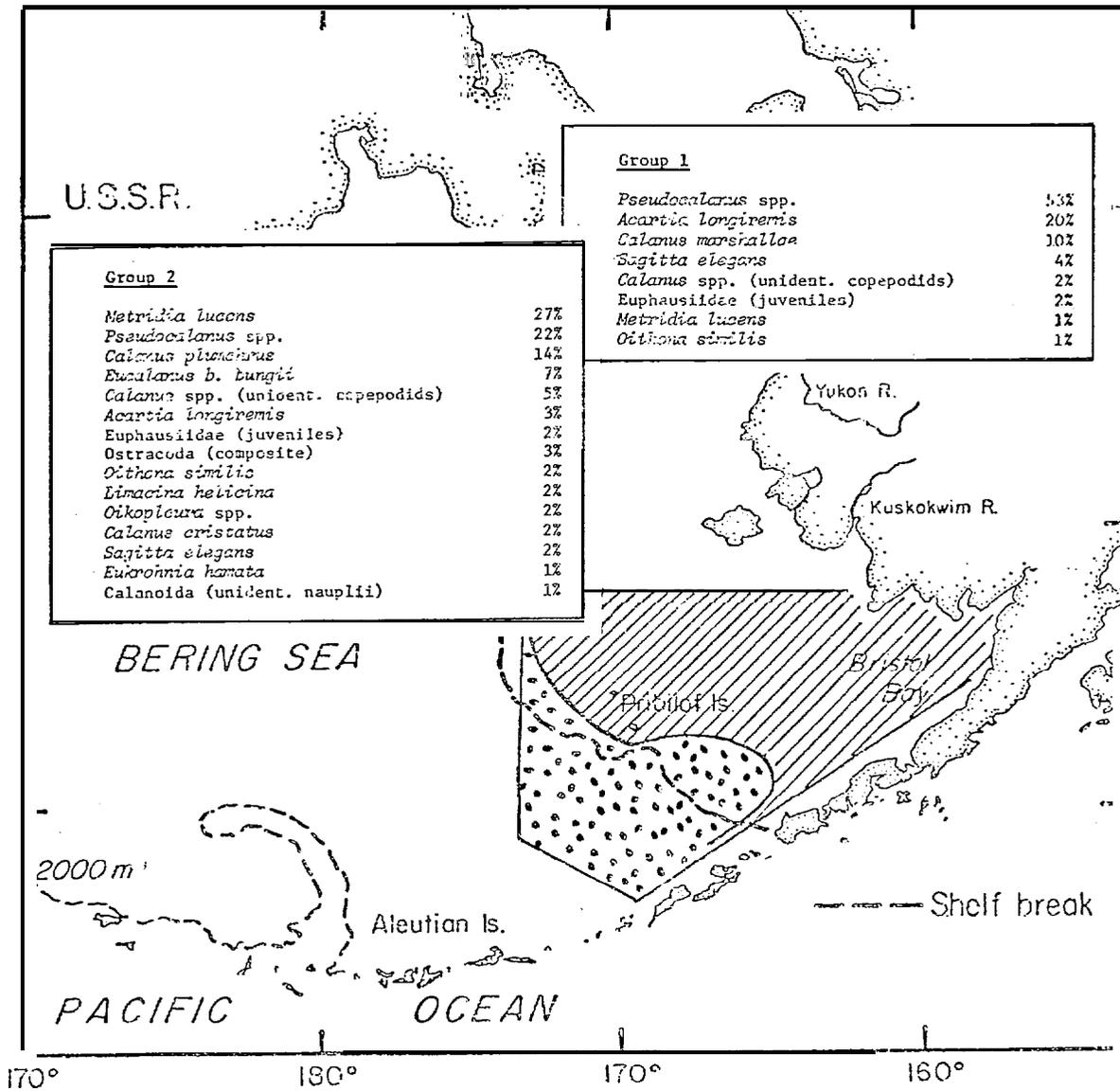


Figure III-2. Distributions of shelf (Group 1, lined) and oceanic (Group 2, dotted) assemblages from R-mode cluster analysis of 1-m net catches.

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 "alike-ness" 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

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

TABLE III-5

CONTINUED

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

TABLE III-5

CONTINUED

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

X

TABLE III-5

CONTINUED

Taxa	No. /m ³		
	>10	>100	>1000
Chordata			
Larvacea			
<i>Fritillaria borealis</i>			
<i>Oikopleura</i> spp.			
Teleostei			
Cyclopteridae (unident.)			
Gadidae (unident.)			
Cottidae (unident.)			
Stichaeidae (unident.)			
Pleuranectidae (unident.)			
<i>Lumpenus</i> 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							
<i>Acartia longiremis</i>	** 7,32	** 1,32	NS 1,32	** 7,32	NS 7,32	NS 1,32	NS 7,32
<i>Calanus glacialis</i>	** 7,32	NS 1,32	* 1,32	** 7,32	NS 7,32	NS 1,32	* 7,32
<i>Calanus plumchrus</i>	* 7,32	NS 1,32	NS 1,32	NS 7,32	NS 7,32	NS 1,32	NS 7,32
<i>Metridia lucens</i>	** 7,32	NS 1,32	** 1,32	NS 7,32	** 7,32	NS 1,32	NS 7,32
<i>Oithona similis</i>	** 7,32	* 1,32	NS 1,32	** 7,32	NS 7,32	NS 1,32	NS 7,32
<i>Pseudocalanus</i> spp.	** 7,32	NS 1,32	NS 1,32	** 7,32	NS 7,32	NS 1,32	NS 7,32
<i>Scolecithricella minor</i>	** 7,32	NS 1,32	NS 1,32	NS 7,32	NS 7,32	NS 1,32	NS 7,32
Chaetognatha							
<i>Sagitta elegans</i>	** 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 ≤ 0.05; ** = P ≤ 0.01; NS = P > 0.05.

TABLE III-7

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
Cnidaria							
Hydrozoa							
<i>Aglantha digitale</i>	NS 1,15	** 3,15	NS 1,15	** 3,15	NS 1,15	** 1,15	NS 3,15
Mollusca							
Pteropoda							
<i>Limacina helicina</i>	NS 1,15	** 3,15	** 1,15	NS 1,15	NS 1,15	** 1,15	* 3,15
Crustacea							
Copepoda							
<i>Acartia longiremis</i>	** 1,15	** 3,15	NS 1,15	* 3,15	NS 1,15	NS 1,15	NS 3,15
<i>Calanus glacialis</i>	** 1,15	** 3,15	* 1,15	NS 3,15	NS 1,15	NS 1,15	NS 3,15
<i>Calanus plumchrus</i>	** 1,15	** 3,15	NS 1,15	NS 3,15	NS 1,15	NS 1,15	NS 3,15
<i>Metridia lucens</i>	NS 1,15	** 3,15	** 1,15	* 3,15	NS 1,15	** 1,15	NS 3,15
<i>Oithona similis</i>	* 1,15	** 3,15	NS 1,15	* 3,15	NS 1,15	NS 1,15	NS 3,15
<i>Pseudocalanus</i> spp.	** 1,15	** 3,15	** 1,15	** 3,15	* 1,15	NS 1,15	* 3,15
<i>Scolecithricella minor</i>	** 1,15	* 3,15	NS 1,15	NS 3,15	NS 1,15	NS 1,15	NS 3,15
Chaetognatha							
<i>Sagitta elegans</i>	** 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; Night3 * = $p \leq 0.05$; ** = $p \leq 0.01$; 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 **inter-zonal** 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 precede 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 $S^\circ/\text{‰}$].) 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 ($2 < \text{cm}/\text{sec}$).

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^o/‰, 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 shelf water and a warmer, more saline Alaska Stream/Bering Sea 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 $44 \text{ mg C/m}^3 \cdot \text{day}$. 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 availa-

bility 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, Homer 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)

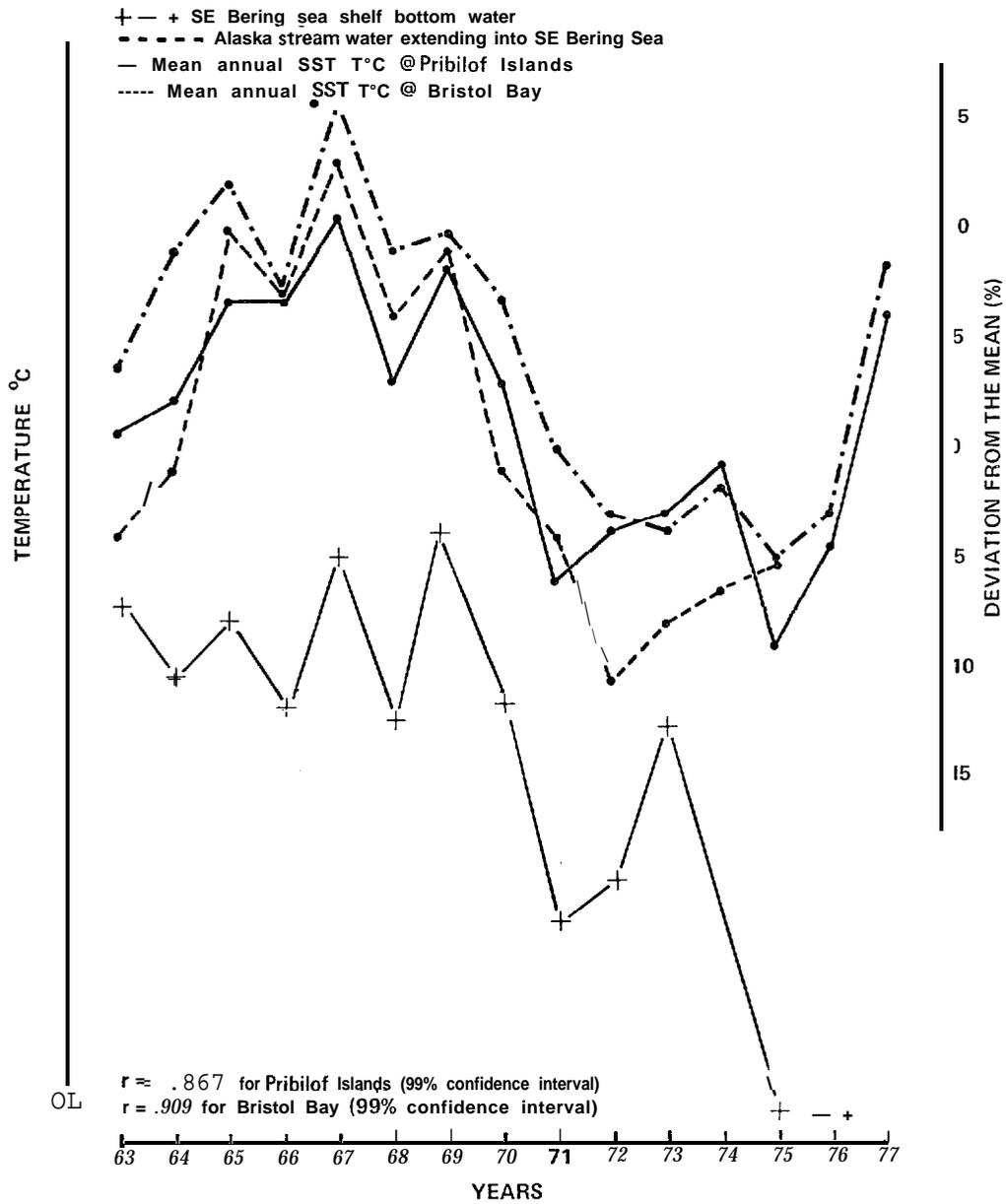


Figure IV-1. Mean annual sea surface and sea bottom temperatures for the S. E. Bering Sea.

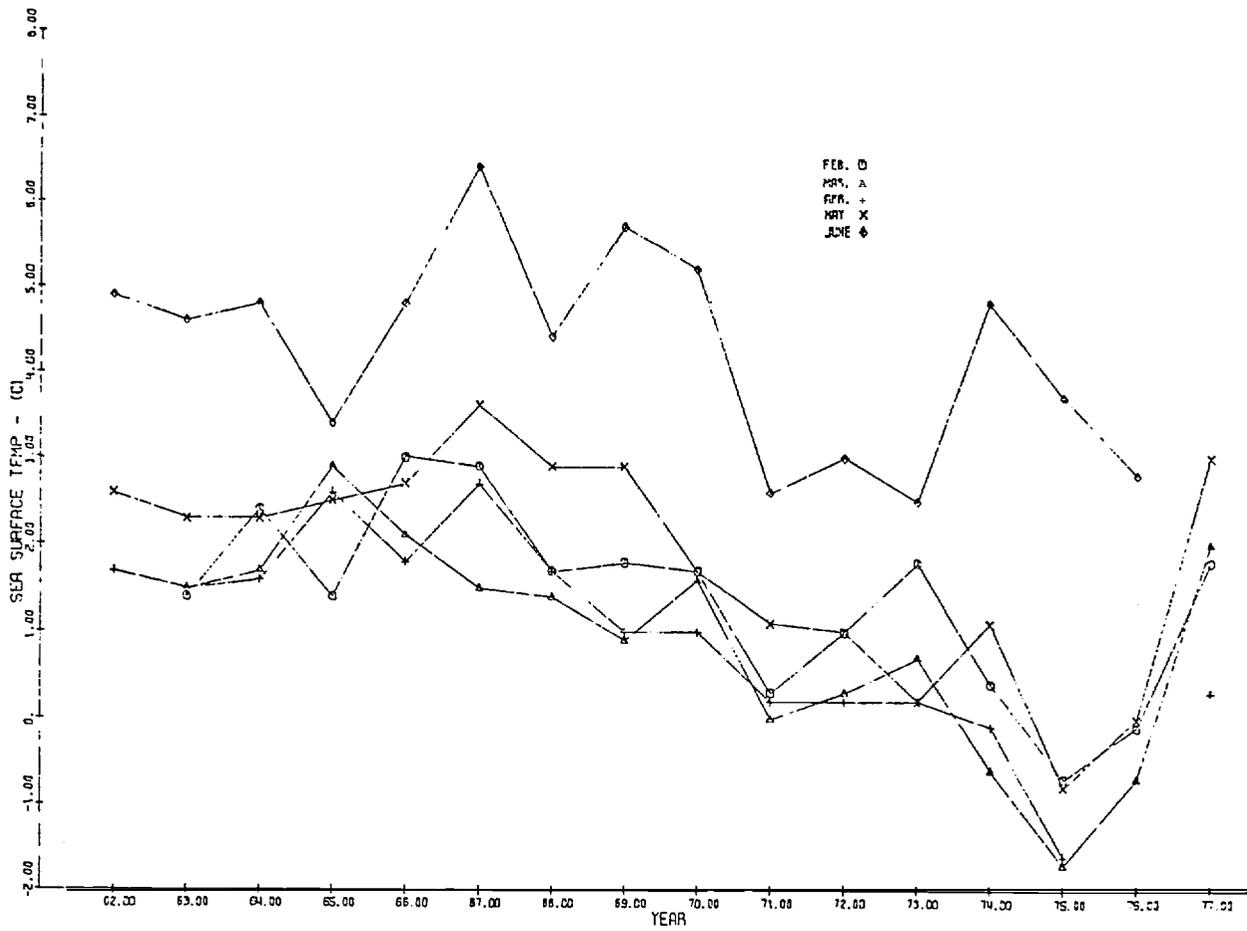
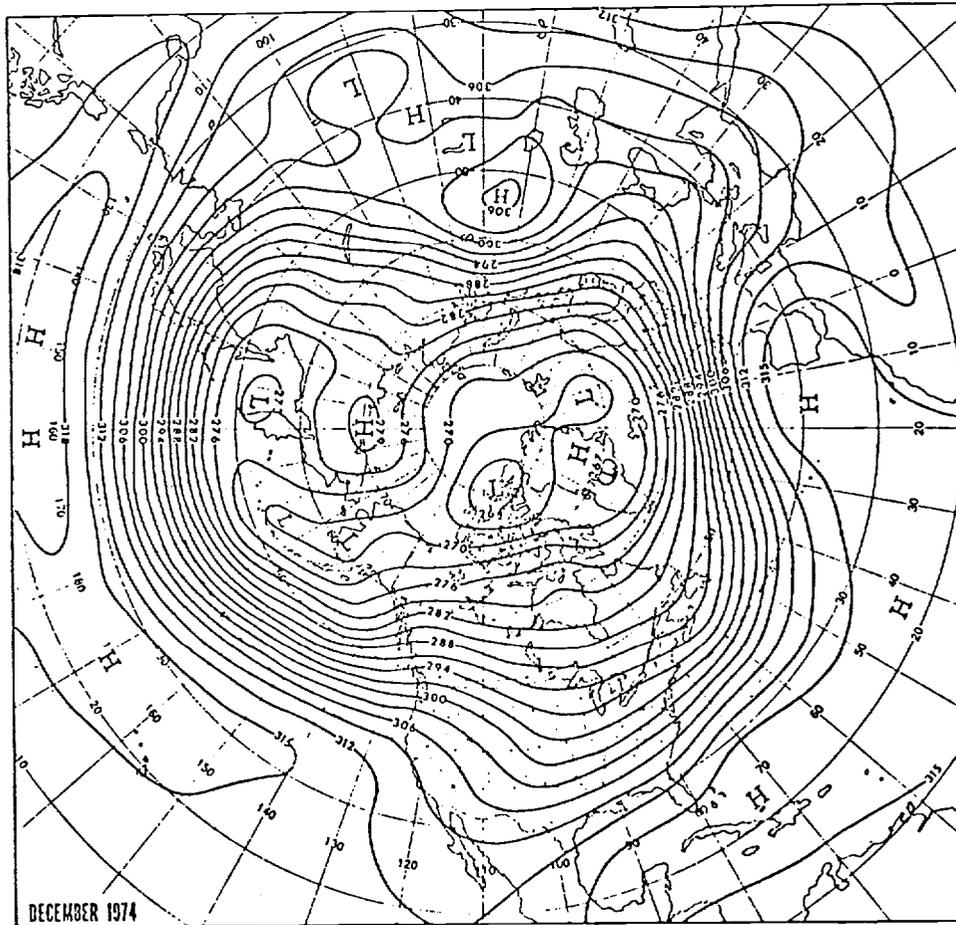


Figure IV-2. Mean monthly sea surface temperatures for the S. E. Bering Sea.



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.

SOUTHERN ICE LIMIT

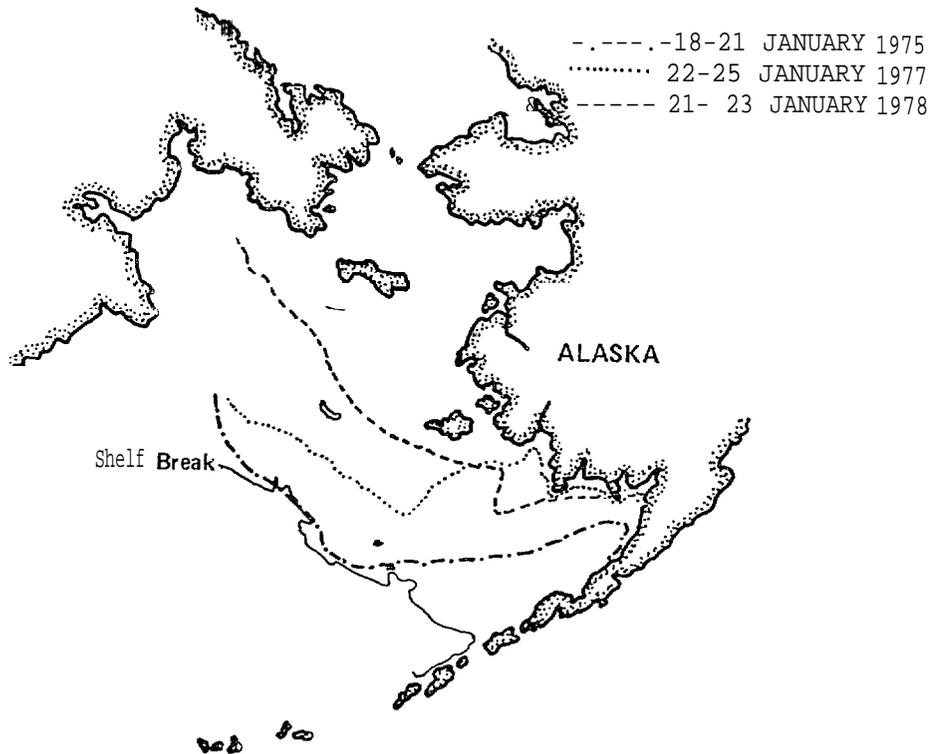
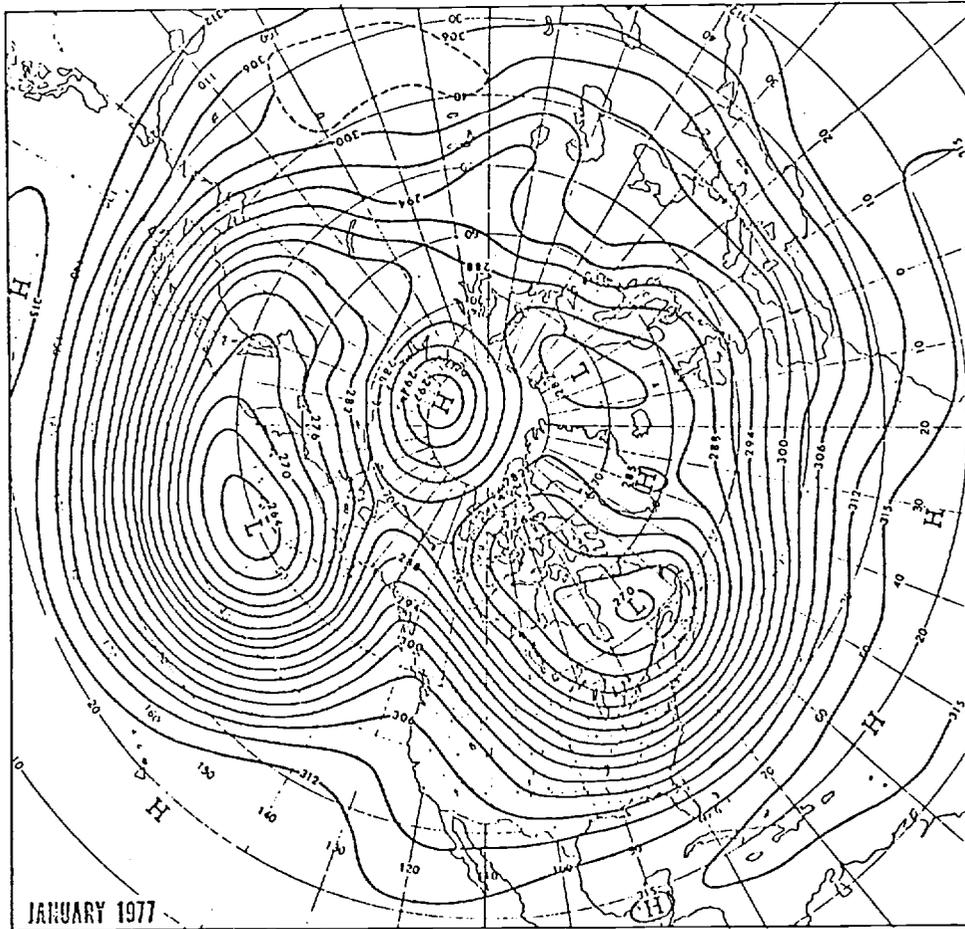


Figure IV-4. Southern ice limit for 1975, 1977, 1978.

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,

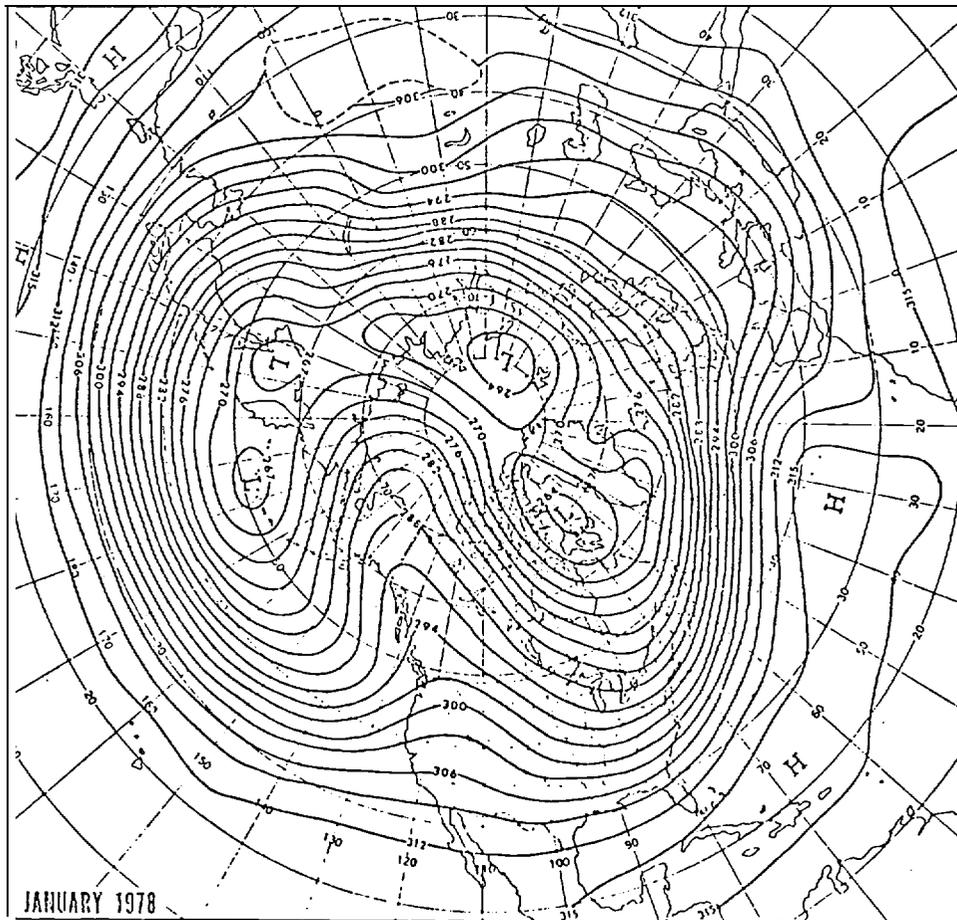


Mean 700 mb height contours (dekameters) for January 1977.

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 700mb contours (dam) for January 1979.

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).

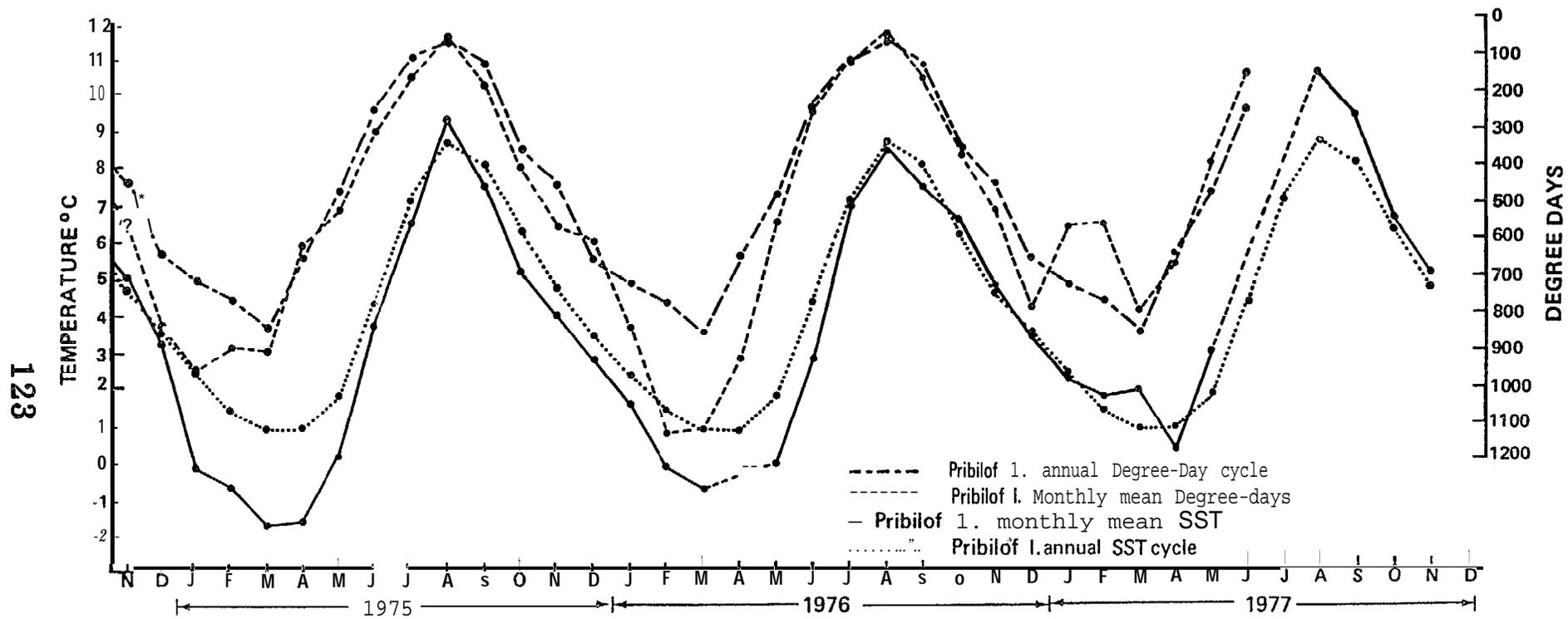


Figure IV-7. Monthly mean sea surface temperatures and degree-day data for the Pribilof Islands for 1975-1977.

13 MAY -27 MAY 1975

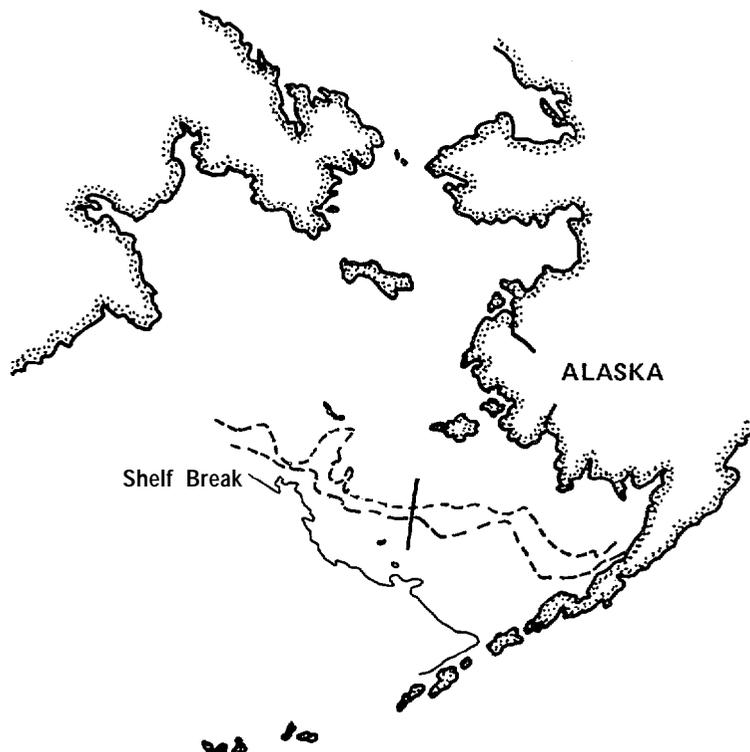


Figure IV-8. 1975 ice edge cruise showing transect.

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 ‰ rising with depth to 32.0 ‰ at the bottom and rising with distance away from the ice to a maximum of 31.8 ‰. 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 shelf water of Coachman and Charnell (1979).

16 MARCH - 7 APRIL 1976

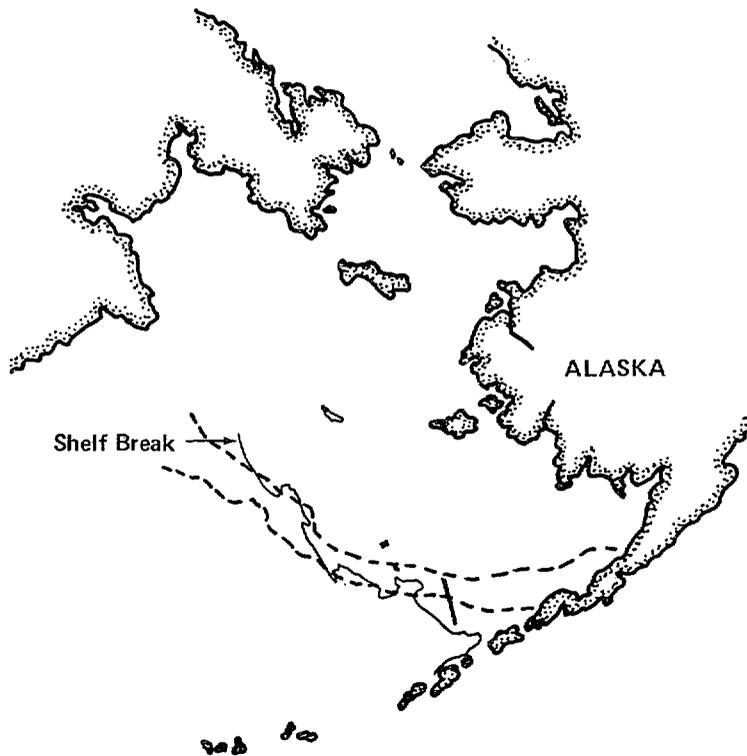


Figure IV-9. 1976 ice edge cruise track showing transect.

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 Gulf of Alaska - Bering Sea source water ($T^{\circ}\text{C} = 3-4^{\circ}\text{C}$) below. The salinity data display these same characteristics of low $S^{\circ}/\text{‰}$ (31.70/0.) 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 ($S^{\circ}/\text{‰} > 32.0$) beneath. The density data also shows the strong pycnocline at 70-90 m.

15 MARCH -5 APRIL 1977

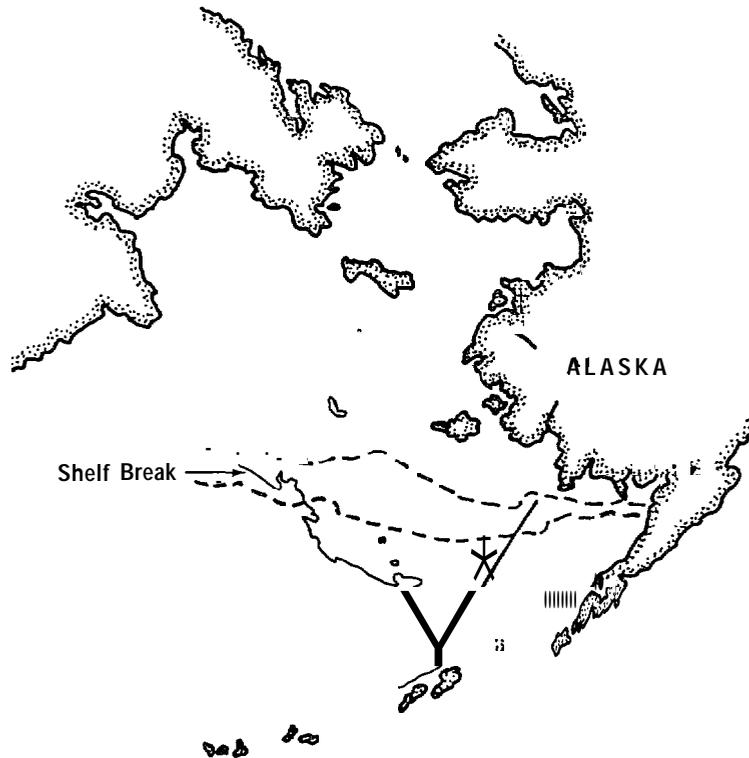


Figure IV-10. 1977 ice edge cruise track showing transect.

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 salinities ($31.6^{\circ}/00$) 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

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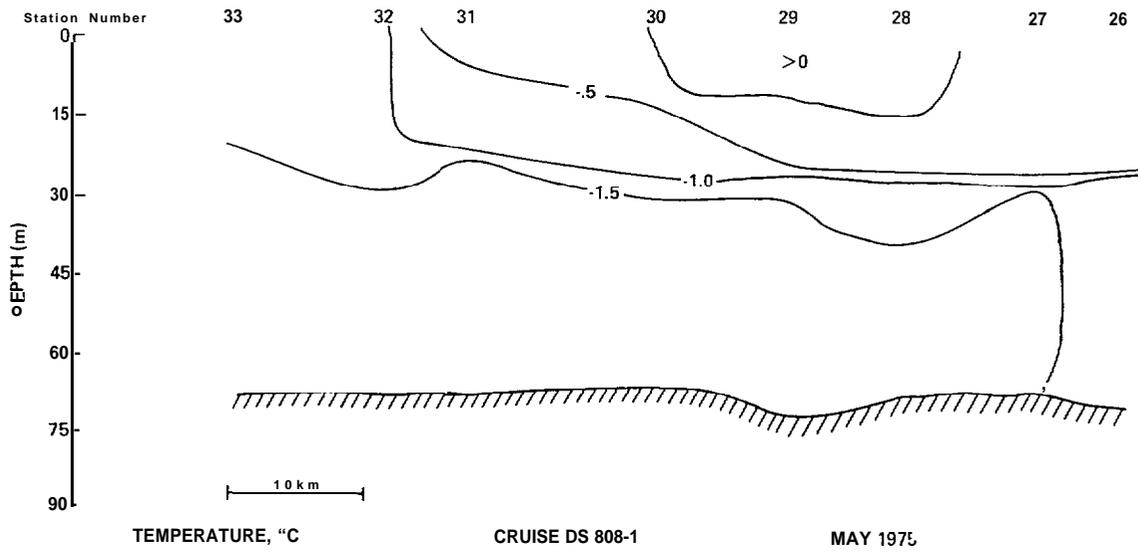
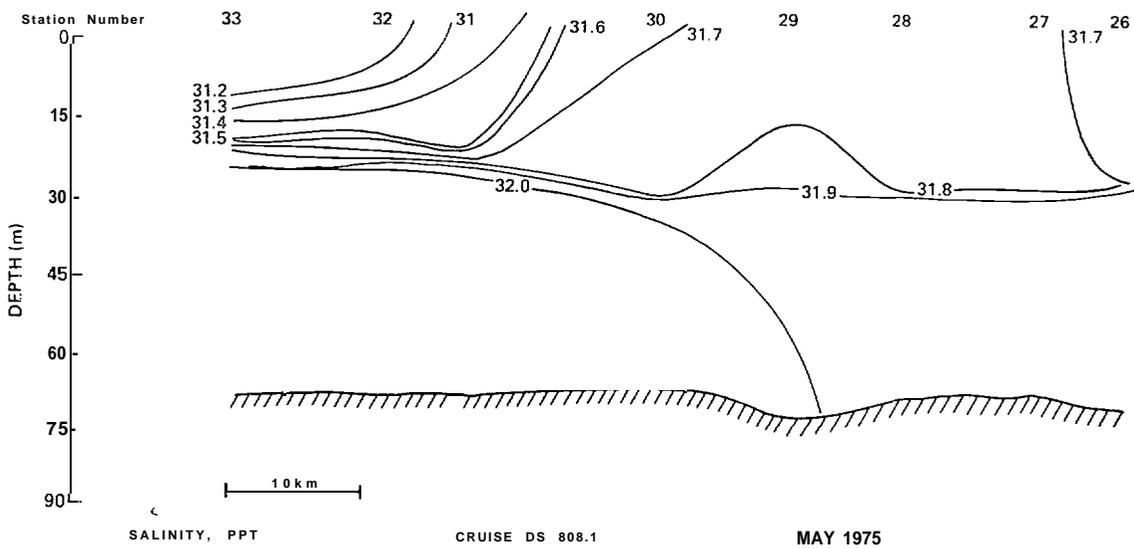
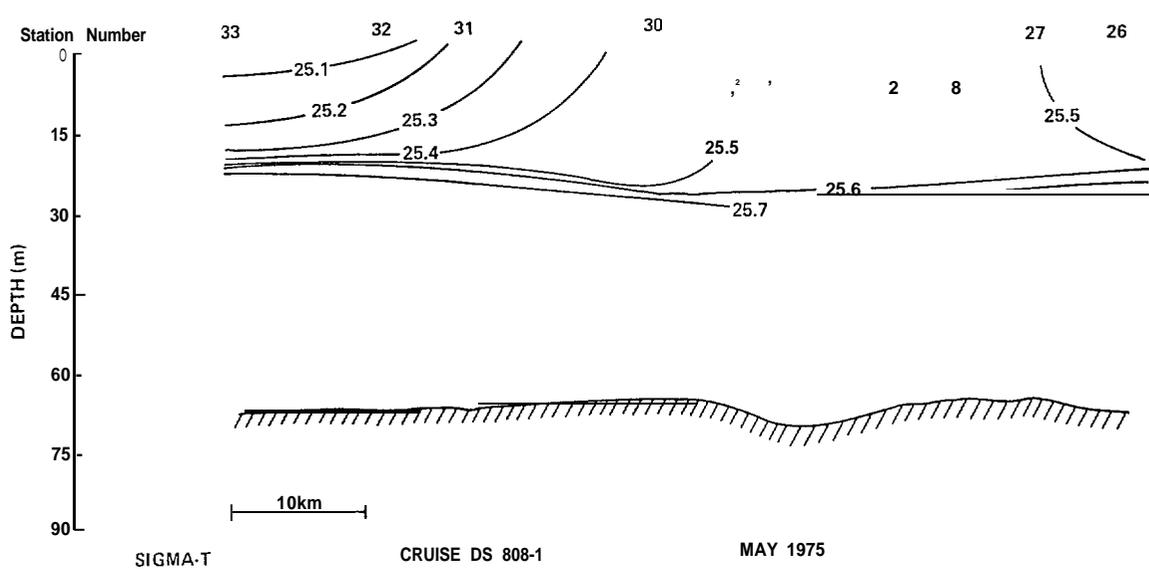


Figure IV-11. Cross section of (a) temperature, (b) salinity, (c) sigma-t, (d) nitrate, (e) ammonia and (f) chlorophyll 1975.

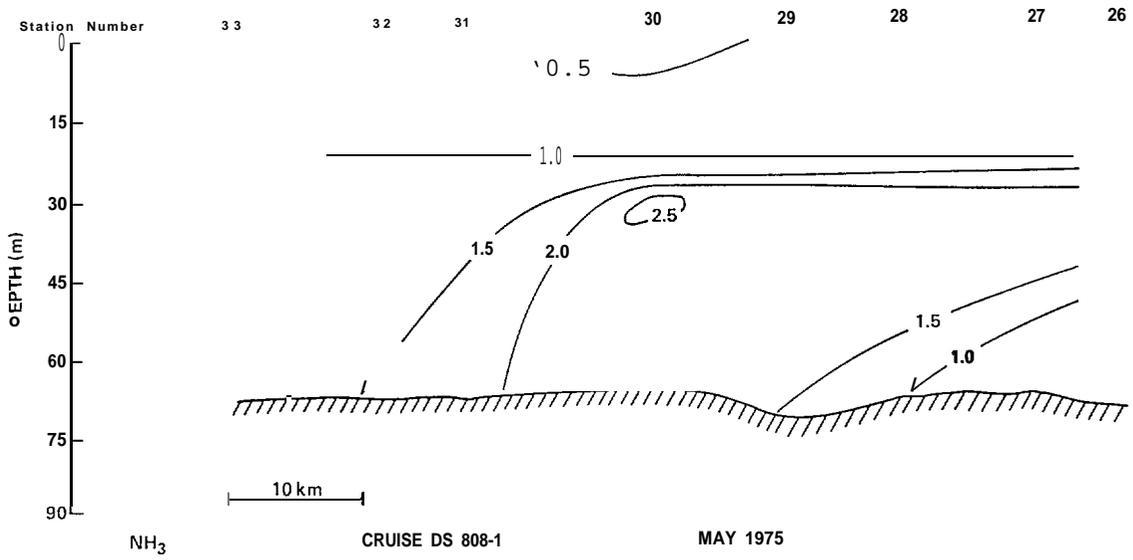
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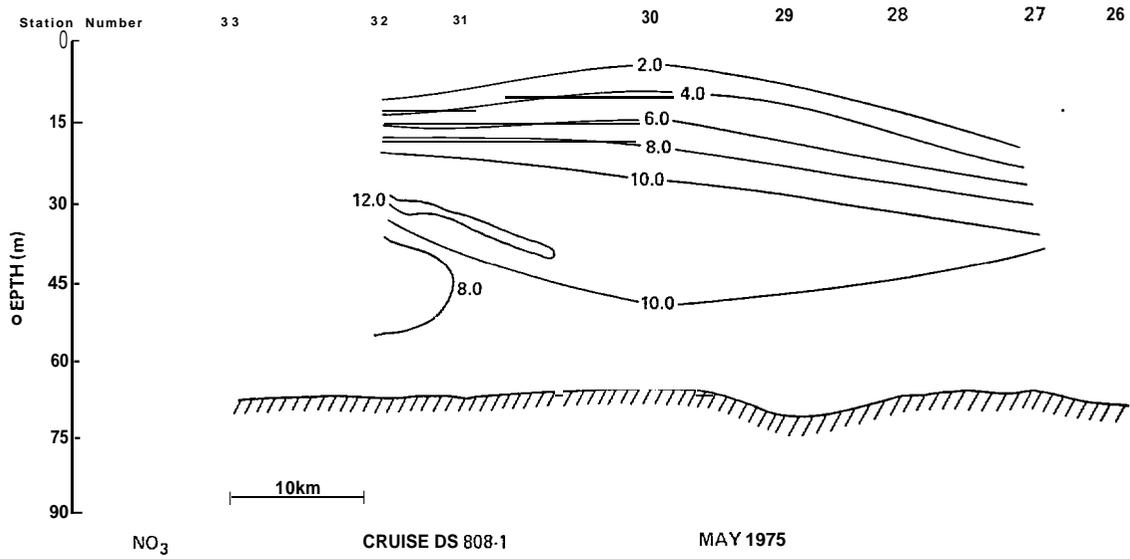
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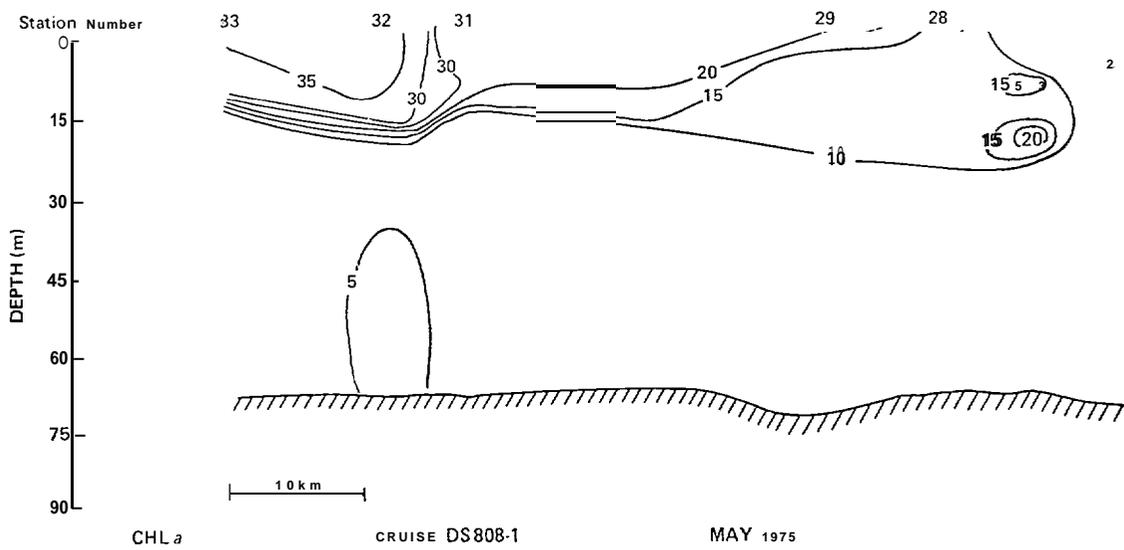
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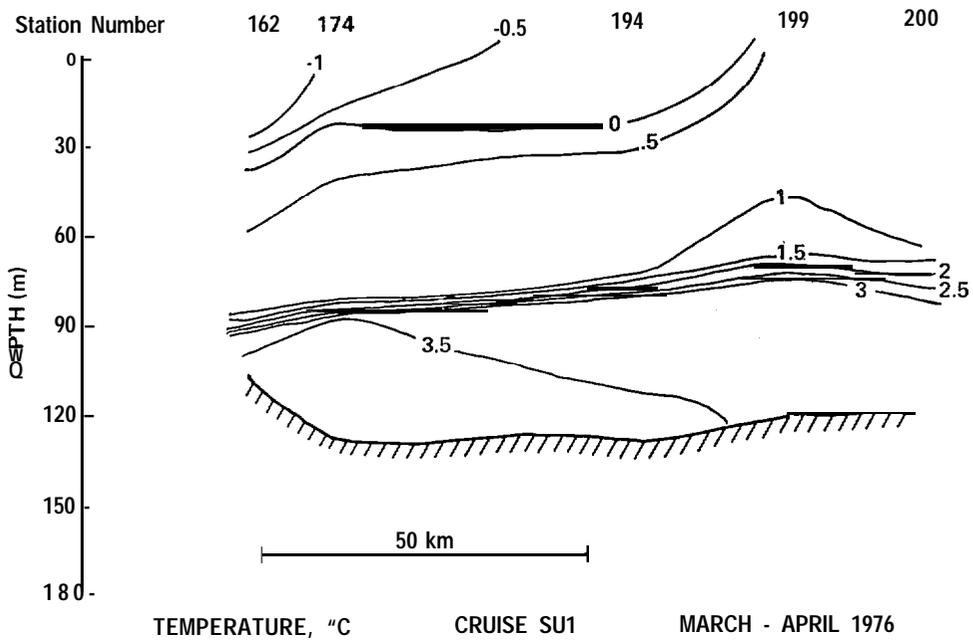
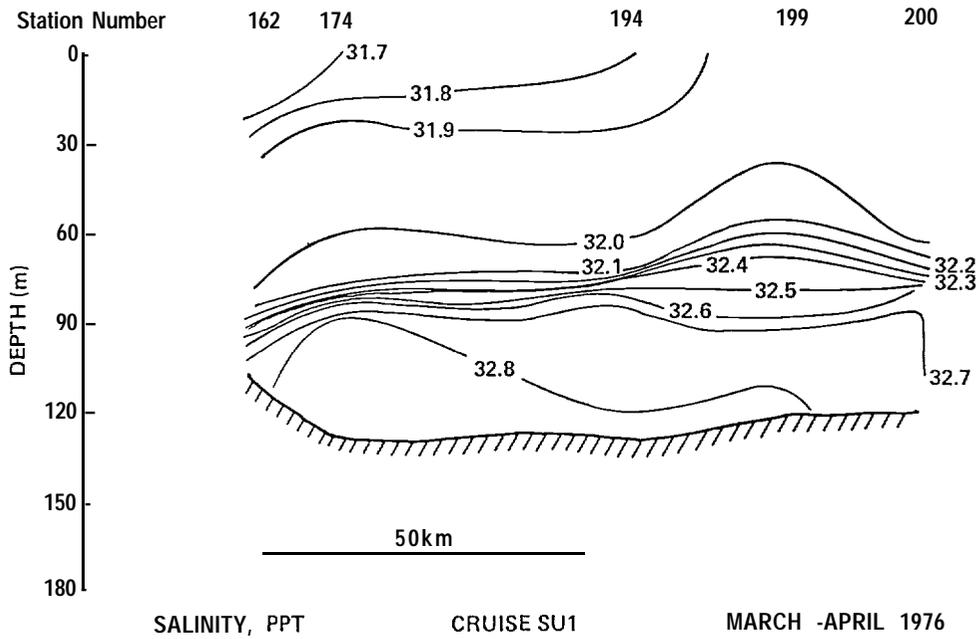
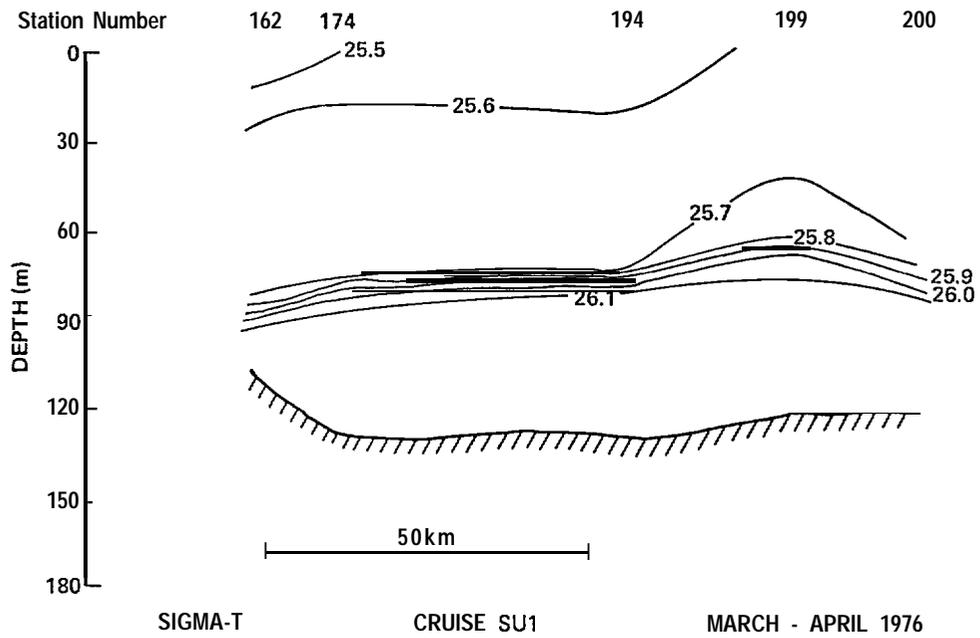


Figure IV-12. Cross section of (a) temperature, (b) salinity, (c) sigma-t, (d) nitrate, (e) ammonia and (f) chlorophyll 1976.

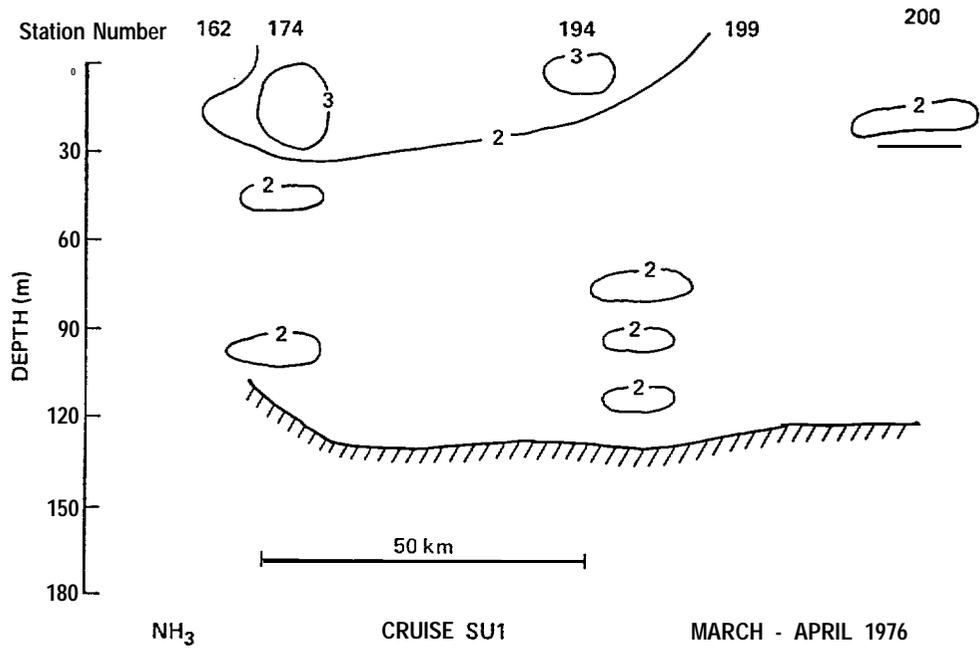
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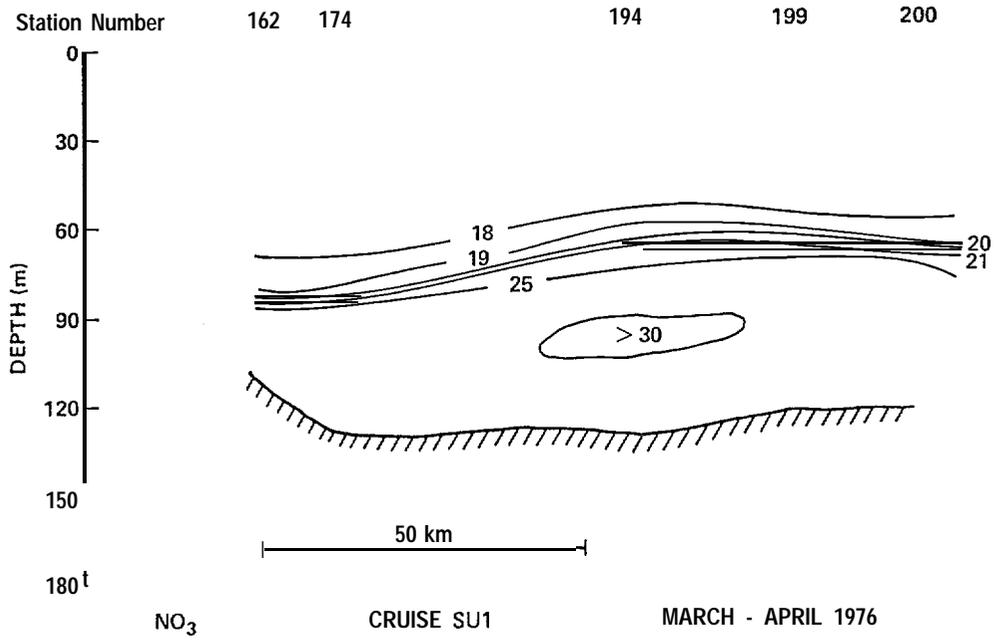
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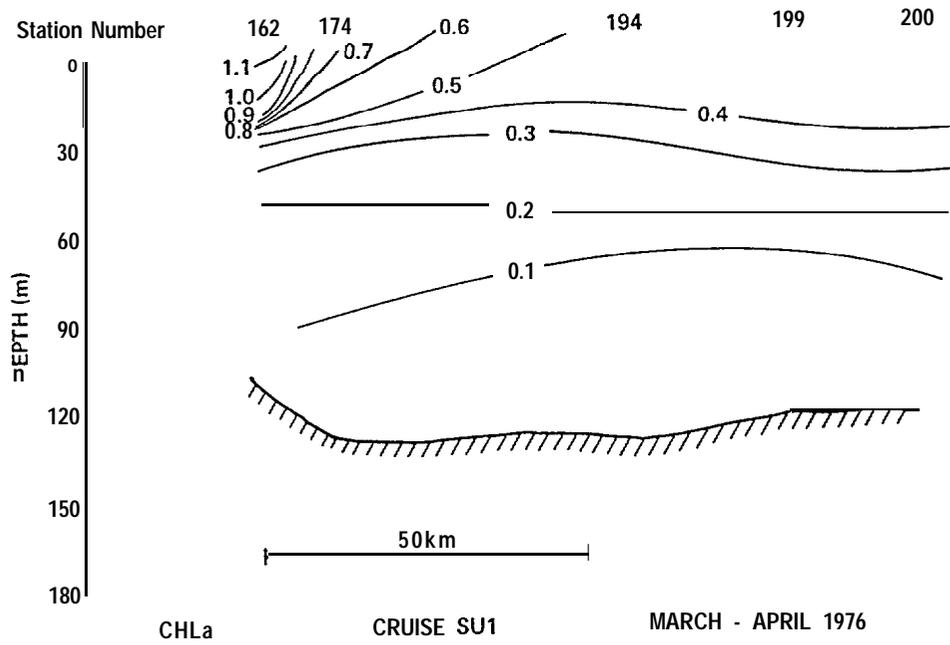
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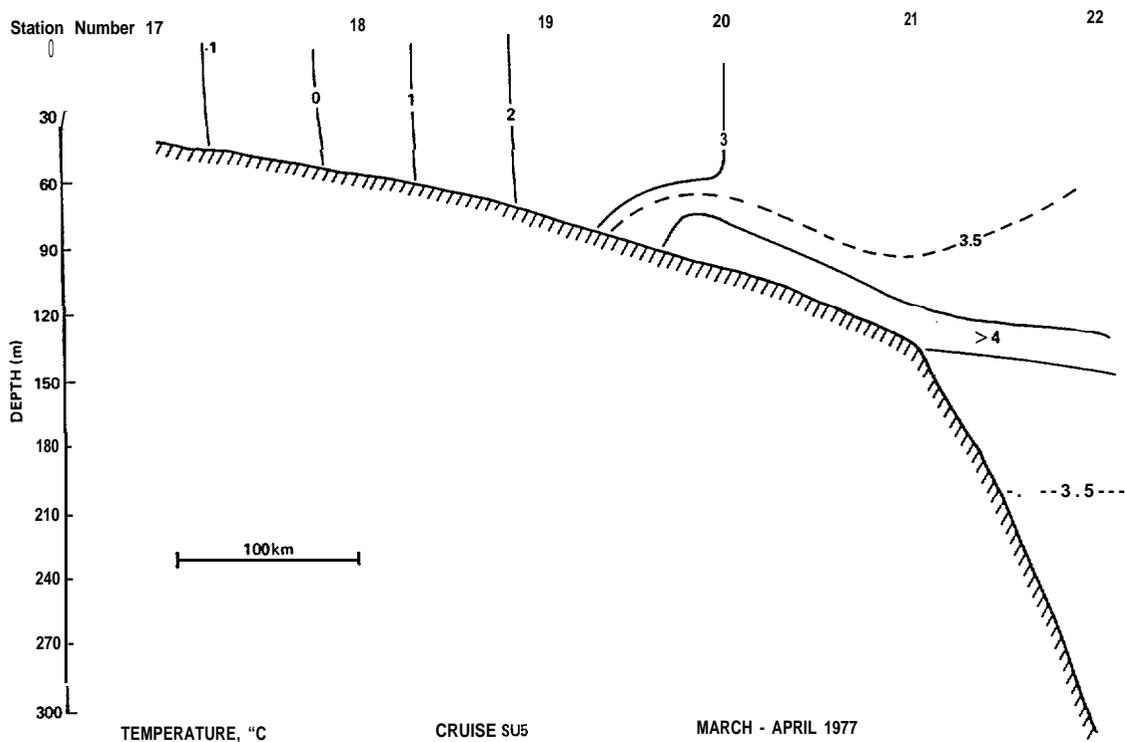
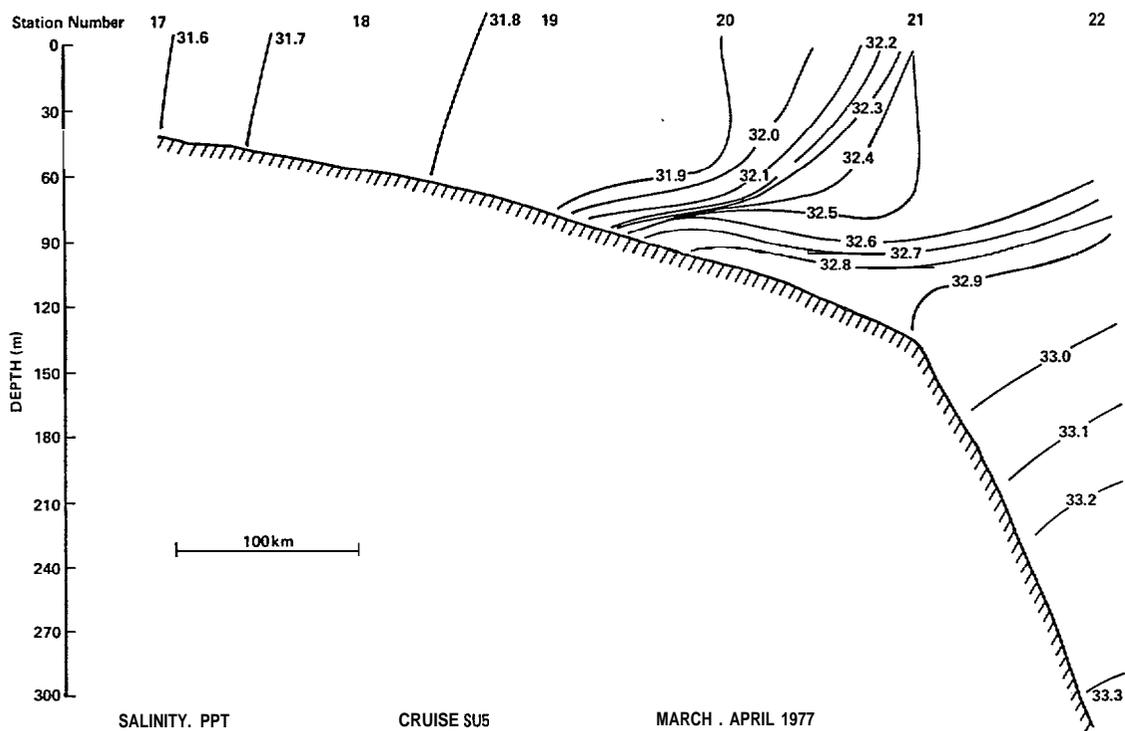
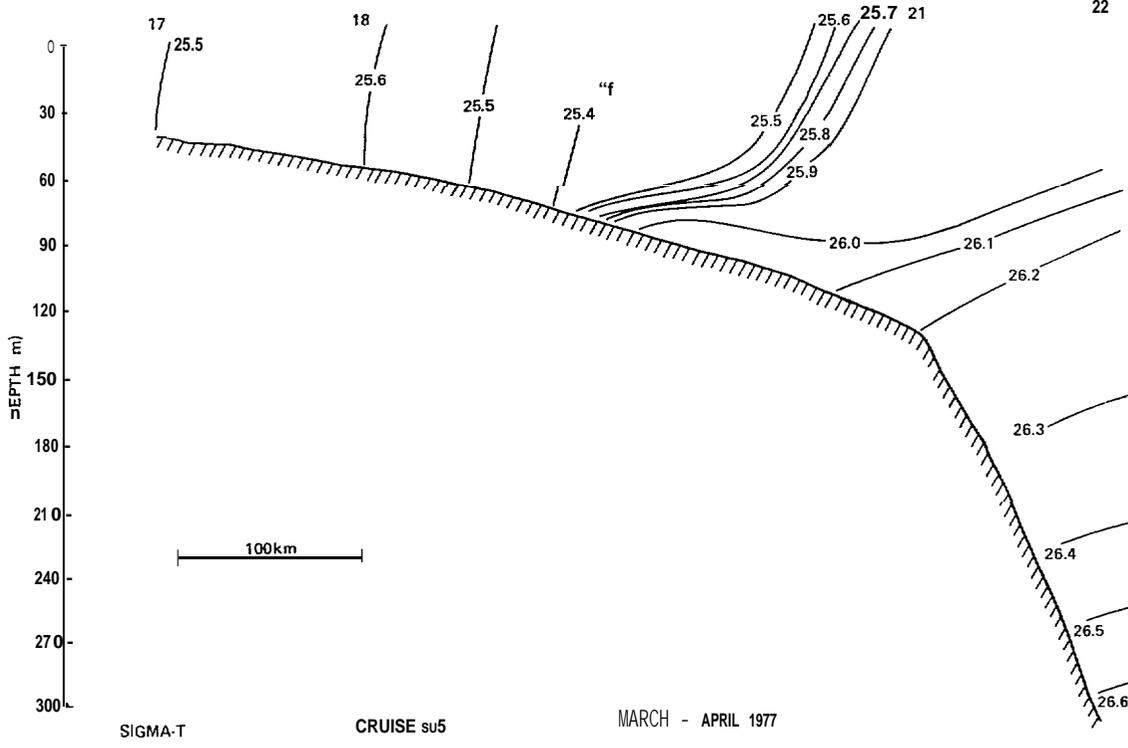


Figure IV-13. Crosssection of (a) temperature, (b) salinity, (c) sigma-t, (d) nitrate, (e) ammonia and (f) chlorophyll 1977.

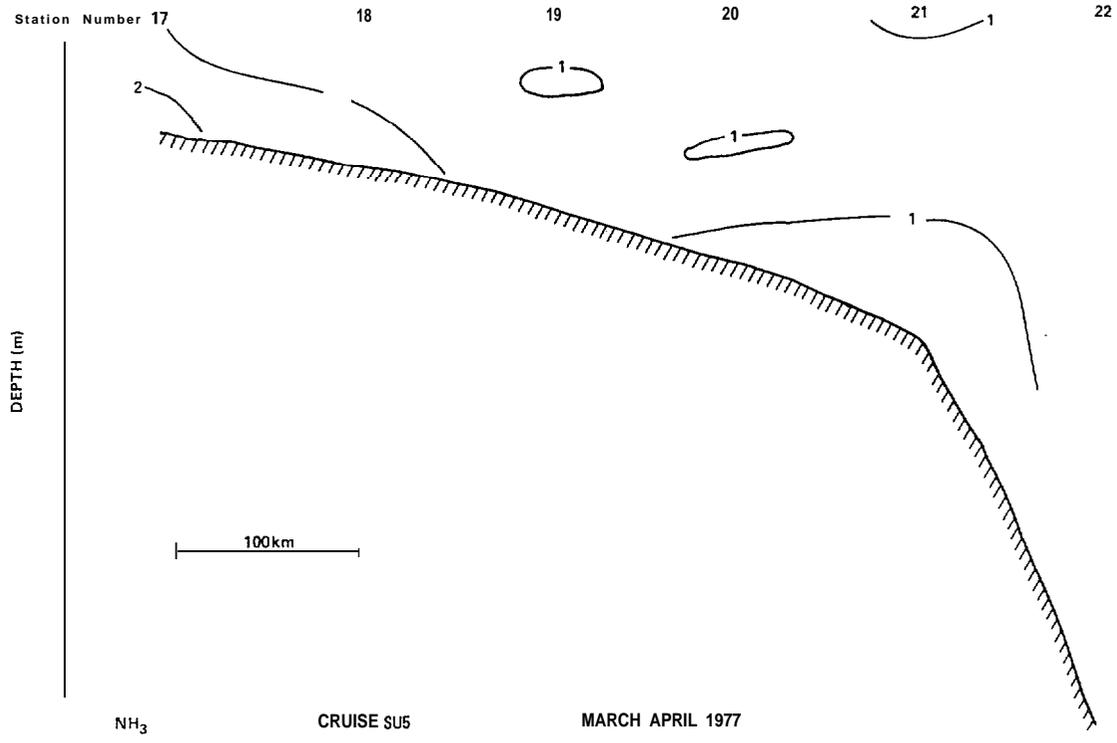
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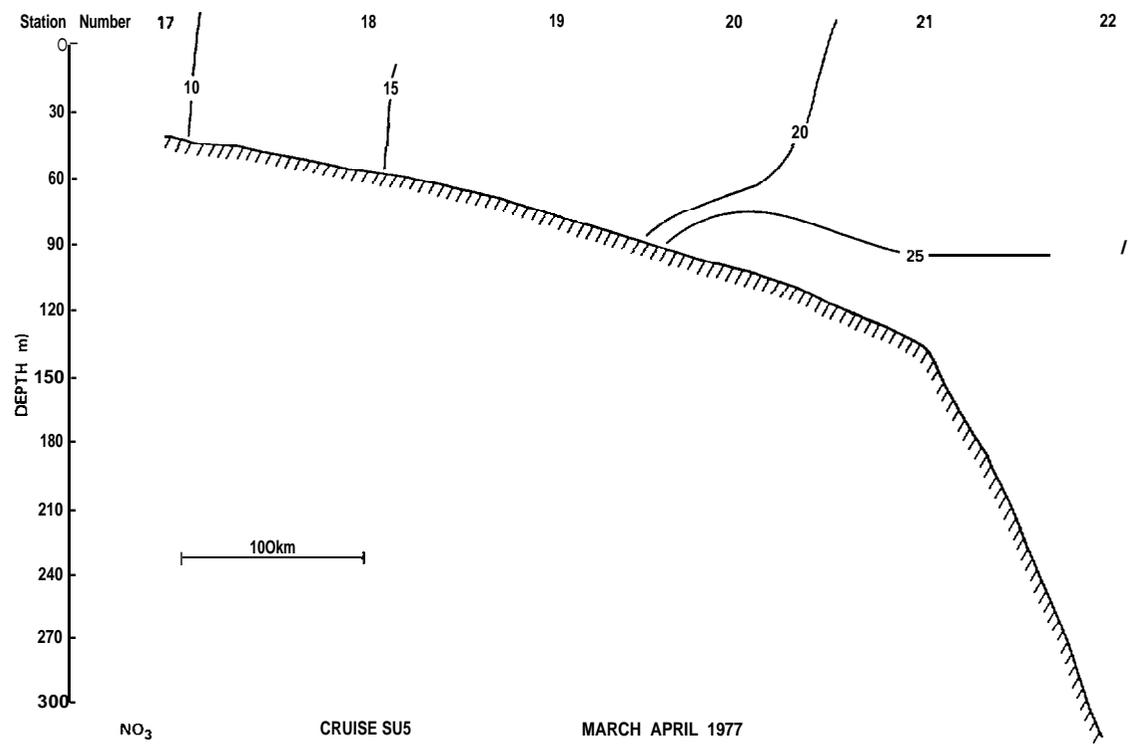
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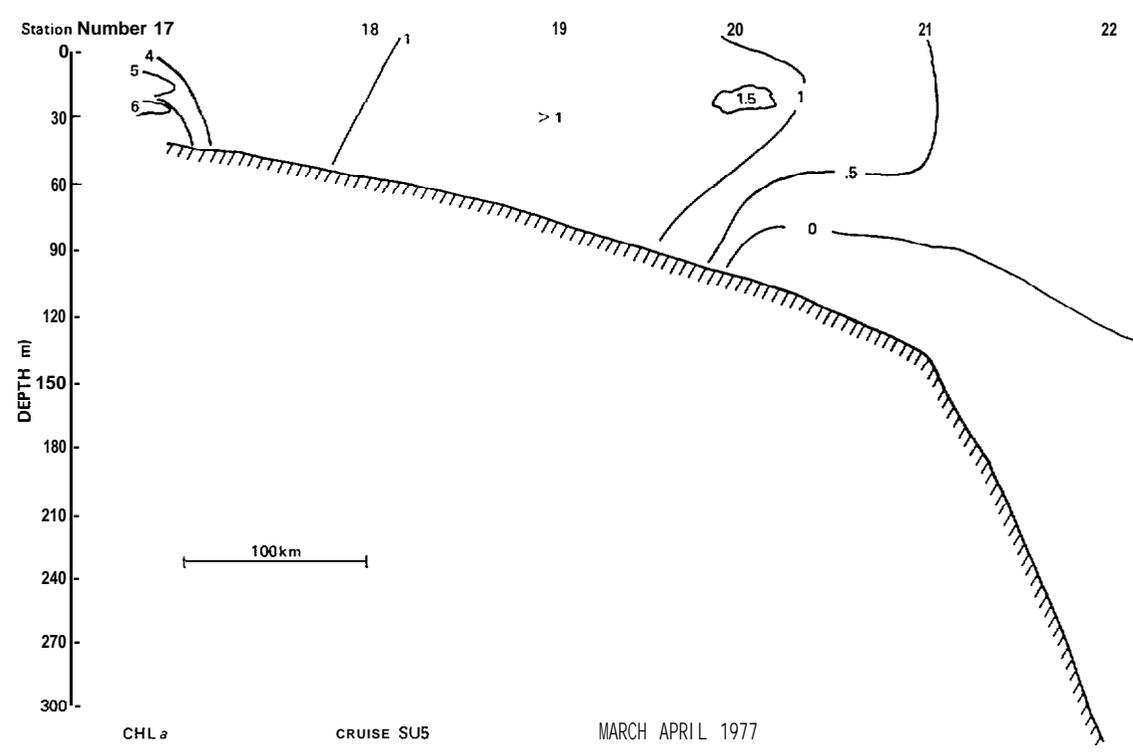
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(1979) is apparent with the inner front in temperature and salinity between stations 19 and 20 on the bottom. The outer front is evident in the surface layers (especially $S^{\circ}/_{\infty}$) between stations 20 and 21. The whole shelf section, except 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 UH1H 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 $64^{\circ}15'36''\text{N}$ to $62^{\circ}52'30''\text{N}$ in latitude and from $166^{\circ}15'36''\text{W}$ to $163^{\circ}20'06''\text{W}$ 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.

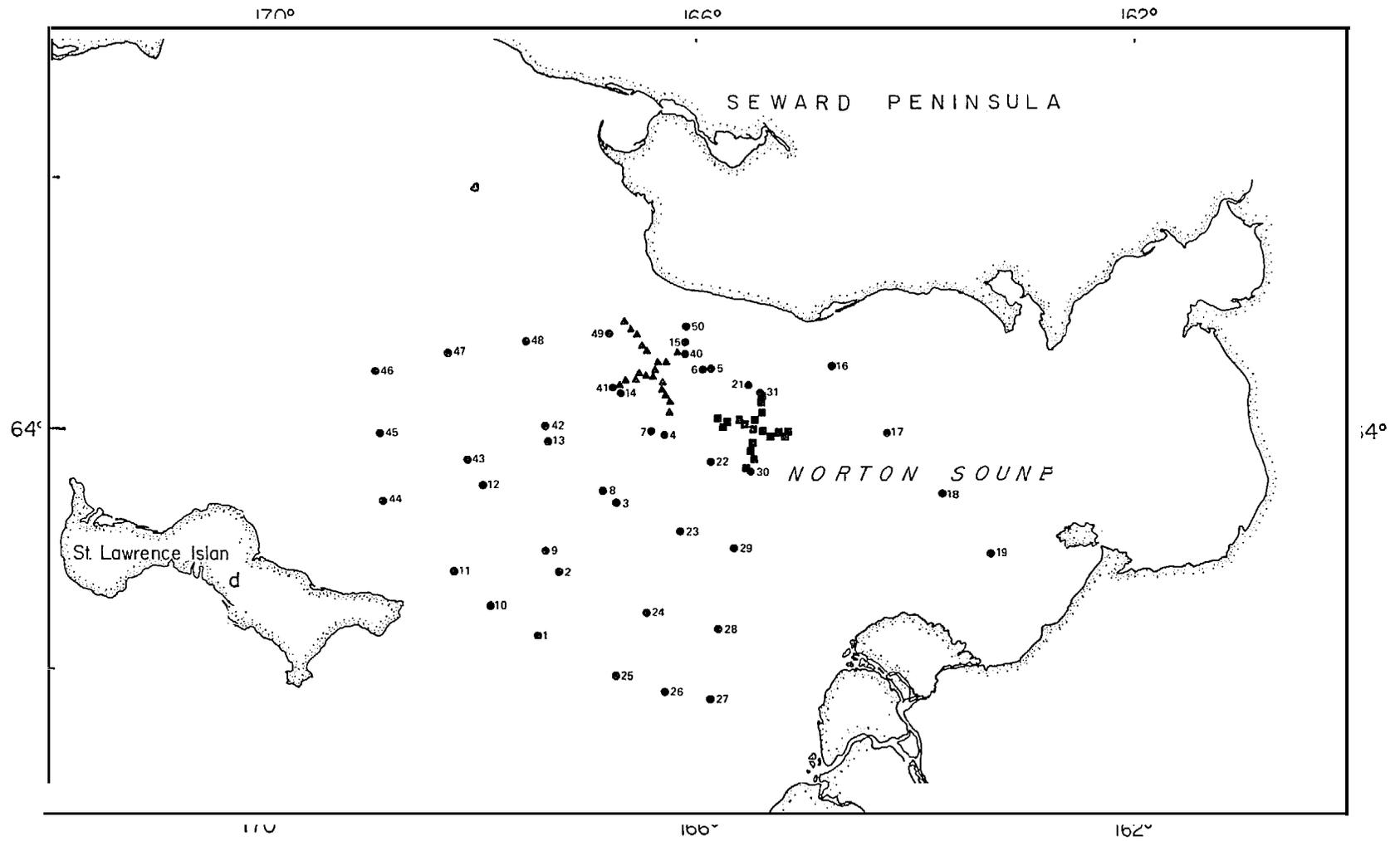


Figure IV-14. Ice algae survey stations, April 1977.

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/m³ chlorophyll *a*), one of the lowest was in the same area at the same time (0.30 mg chlorophyll *a*/m³). Overall, the chlorophyll *a* content of the ice varied from 0.0 to 213.7 mg/m³, 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*/m² 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 (Homer and Alexander, 1972; Clasby, Homer 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 $\mu\text{g-atoms/liter}$, ammonia from 1.4 to 4.7 $\mu\text{g-atoms/liter}$, phosphate from 0.8 to 1.7 $\mu\text{g-atoms/liter}$ and silicate from 12.2 to 42.1 $\mu\text{g-atoms/liter}$. 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 $25 \text{ mg C/m}^3 \cdot \text{hr}$, 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.

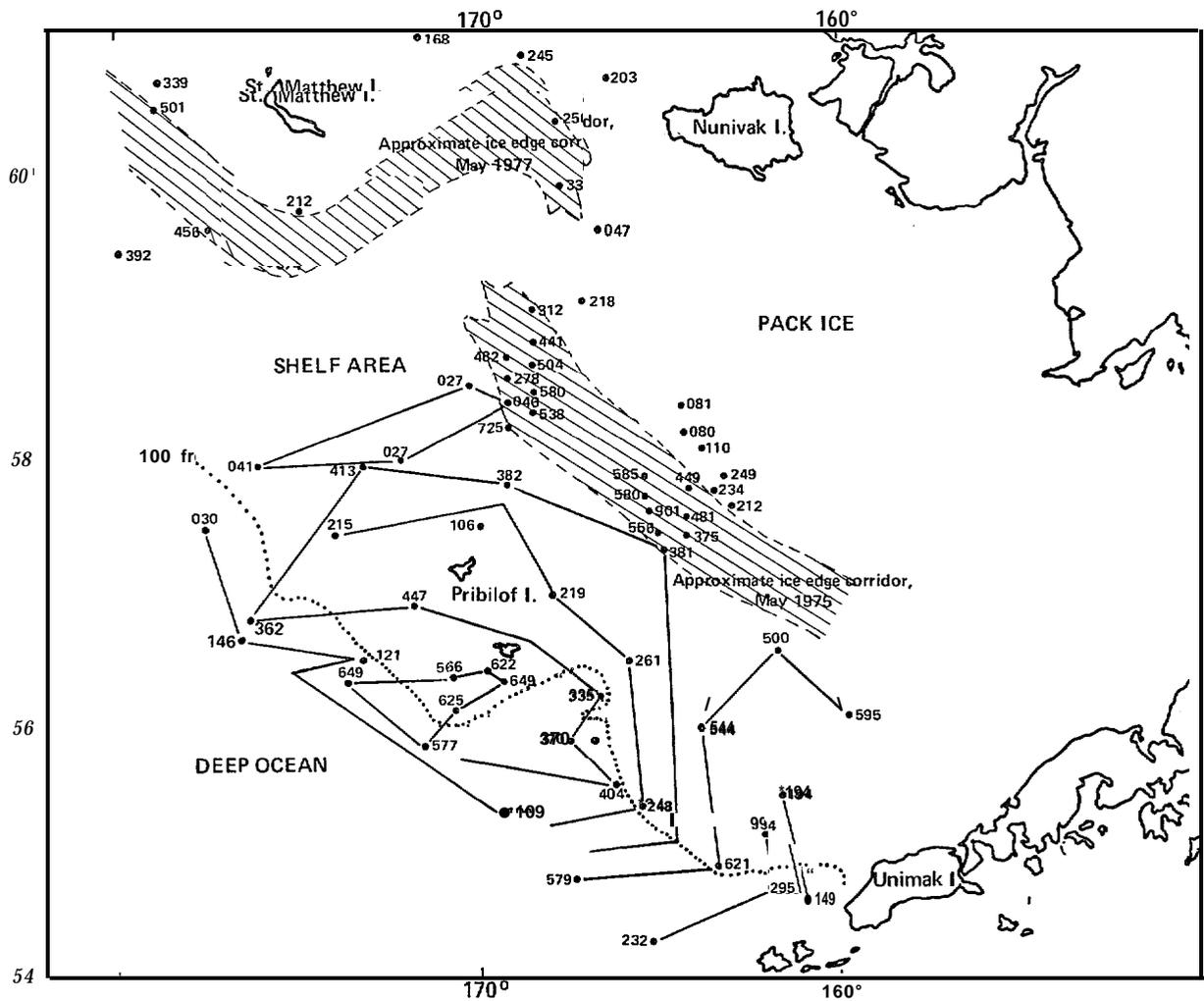


Figure IV-15. Integrated chlorophyll *a* distribution on the Bering Sea shelf.

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

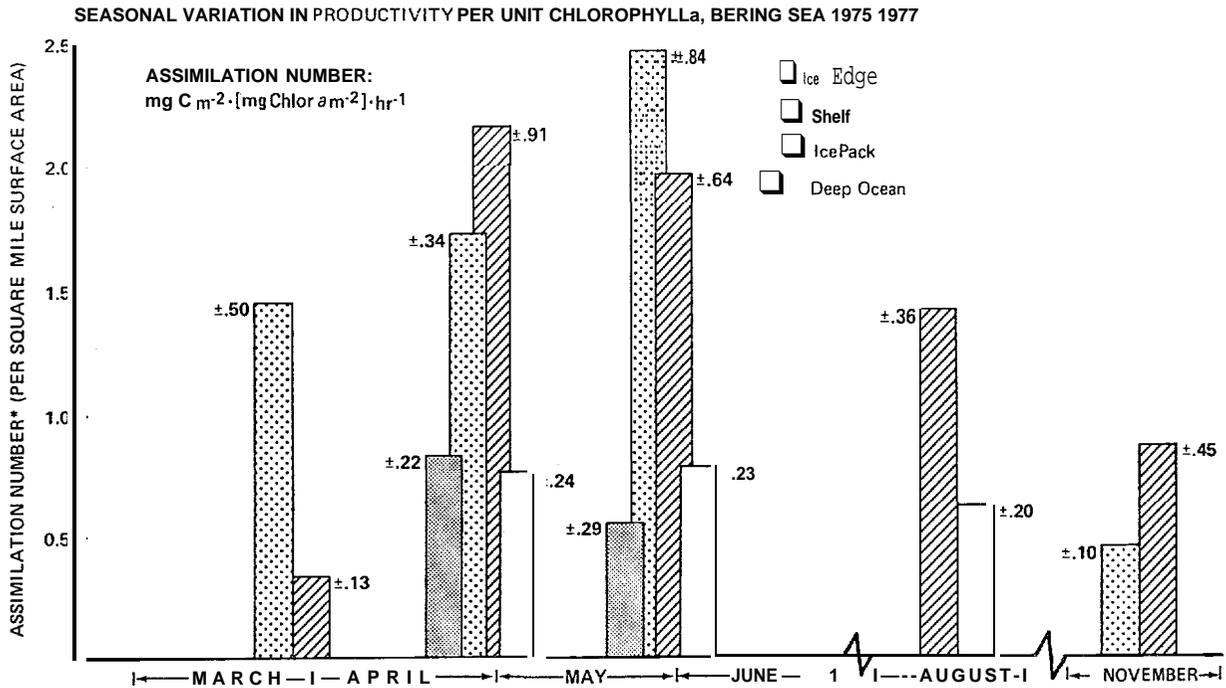


Figure IV-16. Seasonal variation in primary production per unit chlorophyll a.

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

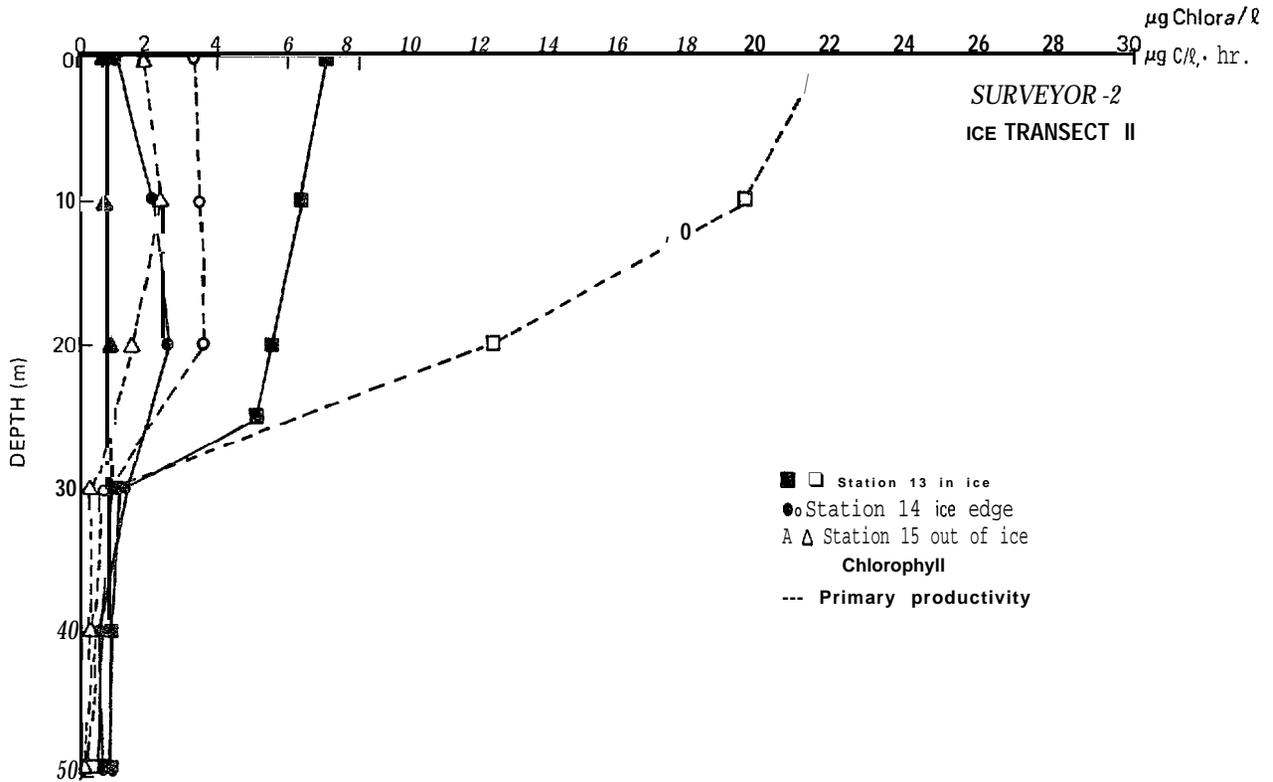


Figure IV-17. Depth profiles of primary production and chlorophyll at three stations at different distances from the ice edge.

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 concentrations 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 $\mu\text{g-atoms/liter}$ in open water, 5-15 $\mu\text{g-atoms/liter}$ 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

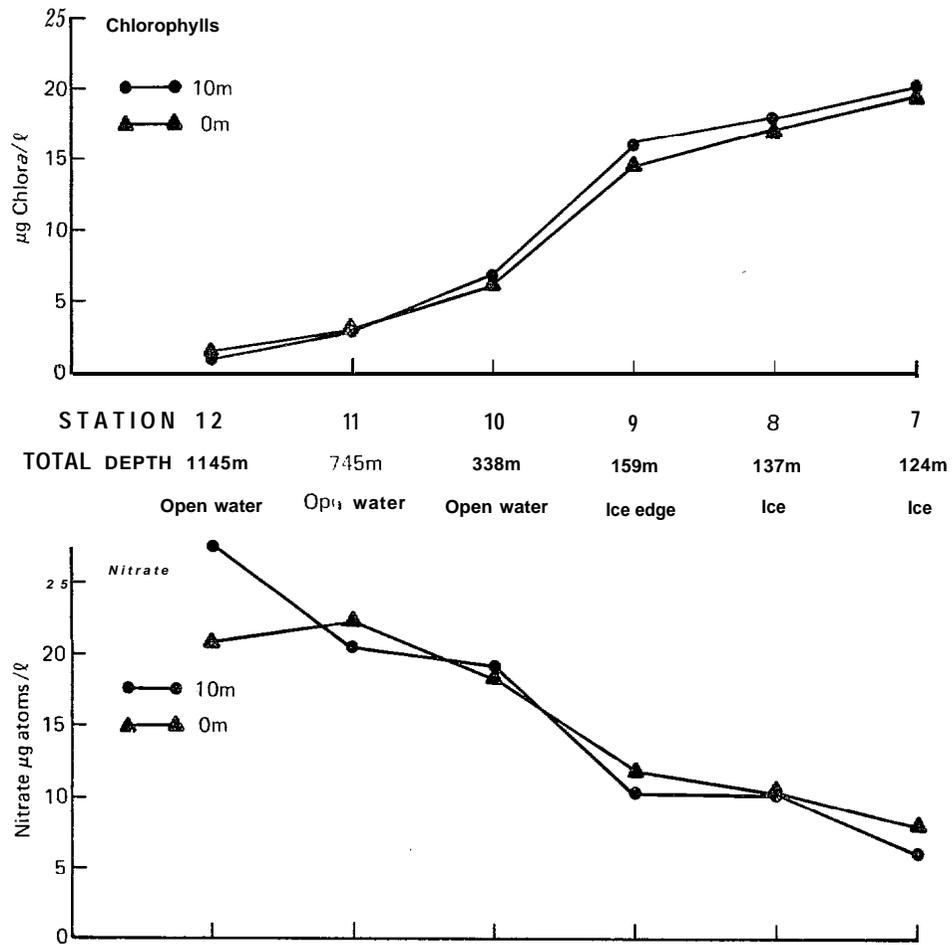


Figure IV-18. Transect showing chlorophyll a and nitrate at 0 and 10 m depths away from the ice.

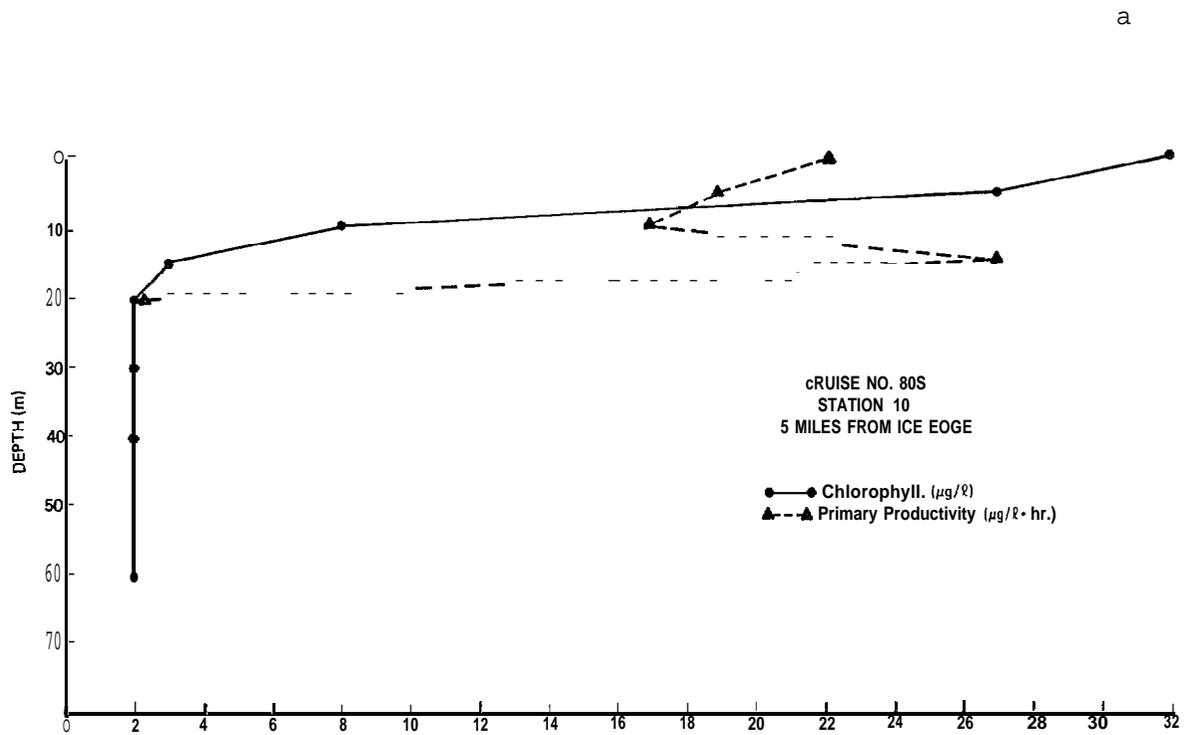
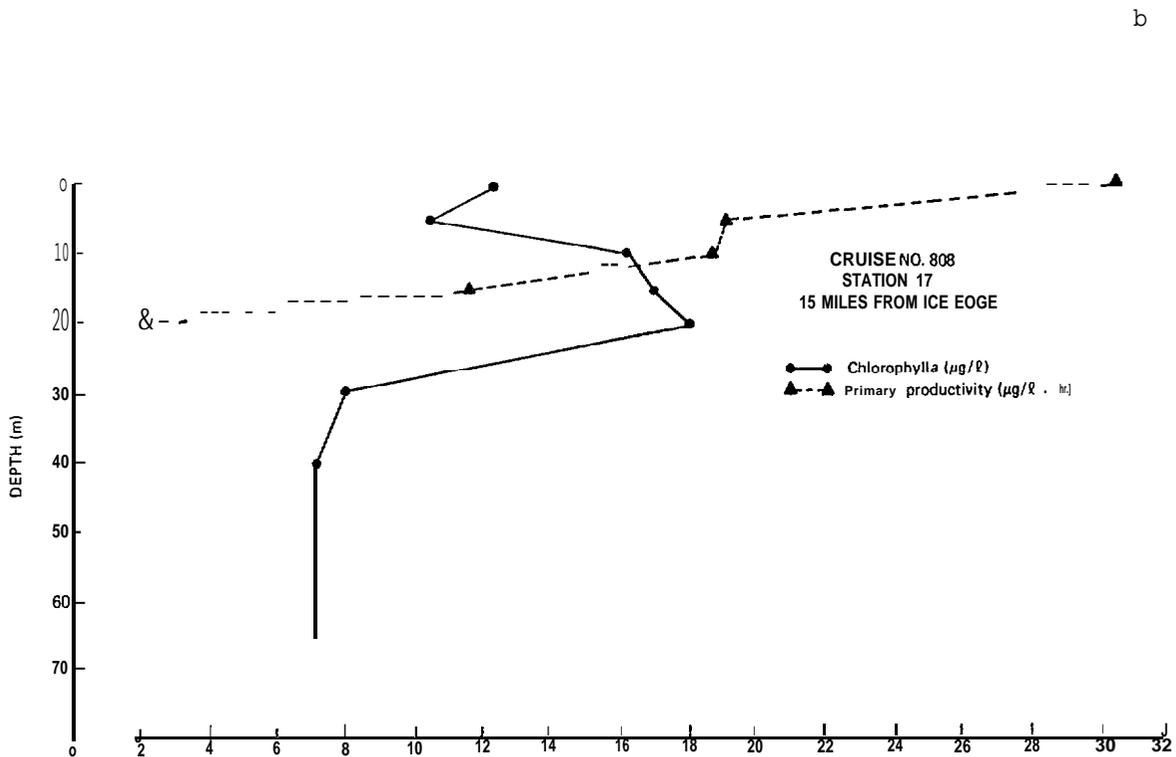


Figure IV-19. Depth profiles for 3 stations [(a) in ice, (b) at ice edge and (c) away from ice] showing primary productivity and chlorophyll a .



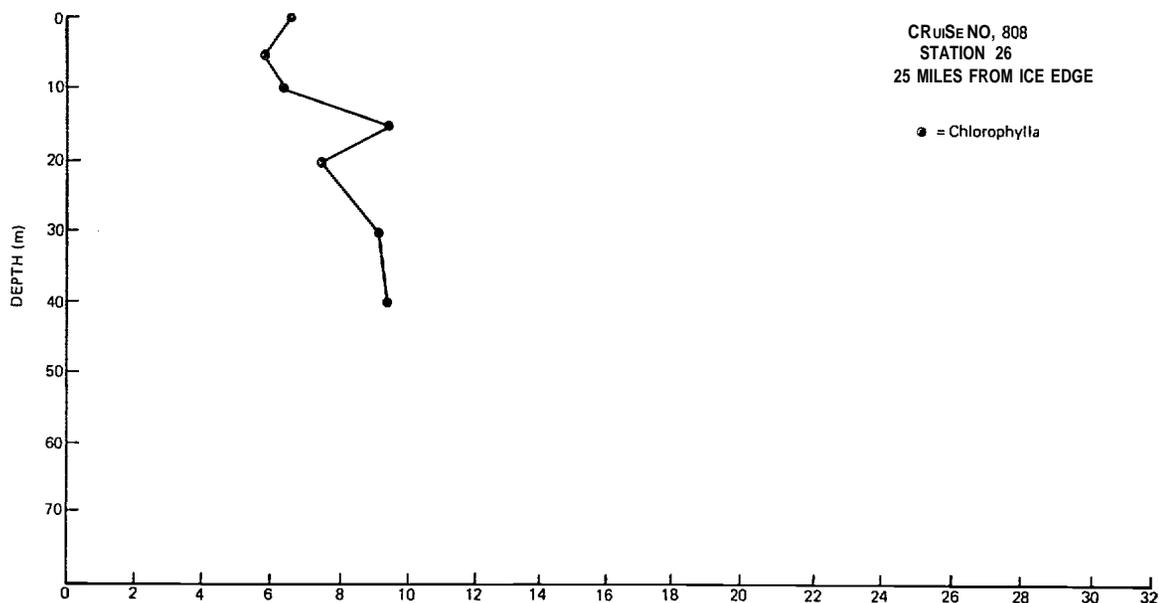


TABLE IV-1

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 Cruises: SV-1, 1976 SV-5, 1977	Ice Stations	1.44	± .50	17
	Shelf Stations	0.34	± .13	5
April & early May Cruises: SV-2, 1976 SV-6, 1977	Ice Edge	1.73	± .34	4
	Ice Pack	0.84	± .22	8
	Shelf	2.16	± .91	6
	Deep Ocean	0.76	± .24	6
May & early June Cruises: 808, 1975 DS-4, 1977	Ice Edge	0.56	± .29	13
	Ice Pack	2.46	± .84	6
	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 Cruises: 815, 1975	Ice Edge	0.45	± .10	2
	Shelf	0.86	± .45	7

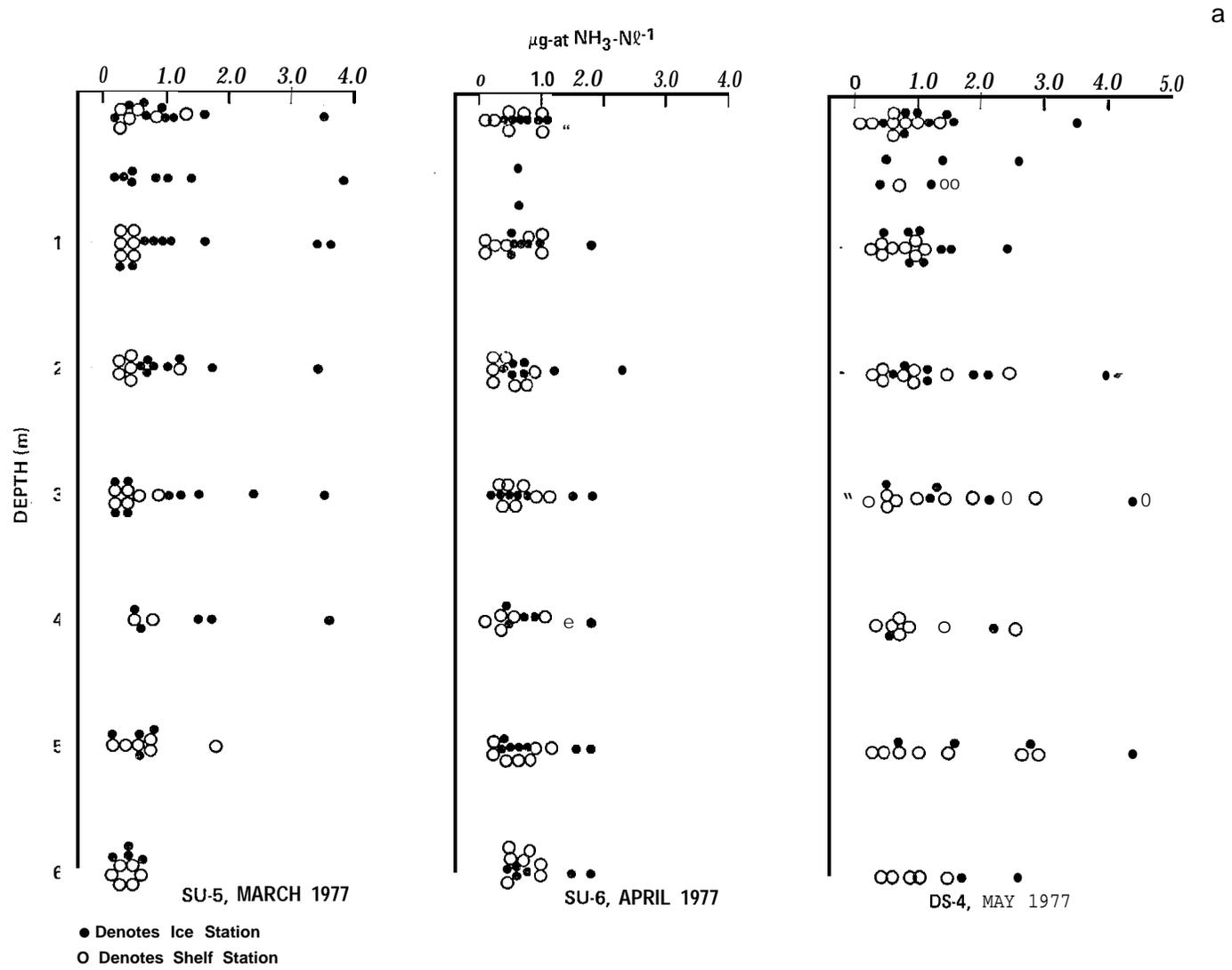
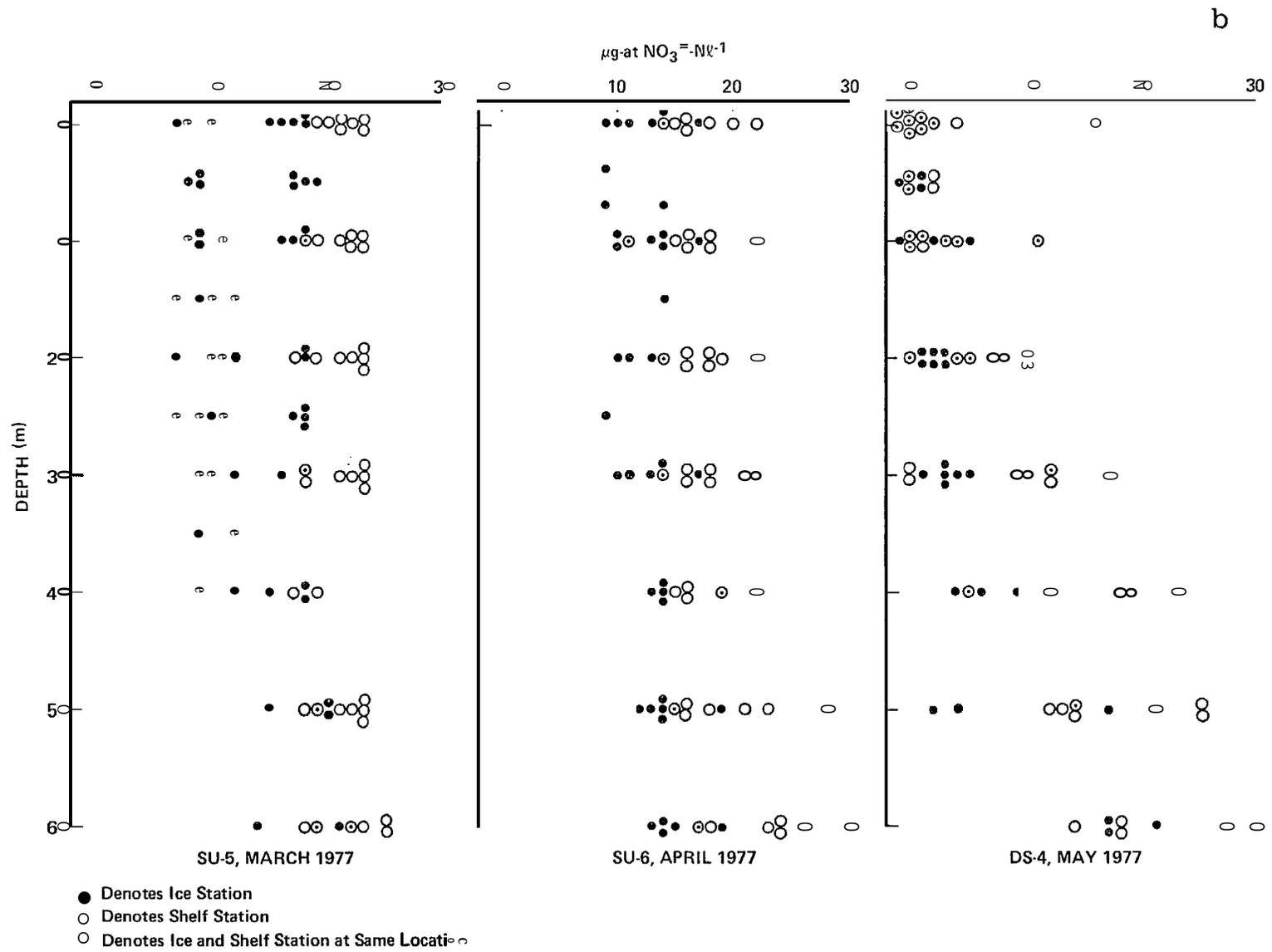


Figure IV-20. Depth profiles in nitrate and ammonia with season.



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

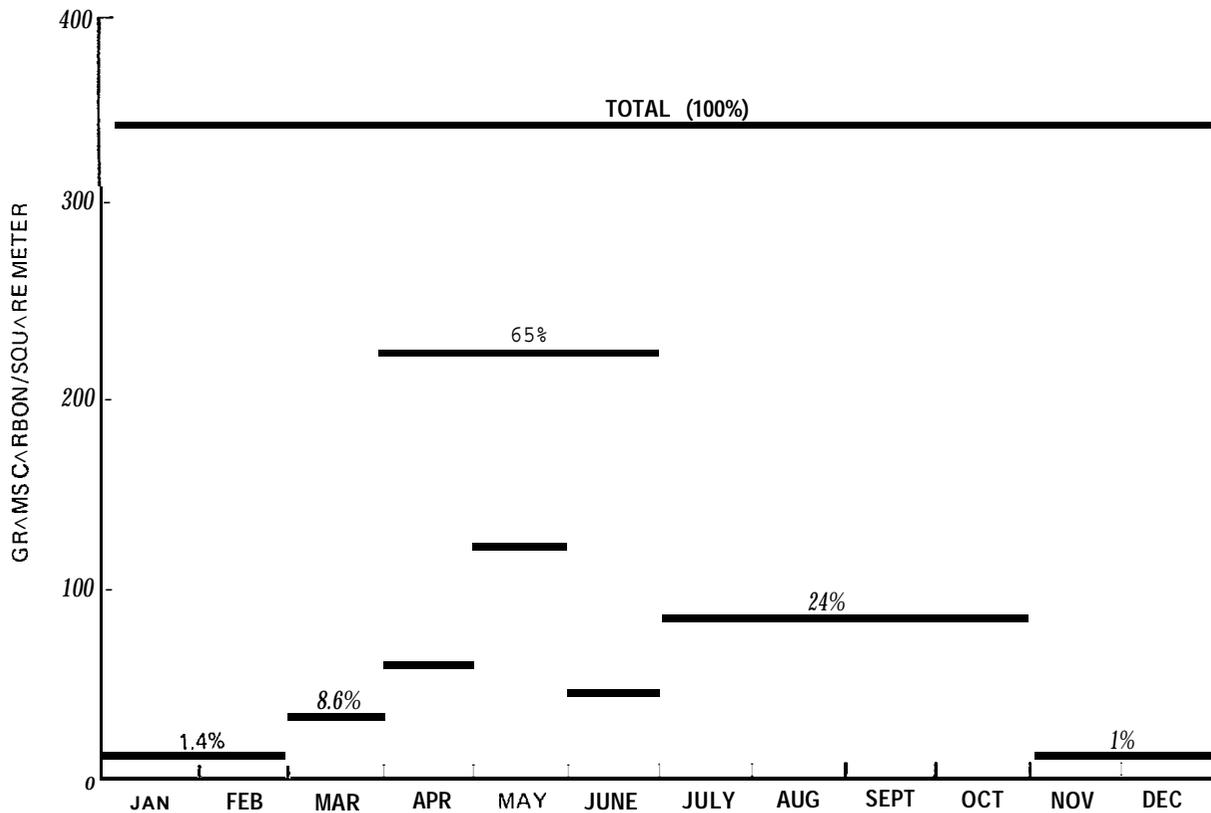


Figure IV-21. Annual distribution of primary production, S. E. Bering Sea shelf.

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 (1-20l) 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/m² day⁻¹ in the open ocean and .1-.3 gC/m² 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

Regime	Ingestion; MgC/m ² /day	
	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 $\mu\text{gC}/1 \text{ hr}^{-1}$. Considering a 20 m photic zone and continuous feeding over 24 hrs, this amounts to a range of ingestion from 0.096 to 0.960 $\text{gC}/\text{m}^2/\text{day}$ 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 assemblage occurring on the shelf in this region.

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CHAPTER V
ICE EDGE MODEL

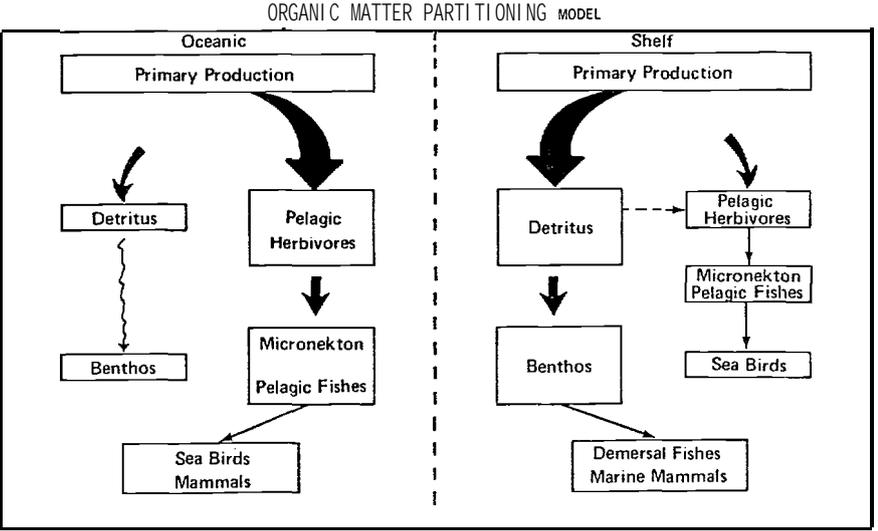
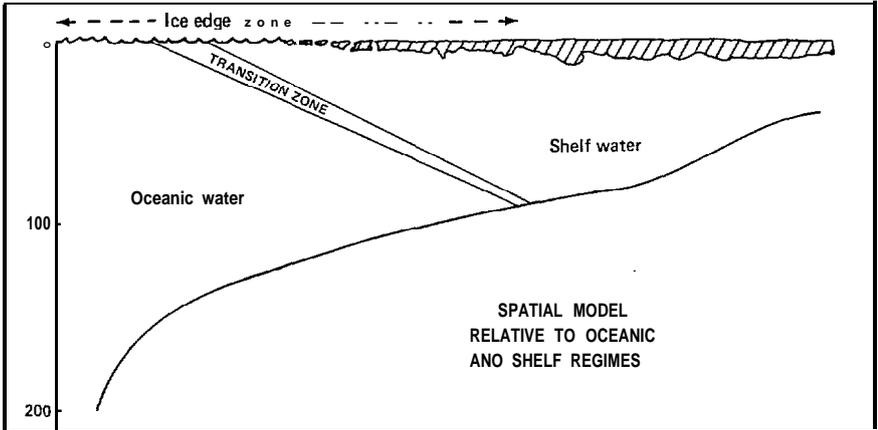
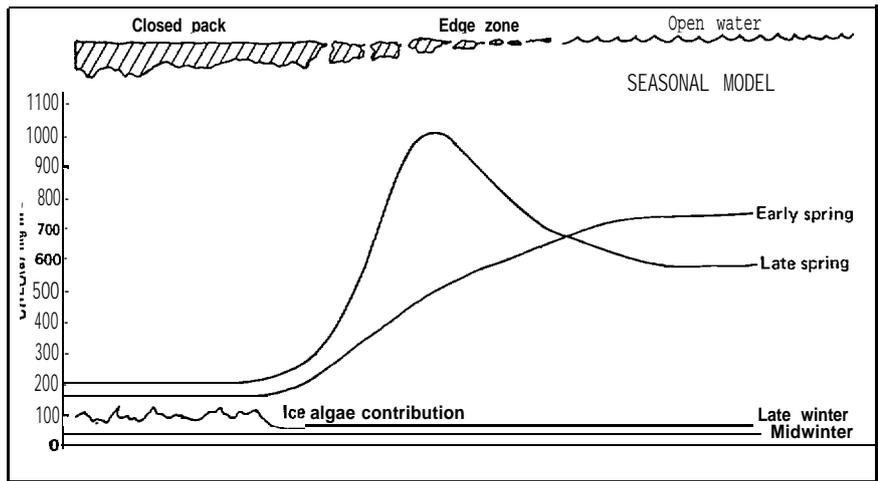


Figure V-1. Conceptual model of the ice-edge ecosystem depicting the seasonal variations in plant stocks, the position of the edge zone relative to the shelf and oceanic waters, and the flow of organic matter in pelagic food webs.

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 preceding 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 $18 \text{ } \mu\text{g-atoms/m}^3$ 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/m²•hr have been measured 20 miles into the broken ice, and 725 mg C/m²•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 changes. 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 affect 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 reestablishment 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 **benthic** system.