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The paradox of pelagic food webs on the Bering-Chukchi continental shelf

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University of Alaska Fairbanks, 1987

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THE PARADOX OF PELAGIC FOOD WEBS ON THE BERING-CHUKCHI CONTINENTAL SHELF

A

THESIS

Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
for the Degree of

Doctor of Philosophy

By

Alan M. Springer, MS

Fairbanks, Alaska

May 1988

THE PARADOX OF PELAGIC FOOD WEBS
ON THE BERING-CHUKCHI CONTINENTAL SHELF

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ABSTRACT

Prolific primary production and spectacular populations of marine birds and mammals in the northern Bering Sea were for many years considered to be a paradox of an environment that should have had low production, as is typical of shallow continental shelves elsewhere. However, a "river" of oceanic water, Anadyr Water, originating along the continental slope of the Bering Sea carries a perpetual supply of nutrients and biota onto this northern shelf that transforms part of the region into one that is extremely productive at all trophic levels. Diatoms grow profusely throughout the ice-free season and, together with oceanic zooplankton advected in the Anadyr stream, provide the energy base for rich pelagic and benthic food webs.

Contrasting with the highly productive pelagic regime is one associated with Bering Shelf Water and Alaskan Coastal Water. Both of these water masses originate over the shallow shelf of the northern and eastern Bering Sea, and are typically nutrient-poor following the spring phytoplankton bloom. Terriginous nutrients introduced by the Yukon and other rivers are not sufficient to elevate primary production above a low level typical of inner shelf regions. The oceanic zooplankton are excluded from this environment, and populations at higher trophic levels are small. The consequence of these contrasting physical regimes is that discrete oceanic and inner shelf food webs coexist in a small geographic region where only a coastal ecosystem is expected.

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ACKNOWLEDGEMENTS

All of the studies that led to the data presented in this thesis were undertaken by a number of people in various roles. Without certain of them it is unlikely that anything would ever have happened that included me, and without others the quality and results of the work would have suffered. Three people stand out in a germinal sense. D.G. Roseneau had prior, credible research experience, and he thus legitimized the original scientific staff, which consisted of himself and me. He helped organize and participated in all of the field work, data analysis and the preparation of seemingly innumerable quarterly, annual and final reports that were required of all OCSEAP investigators. D.W. Norton, formerly in the Arctic Project Office of the Outer Continental Shelf Environmental Assessment Program (OCSEAP), which funded most of the seabird studies, was extremely persevering in obtaining continuing funding for the work, and forthright in his encouragement for us to stay with it. Finally, L.G. Swartz, who conducted the first thorough seabird colony study in Alaska at Cape Thompson in 1959-61, agreed to accompany us there in the first summer of our work so that we could intercalibrate the field methodology to better compare results separated in time by some 15 years. His commitment added the expertise necessary to get the study off of the ground.

E.C. Murphy joined us after the first year, and eventually took primary responsibility for the work at the Bluff colony in Norton Sound. His knowledge of statistics and fortitude in the field both

added considerably to our collective ability to first obtain data and then to properly analyze it. C.P. McRoy, R.T. Cooney and H.J. Niebauer were extremely patient and helpful when I first began coming around the Institute of Marine Science to ask about the ocean, for none of us had any previous formal experience with oceanography. It was clear that the variability we were seeing in seabird populations during the late 1970's was directly related to the ocean in some way, and their insights led to many of the ideas discussed in the following pages. In 1979, K. Ahlnaes introduced me to satellite imagery, which proved to be particularly helpful to our understanding of the physical environment. A few years later, Peter McRoy went so far as to accept me as a student. His insistence that I learn about something other than birds, both in the class room and in the field, was perhaps the most important factor in my subsequent education.

Many people assisted in the field work over the years, and their diligence and enthusiasm, for the most part, made our studies successful. One in particular, Martha Johnson (presently M. Springer) deserves special credit. She accompanied us into the field each summer and flailed away with us during each winter analysis and report writing period. She has truly been a stalwart of the operation.

Funding for these studies was provided by the National Oceanic and Atmospheric Administration and the Minerals Management Service through the OCSEAP, and by the National Science Foundation, Grants DPP-8300916, DPP-7623340, and DPP-8405286 for the project ISHTAR (Inner SHelf Transfer and Recycling). Satellite imagery was provided by the NOAA/NESDIS CDA Station in Fairbanks.

INTRODUCTION

The Bering Sea has long been important to many nations because of its vast renewable resources, particularly fishes and marine mammals. Although not important in the international economy, marine birds are extremely abundant and are utilized by most native residents. The environmental, biological and ecological reasons for such plentiful populations of marine animals at high trophic levels remained obscure well into the 1970's (Hood and Kelley 1974, including papers therein and cited therein), and it was not until late in that decade that significant progress was made toward an understanding of how the Bering Sea ecosystem works (Hood 1986, including papers therein and cited therein).

Primarily because there are no major fisheries in the northern Bering Sea or southern Chukchi Sea, i.e., on the Bering - Chukchi continental shelf, comprehensive, integrated oceanographic investigations of this region were not undertaken until the mid-1980's. This is surprising, since a number of unrelated parochial studies and local knowledge all indicated that the region was extremely productive of marine mammals and birds, if not of commercially important fishes, and that the production base, that is the annual growth of phytoplankton, was unusually high for such a shallow continental shelf area apparently far removed from sources of essential nutrients.

The work reported here began in 1976 with descriptive studies of seabird colonies in the eastern Chukchi Sea. One of the major goals of that and subsequent work was the elucidation of seabird food habits and trophic dependencies. Seabirds are the most numerous, diverse and conspicuous of the upper trophic level vertebrates in pelagic food webs in this region, and because of their accessibility, they have proved to be excellent subjects for studying pathways of energy flow. Clear patterns in the distribution of seabird species and numbers, and highly variable levels of reproductive success between years in some species throughout the region all seemed to be related to food availability, and thus provoked a number of ecosystem-level questions concerning meteorology, oceanography, primary and secondary productivity, levels of interannual variability in these factors, and the relationship of any or all of them to the biology of the birds. The answers to many of these questions are emerging, and we now have a much improved understanding of most of the larger, general features that make the Bering - Chukchi shelf one of the spectacular marine areas in the world. It is the purpose of this thesis to describe the current state of knowledge regarding the principal pelagic food webs in this region.

The following chapters describe pelagic production regimes, from phytoplankton, the primary producers, to zooplankton and birds. Fishes, which stand between the zooplankton and certain species of birds, are difficult to study and information about them has come indirectly from detailed analyses of prey remains recovered from the birds. The order of the chapters mirrors the trophic order, with Chapters 1 and 2 devoted to primary production and zooplankton communities, respectively. Chapter 3 describes the relationships of avian planktivores to their prey in the northern Bering Sea, the northern limit of their breeding range, and compares the situation there to that in other hydrographic and biological domains to the south. Chapters 4 and 5 describe the food habits of piscivorous seabirds on the Bering - Chukchi shelf in relation to the average environmental conditions, as well as to environmental variability.

CHAPTER 1

Patterns of Primary Production

INTRODUCTION

Physical processes that resupply nutrients to the euphotic zone during summer over temperate and high-latitude continental shelves are crucial to regional production regimes. In general, much of the annual primary production away from upwelling areas occurs during the spring bloom, at which time nutrients are stripped from the whole water column in coastal areas less than about 50 m deep and from the upper mixed layer, above the seasonal pycnocline, over the deeper middle and outer shelf. Cross-shelf diffusion and advection are often slow, and this is related, in part, to the presence of physical structural fronts that impede horizontal exchange (Coachman and Walsh 1981). However, these fronts can facilitate the vertical transport of nutrients, enhancing local production (Iverson et al. 1979). If the front is located near an ice edge, diffusion can replenish nutrients in localized physical cells where it is thought that primary production is temporarily high prior to the spring bloom (McRoy and Goering 1974; Niebauer and Alexander 1985). On a larger scale, wind-induced mixing of nutrient-rich water from beneath the pycnocline into the euphotic zone after the termination of the bloom can increase annual primary production by as much as 30% in the New York Bight (Walsh et al. 1978) and the southeastern Bering Sea (Sambrotto and Goering 1983). Likewise, subsurface intrusions of Gulf Stream water onto the continental shelf of the southeastern United States can yield an additional 15% to the annual production there (Yoder et al. 1985).

The continental shelf of the northern Bering and southern

Chukchi seas, beginning several hundred kilometers from the shelf break (Fig. 1), is generally less than 50 m deep, and geographically is an inner shelf environment. The feature that distinguishes the Bering Strait region from other shallow continental shelves is the flow of water through the narrow, shallow strait, predominantly from south to north, and the origins of the water masses that constitute that flow. As a result, the area receives a continual supply of nutrients that promotes abundant phytoplankton growth throughout summer.

Three water masses comprise the bulk of the primarily barotropic flow through Bering Strait. Total transport averages about 0.8 Sv (1 Sv = 10^6 m^3 s^{-1}) to the north on an annual basis, but it is generally higher in the summer, up to about 1.5 Sv (Coachman 1986). Alaskan Coastal Water, in the east, originates in the southeastern Bering Sea. It has a low salinity owing to fresh water input from mainland rivers, is further diluted by the Yukon River which empties into Norton Sound, and warms rapidly in summer following the retreat of sea ice. Anadyr Water, in the west, is a high-salinity water mass that is a northern branch of the Bering Slope Current (Coachman et al. 1975; Kinder et al. 1975). It originates along the shelf break at about 100-200 m and consequently contains nutrients at high concentrations characteristic of the Bering Sea basin. The nutrients are conserved during the northward transit across the continental shelf apparently because Anadyr Water remains sequestered beneath the euphotic zone until it reaches the shallow Bering Strait area. Typical nitrate concentrations throughout summer in Anadyr Water on

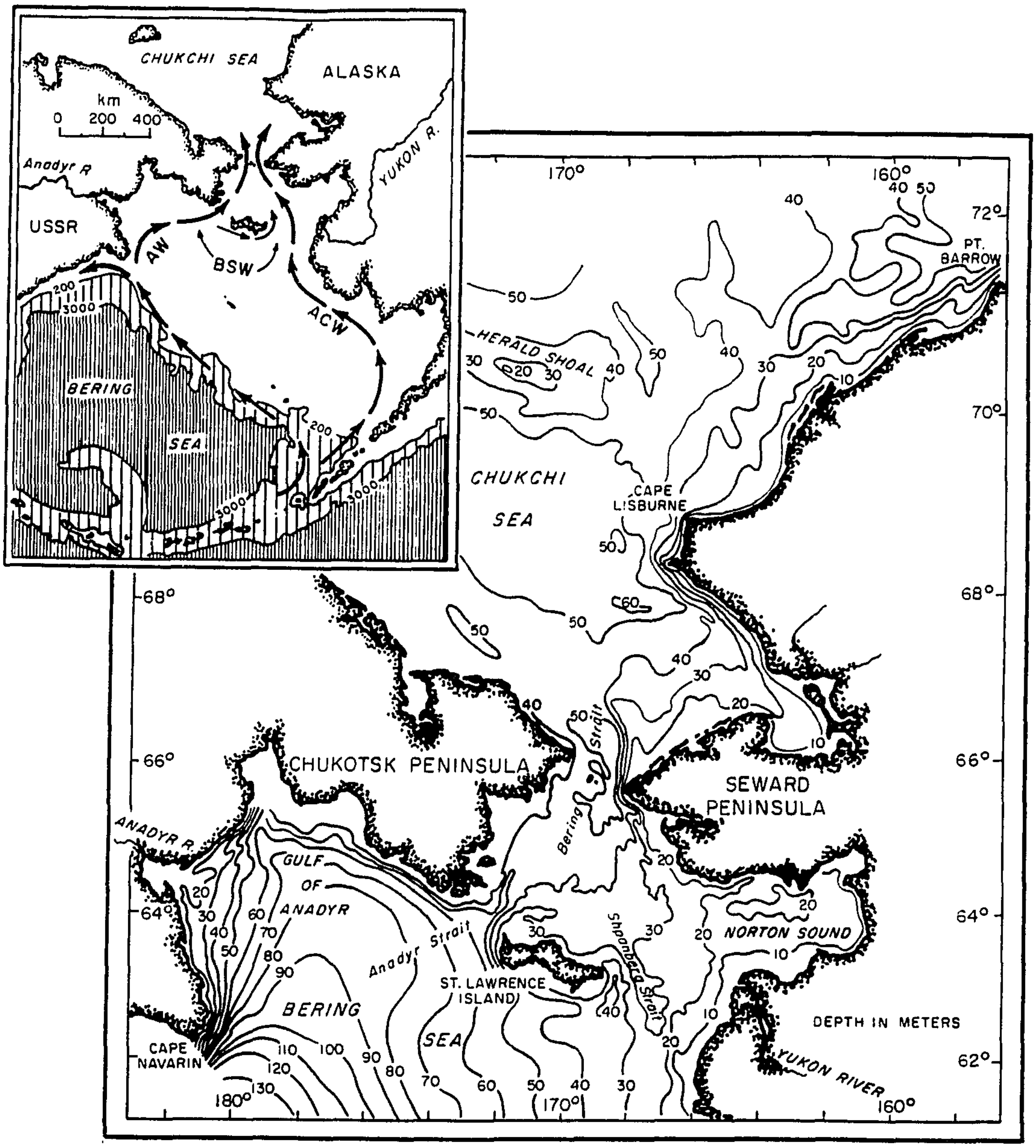

Figure 1. The Bering-Chukchi shelf, with generalized circulation patterns and origins of the principal water masses flowing north through Bering Strait (from Coachman et al. 1975). In the inset AW = Anadyr Water, BSW = Bering Shelf Water, and ACW = Alaskan Coastal Water.

the Bering-Chukchi shelf are in the range of 20-30 ug at l^{-1} (Husby and Hufford 1969; McRoy et al. 1972, this study), and the advective nitrate flux in Anadyr Water is comparable to that in the Peruvian upwelling system (Walsh et al. 1988). Anadyr Water and Alaskan Coastal Water are separated by Bering Shelf Water which originates on the northern shelf south of St. Lawrence Island. Because of similar densities, Anadyr and Bering Shelf waters are well-mixed along their boundary and a sharp front is not always present between them as it is between Bering Shelf Water and Alaskan Coastal Water. The nominal boundaries separating Anadyr Water from Bering Shelf Water from Alaskan Coastal Water are the 32.5 ppt and 31.7 ppt isopleths, respectively (Coachman 1986).

Rapid phytoplankton growth (2-4 g C m^{-2} d^{-1}) has been measured previously in the Bering Strait region at various times during summer (McRoy et al. 1972; Sambrotto et al. 1984), and Sambrotto et al. (1984) estimated a yearly carbon production of 324 g m^{-2} over 2.12 x 10^4 km^2 of the northwestern Bering Sea shelf. The apparent paradox of such high productivity in an inner shelf environment was solved by knowledge of the source of Anadyr Water. In this chapter I describe the primary production regime on the Bering-Chukchi shelf in light of more extensive data from 1985 - 1987. Patterns of phytoplankton production and biomass indicate a highly dynamic system, with large spacial and temporal variability.

METHODS

The work was carried out onboard the RV *Alpha Helix* and the RV *T.G. Thompson* on cruises during July - September 1985 - 1987 (Fig. 2). The study area extended from Anadyr and Shpanberg straits north to 69° or 70° N latitude, depending on the extent of seasonal sea ice and the duration of the various cruises. I was unable to sample west of the United States - Soviet Union Convention Line because of international politics. Water column temperature and salinity were profiled with a Neil Brown CTD, and discrete 5 l water samples were collected at 5 m intervals between the surface and near bottom at all stations. Subsamples from each depth were analysed for chlorophyll-*a* using a Turner - Designs fluorometer and an acetone extraction fluorescence procedure similar to that described by Parsons et al. (1984). Additional subsamples were taken from each depth for dissolved nutrient analyses, which were done on a Technicon Autoanalyser onboard the ship.

Primary productivity measurements were made at a subset of the survey stations. Subsurface light penetration was determined with a LI-COR underwater sensor, and 30 l water samples were collected from 5 depths corresponding to 100%, 50%, 30%, 15% and 1% of the surface irradiance. Subsamples from each depth were taken for the determination of dissolved nutrient concentrations and carbon and nitrogen uptake rates. The results of the nutrient analyses other than nitrate (Whitledge unpubl. data) and nitrogen uptake rate measurements (Hansell and Goering unpubl. data) will be reported

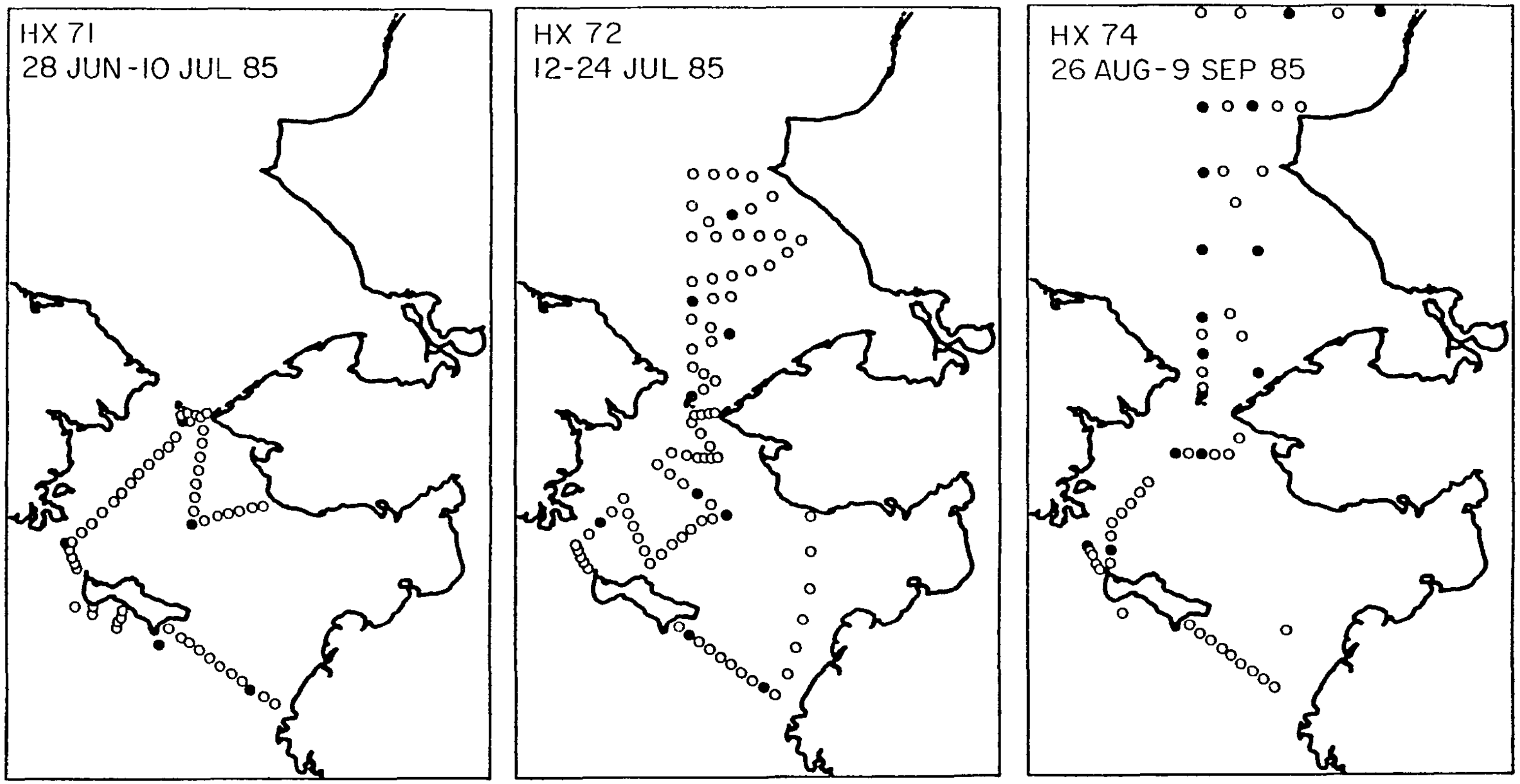

Figure 2a. Locations of stations sampled on selected cruises in 1985. Carbon uptake rates measured at stations identified by solid circles.

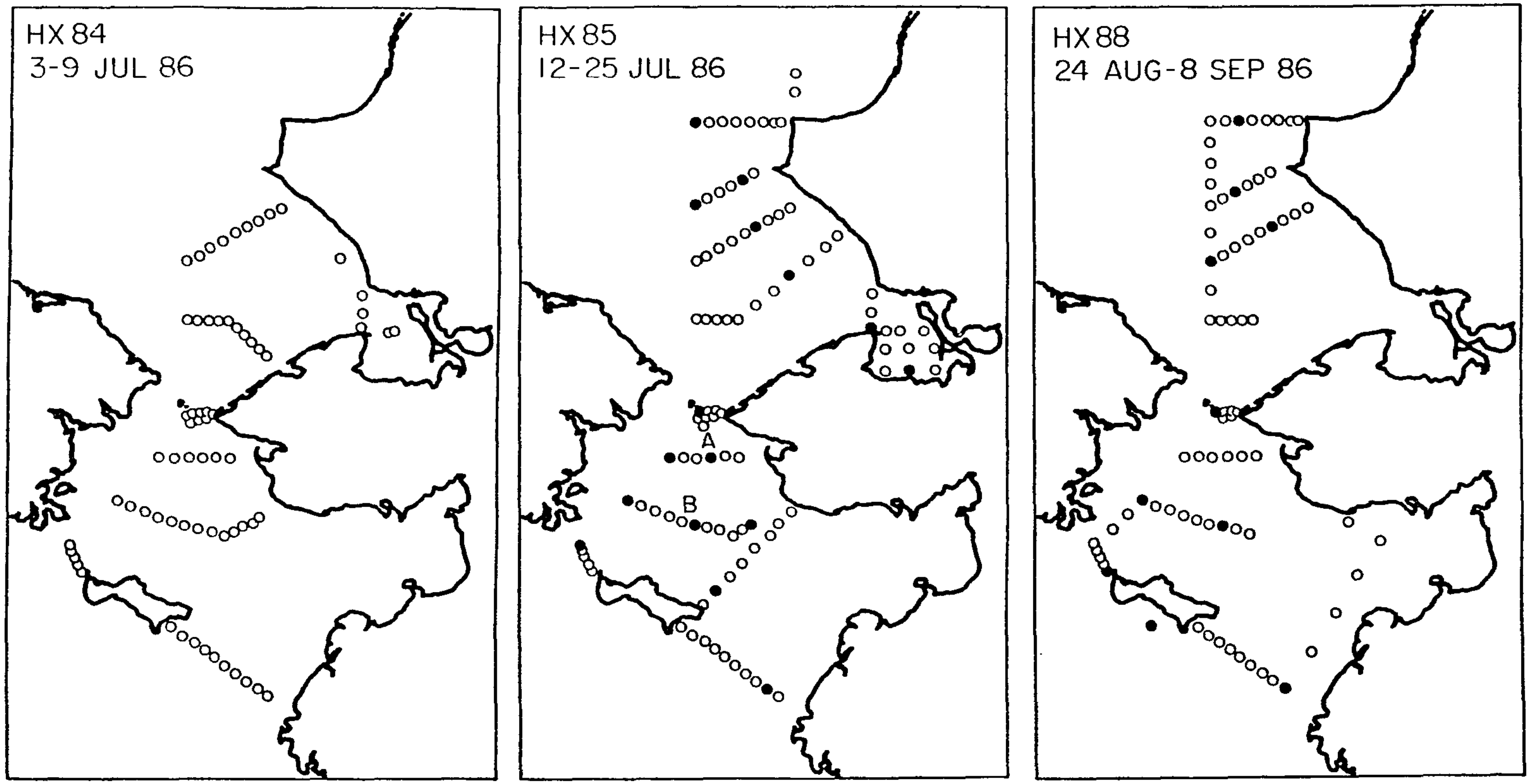

Figure 2b. Locations of stations sampled on selected cruises in 1986. Carbon uptake rates measured at stations identified by solid circles.

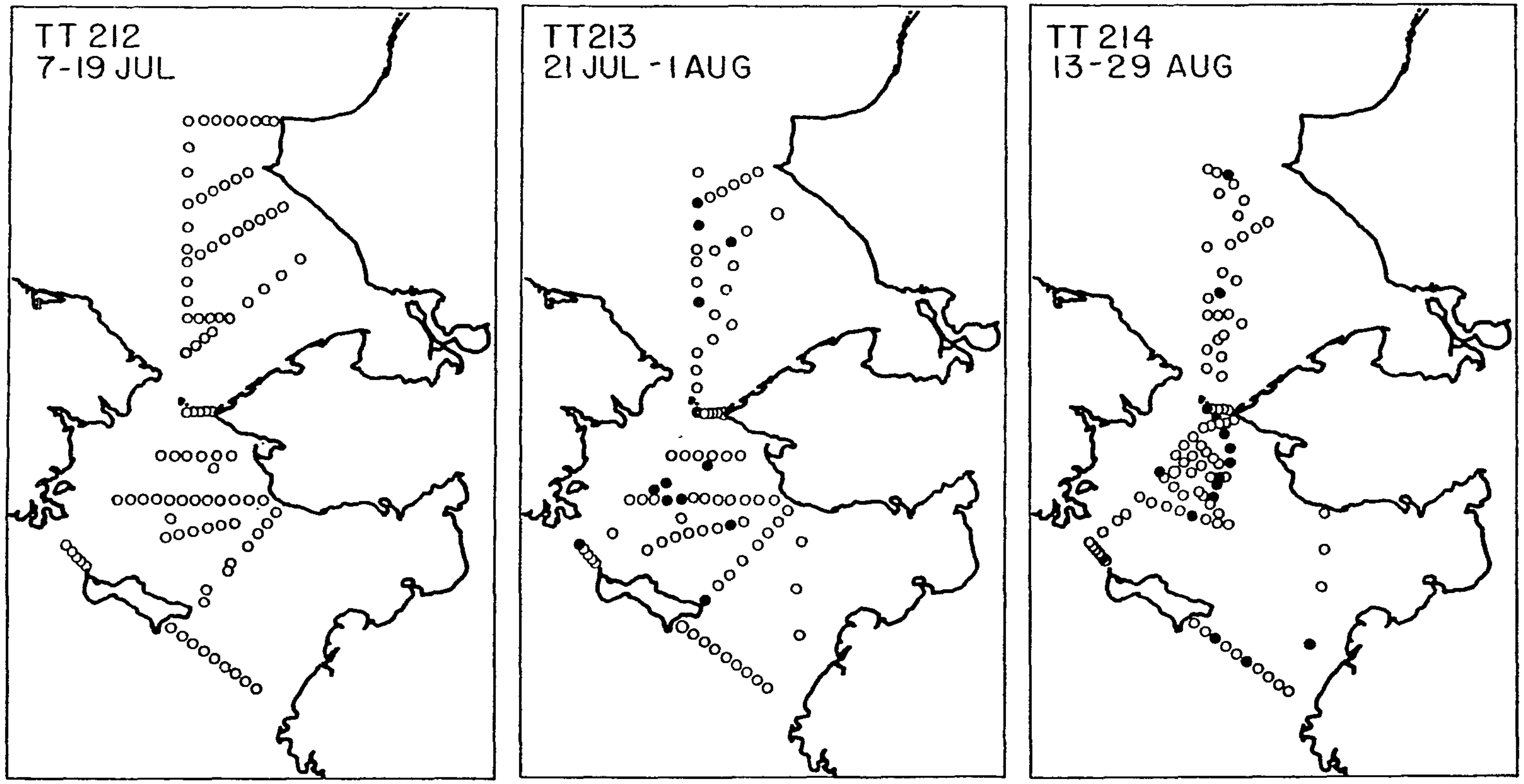

Figure 2c. Locations of stations sampled on selected cruises in 1987. Carbon uptake rates measured at stations identified by solid circles.

elsewhere.

Carbon productivity samples were collected in 175 ml bottles, 2 light bottles and 1 dark bottle, inoculated with 5 uCi ^{14}C-labelled sodium bicarbonate and incubated on deck for about 4 hr at simulated light intensities corresponding to the respective sampling depths using perforated nickel screens. The incubators were bathed in seawater taken from a depth of about 2 m. At the end of the incubation period the samples were filtered through Gelman A/E glass fiber filters, the filters were sealed in scintillation envelopes with 3 ml Scintiverse (Fisher brand SO-X-1), and the activity was counted on a Beckman liquid scintillation counter. Additional subsamples from each light depth were preserved in Lugol's solution for elucidation of the principal taxa of phytoplankton. Incident photosynthetically active radiation (400 - 700 nm) during each day and incubation period was measured with a LI-COR quantum sensor.

In an earlier, related study of pelagic food webs in the coastal zone of the eastern Chukchi Sea, I collected water samples for chlorophyll every few days from June 17 - August 28, 1983 at a station near Cape Lisburne. The station was located about 3 km east of the Cape and 2 km from shore in 15 m of water. Water samples from three depths (1 m, 5 m and 15 m) were filtered in the field, buffered with magnesium carbonate, and frozen until they could be returned to the laboratory and analysed using the same procedure as that used for the shipboard samples. The absolute values determined for chlorophyll in these samples are probably somewhat lower than actual, but the pattern of seasonal change should be accurate.

To compare estimates of daily primary production between cruises in the region of enhanced phytoplankton growth, or the plume, I defined the plume as the region where integrated chlorophyll was greater than 25 mg Chl m^{-2} between 0-15 m, which corresponded approximately to the depth of the euphotic zone. Although the average depth of the 1% light level was 22 m, little carbon uptake occurred at that depth - most of the growth occurred above the 15% light depth, which was closer to 15 m. I then determined the surface area between adjacent isopleths for the plume south of Bering Strait, estimated the average daily production in each contour interval using the appropriate regression equations from Table 1, and summed the results for each interval to give an estimate of the total daily production within the plumes. The standing stock of phytoplankton carbon in the plumes was estimated in a similar manner, by calculating the standing stock of chlorophyll and then converting it to carbon using a carbon:chlorophyll ratio of 45:1 (see Walsh et al. 1988). The standing stock of phytoplankton carbon beneath the euphotic zone, defined here as the bottom layer, was calculated in the same way, but using the integrated chlorophyll values between 20 m and the bottom. Because the survey coverage of the shelf north of Bering Strait was relatively incomplete, I did not attempt these analyses for that region.

RESULTS

Boundary conditions

In 1985, Anadyr Water (salinity > 32.5 ppt) in Anadyr Strait was overlain by coastal water (salinity < 31.8 ppt) from at least July through early September, as illustrated in Fig. 3. The coastal water apparently originated in the northwestern Bering Sea, particularly the Gulf of Anadyr where the Anadyr River discharges. Layering by coastal water in 1986 was confined to the central and western part of Anadyr Strait, with Bering Shelf Water (32.5 ppt > salinity > 31.8 ppt) overlying and replacing Anadyr Water and coastal water in the eastern strait throughout summer (Fig. 4). The water mass distribution across Anadyr Strait in 1987 was similar to 1985 (Fig. 5), with coastal water overlying Anadyr and Bering Shelf Water across the whole strait. Although rich in nutrients, the purest Anadyr Water (water with the highest salinities) carried low stocks of phytoplankton. The relatively abundant chlorophyll beneath the pycnocline in eastern Anadyr Strait in 1987 was probably produced upstream from recent growth like that seen beneath Station 14 in Fig. 5. Bering Shelf Water and Alaskan Coastal Water in Shpanberg Strait were low in both nutrients and chlorophyll.

There appears to have been a localized "island effect" on primary production under conditions that brought Anadyr Water, i.e., nutrients, near St. Lawrence Island in 1985 and 1987. Chlorophyll was relatively concentrated near the island in eastern Anadyr Strait and western Shpanberg Strait during both years (Figs. 3 & 5). Such was

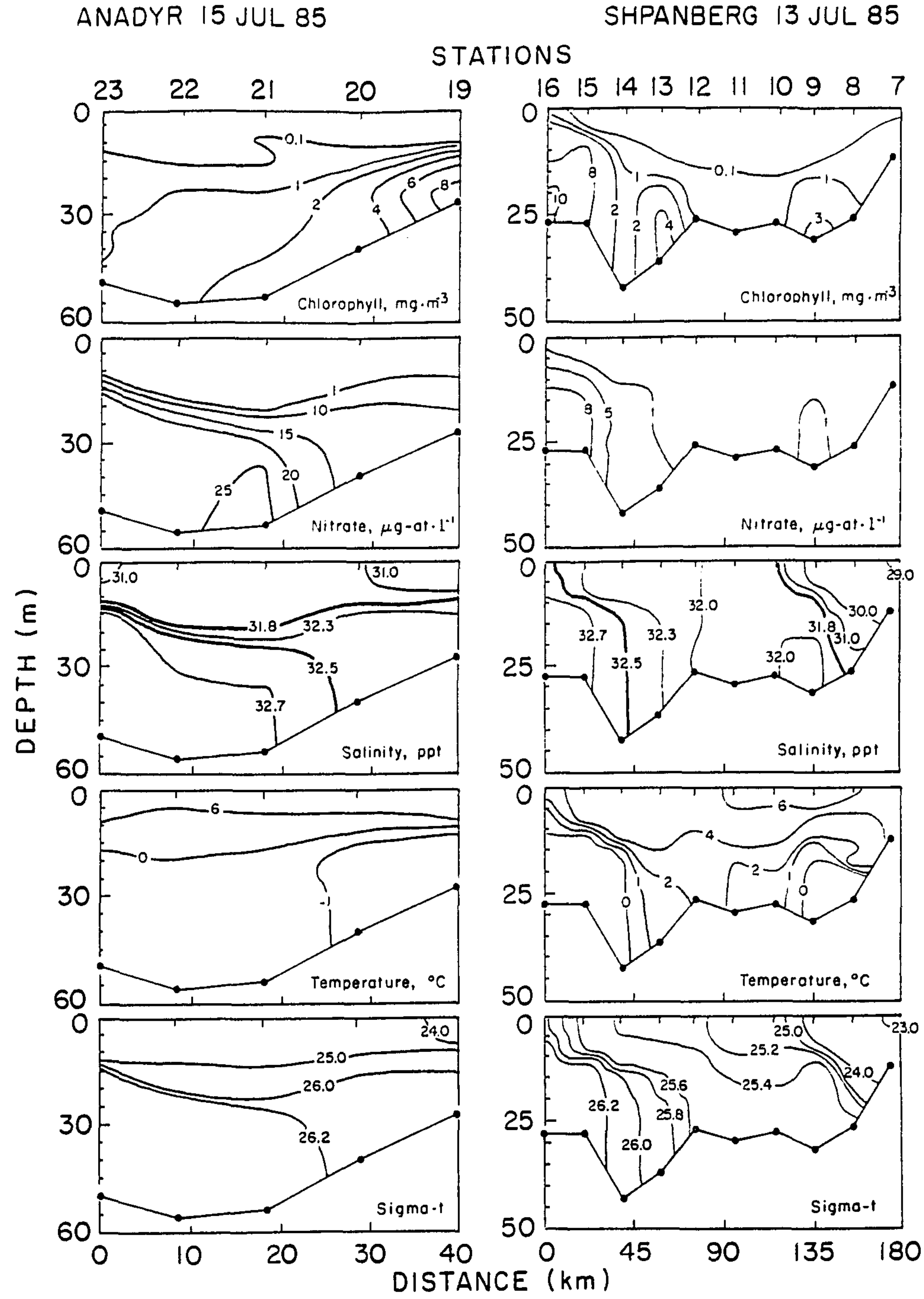

Figure 3. Vertical cross-sections through Anadyr Strait and Shpanberg Strait in mid-July 1985.

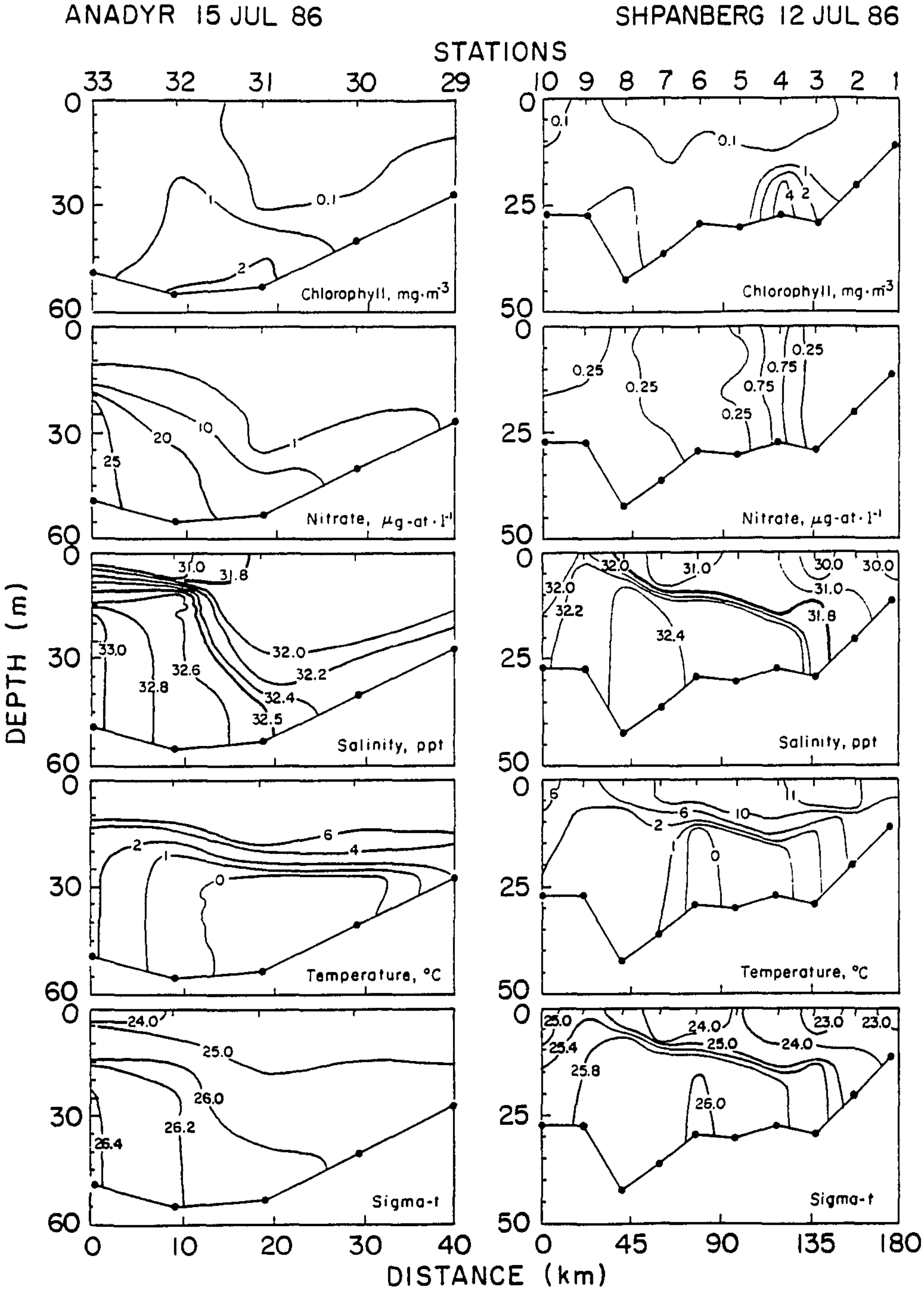

Figure 4. Vertical cross-sections through Anadyr Strait and Shpanberg Strait in mid-July 1986.

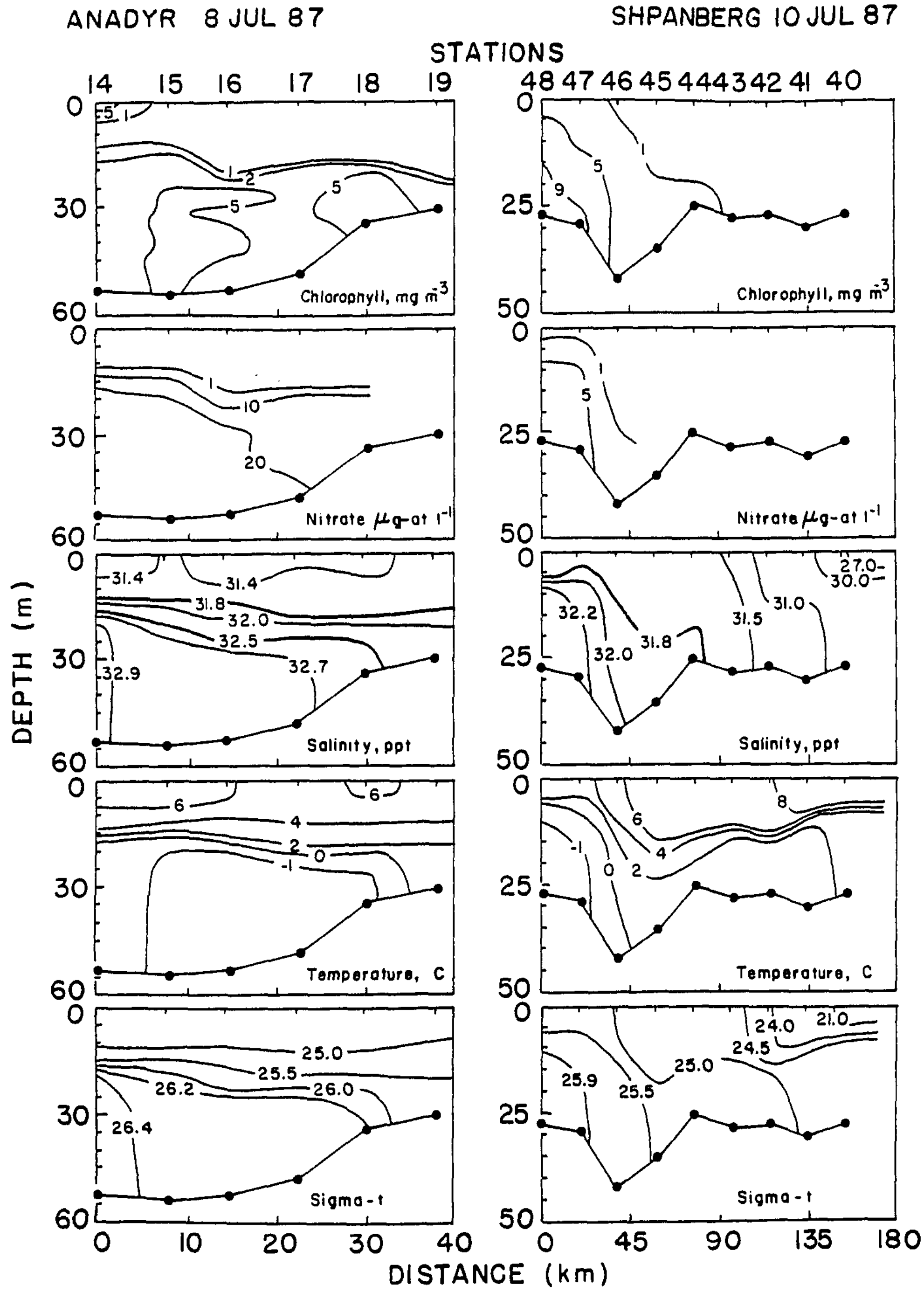

Figure 5. Vertical cross-sections through Anadyr Strait and Shpanberg Strait in mid-July 1987.

not the case, however, at any time in 1986 (Fig. 4). The difference appears to be related to the distribution of Anadyr Water during the three years. In 1985 and 1987, Anadyr Water apparently occupied a greater proportion of Anadyr Strait and extended farther east than in 1986. Moreover, in 1985 and 1987 a portion of Anadyr Water split off of the main flow and travelled around the southern and eastern sides of St. Lawrence Island. Such a flow pattern is indicated by the presence of high-salinity, high-nitrate water in western Shpanberg Strait. This flow pattern was further confirmed by the presence of oceanic zooplankton, which are carried in the Anadyr stream, in the waters of western Shpanberg Strait (Chapter 2).

Areal biomass distribution

Phytoplankton biomass, as represented by chlorophyll, was concentrated in two persistent areas, or pools, one north and one south of Bering Strait, connected by a narrow band between them (Figs. 6-8). Elsewhere, chlorophyll was usually less than about 10-20 mg m^{-2}. The distribution of chlorophyll corresponded to the mixing zone of Anadyr Water with Bering Shelf and Alaskan Coastal water. The highest concentrations in the two pools tended to occur near the center of east-west "loops" in the otherwise northward trajectory of the current through the area, particularly north of Bering Strait. The loops traced streamlines in the currents, which are guided by the bottom topography (compare Fig. 1 to Figs. 6-8), as described for the region by Coachman et al. (1975).

Cross-sections through the chlorophyll pool south of Bering

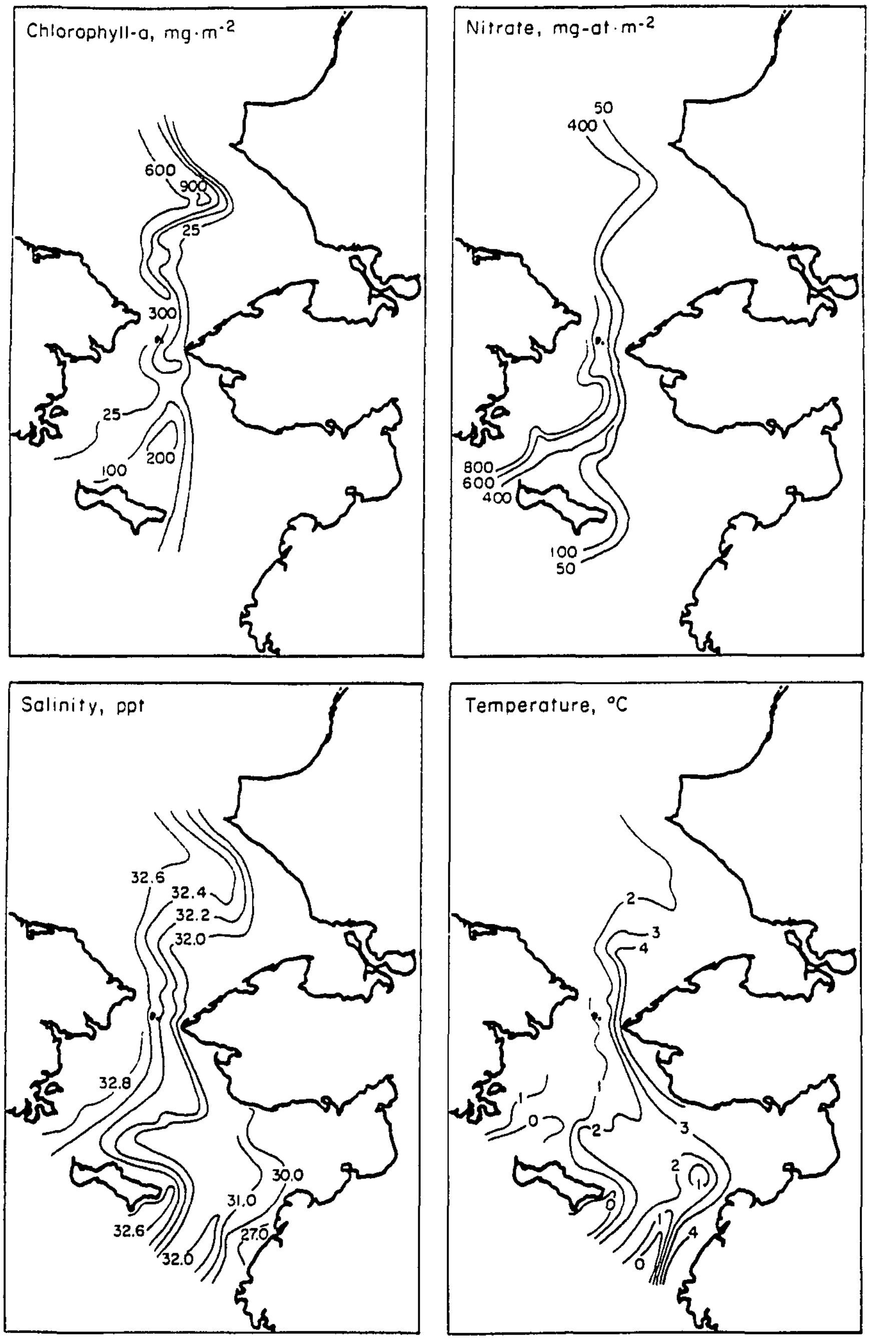

Figure 6. Distribution of chlorophyll, nitrate, bottom salinity and bottom temperature on the Bering-Chukchi shelf, 12-24 July 1985.

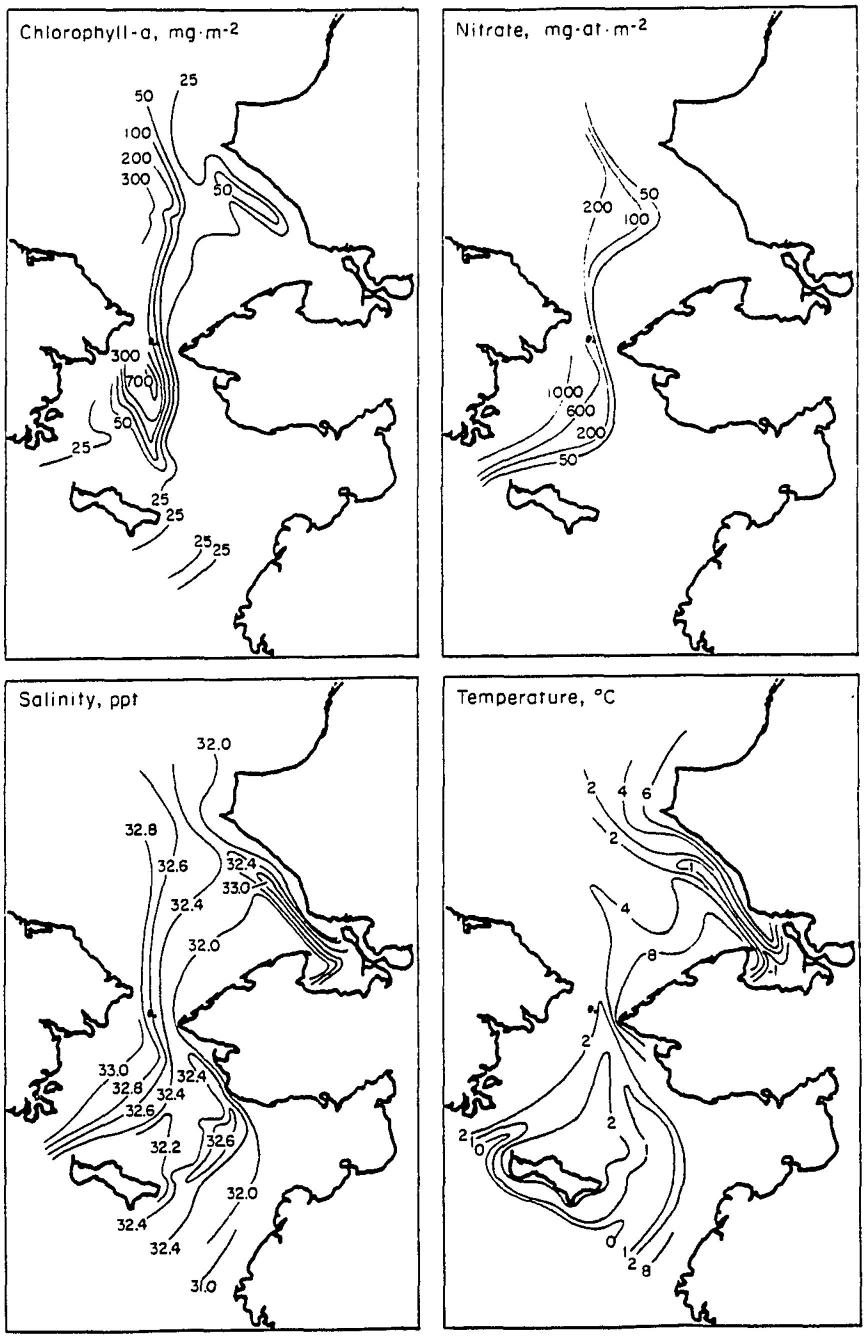

Figure 7. Distribution of chlorophyll, nitrate, bottom salinity and bottom temperature on the Bering-Chukchi shelf. 11-26 July 1986.

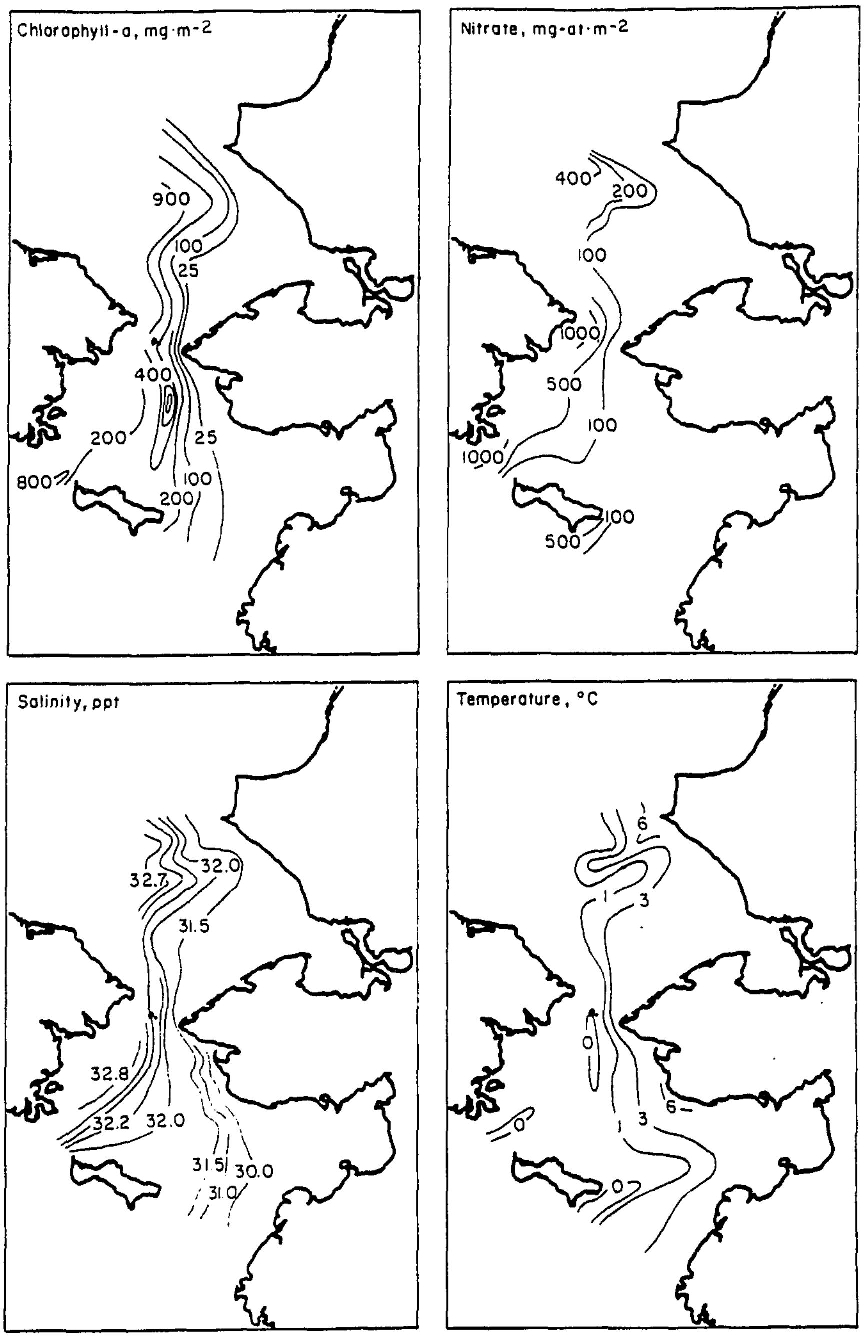

Figure 8. Distribution of chlorophyll, nitrate, bottom salinity and bottom temperature on the Bering-Chukchi shelf, 20 July - 2 August 1987.

Strait show that phytoplankton biomass was consistently greatest west of fronts between Anadyr and Bering Shelf water. For example, in 1986, the concentration of chlorophyll was highest on transect A on July 16, when vertical stratification of the water column was strong and the pycnocline and nutricline were shallow toward the western end of the transect (Fig. 9). The pycnocline was formed by shelf and coastal water over-riding Anadyr Water. Phytoplankton were growing just beneath the pycnocline at a depth of 10-15 m, and biomass apparently was accumulating and settling at the front between Anadyr Water and Bering Shelf Water. Chlorophyll was low in the core of Anadyr Water near the bottom beneath the level of rapid growth. Nine days later on July 25, vertical density stratification was slight and very near the surface in the western half of the transect, and resulted primarily from surface heating of Anadyr Water (Fig. 9). Phytoplankton were growing near the surface where nitrate was plentiful, and chlorophyll was more uniformly distributed throughout the water column below, probably because of the absence of a density gradient. The pycnocline and nutricline were deeper on transect B on July 14 and 15, about 15-20 m, and were formed by Bering Shelf Water overriding Anadyr Water from the east (Fig. 10). Again, chlorophyll was most concentrated just beneath the pycnocline and west of the front between the two water masses.

The cross-sections shown in Figs. 9 & 10 illustrate the level of temporal variability that can exist in biomass distribution, and presumably in primary production. Not surprisingly, day-to-day changes are probably small, while weekly changes can be large.

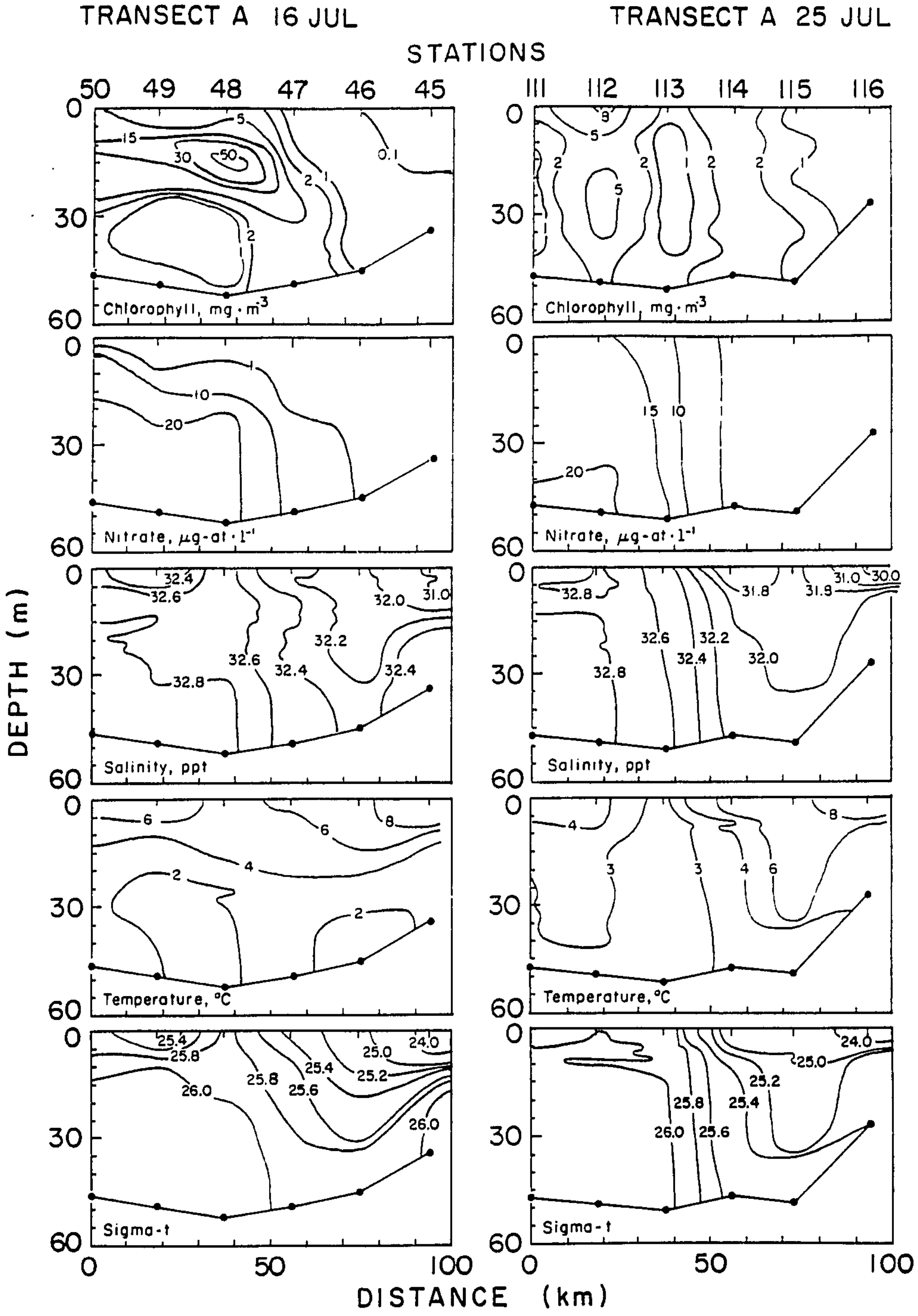

Figure 9. Vertical cross-sections through the southern chlorophyll pool taken 1 week apart in July 1986. See Figure 2, HX85, for transect location.

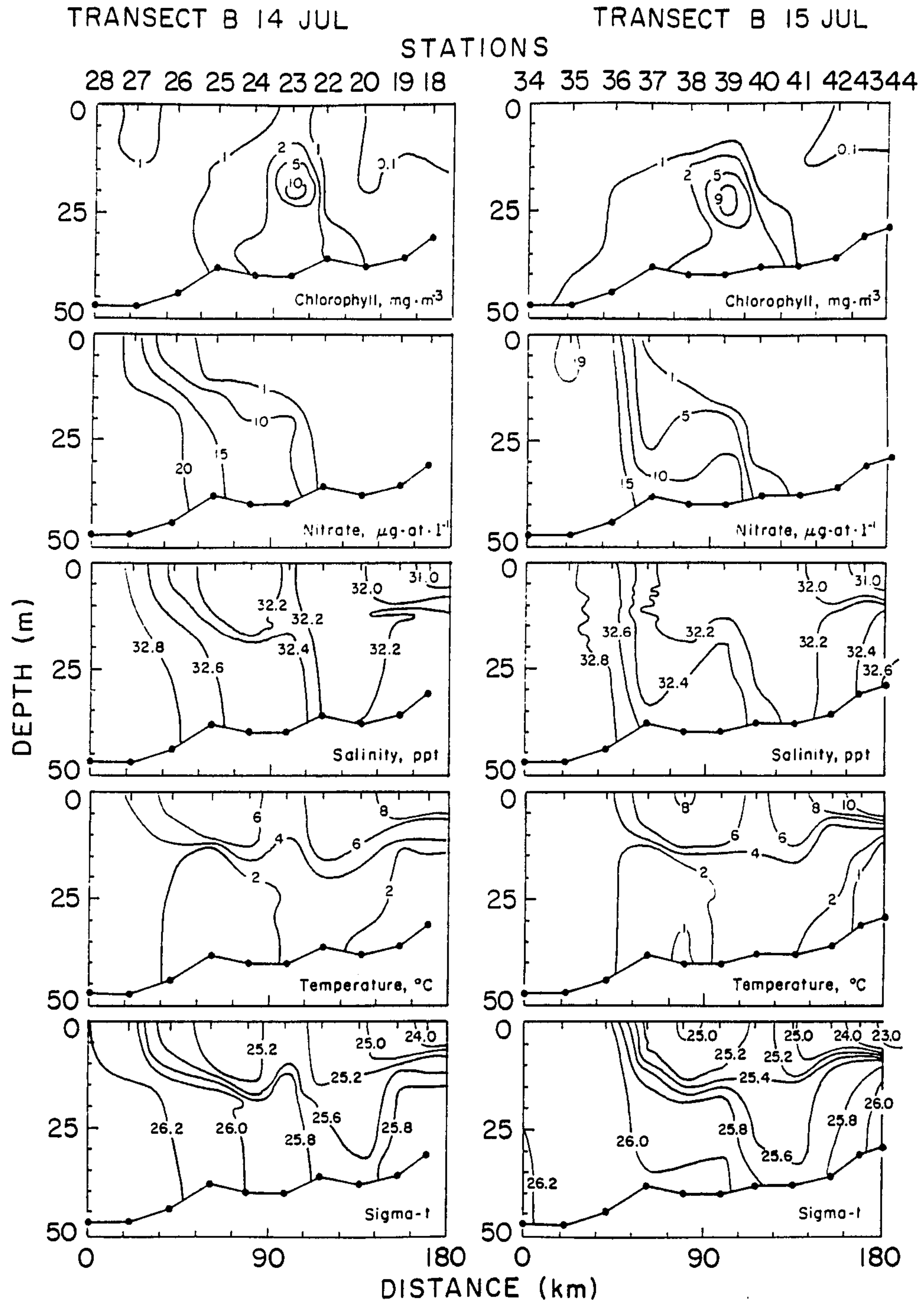

Figure 10. Vertical cross-sections through the southern chlorophyll pool taken 1 day apart in July 1986. See Figure 2, HX85, for transect location.

South of Bering Strait, the standing stock of phytoplankton carbon in the plume (based on a carbon:chlorophyll ratio of 45:1) was not a good predictor ($r = 0.71$, $P > 0.05$) of the amount of carbon in the bottom layer on 6 cruises where reliable contours could be drawn (Table 1). Also, the correlation between the areal extent of the plume and the area of elevated chlorophyll in the bottom layer (Table 1) was not significant ($r = 0.65$, $P > 0.05$). Relations between the chlorophyll stocks and areas in the plume and the bottom layer for three of those cruises (shown in Figs. 6-8) are illustrated in Figs. 11-13. There was, however, a strong correlation ($r = 0.97$, $P < 0.01$) between the area of elevated chlorophyll in the bottom layer and the highest integrated value of chlorophyll (surface to bottom) in western Shpanberg Strait (Table 4).

Primary productivity

Carbon uptake was significantly correlated with biomass in the euphotic zone for all cruises (Table 2). Uptake rates within the production plume ranged between about 1-16 gC m^{-2} d^{-1}, while outside of the plume rates were usually less than 1 gC m^{-2} d^{-1} (Figs. 11-13). The averages of the assimilation numbers (P^B) ranged between 2.0-6.7 mgC mgChl-a^{-1} h^{-1}, and those of the photosynthetic index (P.I.) ranged between 31-75 mgC mgChl-a^{-1} d^{-1} (Table 3).

Growth efficiencies, or α (mgC $mgChl^{-1}$ E^{-1} m^2), for all productivity stations varied by a factor of over 20, with about half of the stations having values below 2 and about half with values above 2.0. Variable irradiance did not explain a significant portion of the

Table 1. Sizes of the regions south of Bering Strait with concentrations of chlorophyll > 25 mg m^{-2} in the plume and the bottom layer, the standing stock of phytoplankton carbon in the two regions (derived from chlorophyll concentrations within the 25 mg Chl m^{-2} isopleths using a carbon:chlorophyll ratio of 45:1), and the highest water column level of chlorophyll in western Shpanberg Strait.

	Area (x10^{-10} m^2)		Carbon Standing Stock (x10^{-10} g)		Chlorophyll (mg m^{-2})
Station	Plume	Bottom layer	Plume	Bottom layer	Water column
HX72	0.48	2.7	1.4	11	193
HX84	0.74	1.7	2.6	4.0	97
HX85	0.63	1.1	3.6	4.1	33
HX88	0.92	1.3	2.0	4.5	94
TT212	1.0	3.5	5.5	15	211
TT213	2.1	3.9	5.8	22	259

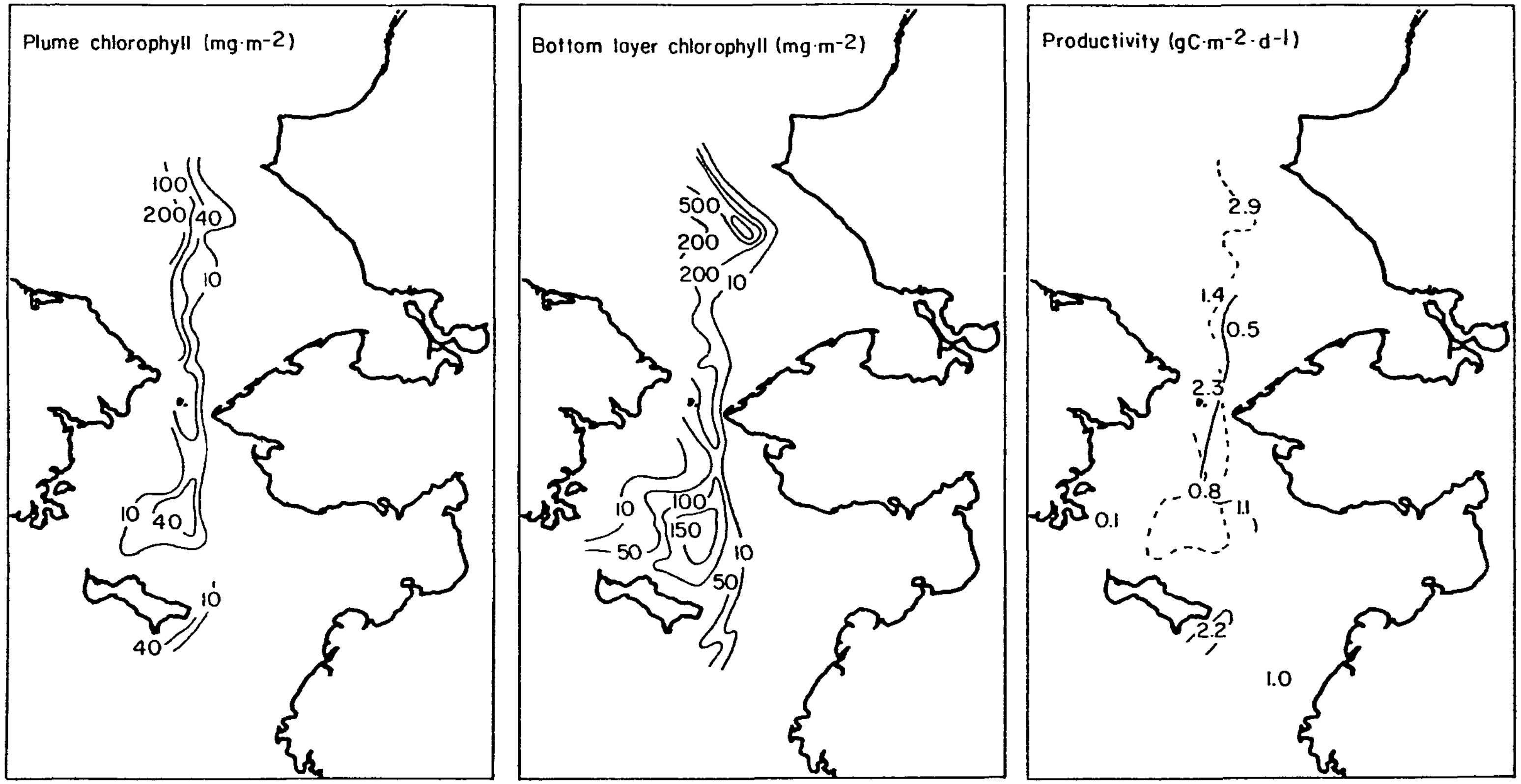

Figure 11. Distributions of plume and bottom layer chlorophyll and carbon uptake rates on the Bering-Chukchi shelf, 12-24 July 1985. The dotted line on the right panel is the 10 mg Chl m^{-2} isopleth from the right panel.

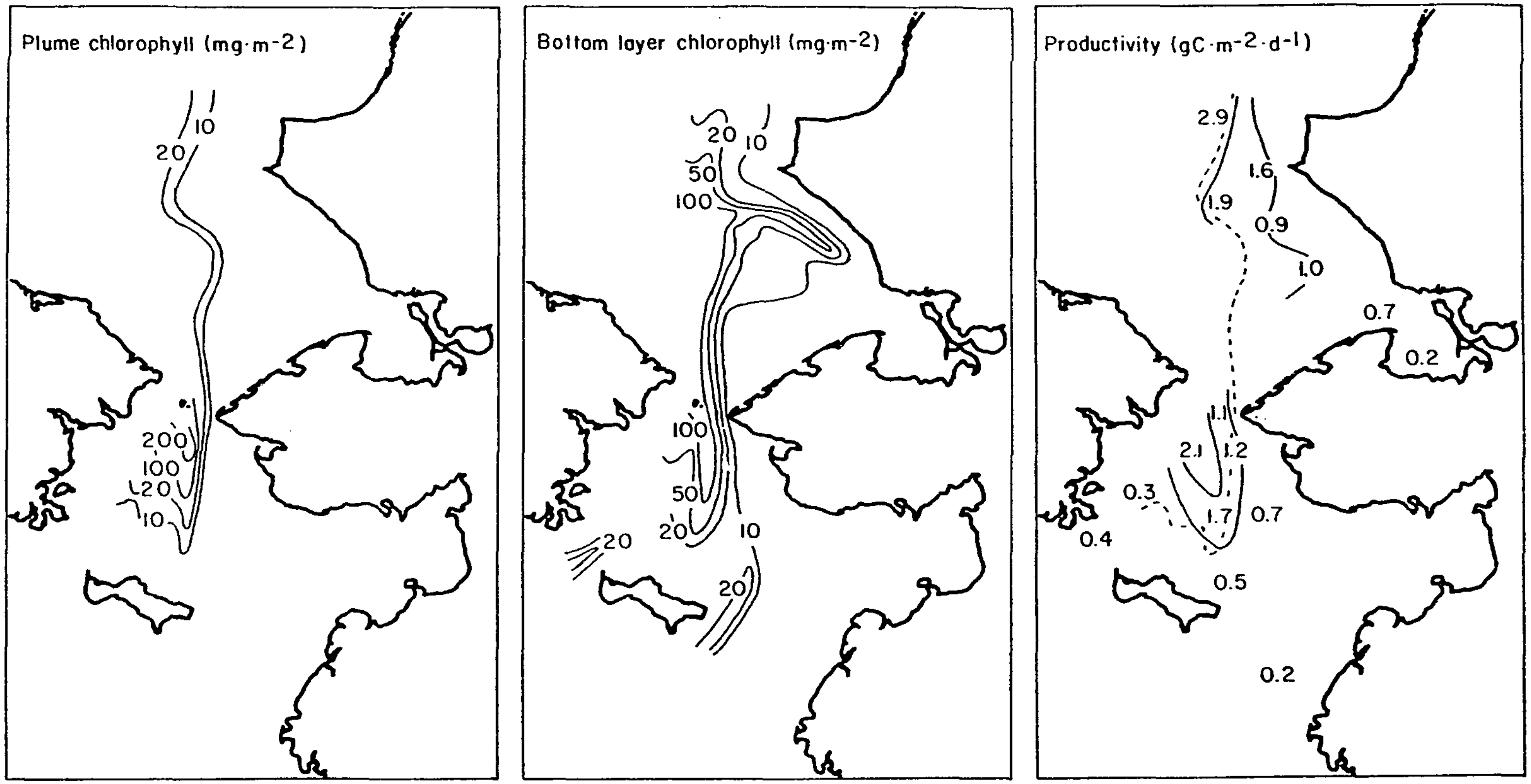

Figure 12. Distributions of plume and bottom layer chlorophyll and carbon uptake rates on the Bering-Chukchi shelf, 11-26 July 1986. The dotted line on the right panel is the 10 mg Chl m^{-2} isopleth from the right panel.

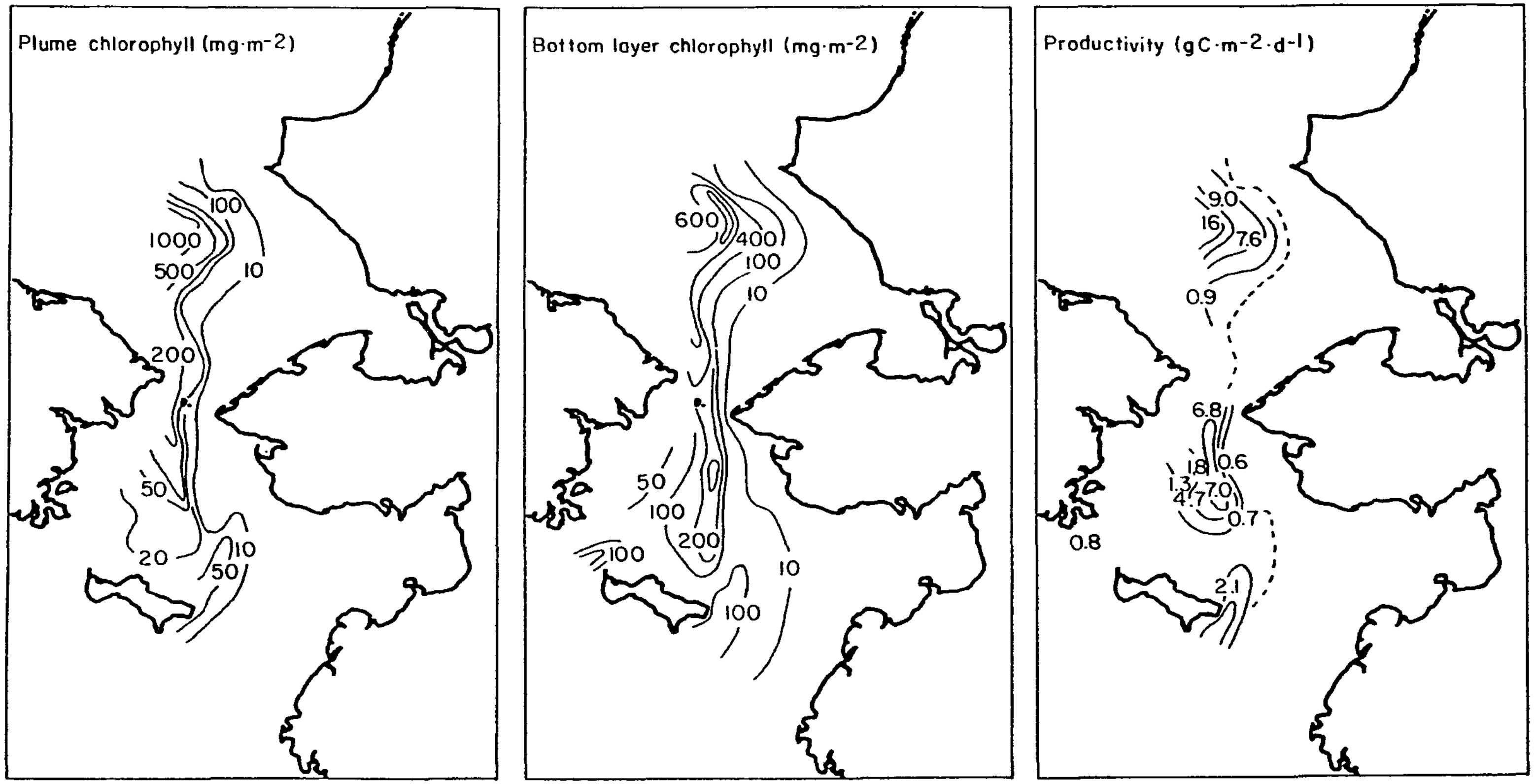

Figure 13. Distributions of plume and bottom layer chlorophyll and carbon uptake rates on the Bering-Chukchi shelf, 20 July - 2 August 1986. The dotted line on the right panel is the 10 mg Chl m^{-2} isopleth from the right panel.

Table 2. Regression results for carbon production (mgC m^{-2} d^{-1}, = y) *v* biomass (mgChl m^{2}, = x), where y = Ax + B; r = correlation coefficient; n = number of stations. Production and biomass integrated between surface and 1% light depth. See Fig. 3 for cruise dates. Significance level of r = 0.05, + = significant.

Cruise	A	B	r	Sig.	n
HX71	28	191	.98	+	5
HX72	21	452	.86	+	9
HX74	15	936	.61	+	14
HX85	37	450	.75	+	16
HX88	26	183	.79	+	10
TT213	17	1621	.58	+	20
TT214	26	535	.59	+	17

Table 3. Geometric mean values and ranges of assimilation numbers (P^B = mgC mgChl^{-1} h^{-1}) and productivity indices (P.I. = mgC mgChl^{-1} d^{-1}). See Fig. 3 for cruise dates.

Cruise	P^B	Range	P.I.	Range	n
HX71	4.6	1.9-12	54	22-134	5
HX72	2.9	1.2-7.3	36	15-84	9
HX74	3.7	2.1-6.5	47	24-91	14
HX85	6.7	3.1-14	75	45-124	16
HX88	3.2	1.4-6.9	33	15-75	10
TT213	2.6	1.0-6.4	33	14-79	20
TT214	2.0	0.97-4.3	31	11-84	17

variability in P^B values (Table 3). However, if the stations in the two groups ($\alpha < 2$ and > 2) are considered separately, the correlations between irradiance and P^B are improved, particularly for the $\alpha < 2$ group (Table 4). The geometric mean of the light utilization index values (Ψ) for stations with $\alpha < 2$ was 0.52 mgC mgChl-a^{-1} E^{-1} m^2 (range = 0.28 - 1.0).

Areal production

The estimated daily production within the plume varied between cruises, and was highly correlated with chlorophyll in the upper 15 m of the water column (Fig. 14). It was considerably higher in 1987 than in 1985 or 1986. The ratio of daily production to biomass, an estimate of the specific growth rate, averaged 0.96 d^{-1} (range = 0.73-1.3 d^{-1}).

Flora

The phytoplankton community in the plume was dominated by typical boreal diatoms, such as *Chaetoceros* and *Thalassiosira*. Flagellates greatly outnumbered diatoms at stations outside the plume. The correlation coefficients for the diatom : flagellate ratio compared to α for 5 stations on each of HX72 and HX74 were -0.74 and -0.86, respectively, with the growth efficiency (α) increasing as the diatom : flagellate ratio decreased.

Spring bloom

The presence of sea ice precluded extensive sampling during

Table 4. Regression results for assimilation number (P^B = mgC mgChl^{-1} h^{-1}, = y) vs irradiance (Einsteins m^{-2} h^{-1}, = x), where y = Ax + B; r = correlation coefficient; n = number of stations; α = mgC mgChl^{-1} E^{-1} m^2. The slope of the regression equation (A) = the light utilization index (Ψ). See Fig. 3 for cruise dates. Significance level of r = 0.05; + = significant, - = not significant.

Cruise	A	B	r	Sig.	n
α < 2.0					
HX71	.24	2.6	1		2
HX72	.46	2.7	.30	-	7
HX74	.90	.11	1		2
HX85	.53	.56	.99	+	6
HX88	.43	.38	.95	+	4
TT213	1.6	-.92	.90	+	11
TT214	.32	.83	.34	-	13
α > 2.0					
HX71	.11	1.1	.95	-	3
HX72	-.12	5.2	1		2
HX74	.61	5.2	-.14	-	12
HX85	.12	1.1	.60	+	10
HX88	.17	.66	.64	-	6
TT213	4.9	-.24	.80	+	9
TT214	-2.8	7.5	-.61	-	4
All Stations					
HX71	.06	2.2	.40	-	5
HX72	.002	3.6	.01	-	9
HX74	.06	1.3	-.26	-	14
HX85	.08	1.7	.33	-	16
HX88	.15	.87	.61	-	10
TT213	.99	2.1	.28	-	20
TT214	.58	1.0	.20	-	17

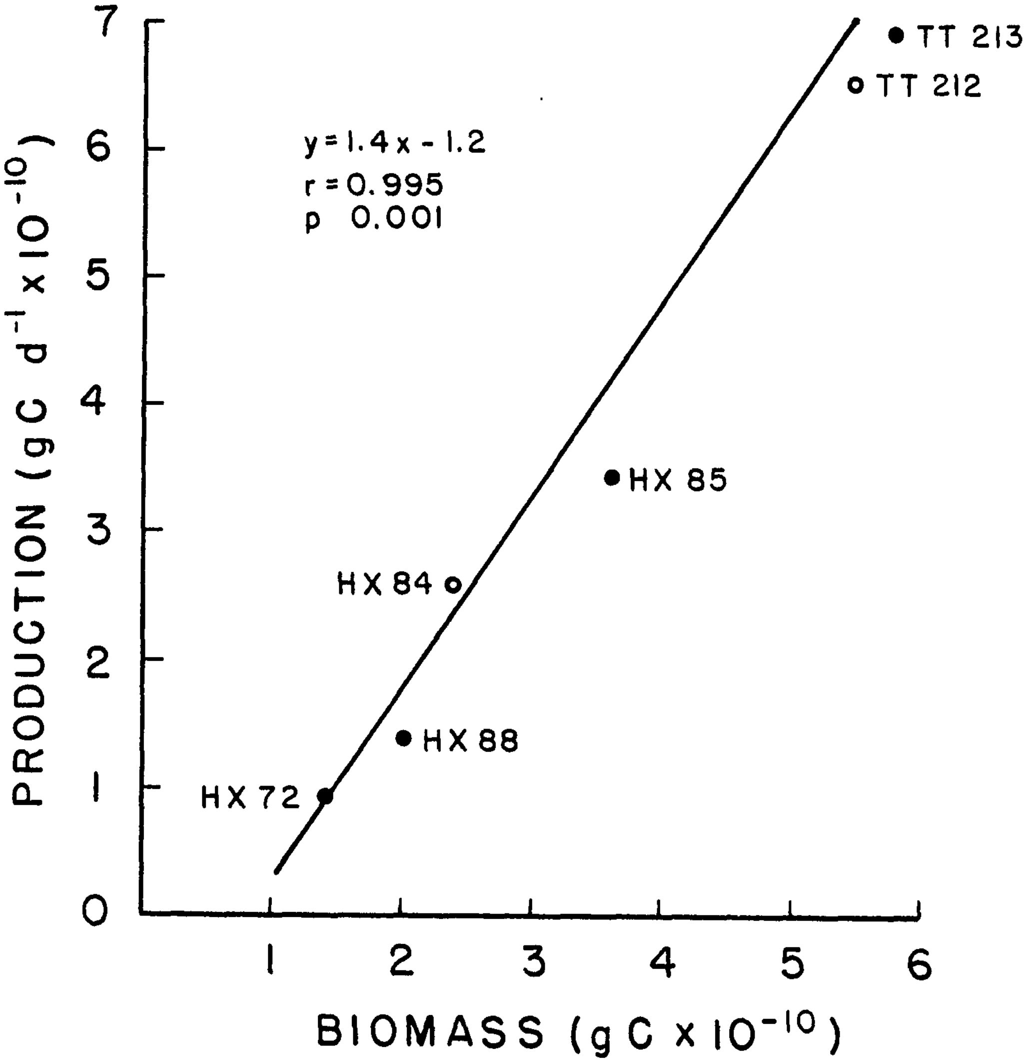

Figure 14. Relation between the estimated daily production and plume chlorophyll south of Bering Strait.

the period of the spring bloom in all years. Chlorophyll concentrations were high in the ice-free region south of Bering Strait during May 28 - June 4, 1986 (Fig. 15). Because ice cover was still extensive, these concentrations might be representative of the spring bloom. However, the presence of oceanic zooplankton throughout most of the survey area at that time confirms the presence of Anadyr Water (Chapter 2), which could also explain the high phytoplankton biomass. Oceanic zooplankton were absent from only two stations during this cruise, those nearest the mainland coast where chlorophyll was low.

The 1983 chlorophyll time series from Cape Lisburne shows the abruptness and magnitude of the decline in production following nutrient depletion in early summer (Fig. 16). This series probably did not include the full bloom period, since open water had been present for several days prior to our first sampling.

DISCUSSION

The plume

The size of the area south of Bering Strait that I have defined as the plume has been smaller on all of our cruises than the area estimated by Sambrotto et al. (1984), averaging about 0.87 x 10^{10} m^2 (range = 0.52-1.4) compared to 2.1 x 10^{10} m^2. The difference arises from the fact that I am considering all waters inside the 25 mg Chl m^{-2} isopleth as the plume, while they defined the plume on the basis of reported nutrient and chlorophyll distributions, and by making the logical, but erroneous, assumption that productivity was

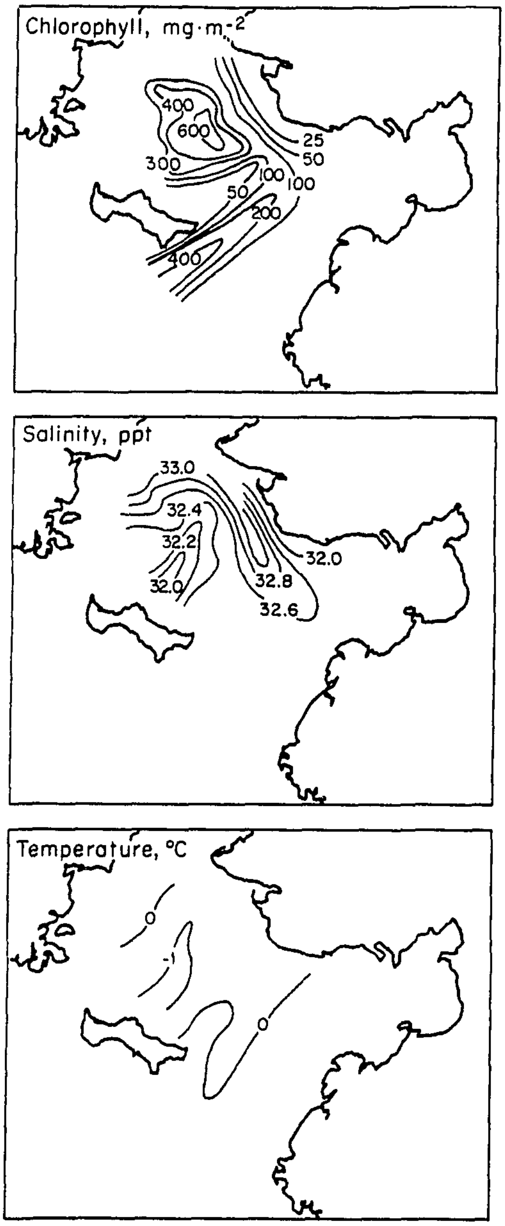

Figure 15. Areal distribution of chlorophyll, bottom salinity and bottom temperature, 28 May - 4 June 1986.

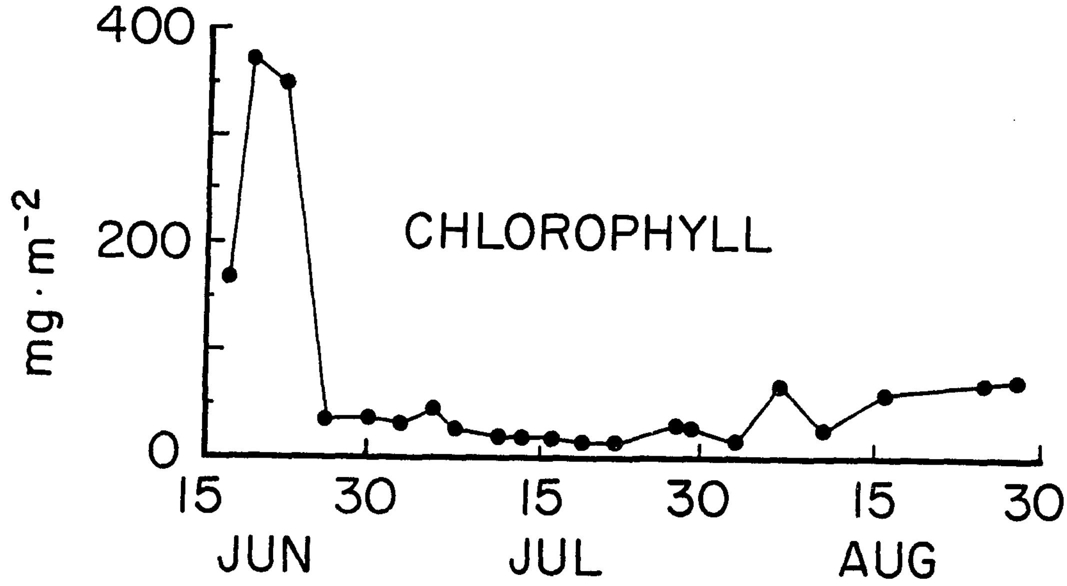

Figure 16. Chlorophyll time series from Cape Lisburne in 1983.

high wherever nutrients and chlorophyll were high. This raises the question of why growth is not greater in Anadyr Water in the western strait area, north and west of St. Lawrence I., where euphotic zone nutrients are high.

One explanation is that turbulence in the Anadyr stream generally is sufficiently great that the critical depth criterion for net phytoplankton production is not met. The water depth is between 30 - 55 m, while the 1% light depth is seldom deeper than about 20 - 30 m. Hydrographic data taken along the Convention Line between Anadyr Strait and Bering Strait indicate that the water column is often well-mixed in this region. Chlorophyll was consistently most concentrated, i.e., phytoplankton growth was highest, just beneath the pycnocline when the water column was stratified. Sufficient stratification apparently can be generated in several ways - for example, by simply heating the surface of Anadyr Water, or by the layering of coastal or shelf water over Anadyr Water from either the west or the east. The displacement of the whole plume downstream from St. Lawrence Island might further be related to current speeds and the time needed for diatom populations to respond to a regime of abundant light and nutrients.

Variability in the flow field, and the resulting nutrient and phytoplankton distributions, is substantial at time scales of a month and year (Figs. 3 & 4), and at the scale of a week. The range of daily variability is probably always much smaller. Variability in the flow field and in vertical stability apparently derives principally from wind forcing, which can significantly affect the transport and trajectory of Anadyr Water through Anadyr Strait (Nihoul et al. 1986), the mixing depth, and thus the ensuing production regime. Such variability might explain why the low areal production value for HX72 (mid-July 1985) was inconsistant with the relatively high chlorophyll inventory beneath the pycnocline.

The area of the northern shelf with elevated bottom layer chlorophyll (mean = 2.1×10^{10} m^2) was always larger than the area of the plume (mean = 0.87×10^{10} m^2). Although the bottom layer area was not significantly correlated with the area of the plume, it was well correlated with the highest value of integrated chlorophyll (surface to bottom) in western Shpanberg Strait ($r = 0.97$, $P < 0.01$). This relation suggests that an important factor governing the areal distribution of phytoplankton biomass on the northern shelf of the Bering Sea is the amount of Anadyr Water that flows around the south side of St. Lawrence I. and through western Shpanberg Strait. Such a flow pattern transports a considerable biomass of phytoplankton onto the northcentral shelf that was apparently grown upstream as well as locally - the two productivity stations occupied near eastern St. Lawrence I. both had uptake rates of over 2 gC m^{-2} d^{-1} (Figs. 11 & 13).

The size of the area of elevated chlorophyll in the bottom layer south of Bering Strait averaged 2.1×10^{10} m^2, which is the same size as the area of the plume estimated by Sambrotto et al. (1984). This area, however, was 2.4 times larger than that of the plume (0.87×10^{10} m^2) during 1985-1987. Therefore, it appears that Sambrotto et al. (1984) overestimated the extent of the region of high production on a daily or weekly basis, but they were accurate in estimating the size of the area affected by it.

Growth efficiencies

The average values of P^B for all cruises were higher than the value of 1.5 mgC $mgChl^{-1}$ h^{-1} reported for the southern Chukchi Sea by Hameedi (1978), who commented on the low assimilation efficiency of the phytoplankton compared to that reported from high arctic stations, which ranged between 3.6 and 7.2 mgC $mgChl^{-1}$ h^{-1} (Smith and English 1973; Pautzke 1974; cited in Hameedi 1978) and which are similar to ours. All of these values are still only about half of the unusually high P^B values of around 15 mgC $mgChl^{-1}$ h^{-1} found on the continental shelf of the southeastern United States (Yoder et al. 1985).

Harrison et al. (1982) reported mean photosynthetic index (P.I.) values of 4.0 mgC $mgChl\text{-}a^{-1}$ d^{-1} for Baffin Bay and 6.7 mgC $mgChl\text{-}a^{-1}$ d^{-1} for all waters in the eastern Canadian Arctic up to 80° N. Our mean P.I. values ranged from 31-75 mgC $mgChl\text{-}a^{-1}$ d^{-1}, indicating a much higher daily efficiency.

The lack of a correlation between P^B and irradiance, and the highly variable values of Ψ for all stations combined differs from the observations of Falkowski (1981) for the New York Bight, where Ψ was valid over three orders of magnitude of chlorophyll, as well as highly variable nutrient and temperature conditions and species composition of the community. The average value of ψ for stations with $\alpha < 2$, 0.58, was similar to measured and modeled estimates in other high-latitude regions (Falkowski 1981, Yoder et al. 1985).

Annual production

Using the estimates of the total daily production (gC d^{-1}) in the plume and the area (m^2) of the plume for cruises where contouring was reliable south of Bering Strait, I calculated an average daily productivity value for the plume. The estimates ranged between 1.5-5.4 gC m^{-2} d^{-1}, with a mean of 2.7 gC m^{-2} d^{-1}, which supports the estimate made by Sambrotto et al. (1984) of 2.7 gC m^{-2} d^{-1}. Sambrotto et al. further calculated an annual production value of 324 gC m^{-2} y^{-1} using the daily rate and an annual growing season of 120 days, which integrated seasonal changes in irradiance and ice cover. The principal difference between their results and mine, therefore, is in the estimate of the area of rapid growth.

Still higher production would be expected in the southern Chukchi Sea, where euphotic zone chlorophyll reached over 1000 mg m^{-2} and productivity reached 16 gC m^{-2} d^{-1} (McRoy et al. in prep). Concurrent benthic process studies found anoxic sediments and a reduced stock of invertebrate macrofauna near the center of the pool in the southern Chukchi Sea, which could have resulted from a heavy rain of phytodetritus (Grebmeier 1987; Henriksen and Blackburn unpubl. data).

Productivity at stations outside of the plume on four cruises where carbon uptake rates were measured and where I was able to reliably contour the chlorophyll distribution averaged 0.50 gC m^{-2} d^{-1} (range = 0.27-0.92, n = 13). During a growing season of 120 days (Sambrotto et al. 1984), 60 gC m^{-2} would be fixed. Assuming an average productivity of 2.0 gC m^{-2} d^{-1} during the intense spring bloom period (Walsh and McRoy 1986), which lasts about 10 days in the southeastern Bering Sea (Sambrotto and Goering 1983), an additional 20 gC would be fixed, yielding a total of 80 gC m^{-2} y^{-1}.

Neither the estimate of Sambrotto et al. (1984) for annual production in the plume nor my estimate of annual production elsewhere includes the contribution from epontic algae, which may be in the order of 20% of the annual production for shelf waters in the Bering Sea (McRoy and Goering 1976), or from ice edge blooms which are thought to predate and to be distinct from the major spring bloom in the Bering Sea (Niebauer and Alexander 1985). Because epontic algae may tend to be nutrient (NO_3) limited (Maestrini et al. 1986), production by this community might be relatively high under the ice bathed by Anadyr Water.

CONCLUSIONS

The flow of water through Bering Strait is the only connection between the Pacific and Arctic oceans, and is an unusual example of a physical process that supplies nutrients to a shallow continental shelf during the summer production season. An estimated average of 0.87 x 10^4 km^2 of the continental shelf south of Bering Strait, and probably an even larger area in the southern Chukchi Sea, experienced high primary production following the spring bloom in 1985-1987. Phytoplankton growth rates were elevated in a plume that ran generally south - north through Bering Strait, with persistent pools of high productivity and phytoplankton biomass in the northern Bering and southern Chukchi seas. The pools corresponded to regions of stability in loops of the stream lines where Anadyr Water mixed with Bering Shelf Water and Alaskan Coastal Water.

An even larger area over the shelf beneath the euphotic zone between St. Lawrence I. and Bering Strait (mean = 2.1×10^4 km^2) exhibited elevated phytoplankton biomass (as chlorophyll). The size of this area on individual cruises was not well correlated with the size of the plume, but was strongly correlated with the water column concentration of chlorophyll in western Shpanberg Strait, which reflected the relative proportion of Anadyr Water flowing south around St. Lawrence I. rather than through Anadyr Strait. The flow of Anadyr Water through western Shpanberg Strait carried phytoplankton biomass grown upstream onto the northcentral shelf and promoted locally high productivity, thereby enlarging to the east the size of the area influenced by flow through Anadyr Strait.

The fertilization of these shelf waters by physical processes maintained the flora in eutrophic bloom conditions, and interrupted normal community development in the plume. Large, chain-forming diatoms flourished among the phytoplankton, while elsewhere, small, solitary diatoms and flagellates typical of oligotrophic waters and later successional communities dominated.

As a result, the structure of food webs supported by the two production regimes is dramatically different. Most of the diatom production in the plumes goes to the bottom. South of Bering Strait the flux is sufficient to support dense benthic faunal populations, up to an average of 5000 individuals m^{-2} of ampeliscid amphipods and tellinid bivalves (Stoker 1981; Grebmeier 1987), which in turn support a large biomass of walruses and gray whales (Frost and Lowry 1981a; Fay 1982). Near the center of the pool in the southern Chukchi, however, the diatom fallout might be great enough to account for anoxic sediments and a dominant microbial food web. Whereas the macrofaunal community accounts for about 60-70 % of the total carbon mineralization in the northern Bering Sea, microbes contribute about 50-95% in the southern Chukchi Sea (Grebmeier 1987; Henriksen and Blackburn, unpubl. data).

The phytoflagellates are thought to participate in an efficient pelagic microheterotrophic food web (Andersen 1986), and they also undoubtedly go through a more direct route via herbivorous zooplankton to fishes and birds (Chapter 2; Springer et al. 1987). Benthic biomass outside of the plume is only about 10 - 50% of that under the plume, and the diversity and number of marine birds along the mainland coast are very low compared to the islands (Sowls et al. 1978). The juxtaposition of such highly contrasting environments and food webs within a small geographic area will continue to provide an unusual opportunity to follow patterns of community structure and development, energy production and allocation, and the effects on biological processes of dynamic physical variability at time scales of days, seasons and years.

CHAPTER 2

Zooplankton Communities

INTRODUCTION

The continental shelf of the northern Bering Sea and southern Chukchi Sea has been recognized for many years as a region of unusually high marine production at several trophic levels, from primary producers (McRoy et al. 1972) to benthic invertebrates (Stoker 1981), seabirds (Fay and Cade 1959; Bedard 1969a,b), and marine mammals (Nasu 1974; Fay 1982). The abundant flora and fauna seemed paradoxical, since the region is generally less than 50 m in depth and distant from the known source of nutrients at the shelf edge, several hundred kilometers in either direction, that could support such dense populations of marine biota. However, recent studies have greatly improved our understanding of the physical processes on the Bering-Chukchi shelf, and the conclusion which has emerged is that the advection of oceanic water from far to the south is responsible for the biological richness (Sambrotto et al. 1984; Springer and Roseneau 1985; Springer et al. 1987; Walsh et al. 1988; Chapter 1).

The oceanic water, Anadyr Water, is the northern branch of the Bering Slope Current that originates along the continental shelf break of the Bering Sea (Coachman et al. 1975; Kinder et al. 1975) (Fig. 17). It is a marine "river" flowing north through western Bering Strait and carrying abundant nutrients onto the shallow northern shelf. The nutrients, primarily nitrate, allow for prolific primary production throughout summer over a large portion of the Bering Strait region (McRoy et al. 1972; Sambrotto et al. 1984; Chapter 1).

In addition to nutrients, and probably more important to

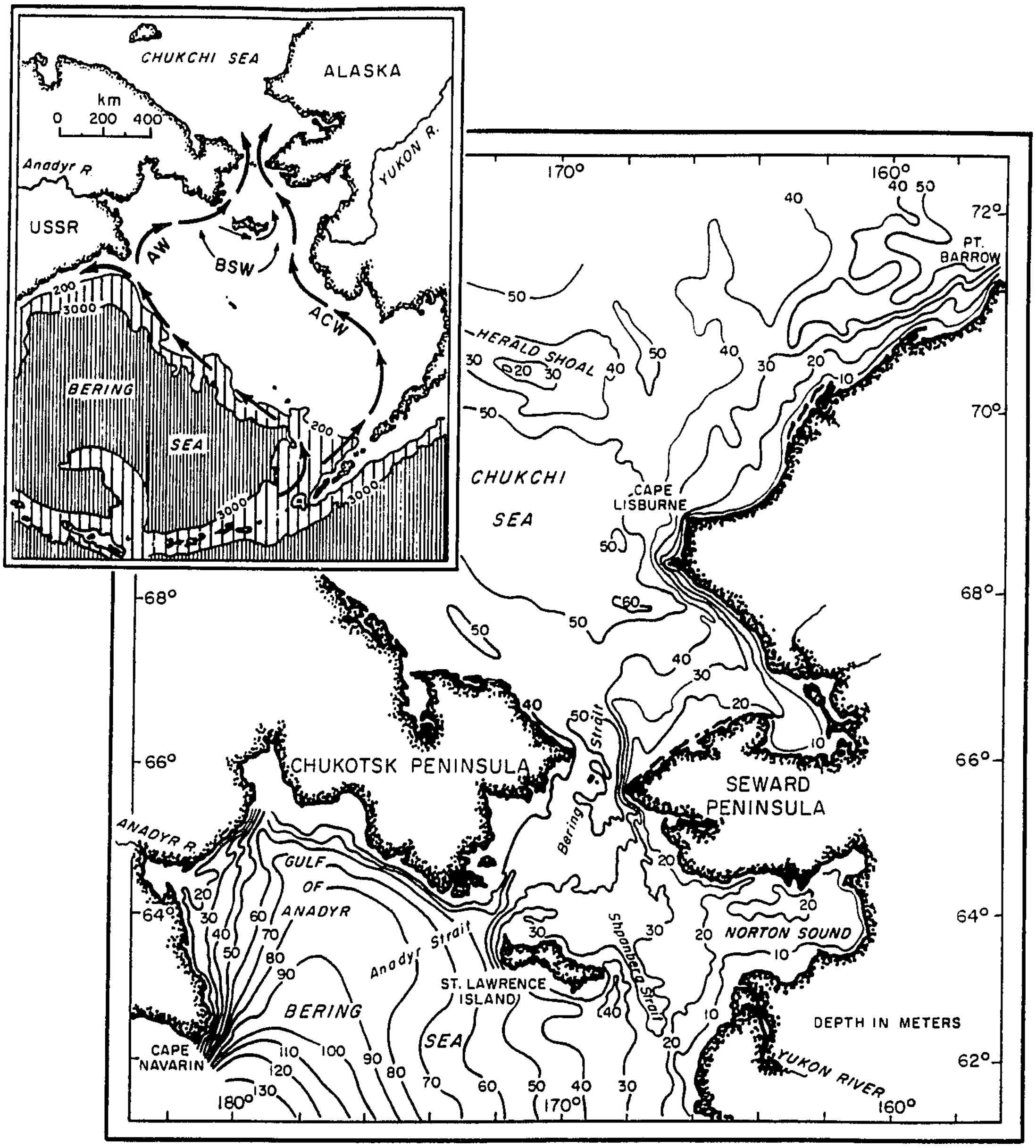

Figure 17. The Bering-Chukchi shelf, with generalized circulation patterns and origins of the principal water masses flowing north through Bering Strait (from Coachman et al., 1975). In the inset AW = Anadyr Water, BSW = Bering Shelf Water, and ACW = Alaskan Coastal Water.

pelagic food webs on the northern self, Anadyr Water carries with it a considerable biomass of oceanic zooplankton. An obvious example of the trophic importance of the zooplankton are the immense populations of auklets (*Aethia* spp.) in the northern Bering Sea that feed primarily on *Neocalanus cristatus* and *N. plumchrus* (Bedard 1969a; Springer and Roseneau 1985). Although these and other oceanic species of zooplankton are normally excluded from the expansive shelf shoreward of the middle front in the southern Bering Sea (Iverson et al. 1979; Cooney 1981; Smith and Vidal 1984), they are known to enter the Chukchi and Beaufort seas (Johnson 1956, 1958; Wing 1974) and even the Arctic basin (Johnson 1963), and their presence there has, in a general sense, been attributed to the flow of water through Bering Strait.

In the southeastern Bering Sea, the herbivorous zooplankton of the oceanic and outer shelf domains, primarily the large calanoid copepods *Neocalanus cristatus*, *N. plumchrus*, *Eucalanus bungii* and *Metridia pacifica* (Cooney 1981; Smith and Vidal 1984), apparently can control the spring diatom bloom (Kokur 1982), and are important in the allocation of carbon to pelagic and benthic food webs (Cooney and Coyle 1982; Dagg et al. 1982; Dagg and Wyman 1983). Because the biomass of oceanic species advected onto the northern shelf is substantial, as indicated by the numbers of planktivorous seabirds, they could be important in regional carbon budgets there as well. To assess this possibility I sampled the zooplankton as part of ISHTAR (Inner SHelf Transfer and Recycling), a continuing, multidisciplinary study of the oceanography of the Bering-Chukchi continental shelf.

The primary objectives of the zooplankton study were to determine the distribution of the oceanic community in the study area and to estimate their biomass.

METHODS

Vertical tows from about 1 m above the bottom to the surface were made during cruises of the RV Alpha Helix in the summers of 1985 and 1986 (Fig. 18). No samples could be taken west of the United States - Soviet Union Convention Line because of international politics. A 1 m diameter, 505 um mesh net was used on all cruises except HX72 (12-24 July 1985), when a 0.5 m diameter, 303 um mesh net was used. The larger net did not adequately sample small species of zooplankton, i.e., those smaller than Pseudocalanus spp., so they are considered below only for HX72. The smaller species are the subject of a related study of pelagic food webs in the coastal zone (Springer et al. 1987, unpubl. data). All samples were preserved in 5% formalin in seawater.

To estimate the biomass of zooplankton, I weighed individuals of most species after drying them at 65°C for 12 hours and corrected the weights for an estimated 40% loss due to formalin preservation (Vidal and Smith 1986), or I relied upon literature values (Harris 1985; Vidal and Smith 1986). Sagitta elegans were divided into three size groups, small, medium and large; Oikopleura spp. and Aglanthe digitale were divided into two groups, small and large, and the average weight of the groups was determined. Individuals in each

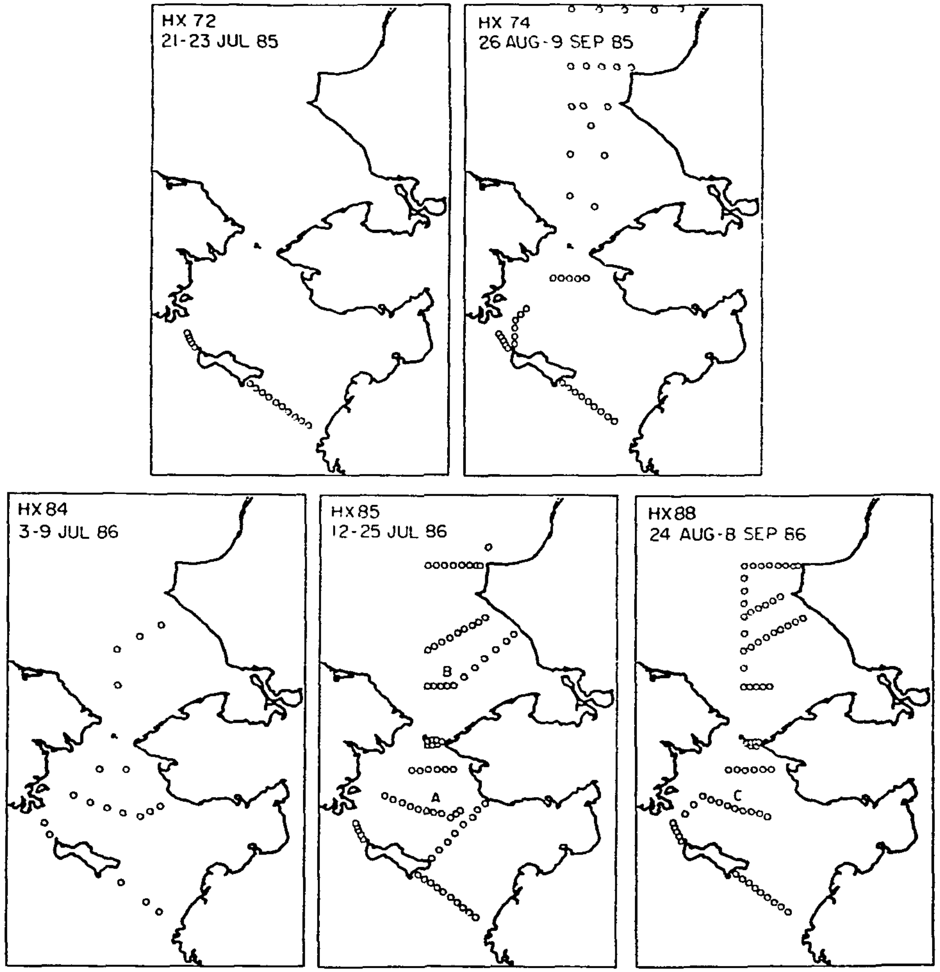

Figure 18. Locations of stations sampled for zooplankton in 1985 and 1986.

sample were then tallied by group so that a more appropriate estimate of biomass could be made. A single weight was used for each species of copepod except *Calanus marshallae*, which was divided into two weight groups represented by stage III copepodids and adults.

The boundary between Anadyr Water and Bering Shelf Water occurred at a salinity of about 32.5 ppt in 1985 and 1986 (Coachman 1986); that is, water with a salinity of 32.5 ppt consisted of approximately equal proportions of the two water masses. Oceanic copepods, however, frequently crossed this isopleth and on several cruises were found in waters with bottom salinities as low as 32.0 ppt, particularly north of Bering Strait. Since there was no difference between copepod numbers west of 32.5 ppt, the nominal boundary, and numbers between 32.5 and 32.4 ppt (Kruskall-Wallis test, $p < 0.05$), we used the 32.4 ppt isopleth of bottom salinity and the 32.4 ppt envelope to partition shelf waters for subsequent analyses.

To assess spatial and temporal variability in zooplankton numbers and biomass, I first determined if there were differences from west to east of the 32.4 ppt isopleth of bottom salinity and from south to north of Bering Strait by comparing the values in four quadrants - southwest, northwest, southeast and northeast. Adjacent quadrants west and east of 32.4 ppt were lumped if no significant differences were found between them (Kruskall-Wallis test, Multiple Comparisons Procedure, $p < 0.05$) and they were then compared to each other, i.e., west versus east.

I estimated the flux of zooplankton biomass into the study area in two ways. In Method 1 I assumed that most of the individuals of oceanic origin were contained within the 32.4 ppt cross-sectional envelope in Anadyr Strait, which marked the nominal boundary between Anadyr Water and water from elsewhere. Results from vertically stratified sampling over Anadyr Water in 1987 supported that assumption (Springer et al. unpubl. data). Based on cross sections presented by Coachman et al. (1975), I extended the boundary from its depth at our western-most station in Anadyr Strait to near the Siberian coast. I could then estimate the concentration of zooplankton in the water mass, i.e., the biomass m^{-3}, and an approximate volume percent of Anadyr Water in Anadyr Strait. By using transport data from the same periods during summer, presently available for 1985 only, I estimated the transport of biomass of oceanic species into the study area. This method was modified for estimating the transport of total zooplankton by calculating the concentration of animals using the full sampling depth and by using the total transport through Anadyr Strait. The transport of zooplankton through Shpanberg Strait was calculated using this modification. In Method 2 I used the width of each strait (Anadyr Strait = 85 km, Shpanberg Strait = 175 km) the average velocity of the water flowing through them at the time of each cruise (about 45 and 40 cm s^{-1} in Anadyr Strait on HX72 and HX74, respectively, and about 10 and 15 cm s^{-1} in Shpanberg Strait on HX72 and HX74, respectively) and the average biomass (m^{-2}) of zooplankton for each transect to estimate the flux.

I have reported data for only those taxa of zooplankton that were either abundant or had distributions diagnostic of hydrographic conditions and circulation. I used the transects from cruise HX72 (21-23 July 1985) to illustrate the distribution of zooplankton across Anadyr Strait and Shpanberg Strait, the "zooplankton boundary conditions," because the samples were collected with a smaller mesh net that better represented all species. My sampling coverage of the study area was most complete on HX85 (12-25 July 1986), and I have used these data to illustrate the general pattern of areal distribution of the zooplankton north of Anadyr and Shpanberg straits.

Most samples were obtained as part of the ISHTAR project. Additional samples of zooplankton were provided by R. Highsmith for the period 28 May - 4 June 1986. All of the unpublished physical data referred to throughout this paper were taken from ISHTAR hydrographic reports for 1985 and 1986 (Institute of Marine Science, University of Alaska, Fairbanks), and the nutrient data are from T. Whitledge (unpubl. data).

RESULTS

Hydrography

The northward flow of water through Bering Strait is primarily barotropic, resulting from a north - south atmospheric pressure differential that tilts the sea level down toward the north (Coachman et al. 1975). The calculated mean annual transport has varied between 0.56 - 0.91 Sv during the past 85 years, and is generally well-correlated with the north - south component of the local wind (Coachman MS). On average, the transport is larger and less variable in the summer months, 1.1 + 0.2 Sv, than in the winter, 0.4 + 0.4 Sv.

The origins of the three principal water masses on the northern shelf differ, which leads to distinctive physical and chemical signatures of each. Anadyr Water originates at depth along the continental slope of the Bering Sea, Bering Shelf Water originates over the middle shelf of the northern Bering Sea south of St. Lawrence Island, and Alaskan Coastal Water originates over the inner shelf of the southeastern Bering Sea (Coachman et al. 1975; Kinder et al. 1975). Alaskan Coastal Water is further freshened by the discharge of the Yukon River into outer Norton Sound. The nominal boundaries separating Anadyr Water from Bering Shelf Water, and Bering Shelf Water from Alaskan Coastal Water are defined as the 32.5 ppt and 31.8 ppt isopleths, respectively, across Anadyr Strait and Shpanberg Strait (Coachman 1986). Cross sections through these two straits in mid-July of 1985 and 1986 illustrate the hydrographic boundary conditions on the northern shelf and interannual variability in the flow fields (Fig. 19).

Anadyr Water was prominent in Anadyr Strait in summer of both years, but was replaced in the eastern strait by Bering Shelf Water. Both of these water masses were overlain by coastal water, in this case coastal water originating along the Siberian coast. Anadyr Water occupied a greater proportion of Anadyr Strait in 1985 than in 1986, and part of it traveled eastward around the south side of St. Lawrence Island in 1985, entering the study area through western Shpanberg Strait. Bering Shelf Water and Alaskan Coastal Water accounted for the remainder of the volume in Shpanberg Strait in 1985 and for the

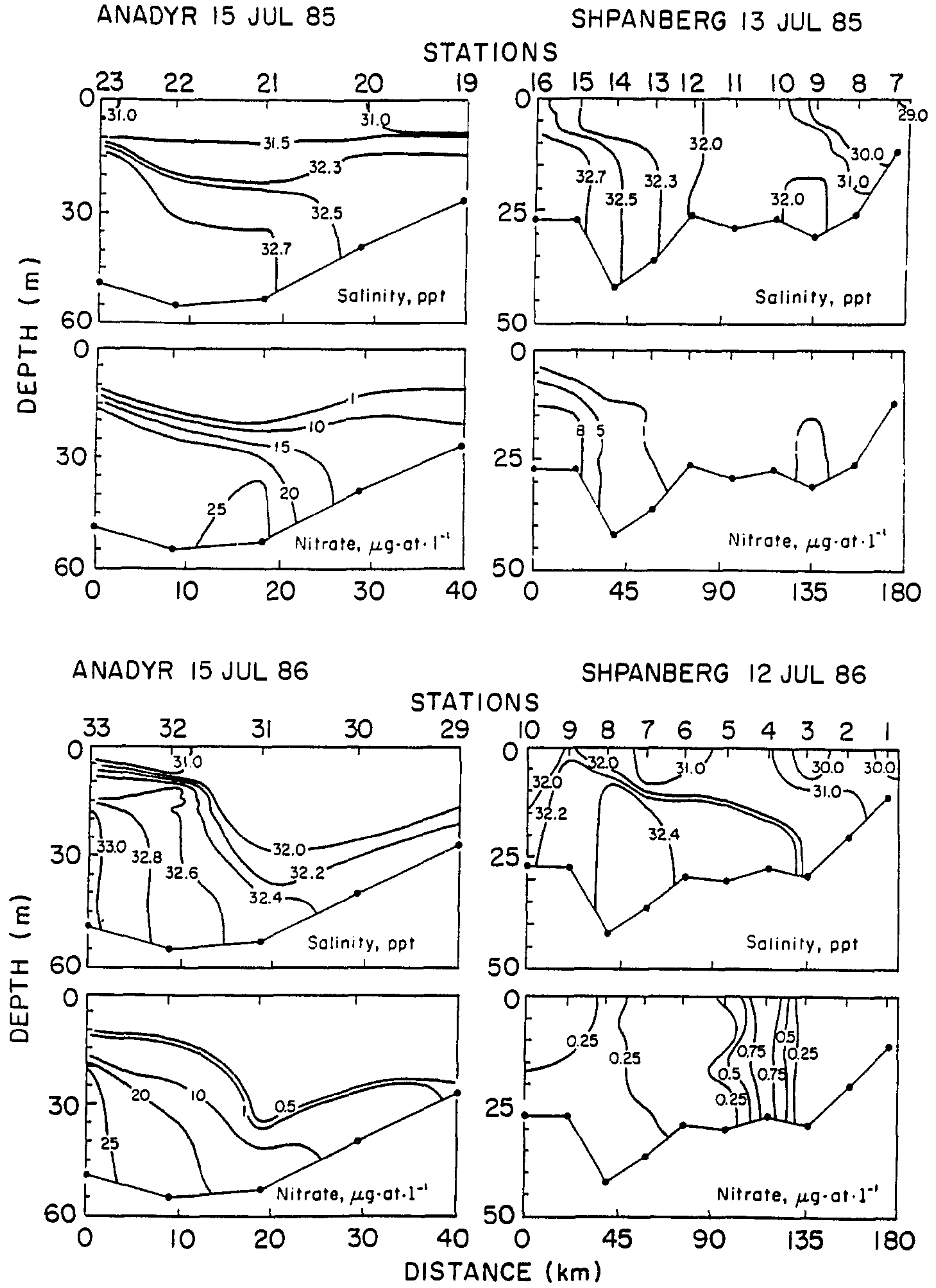

Figure 19. Cross-sections of salinity and nitrate in Anadyr and Shpanberg straits in mid-July 1985 and 1986. High salinity and nitrate are indicative of Anadyr Water in Anadyr Strait in both years, and in western Shpanberg Strait in 1985 only.

total volume in 1986.

North of Anadyr and Shpanberg straits, topographic steering led to general circulation patterns that tended to conform to the bathymetry (Fig. 20, compare isopleths of bottom salinity and integrated nitrate to bathymetry in Fig. 17), as described for this region by Coachman et al. (1975). Anadyr Water was held to the west by the lighter shelf and coastal waters, except in a broad mixing region in the southern Chukchi Sea where the flow looped eastward.

Zooplankton boundary conditions

Among the copepods, the oceanic species *Neocalanus cristatus*, *N. plumchrus*, *Eucalanus bungii* and *Metridia pacifica* occurred predominately in Anadyr Strait (Fig. 21). Small numbers were occasionally found in western Shpanberg Strait in 1985 presumably because of the eastward flow of Anadyr Water south of St. Lawrence Island. *Calanus marshallae* predominated in Bering Shelf and Alaskan Coastal water in Shpanberg Strait, but was replaced in eastern Shpanberg Strait by *Pseudocalanus* spp. and by *Eurytemora* spp. and *Acartia longiremis* which are typical nearshore species (Cooney 1981). *Pseudocalanus* spp. and another small copepod, *Oithona similis*, were generally wide-spread and abundant compared to the rest. *Centropages abdominalis* was not encountered in Shpanberg Strait on this cruise, but was common there at other times.

Euphausiid furcilia, primarily *Thysanoessa raschii*, and the larvacean *Oikopleura* spp. were abundant in Anadyr Strait but not Shpanberg Strait (Fig. 22). *T. raschii* is apparently most abundant

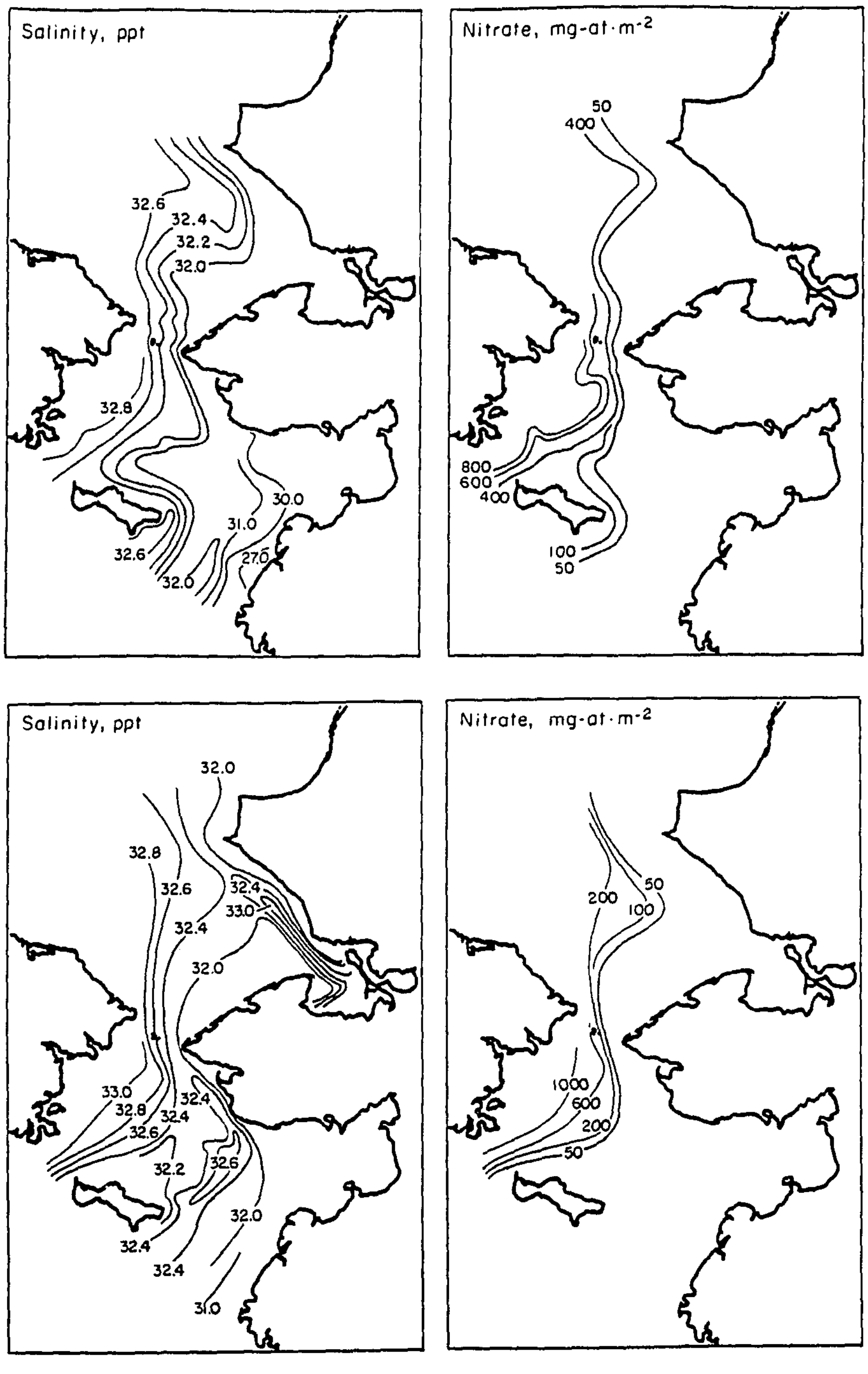

Figure 20. Areal distribution of bottom salinity and integrated nitrate, 12-24 July 1985 (above) and 11-26 July 1986 (below).

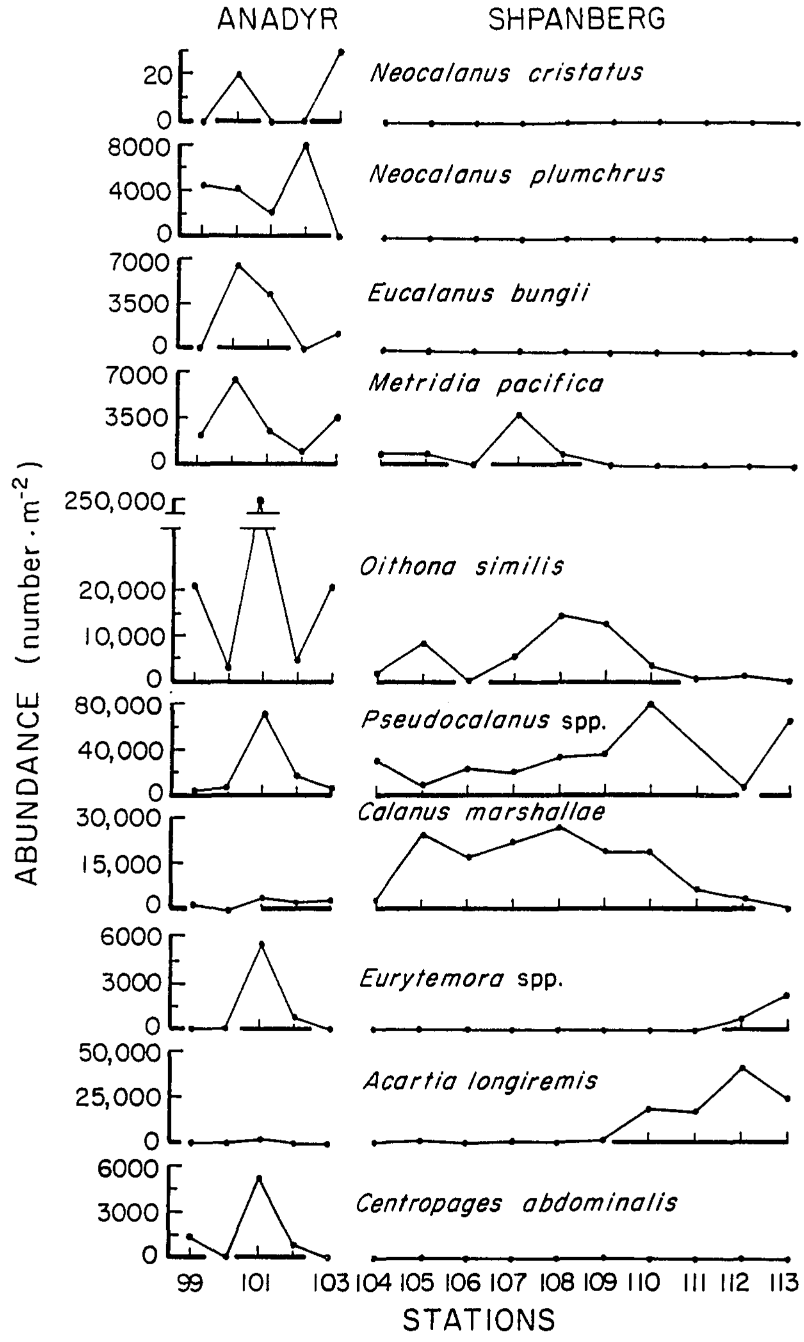

Figure 21. Distribution of abundance of copepods across Anadyr and Shpanberg straits, 21-23 July 1985.

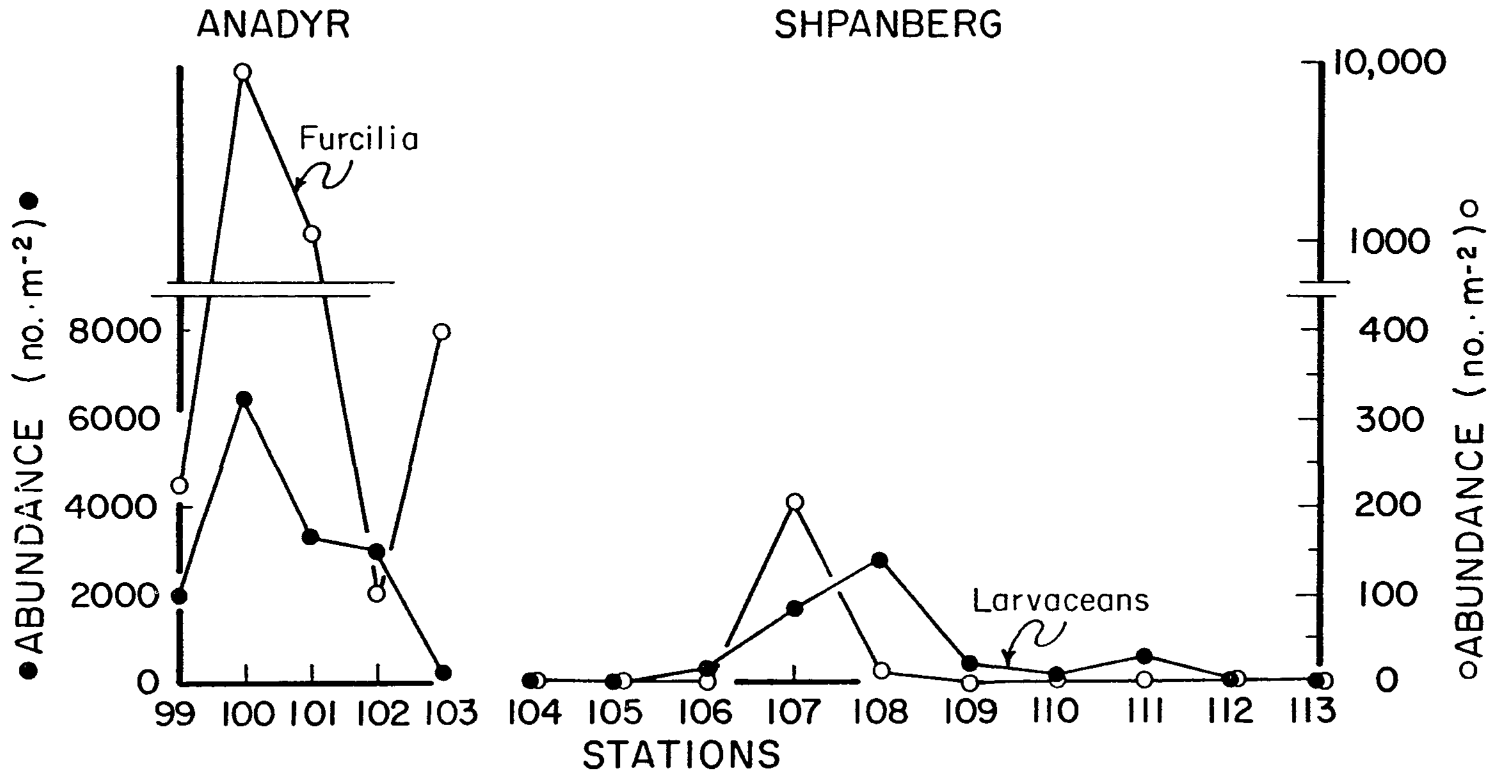

Figure 22. Distribution of abundance of <u>Oikopleura</u> spp. and <u>Thysanoessa</u> <u>raschii</u> furcilia across Anadyr and Shpanberg straits, 21-23 July 1985.

over the shelf of the northwest Bering Sea and is replaced by *T. longipes* in oceanic water off the shelf (Motoda and Minoda 1974). Larvaceans are considered oceanic species that do not effectively penetrate shelf waters (Cooney 1981; Shiga 1982). However, the abundance of individuals in Anadyr Strait, in the range of 2000 - 6000 m^{-2} at all but the eastern-most station, was as high as the highest values (3000 - 4500 m^{-2} south of Kamchatka) in the N. Pacific, including the Bering Sea, reported by Shiga (1982).

Sagitta elegans and *Aglanthe digitale*, the dominant carnivores, were more or less evenly distributed across both straits (Fig. 23). *S. elegans* in Anadyr Strait were generally larger than those in Shpanberg Strait, however, and juvenile *A. digitale* were present in Anadyr Strait, but not Shpanberg Strait, indicating differences in the production regimes of the two water masses. *Eukronhia hamata*, an oceanic chaetognath (Bieri 1959; Kotori 1976), occurred at one station in Anadyr Strait on 13 July 1985 (HX72), as well as at stations in and near Anadyr Strait on other cruises.

Limacina helicina entered the study area principally through Anadyr Strait, and most *Clione limacina* entered through western Shpanberg Strait (Fig. 24). According to Motoda and Minoda (1974), both species of pteropods are distributed mainly over the central and western Bering Sea, but also occur over the eastern shelf.

Copepods accounted for about half of the estimated dry weight biomass of zooplankton in Anadyr Strait, except near St. Lawrence Island where there was little else (Fig. 25). After copepods, the biomass of the pteropods and larvaceans were next highest, with the

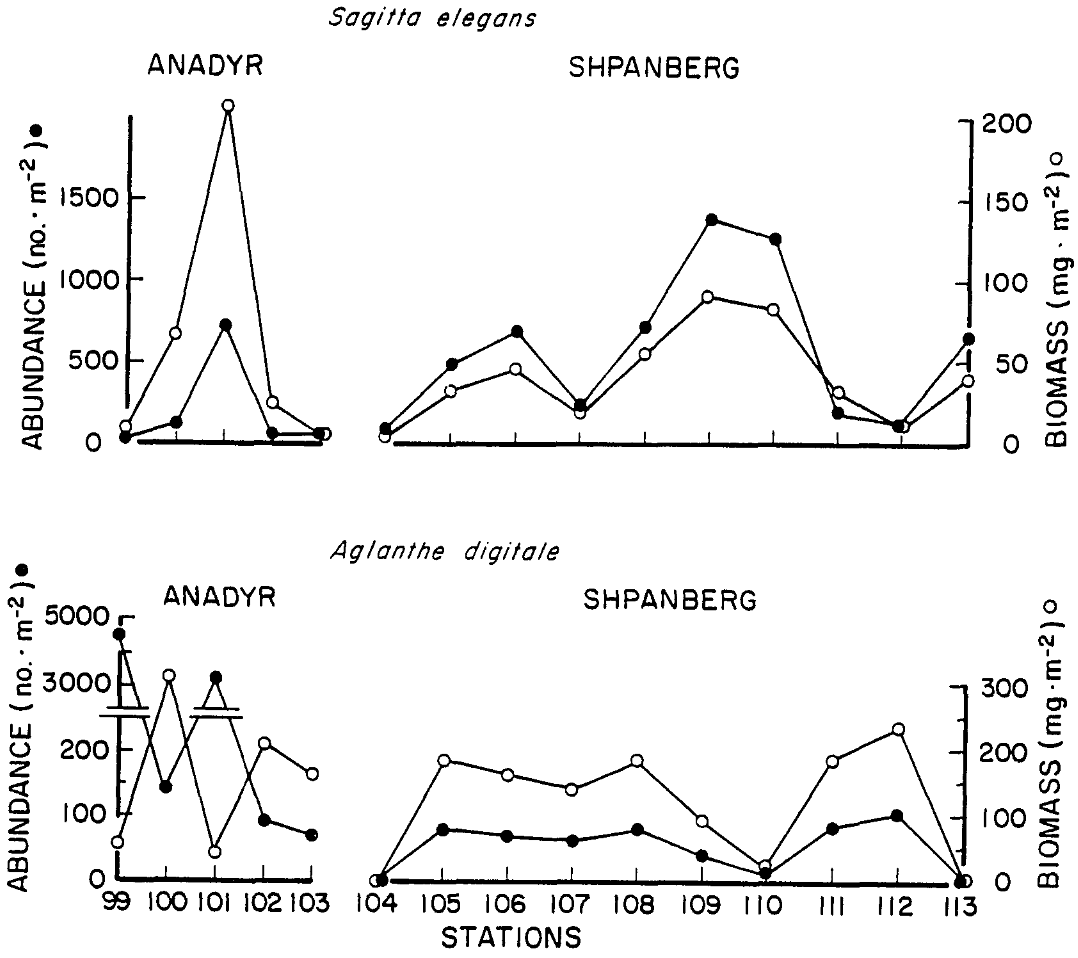

Figure 23. Distribution of abundance and biomass of Sagitta elegans and Aglanthe digitale across Anadyr and Shpanberg straits, 21-23 July 1985.

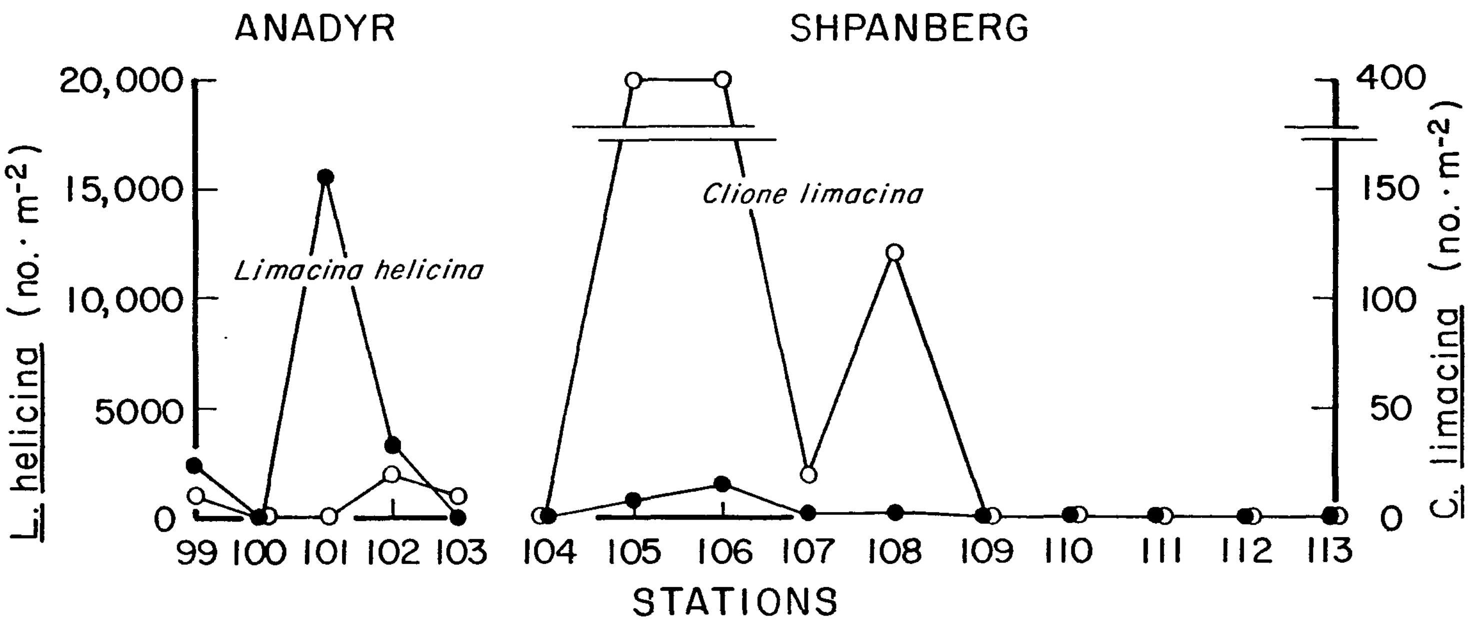

Figure 24. Distribution of abundance of Clione limacina and Limacina helicina across Anadyr and Shpanberg straits, 21-23 July 1985.

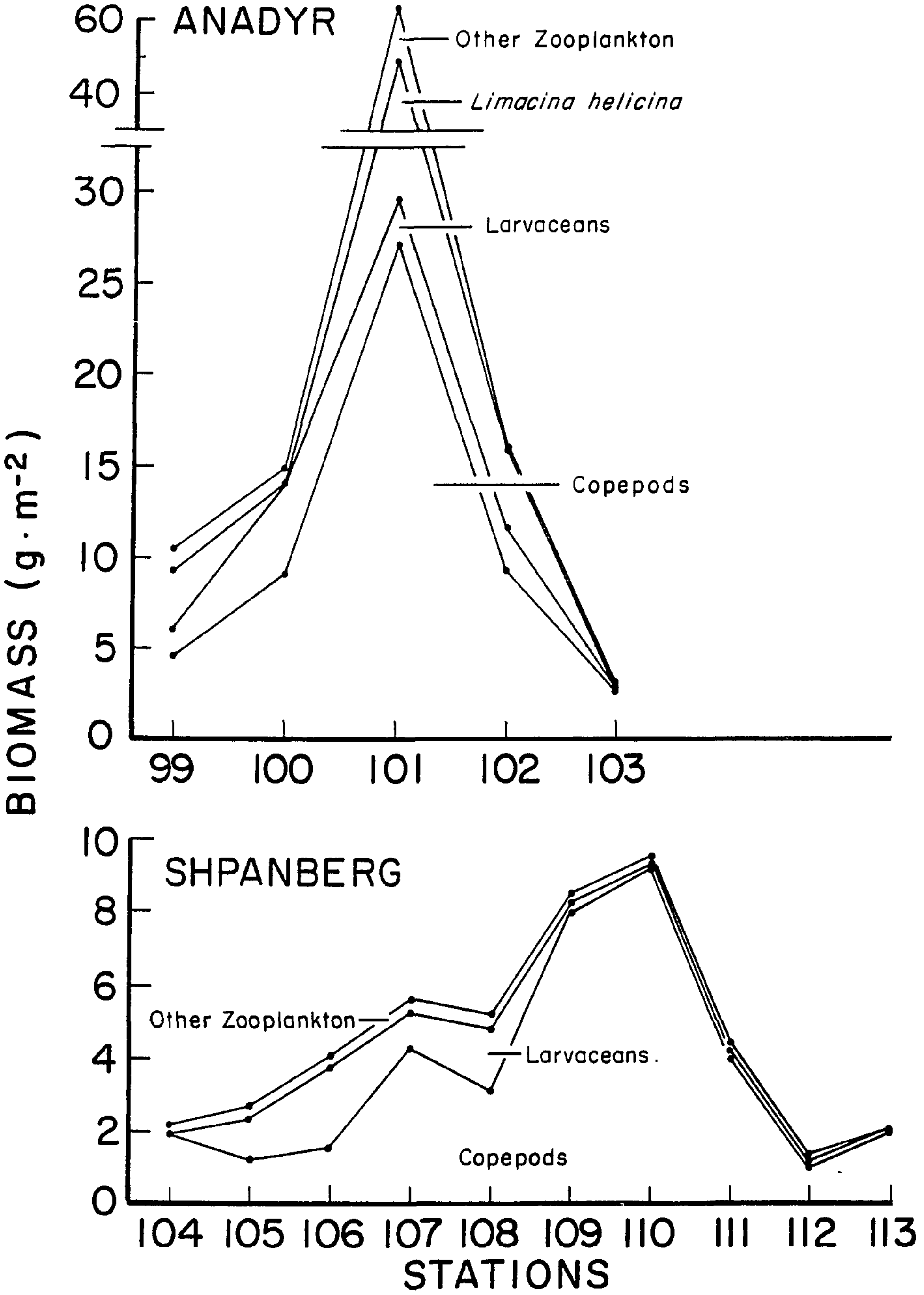

Figure 25. Distribution of zooplankton biomass across Anadyr and Shpanberg straits, 21-23 July 1985.

contribution from other taxa being relatively small. Because of their large size during mid-July 1985, the larvaceans contributed up to nearly 5 g dry weight m^{-2}, or 37%, to the total biomass of the herbivores in Anadyr Strait. Although often quite numerous, the juvenile euphausiids were of relatively minor importance in terms of biomass, contributing at most about 1 g dry weight m^{-2}, or about 7%, to the total. The large biomass of the "Other zooplankton" category at Station 101 was due to an unusual abundance of juvenile *Parathemisto* spp. Copepods and larvaceans were the dominant taxa in the western part of Shpanberg Strait, except near St. Lawrence Island where larvaceans were uncommon, as they were nearshore in eastern Anadyr Strait (Fig. 25). Copepods predominated across the eastern portion of Shpanberg Strait. Taxa other than copepods and larvaceans were not important anywhere.

The four oceanic species of copepods, *Neocalanus cristatus*, *N. plumchrus*, *Eucalanus bungii* and *Metridia pacifica*, contributed 70% - 90% of the copepod biomass in Anadyr Strait in July 1985, while *Calanus marshallae* accounted for a similar proportion in Shpanberg Strait (Fig. 26). The geometric mean copepod biomass (9.0 g dry weight m^{-2}) and highest value (27 g m^{-2}) at the five stations in Anadyr Strait are similar to estimates of peak standing stocks of 9.9 g m^{-2} (Ikeda and Motoda 1978), 8 - 40 g m^{-2} (Cooney 1981) and 10 - 14 g m^{-2} (Vidal and Smith 1986) over the continental slope and outer shelf of the southeastern Bering Sea. The mean biomass in Shpanberg Strait, excluding the three western-most stations where Anadyr Water contributed substantially to the total flow, and the two eastern-most,

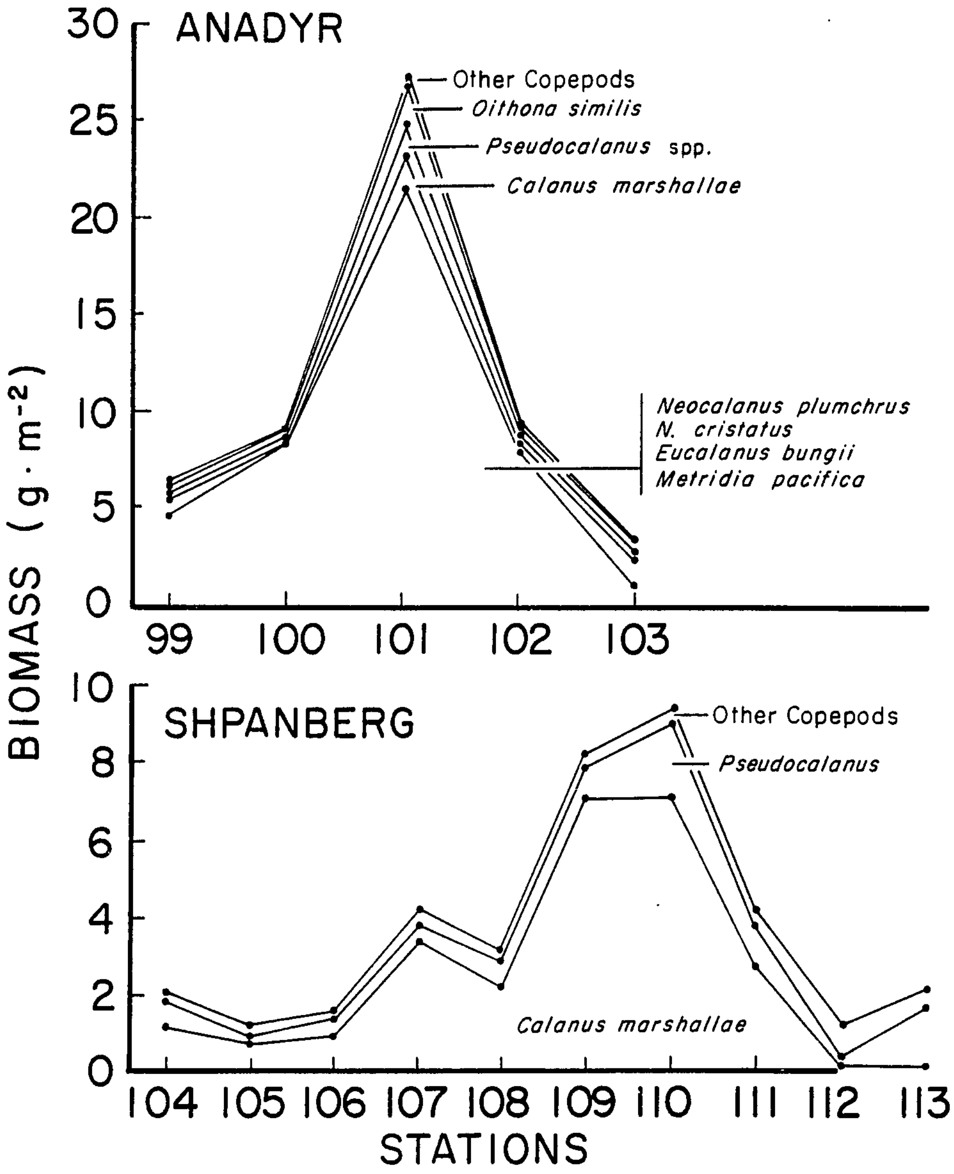

Figure 26. Distribution of copepod biomass across Anadyr and Shpanberg straits, 21-23 July 1985.

nearshore stations, was 5.2 g dry weight m^{-2}. This value is similar to the estimate of a peak standing stock of 3.9 g m^{-2} in the middle domain of the southeastern Bering Sea in August 1975 (Cooney 1981), and an estimated range of about 2.5 - 6.0 g m^{-2} over the northern shelf reported by Motoda and Minoda (1974). It was nearly 4 times greater than copepod biomass over the middle domain in early June 1980 (Vidal and Smith 1986), but this might be expected since the middle shelf community reaches its greatest biomass several weeks after that of the oceanic community. The average copepod biomass at the two nearshore stations in Shpanberg Strait, numbers 112 and 113, was 1.5 g m^{-2}, of which about half was _Pseudocalanus_ spp. and half was _Acartia longiremis_. This value is similar to a previous estimate of 1.3 g m^{-2} in the nearshore zone of the southeastern Bering Sea in August 1975, the apparent period of peak zooplankton abundance there (Cooney 1981).

Areal distributions

The areal distributions of the zooplankton over the shelf between St. Lawrence Island and Bering Strait on all cruises conformed to their distributions in Anadyr and Shpanberg straits. The oceanic copepods generally were found west of the 32.4 ppt isopleth of bottom salinity (Fig. 27), where they were always significantly more abundant, with numbers 33 - 619 times greater and biomass 26 - 1005 times greater west of 32.4 ppt than east of it. Eastward excursions across 32.4 ppt by the oceanic species were greater north of Bering Strait, probably because of turbulence and increased mixing through the strait. In comparison, _Calanus marshallae_ was generally (Fig.

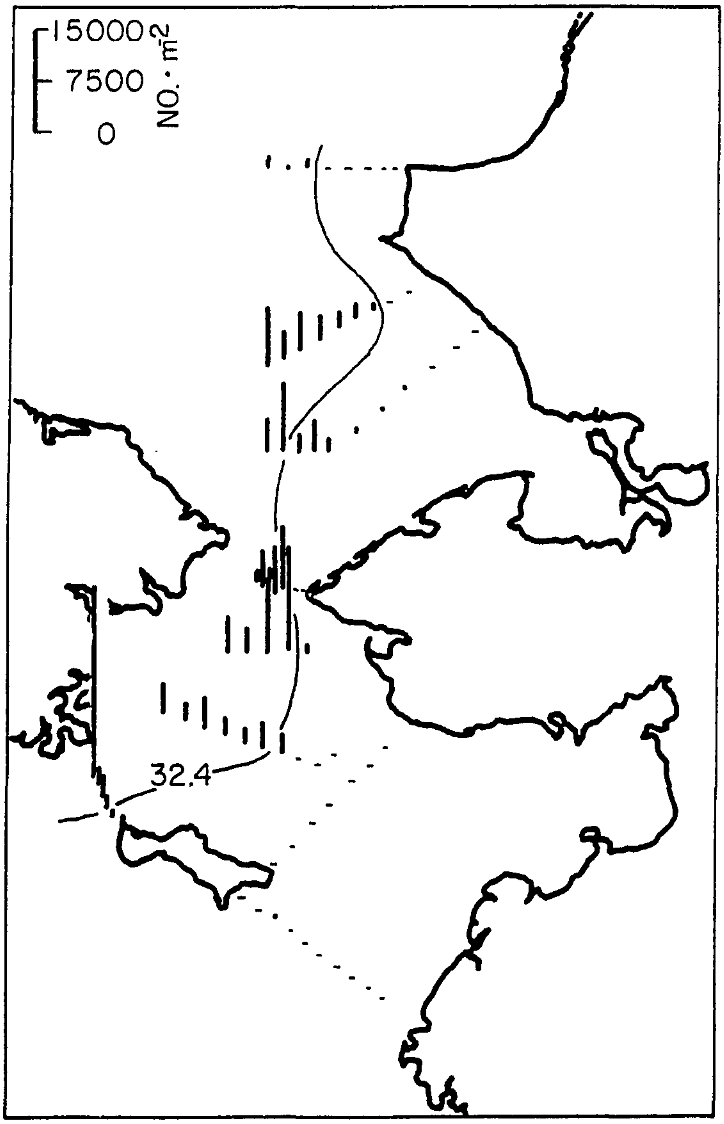

Figure 27. Areal distribution of abundance of oceanic copepods, 11-26 July 1986. Combined numbers of *Neocalanus cristatus*, *N. plumchrus*, *Eucalanus bungii* and *Metridia pacifica*).

28), but not always (Fig. 29) most abundant east of the 32.4 ppt isopleth. The tendency toward westward excursions was particularly pronounced in 1986.

Pseudocalanus spp. was more wide-spread than were the larger copepods, particularly south of Bering Strait (Fig. 30), although it was more abundant west of 32.4 ppt on all but the July 1985 cruise (see below). *Pseudocalanus* is widely distributed in the southeastern Bering Sea also, being common in the oceanic, middle and inner shelf, and nearshore communities (Cooney 1981). Since several species comprise the group of *Pseudocalanus* spp. (Smith and Vidal 1984), differences in numbers across the northern shelf could be due to changing species distributions. *Centropages abdominalis* was absent from many stations, somewhat more in the north, and tended to occur around the perimeter of the sampling area (Fig. 31). *C. abdominalis* is considered to be a neritic species (Motoda and Minoda 1974; Cooney 1981), and probably enters the northern shelf region in both Alaskan Coastal Water and coastal water originating along the Siberian coast that is entrained in the overall northward flow.

Euphausiid furcilia and the hyperiid amphipod *Parathemisto pacifica* were western species (Figs. 32 and 33), but not necessarily oceanic ones. *P. pacifica* is characteristically found in the western and central Bering Sea, while *T. raschii* is most abundant on the northwest shelf (Motoda and Minoda 1974). Crab and shrimp zoea were shelf taxa that were generally not abundant or evenly distributed (Figs. 34 and 35). *Oikopleura* spp., which is not shown here, was very abundant in Anadyr Strait in mid-July 1985, but was nearly absent

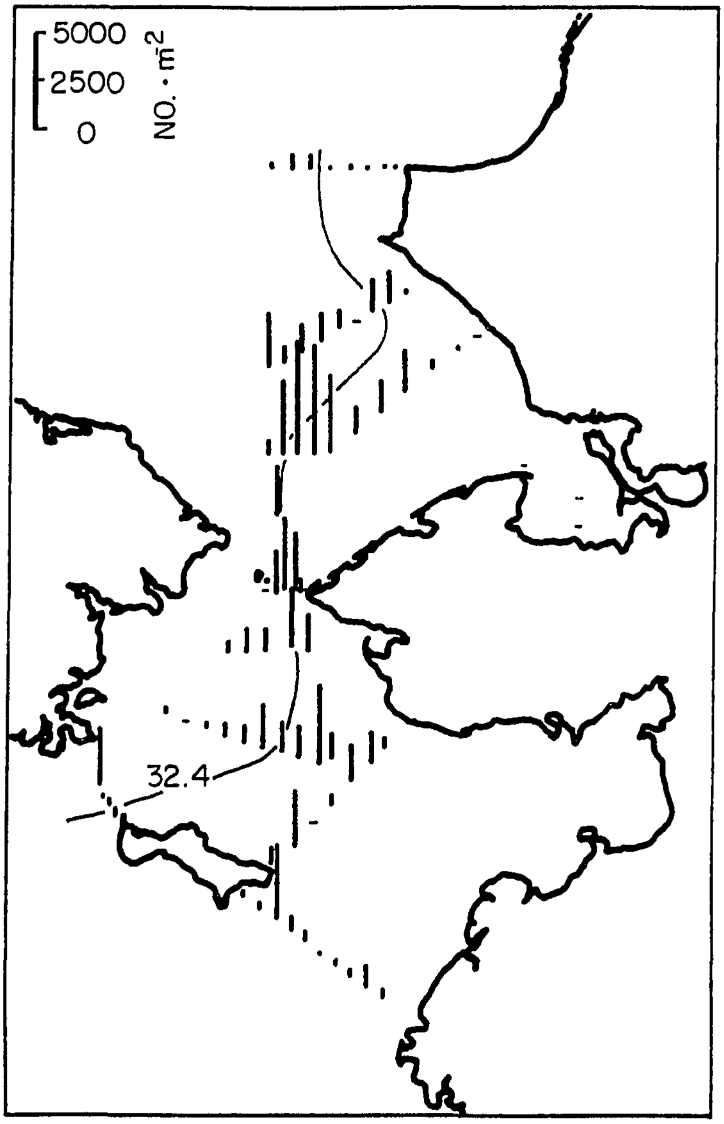

Figure 28. Areal distribution of abundance of *Calanus marshallae*, 11-26 July 1986.

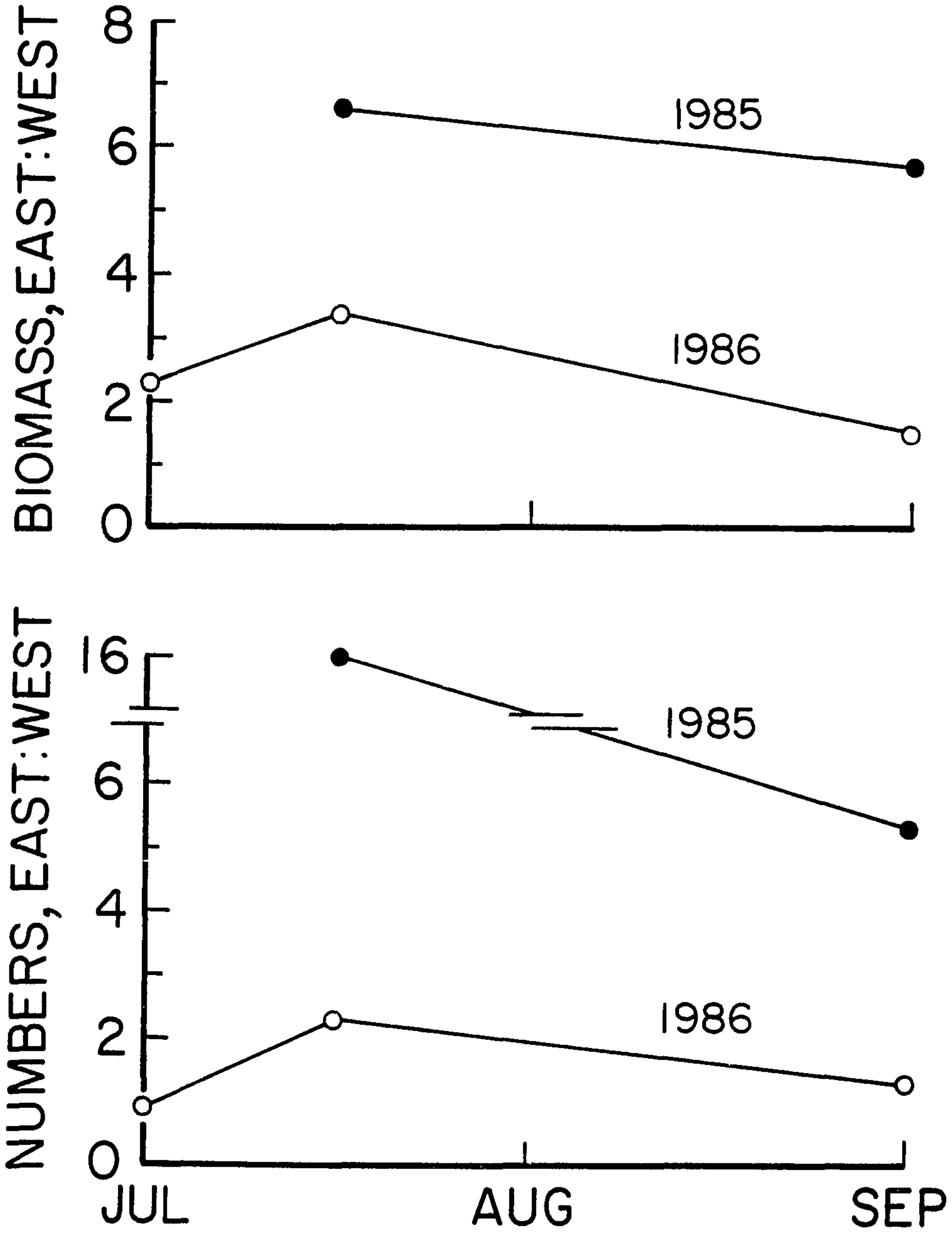

Figure 29. Proportions of *Calanus marshallae* east and west of the 32.4 ppt isopleth of bottom salinity.

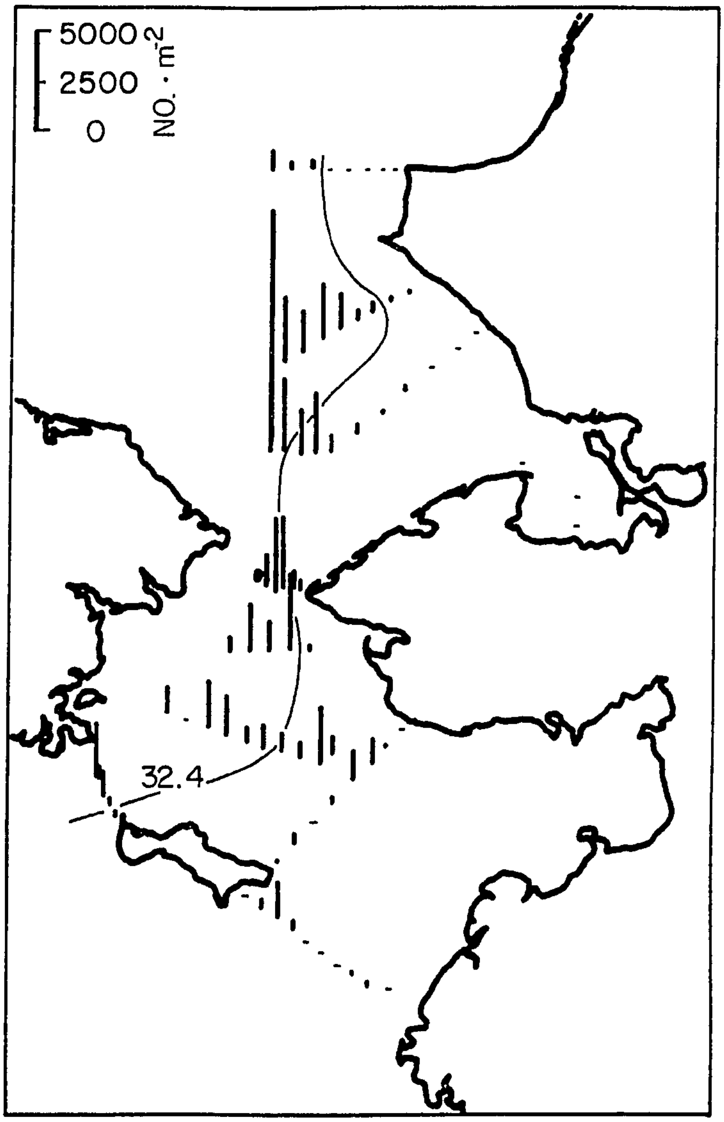

Figure 30. Areal distribution of abundance of Pseudocalanus spp., 11-26 July 1986.

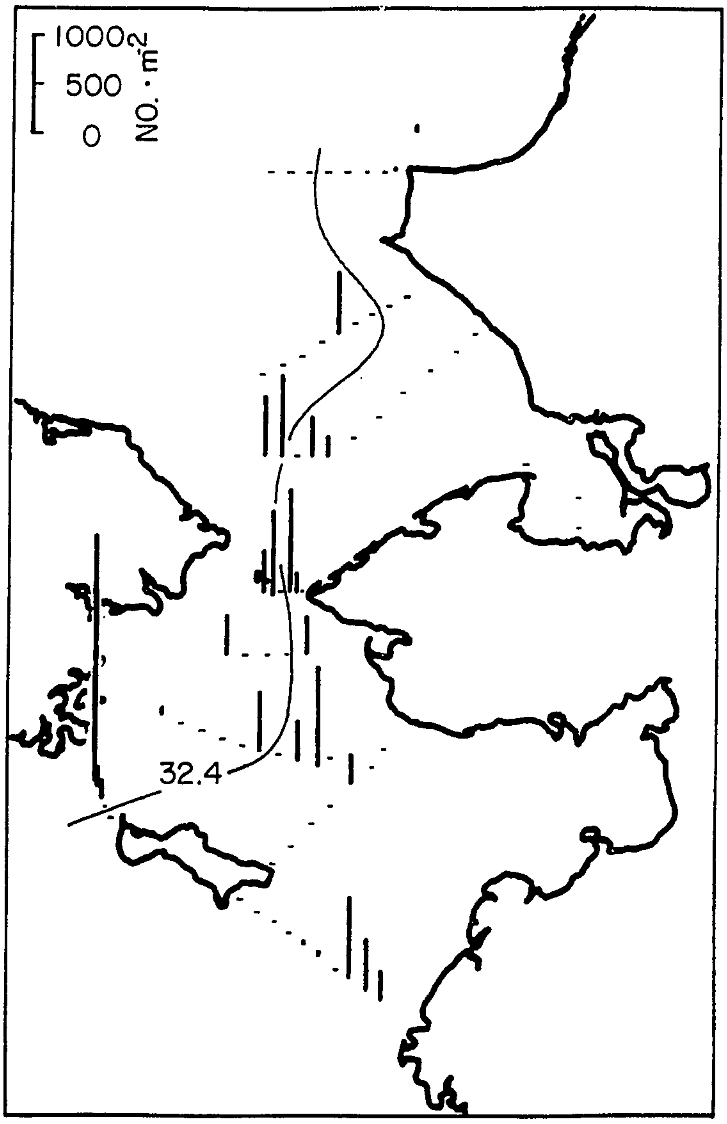

Figure 31. Areal distribution of abundance of _Centropages abdominalis_, 11-26 July 1986.

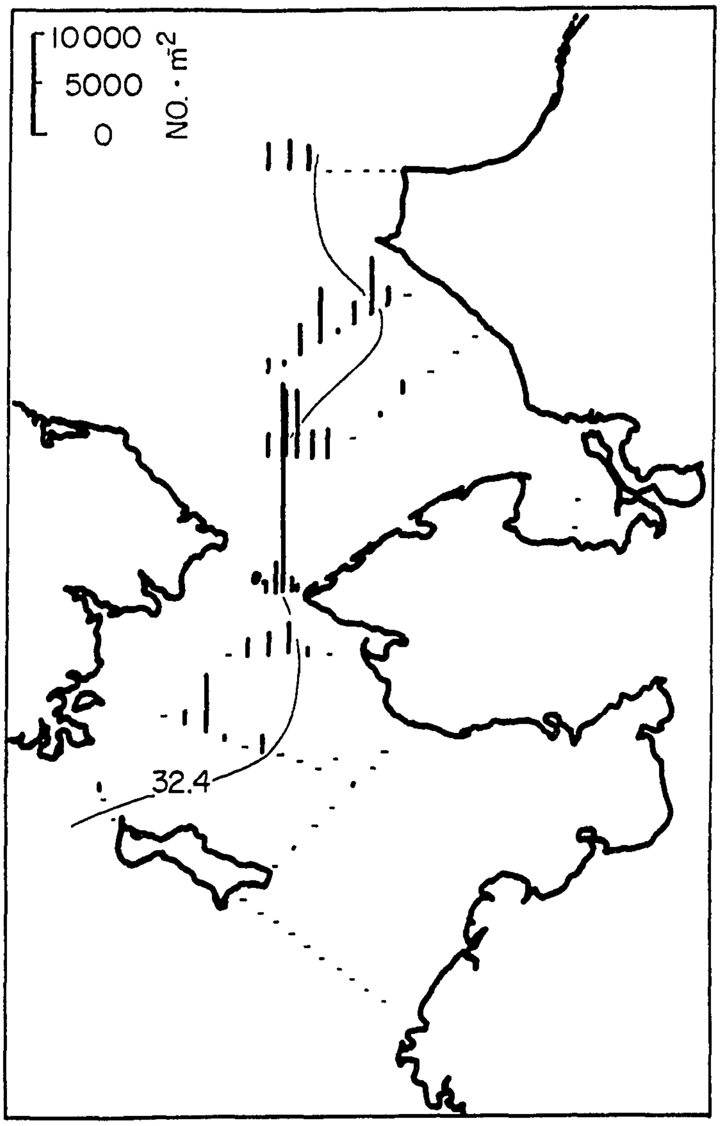

Figure 32. Areal distribution of abundance of *Thysanoessa raschii* furcilia, 11-26 July 1986.

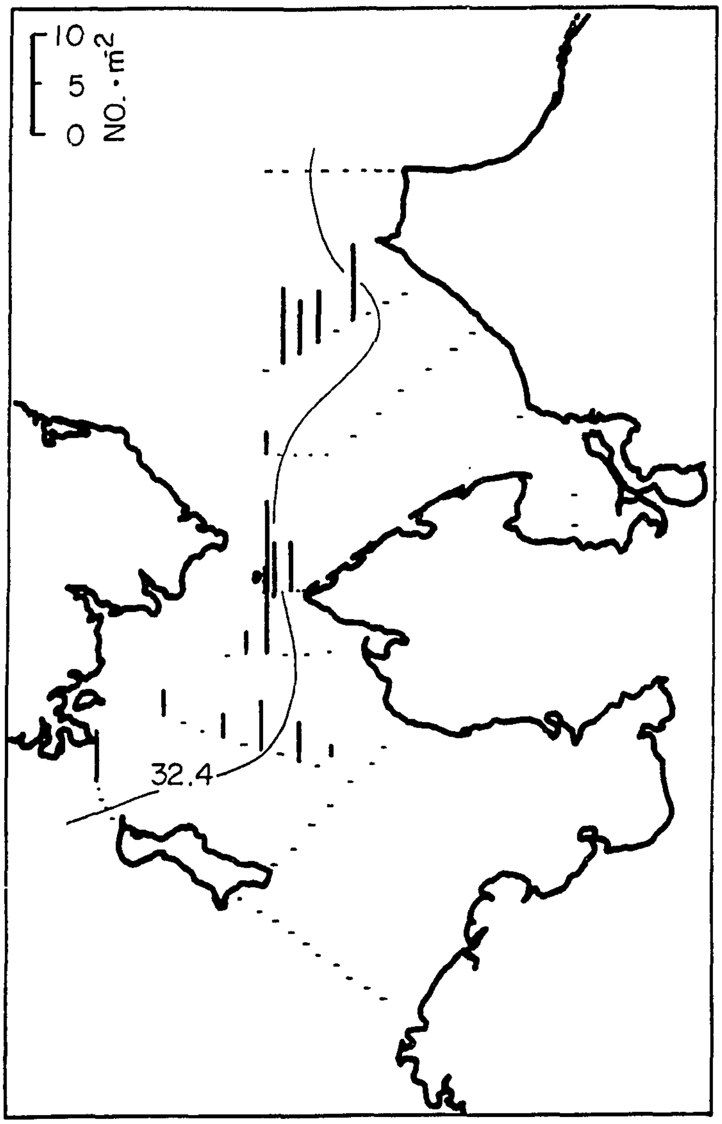

Figure 33. Areal distribution of abundance of *Parathemisto pacifica*, 11-26 July 1986.

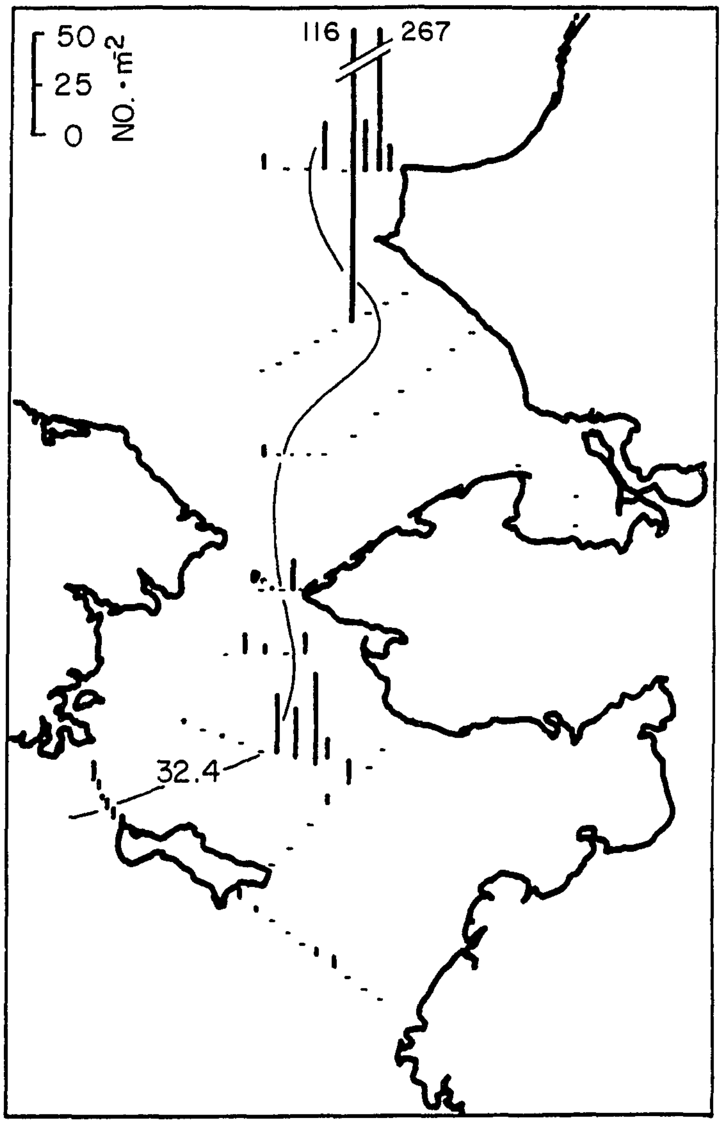

Figure 34. Areal distribution of abundance of crab zoea, 11-26 July 1986.

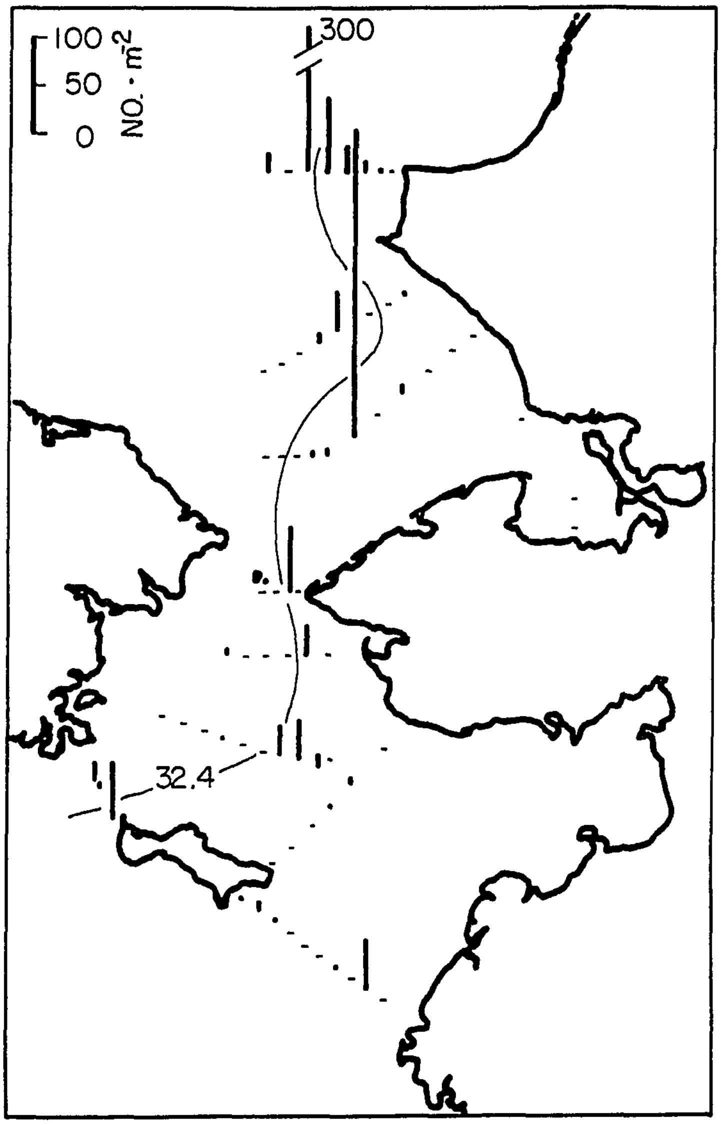

Figure 35. Areal distribution of abundance of shrimp zoea, 11-26 July 1986.

during the same period in 1986, occurring at only 10% of all stations sampled.

Sagitta elegans was wide-spread, but there was a marked difference in the distribution of size classes (Fig. 36). The majority of the larger individuals were confined to the west, i.e., were arriving from the southwest, while the smaller sized individuals were arriving from the east. This pattern for large *Sagitta* was repeated on all cruises, while small ones were occasionally more evenly distributed east to west. Large *Aglanthe digitale* were widely distributed across the shelf both north and south of Bering Strait (Fig. 37). On this cruise, in contrast to the same date in 1985, juveniles were most abundant in shelf water, particularly north of Bering Strait, again suggesting differences in production cycles of *A. digitale* in the two regimes.

Limacina helicina and *Clione limacina* arrived from the southwest, but, by the time they had reached the Chukchi Sea, both had spread far to the east of 32.4 ppt (Figs. 38 and 39). *C. limacina* was significantly more abundant in the southwest than in the southeast, yet it was more abundant in the northeast than in the northwest. Such a skewed distribution indicates that they resided primarily in the surface layer and possibly were carried east by wind-generated surface currents. Their predominance in the surface layer was confirmed in 1987 (Springer et al. unpubl. data).

The dependence of the areal distributions of zooplankton on mixing patterns of Anadyr Water with Bering Shelf and Alaskan Coastal water is further illustrated by comparing vertical cross-sections of

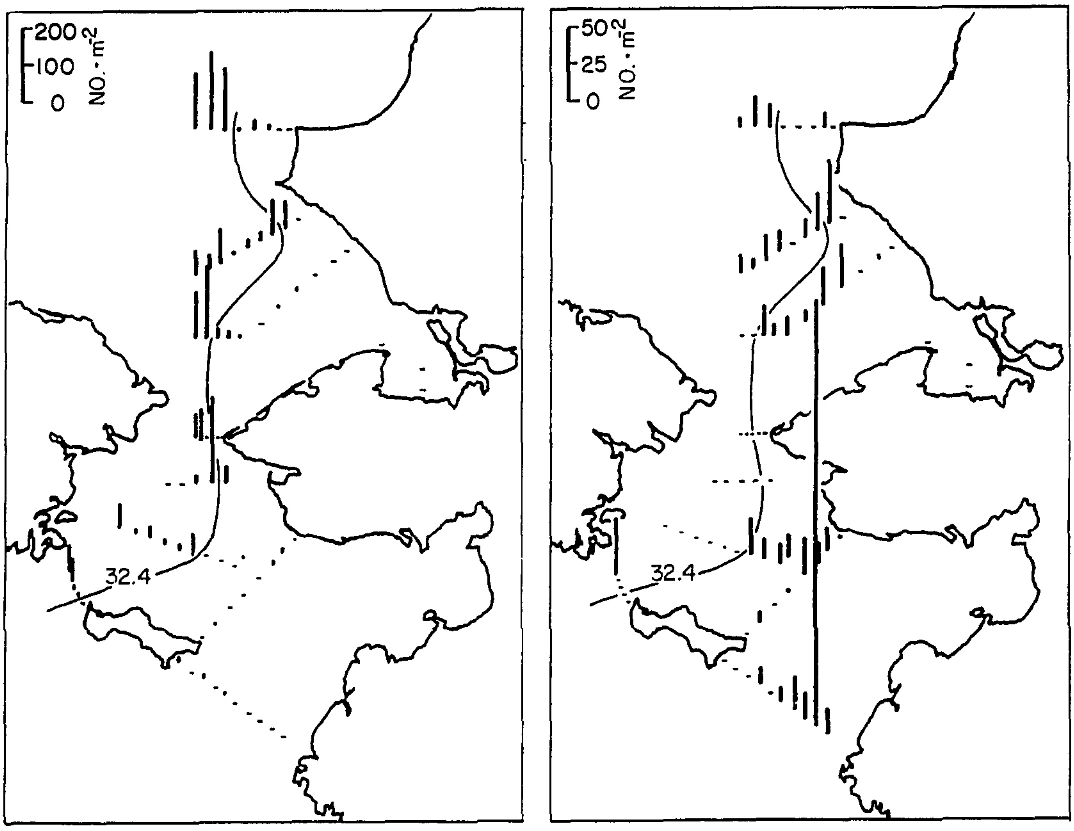

Figure 36. Areal distribution of abundance of large (left) and small (right) Sagitta elegans, 11-26 July 1986.

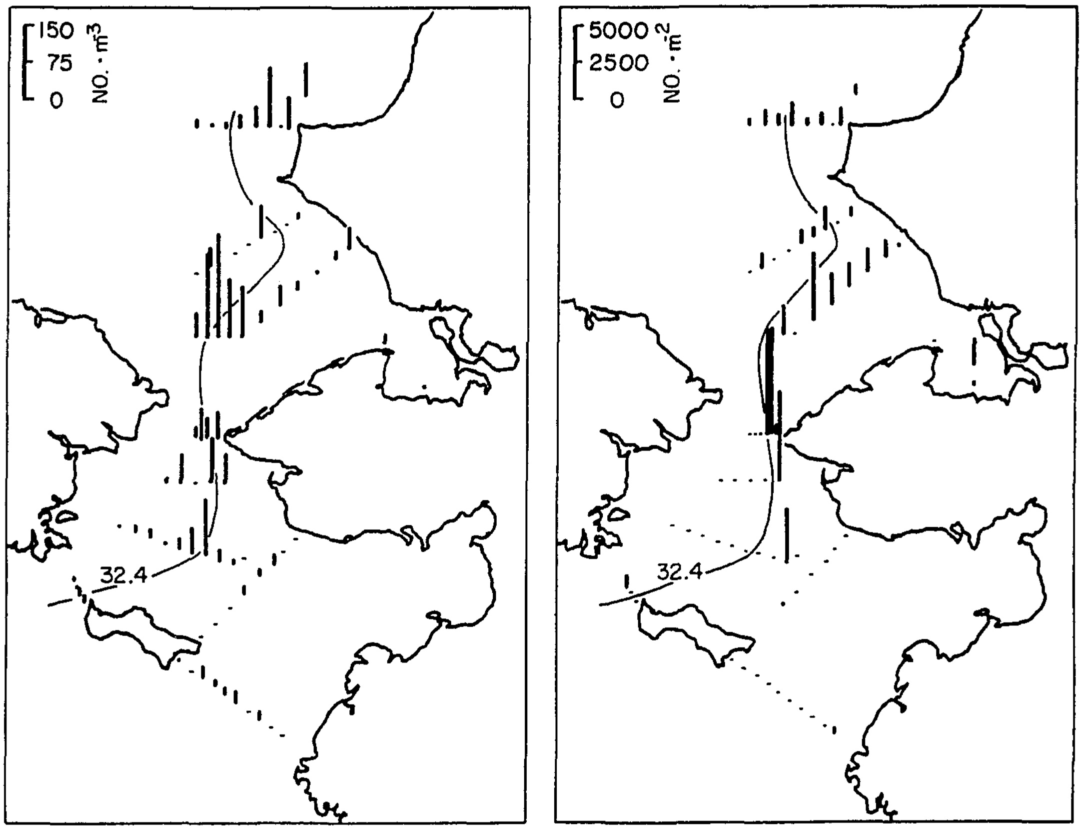

Figure 37. Areal distribution of abundance of large (left) and small (right) *Aglanthe digitale*, 11-26 July 1986.

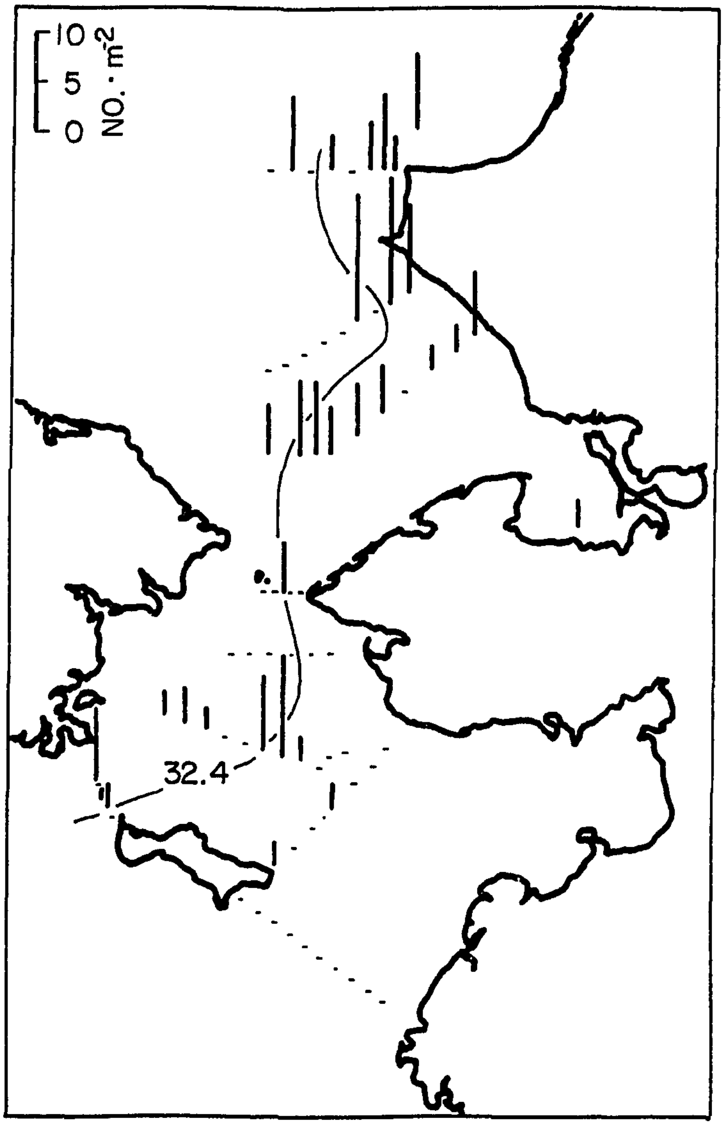

Figure 38. Areal distribution of abundance of _Clione limacina_, 11-26 July 1986.

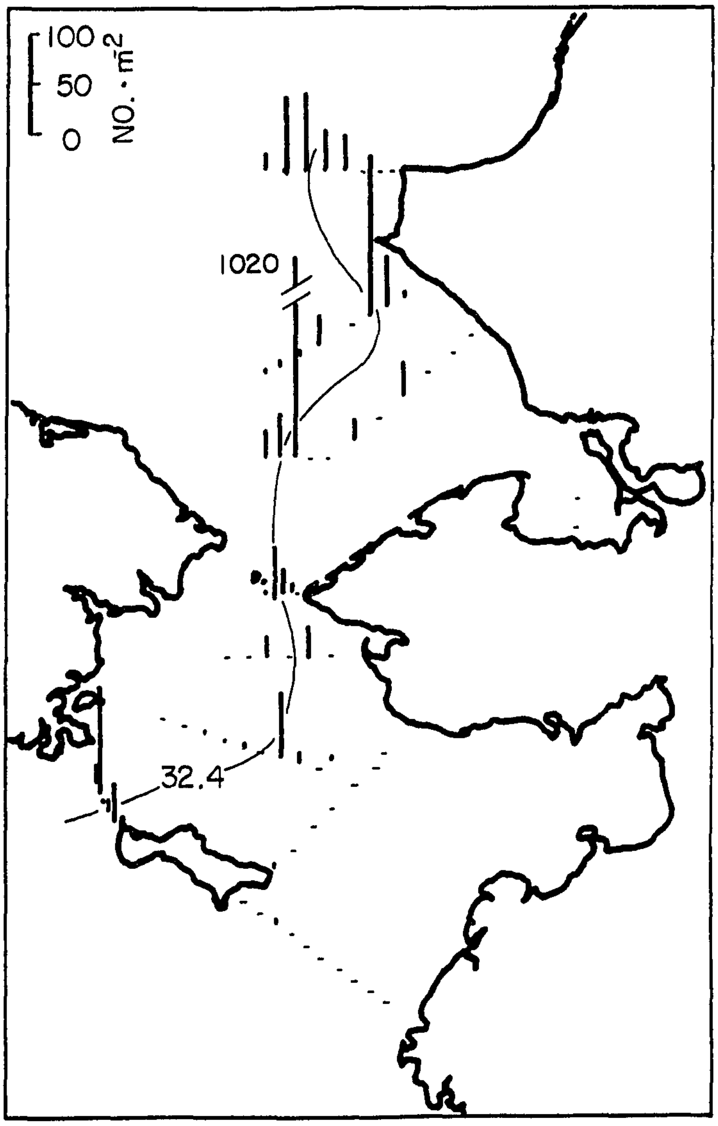

Figure 39. Areal distribution of abundance of *Limacina helicina*, 11-26 July 1986.

salinity to horizontal distributions of copepods north of St. Lawrence Island. Between the island and Bering Strait in mid-July 1986, Anadyr Water and Bering Shelf Water were separated by a front beginning at the surface near Station 26 and continuing from a depth of about 20 m to the bottom between Stations 22 and 23 (Fig. 40). Oceanic copepods declined gradually from west to east as the relative amount of oceanic water declined until Station 22 when they abruptly ended. Calanus marshallae was scarce in the west, increased gradually to the east, with an abrupt increase beginning at Station 23, where the bulk of the shelf water was met. The mixing zone between Anadyr and Bering Shelf water was much broader north of Bering Strait during the same period, and the abundance of oceanic copepods declined steadily over a distance of more than 100 km, while the numbers of Calanus marshallae changed little (Fig. 41).

Six-weeks later, in early September 1986, a thick layer of shelf water overlay Anadyr Water at least as far west as the Convention Line between St. Lawrence I. and Bering Strait (Fig. 42). The oceanic copepods extended east past Station 31 about the same distance as during the previous cruise, and were common in water with salinities as low as 32.0 ppt. Calanus marshallae, on the other hand, apparently underwent a pronounced westward excursion as a result of the upper-layer spreading of shelf water. It was least abundant, and the oceanic species most abundant, at Station 26 where Anadyr Water domed upwards from a depth of about 30 m.

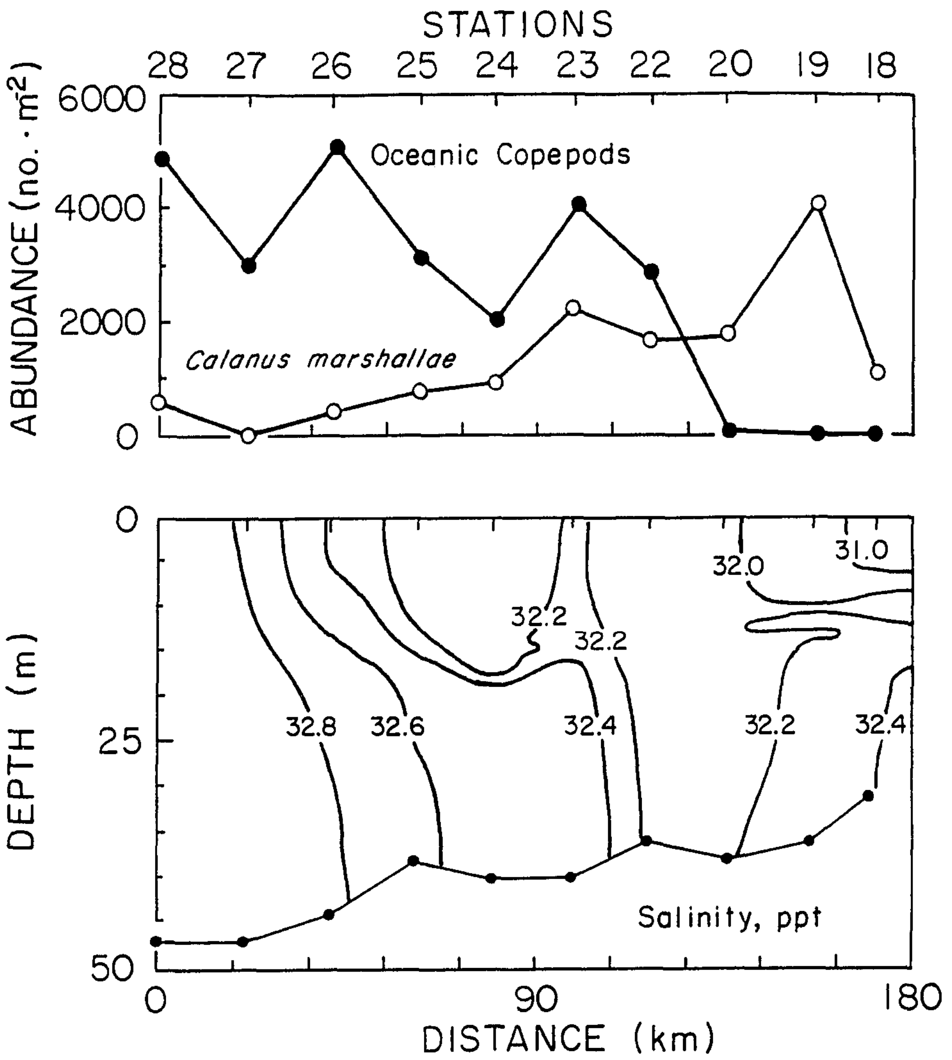

Figure 40. Cross-shelf distribution of salinity and abundance of copepods in the northern Bering Sea (transect A in Fig. 18, HX85), 14 July 1986. Values for the oceanic copepods as in Fig. 27.

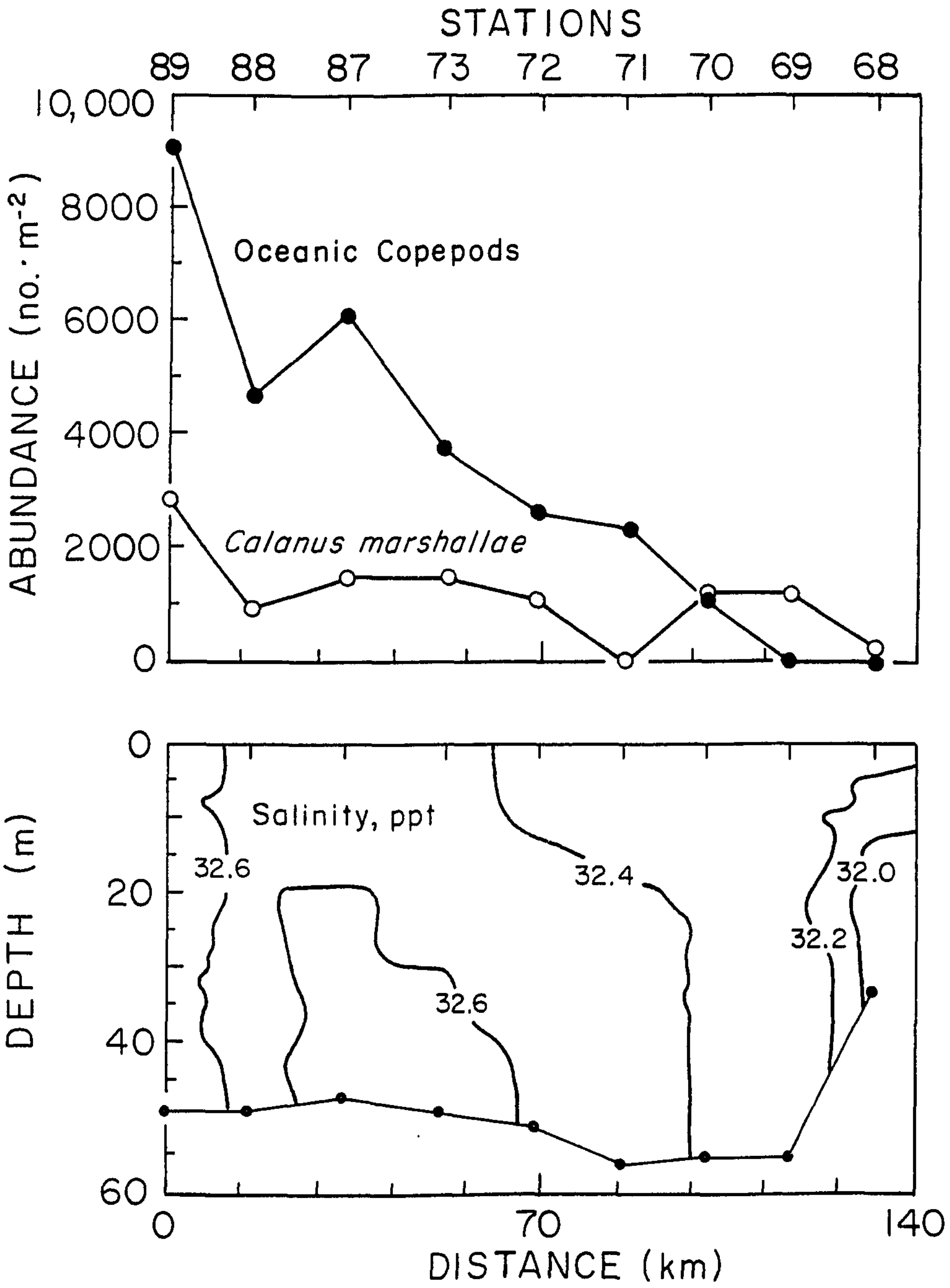

Figure 41. Cross-shelf distribution of salinity and abundance of copepods in the southern Chukchi Sea (transect B in Fig.18, HX85), 19-22 July 1986. Values for the oceanic copepods as in Fig. 27.

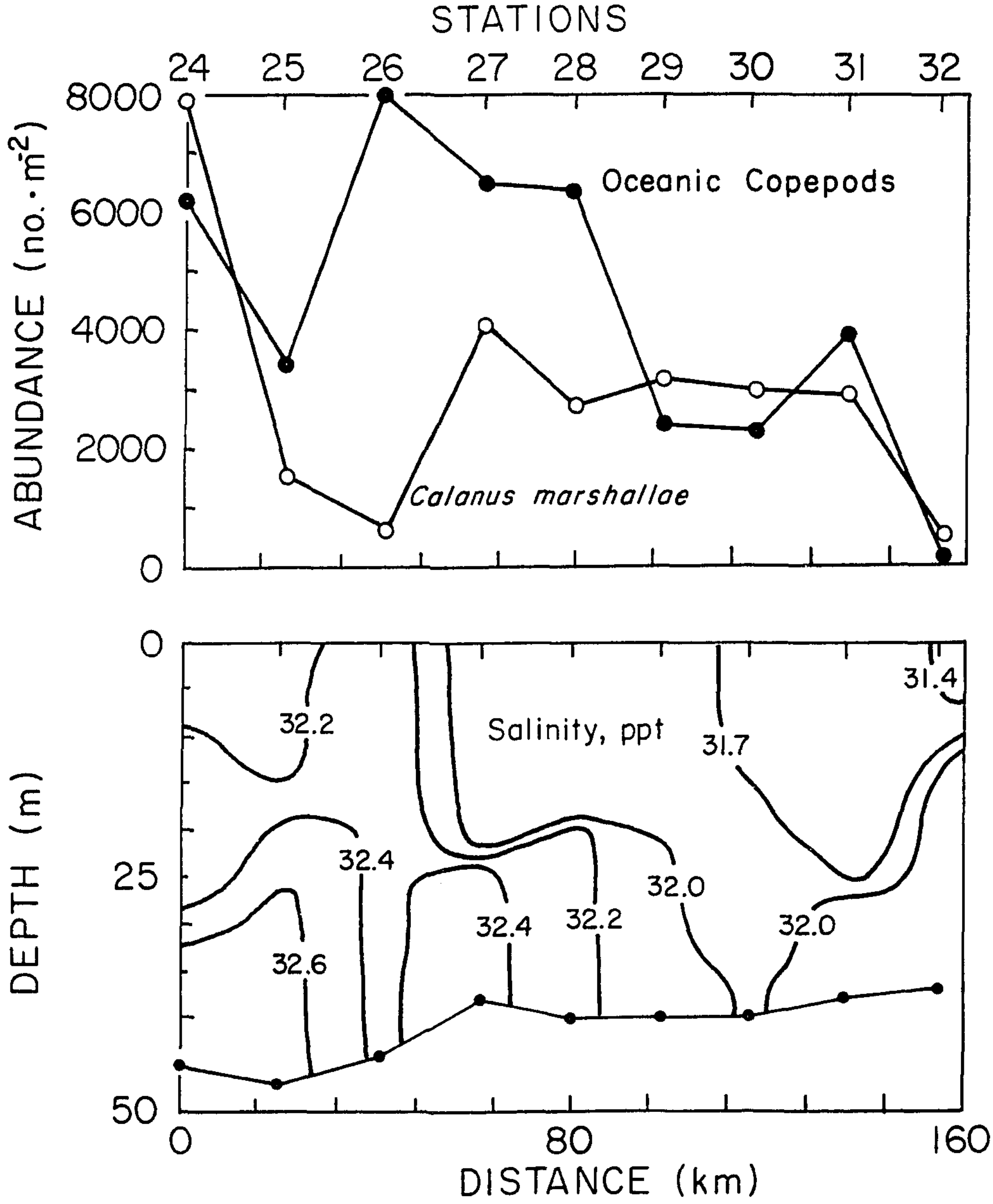

Figure 42. Cross-shelf distribution of salinity and abundance of copepods in the northern Bering Sea (transect C in Fig. 18, HX88), 29 August 1986. Values for the oceanic copepods as in Fig. 27.

Variability

With one exception, the abundance of each of the four oceanic species of copepods west of 32.4 ppt was the same north and south of Bering Strait. This relationship greatly facilitated the analysis of temporal variability, therefore, since nearly all data for each cruise could be reduced to a single value, i.e., the mean number west of 32.4 ppt.

Individually, *Neocalanus cristatus* was the least abundant of the oceanic species (Fig. 43). *N. plumchrus*, *Eucalanus bungii* and *Metridia pacifica* were all about equally abundant in July of both years. Because of the small sample size in mid-July 1985 (HX72), I do not attach too much importance to the apparent difference in numbers between this and other cruises. *N. plumchrus*, but not the other species, declined significantly in abundance in late summer.

In the only case of a north - south difference in abundance of the oceanic copepods, *Metridia pacifica* was about an order of magnitude more numerous in the southwest than in the northwest in early September 1986. This difference possibly represents an influx of *M. pacifica* into the study area, and might indicate a change between years in the development of the population off the shelf. Unlike the other oceanic species which produce one or possibly two cohorts each year, *M. pacifica* apparently reproduces continuously during spring and early summer (Batchelder 1985; Smith and Vidal 1986), and this strategy could lead to a different pattern of abundance between years for them compared to the others.

The combined biomass of the four oceanic species was similar

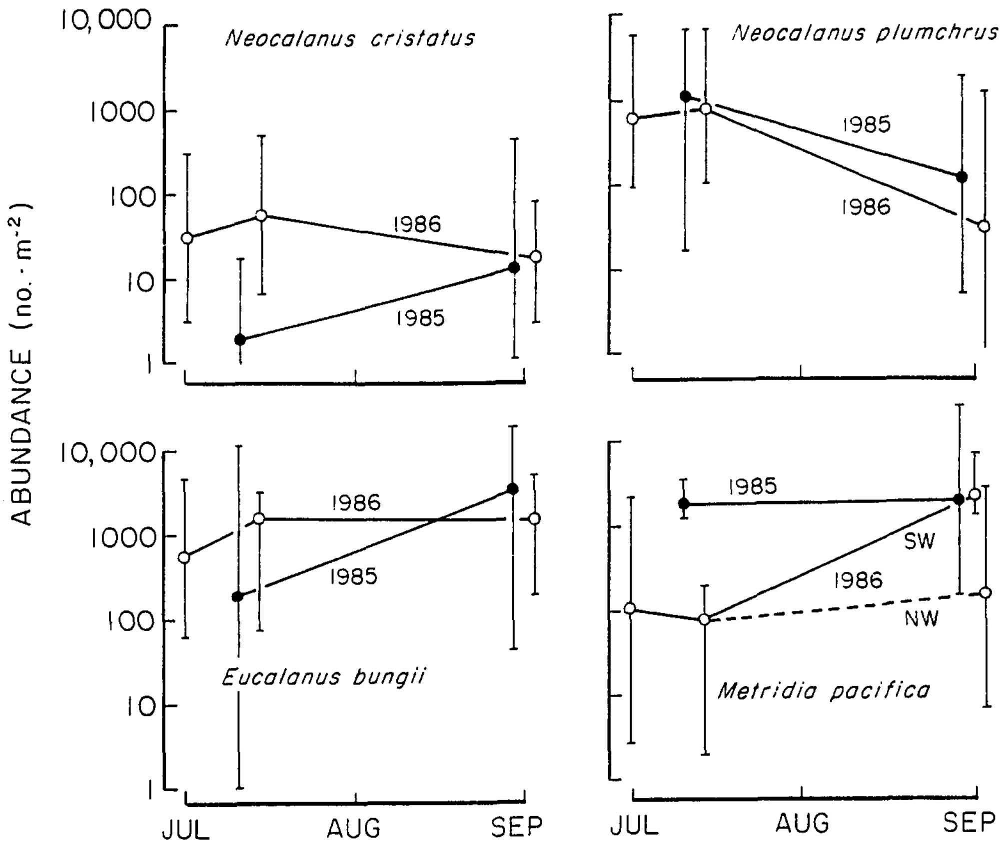

Figure 43. Abundance of oceanic copepods west of the 32.4 ppt isopleth of bottom salinity. Geometric means, range of ± 1 standard deviation.

between years (Fig. 44). The biomass was highest in early July at 4 - 6 g dry weight m^{-2} and declined by about 50% - 60%, to 2 g m^{-2}, by September. Although these trends were not significant, they fit with the expected pattern because of the seasonal decline in biomass in the southeastern Bering Sea (Cooney 1981; Smith and Vidal 1984).

The abundance and biomass of Calanus marshallae east of 32.4 ppt were not different between cruises in either year, except that both were significantly lower in June 1986 than at any other time (Fig. 45). Numbers and biomass were significantly lower throughout 1986 than in 1985.

Pseudocalanus spp. was usually more abundant west of 32.4 ppt (Fig. 46). I have not included data from the July 1985 cruise (HX72) in Fig. 46, since those samples are not comparable with the others because of the smaller net used then. Unlike all other cruises, the abundances east and west on HX72 were not different, and the overall average of 19,000 m^{-2} (range = 6,600 - 55,000) was the highest recorded. Pseudocalanus spp. was significantly more abundant (by a factor of 3 - 4) both east and west of 32.4 ppt in September 1985 than in September 1986.

The numbers of Oikopleura spp. showed distinct spatial and temporal trends (Fig. 47). On both cruises in 1985, large individuals were found only in and near Anadyr Strait, although they were less numerous in September. Some small individuals, as well as large ones, were present in the west in September 1985, but not in July. Only small ones occurred east of 32.4 ppt. In contrast, large individuals were found at just 3 stations in all of 1986, and those were east of

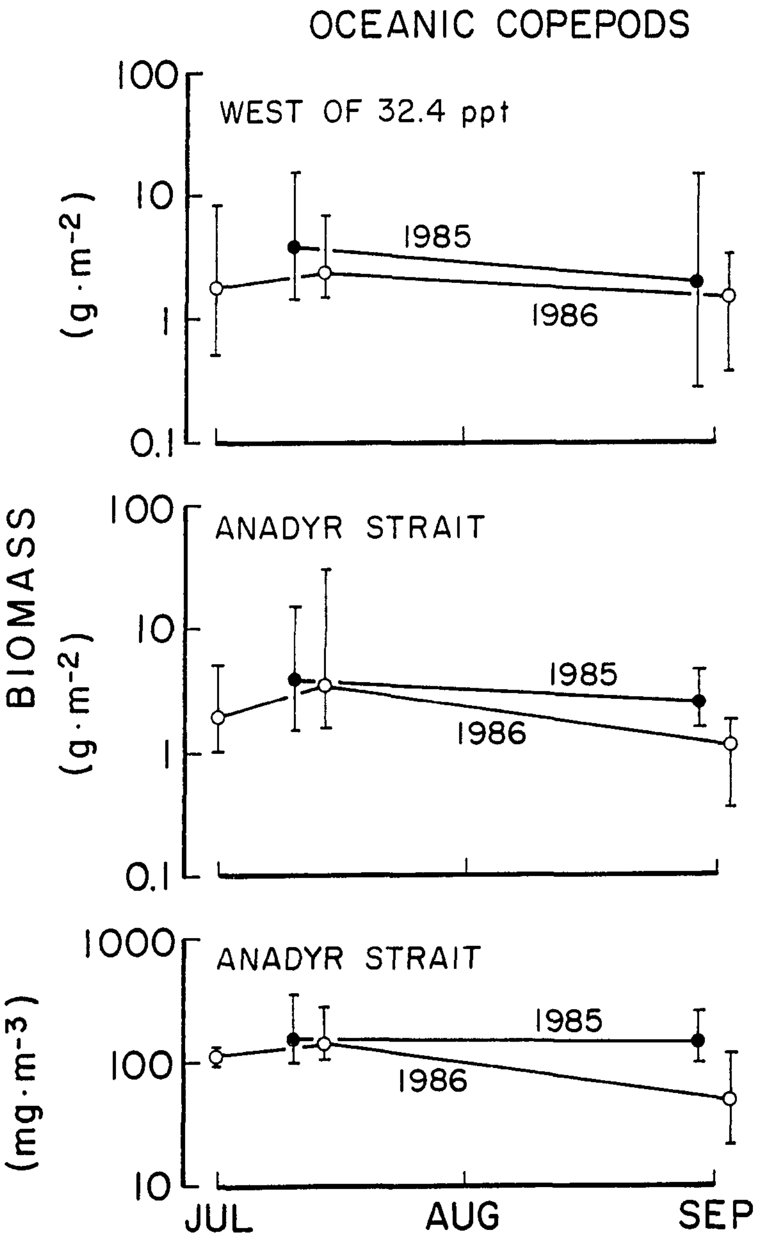

Figure 44. Biomass of oceanic copepods west of the 32.4 ppt isopleth of bottom salinity and in Anadyr Strait. Geometric means, range of ± 1 standard deviation. Values for the oceanic copepods as in Figure 29.

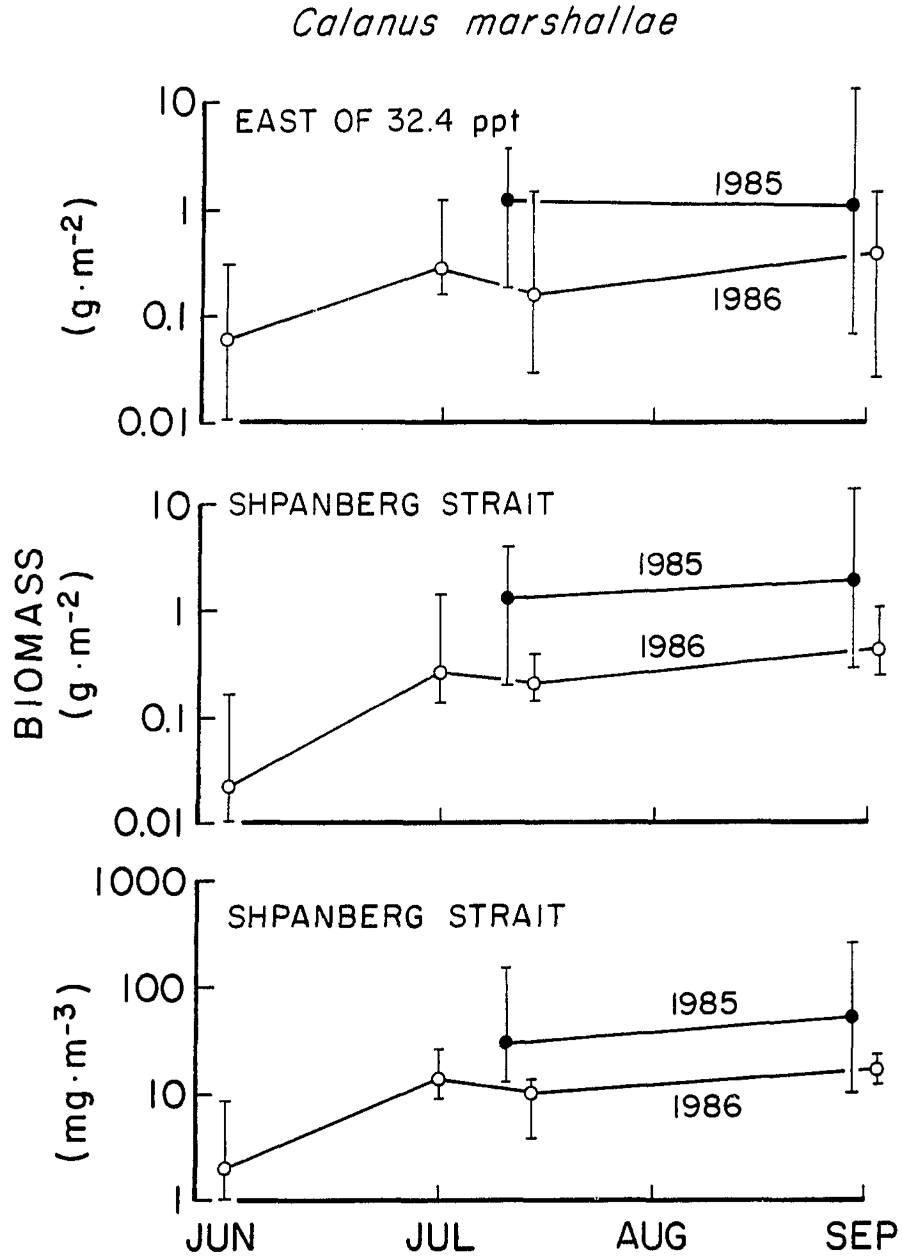

Figure 45. Biomass of Calanus marshallae east of the 32.4 isopleth of bottom salinity and in Shpanberg Strait. Geometric means, range of ± 1 standard deviation.

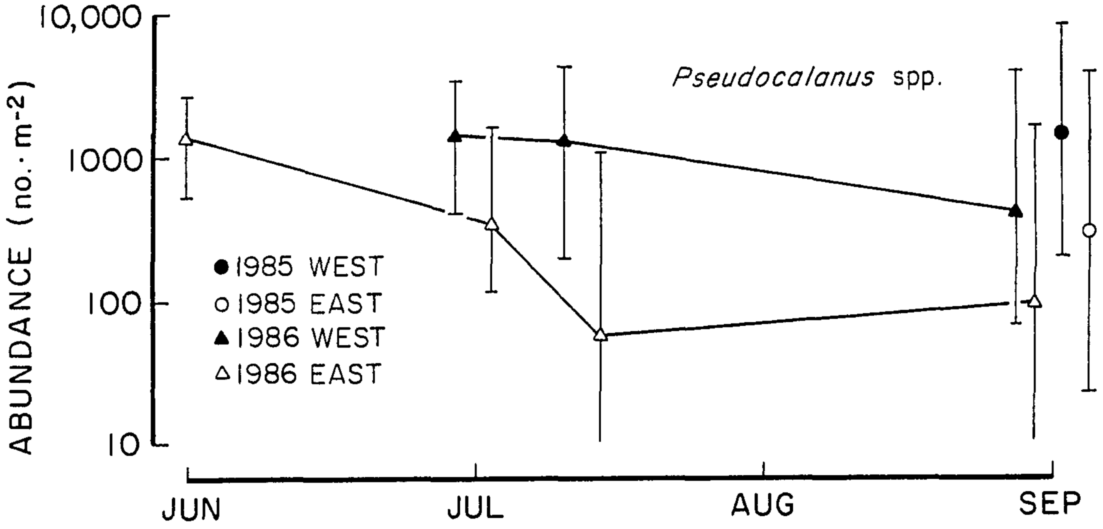

Figure 46. Abundance of Pseudocalanus spp. east and west of the 32.4 ppt isopleth of bottom salinity. Geometric means, range of ± 1 standard deviation.

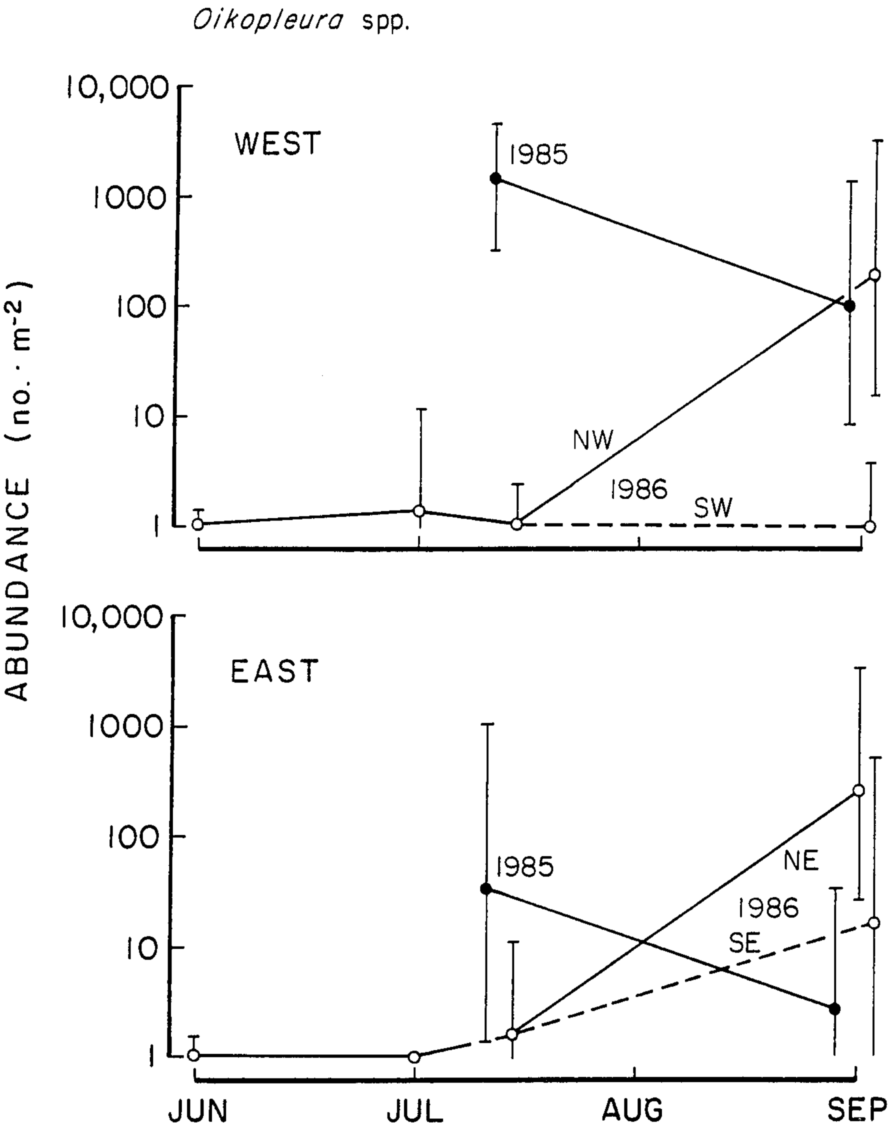

Figure 47. Abundance of Oikopleura spp. east and west of the 32.4 ppt isopleth of bottom salinity. Geometric means, range of ± 1 standard deviation.

32.4 ppt. Also, in 1986 neither adults nor juveniles materialized in the west; the increase in the northwest in September probably resulted from layering of shelf water westward over Anadyr Water. In the east, the numbers of juveniles attained similar maximum values in both summers, but there was apparently a shift in the timing of the production cycle, with 1985 different than 1986 by as much as 6 weeks. The seasonal decrease in numbers in 1985 and the increase in 1986 were both significant.

Large, presumably adult, _Sagitta_ _elegans_ predominated in the western portion of the study area, and exhibited little seasonal or interannual difference in abundance (Fig. 48). The abundance of large individuals in the east also was stable over time, but was significantly lower (by a factor of 5 - 10) than in the west. The east - west difference in abundance was less pronounced for small individuals, except in mid-July 1985 when they were extremely abundant, at least in Shpanberg Strait. Again with the exception of mid-July in the east, interannual differences in abundance were not significant. When all three size classes are considered together, the distribution of biomass was more uniform from east to west than was the distribution of abundance (Fig. 49). There was no difference between years in the combined abundance or biomass of _S._ _elegans_ in the west, but both were significantly lower in the east in 1986 than in 1985 (Fig. 49). Also, both were significantly greater in the west than in the east each year.

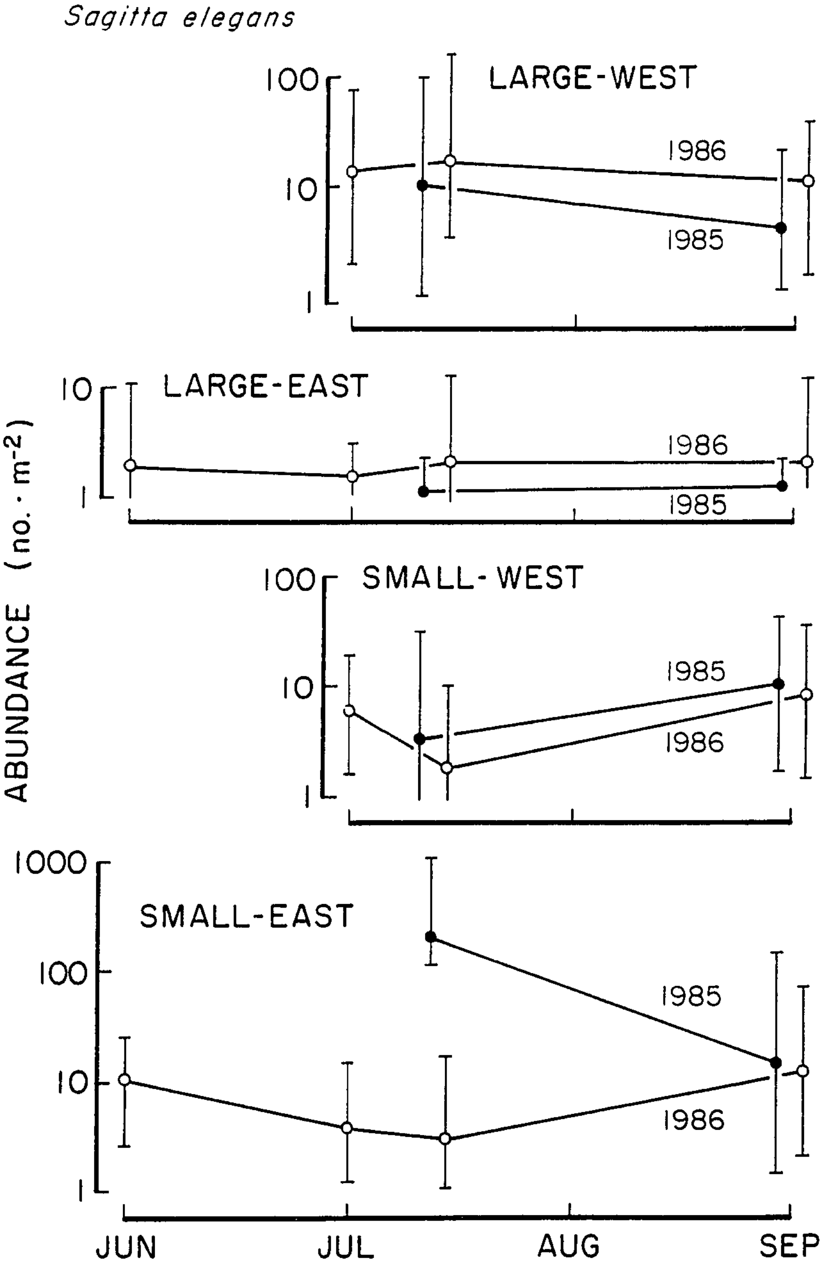

Figure 48. Abundance of large and small Sagitta elegans east and west of the 32.4 ppt isopleth of bottom salinity. Geometric means, range of ± 1 standard deviation.

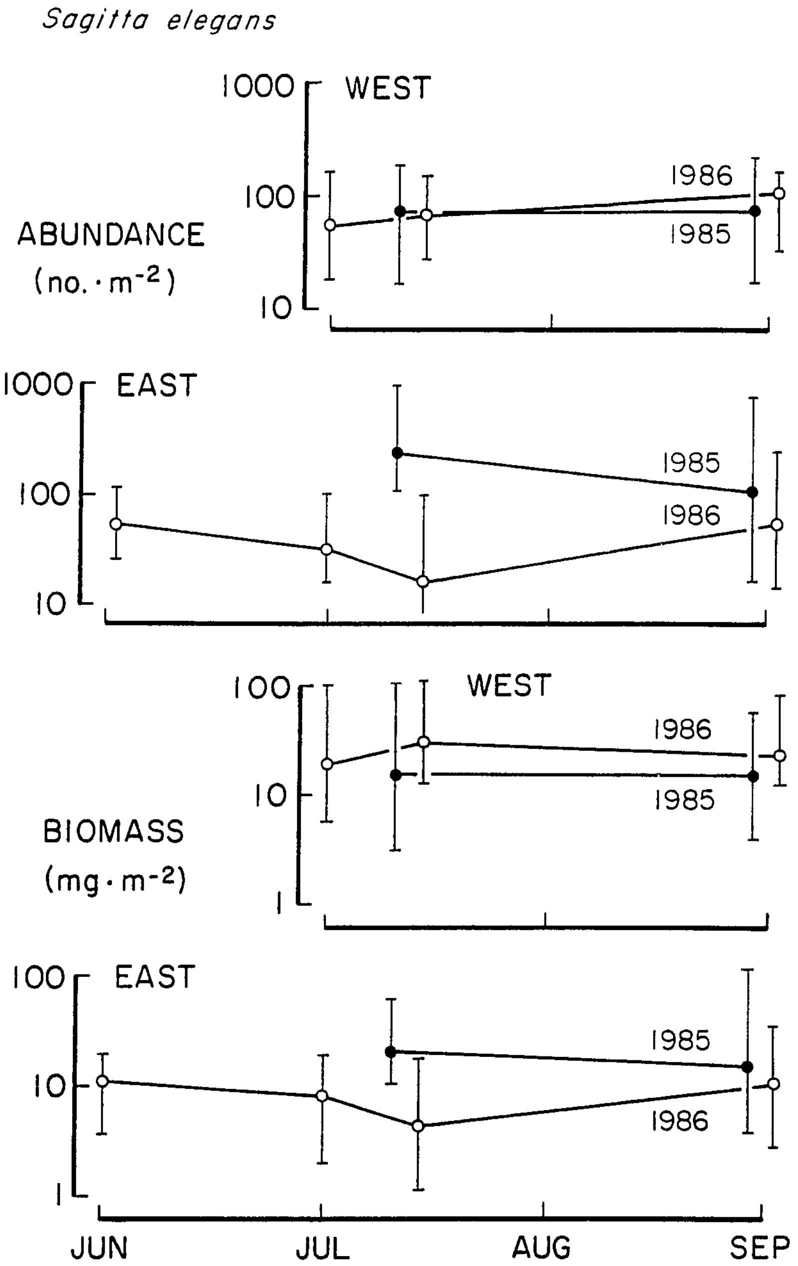

Figure 49. Combined abundance and biomass of all Sagitta elegans east and west of the 32.4 ppt isopleth of bottom salinity. Geometric means, range of ± 1 standard deviation.

Transport

The estimates of the daily transport of zooplankton biomass using the two methods were similar, particularly for Shpanberg Strait (Table 5). The average coefficient of variability (CV) for each pair of estimates in Anadyr Strait (0.17) was much higher than that for Shpanberg Strait (0.05). The CV's of the estimates of transport of total zooplankton using Method 1 and of oceanic copepods and larvaceans using Method 2 through Anadyr Strait were equal (0.17).

The transport of zooplankton through Anadyr Strait apparently declined during summer in 1985 (Table 5). Transport of total zooplankton declined by about 75%, from an average of 45 x 10^9 g d^{-1} to 11 x 10^9 d^{-1}. The change was accounted for by a loss of about 20% in total water transport, from an average of about 1.25 Sv in mid-July to about 1 Sv in early September (Coachman 1986), and by a decline of about 70% in the standing stock of zooplankton, mainly pteropods and larvaceans, from about 14 g m^{-2} to 4.1 g m^{-2}. The transport of oceanic copepods declined by about 30%, and was due primarily to the decline in total transport and to a decline of about 33% in the estimated volume percent of Anadyr Water in the strait, from about 72% to about 48% (Fig. 50). The transport of larvaceans changed the most, falling over 99% mainly because of the large decline in the standing stock. The relationship between the estimated volume percent of Anadyr Water in Anadyr Strait and the biomass of oceanic copepods (Fig. 51), indicates that the transport of zooplankton biomass in 1986 would have been lower than in 1985 unless the current speeds in 1986 were considerably higher than in 1985.

Table 5. Estimated transport of zooplankton biomass through Anadyr and Shpanberg straits. Estimation Methods 1 and 2 are described in the text.

		Transport (g dry weight d^{-1}, x10^{-3})			
		Anadyr Strait		Shpanberg Strait	
Cruise (Date)	Taxon	Method 1	Method 2	Method 1	Method 2
HX72 (21-23 Jul 85)	Total zooplankton	41	35	5.6	6.4
	Oceanic copepods	11	18		
	Calanus marshallae			1.8	2.1
	Oikopleura spp.	4.5	4	0.065	0.073
HX74 (7-8 Sep 85)	Total zooplankton	11	8	7.1	7.1
	Oceanic copepods	10	8		
	Calanus marshallae			4.8	4.5
	Oikopleura spp.	0.014	0.016	0.00036	.00039

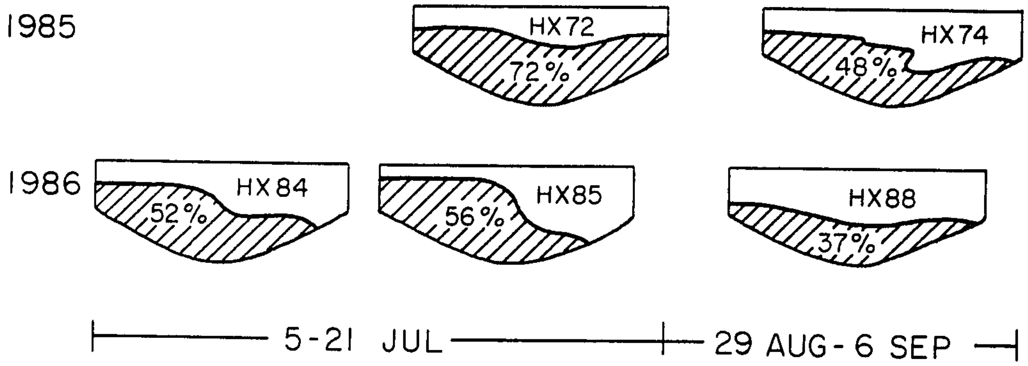

Figure 50. Distribution of Anadyr Water in Anadyr Strait. The values are the approximate percentages of the total cross-sectional volume in Anadyr Strait occupied by water with salinity greater than 32.4 ppt.

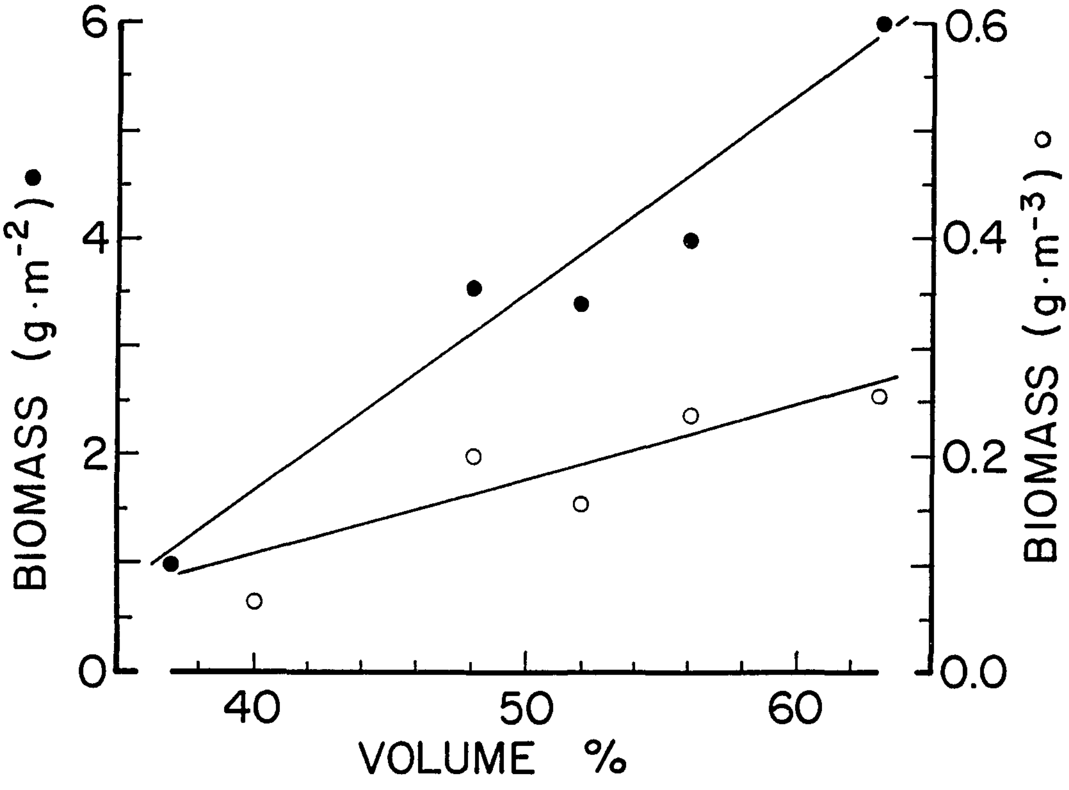

Figure 51. Relations between the estimated biomass of oceanic copepods in Anadyr Water, and the estimated volume percent of Anadyr Water in Anadyr Strait.

The transport of total zooplankton biomass through Shpanberg Strait was lower than through Anadyr Strait, and changed little during summer (Table 5). The transport of Calanus marshallae increased about 240%, from an average of about 2 x 10^9 g d^{-1} to about 4.7 x 10^9 g d^{-1}, in response to an increase in the standing stock (Fig. 45) and a 33% rise in total water transport, from an average of about 0.5 Sv in the first half of July to about 0.75 Sv in late August - early September (Coachman 1986). In contrast, the transport of larvacean biomass declined by over 99%, as in Anadyr Strait.

DISCUSSION

Distribution of zooplankton

Three zooplankton communities occurred on the Bering - Chukchi shelf during the study, one originating primarily in the oceanic domain of the Bering Sea that is advected northward with the flow of Anadyr Water, a second originating over the shelf shoreward of the middle front near the 100 m isobath in Bering Shelf and Alaskan Coastal water, and a third nearshore community. The biomass of herbivores in the oceanic community was dominated by the calanoid copepods Neocalanus cristatus, N. plumchrus, Eucalanus bungii, and Metridia pacifica. They were replaced in waters of primarily shelf origin by Calanus marshallae, the only large copepod normally found inshore of the middle front. Nearshore, C. marshallae declined to low numbers, leaving only small species, particularly Pseudocalanus spp. and Acartia longiremis. Unlike A. longiremis, Pseudocalanus spp. was common in all three communities, but was generally most abundant in Anadyr Water, even though its contribution in terms of total biomass there was small. *Oithona similis* also was wide-spread and at times extremely numerous, but because of its very small size, it contributed little to the overall biomass of copepods.

Other species of zooplankton also were distributed according to the hydrography. *Oikopleura* spp., *Clione limacina*, *Limacina helicina*, *Thysanoessa raschii*, and *Parathemisto pacifica* were all oceanic species, while meroplanktonic crab and shrimp zoea were primarily shelf taxa.

The major carnivores, *Sagitta elegans* and *Aglanthe digitale*, were cosmopolitan species, but there were obvious differences in the distributions of size classes across the shelf. Large *S. elegans* were essentially confined to Anadyr Water, while small and medium-sized individuals were much more abundant in shelf water. Large *A. digitale* were fairly widely distributed, but small ones, like small *S. elegans*, were generally associated with shelf water.

Dynamics

While the distribution of the oceanic zooplankton community over the Bering - Chukchi shelf depended on factors governing the eastward spreading of Anadyr Water, the abundance of the various species at any time was probably more a function of events in their natural history far to the south. Among the important variables over the outer shelf and slope are the timing of the annual production cycles and the levels of reproductive success, which vary considerably between years (Cooney 1981; Motoda and Minoda 1974; Smith and Vidal 1984, 1986), as well as purely physical factors that determine the volume and velocity of water transported first in the Bering Slope Current, and then in the "river" of Anadyr Water.

Of the biological variables, seasonal patterns of abundance of the four oceanic species on the northern shelf appeared to reflect seasonal changes in the abundance of each in the southeastern Bering. In the southeast, *Neocalanus cristatus* and *N. plumchrus* peak earlier than *Eucalanus bungii* and *Metridia pacifica* (Cooney 1981; Smith and Vidal 1986), as they apparently did in the north. There were no differences in abundance between 1985 and 1986, except for *M. pacifica*, which apparently increased earlier in 1985.

Over the outer shelf of the southeastern Bering Sea, copepod biomass increases rapidly beginning in early April and peaks in about mid-May, even though the numbers of each species do not follow this pattern, e.g., *Metridia pacifica*, (Cooney 1981; Smith and Vidal 1984; Vidal and Smith 1986). Anadyr Water travels about 400 km from the point of bifurcation of the Bering Slope Current to Anadyr Strait, and about 800 km from a point mid-way along the slope to the southeast. At an average speed of 20 cm s^{-1}, it would take 3 weeks for an event to propagate north to Anadyr Strait from the fork, and 6 weeks from mid-slope. Six weeks from mid-May, when the biomass over the outer shelf is probably near its peak, is early July, when the biomass on the northern shelf is probably near maximum. *M. pacifica* has a somewhat later, protracted period of peak abundance from May and June to possibly as late as August in the southeastern Bering (Cooney 1981;

Smith and Vidal 1986). The apparent influx of *M. pacifica* to the northern shelf between July and September 1986, therefore, might indicate that the production cycle was later that year than in 1985, when numbers were already high by mid-July in the south and by September in the north.

The biomass of *Oikopleura* spp. exhibited pronounced fluctuations both seasonally and annually. The decline from July to September 1985 could be explained if adults died after spawning, as suggested by Shiga (1982). The differences between 1985 and 1986 might be related to a change in the timing of the annual production cycle, thus I could have missed catching them because of the sampling schedule, or to a change in the annual production of the population. Shiga (1982) reported significant interannual variability in the numbers and size composition of *Oikopleura labradoriensis* off the shelf of the Bering Sea over a period of 13 years.

The flux of oceanic zooplankton onto the northern shelf is further governed by the volume transport of Anadyr Water, which varies seasonally and annually. Although the transport calculations for 1986 are not complete, the proportion of Anadyr Water in the overall flow through Anadyr Strait apparently was less than in 1985. The relationship between the volume percent of Anadyr Water and copepod biomass in Anadyr Strait suggests possibly a compound effect of water transport on biomass flux.

Calanus marshallae, the indicator species of water of shelf origin, was much less abundant in 1986 than in 1985. Like *Metridia pacifica*, its breeding season is protracted and apparently at least two generations are produced (Cooney 1981; Vidal and Smith 1986). At an average current velocity through Shpanberg Strait in the order of 10-20 cm s^{-1} (Coachman 1986), the transit time of plankton from Shpanberg Strait to Bering Strait would be 2-5 weeks, which could allow for changes in biomass through local production and growth to be expressed. Bering Shelf Water was more pervasive in 1986, and it was highly stratified, with temperatures in the upper layers generally warmer than in 1985, while the bottom temperatures were generally colder (Coachman 1986). These changes might be related to the decline in biomass in the east of *C. marshallae* and *Sagitta elegans*.

Food webs and carbon flow

The delivery of nutrients in Anadyr Water to the euphotic zone maintains a sizable area in eutrophic bloom conditions during most of summer, with diatoms producing up to 1-4 g C m^{-2} d^{-1} (Chapter 1). Elsewhere, nutrient depletion during the spring bloom leads to a floral succession from large diatoms to phytoflagellates, and productivity falls to 0.25-1 g C m^{-2} d^{-1}. Although daily production is less than in the region influenced by Anadyr Water, the production efficiency is much higher and this difference seems to characterize energy ascension in the two domains.

Grazing experiments with the oceanic copepods during the spring bloom over the outer shelf of the southeastern Bering Sea indicated rates of consumption of 28 mg C g dry wt^{-1} d^{-1} for the community as a whole (Cooney and Coyle 1982), and about 10% of body carbon d^{-1} $animal^{-1}$ (Dagg et al. 1982). At these rates, the average biomass of oceanic copepods of about 5 g dry wt m^{-2} on the northern shelf west of 32.4 ppt could graze 140 - 500 mg C m^{-2} d^{-1}. At the highest levels of about 20 g dry wt m^{-2}, the community could graze 560 - 2000 mg C m^{-2} d^{-1}. This is a significant fraction of the estimated daily primary production, particularly around the margin of the area of high production over Anadyr Water (Chapter 1). There are presently no estimates of the daily consumption by the larvaceans, but a species of similar size in the northwest Atlantic, Oikopleura vanhoeffeni, can clear up to 15 l d^{-1} $animal^{-1}$ and ingests large species of armored diatoms (Deible and Turner 1985), such as those found in the the northern Bering Sea. At a clearance rate of just 10 l d^{-1}, the population of Oikopleura spp. of 2000 - 6000 animals m^{-2} in Anadyr Strait in July 1985 could clear up to 20 - 60 m^3 d^{-1}, or about 50% - 150% of the water column. Thus, the combined effect of the oceanic grazers could be important in the pattern of carbon flow to pelagic and benthic food webs over part of the area. Nevertheless, persistent and predictable regions of high primary productivity and phytoplankton biomass (Chapter 1) indicate that, on average, the herbivores are unable to fully control the prolific diatom growth.

In 1985 when Calanus marshallae averaged about 1 g m^{-2} outside of the highly productive region and east of 32.4 ppt, they could consume 28 - 50 mg C m^{-2} d^{-1} if they fed at the same rate as the oceanic species. This demand is considerably below the average daily production, but at their highest biomass of about 7 g dry wt m^{-2}, and with the addition of as much as 3 g m^{-2} of small copepods that graze at a rate of about 75 mg C g dry wt^{-1} d^{-1} (Cooney and Coyle 1982), the shelf community could remove about 420 - 575 mg C m^{-2} d^{-1}, which approaches the daily primary production over much of the region. Considering that some of the fixed energy probably passes through microheterotrophs prior to reaching the zooplankton (Andersen 1986; Frost 1987), such a rate is an even greater proportion of that available. In 1986, when C. marshallae was less abundant by a factor of 5-10, the grazing stress would have been considerably lower, with a corresponding increase in the benthic carbon flux.

If the transport of zooplankton biomass through Anadyr Strait estimated for July 1985 was typical for about 45 days in mid-summer, and that estimated for September was typical for 75 days in early and late summer, in the order of 2.9 x 10^{12} g dry weight, or 1.4 x 10^{12} g C, was carried onto the northern shelf during June - September. The flux of shelf species through Shpanberg Strait could add approximately another 30%, bringing the total to about 1.8 x 10^{12} g C. To place this export in perspective, it represents an amount equal to: 1) 15% - 70% of estimates of the total standing stock of zooplankton in the Arctic Basin (calculated from data in Hopkins, 1969); 2) using annual production estimates for the outer domain of 30 - 40 g C m^{-2} (Cooney 1981; Vidal and Smith 1986), 35% to 50% of the calculated annual secondary production over the 13 x 10^{10} m^2 outer shelf domain of the southeastern Bering Sea, the region from which much of the oceanic zooplankton on the northern shelf probably originates; and 3) about an order of magnitude greater than the annual carbon loss to the walleye pollock (Theragra chalcogramma) fishery, which operates primarily over the outer domain and is the largest single-species fishery in the N.

Pacific Ocean (Bakkala et al. 1986).

The most conspicuous beneficiaries of the transport of zooplankton biomass in the northern Bering Sea are the planktivorous auklets, which derive the bulk of their dietary needs from oceanic species. Auklets are endemic to the Bering Sea, and the breeding colonies on islands in the Bering Strait region, principally St. Lawrence I. and the Diomede Islands, contain millions of birds and are probably the largest in the world (Sowls et al. 1978). However numerous, the birds are small - each increment of 10^6 least auklets probably removes in the order of only 2.7 x 10^6 g C d^{-1}, and each 10^6 crested auklets removes about 8.1 x 10^6 g C d^{-1} (Springer et al. 1987). If there are 3 x 10^6 of each species in the region, the combined daily ration would be about 32 x 10^6 g C, or < 0.3% of the daily influx of oceanic copepods through Anadyr Strait in July and September.

Other animals undoubtedly feed on the zooplankton also, including fishes such as Arctic cod (Boreogadus saida) and capelin (Mallotus villosus), which are important in the diets of piscivorous seabirds, primarily murres (Uria spp.) (Springer et al. 1987), as well as marine mammals (Frost and Lowry 1981b). Murres on St. Lawrence I., which has the largest population of all the regional colonies, consume in the order of 1.5 x 10^7 g C d^{-1} of fish biomass (Springer et al. 1987). Nevertheless, fish stocks are apparently low compared to elsewhere, as indicated by the lack of commercial fin-fisheries. The dominant pelagic baleen whale, the bowhead whale (Balaena mysticetus), only migrates through the region in early spring and late autumn.

Since there were generally no differences in the numbers of copepods north or south of Bering Strait, the combined loss to predators appears to be insignificant, and most of the biomass arriving on the shelf of the northern Bering Sea must be added to pelagic and benthic flux calculations in the Chukchi Sea and Arctic Ocean.

CONCLUSIONS

One of the chief working hypotheses of the ISHTAR project is that biological rates and processes on the Bering - Chukchi shelf are determined primarily by the influx of water, nutrients and biota from the south. The data on zooplankton support that concept for the western, oceanic part of the shelf, while local factors, as well as advection, are probably important in the east.

Circulation patterns of the water masses in the northern Bering Sea and southern Chukchi Sea clearly determined the areal distribution of the oceanic and shelf zooplankton communities. Looking at this relationship from the other direction, it can be said that the composition of the zooplankton in a given location was apparently a reliable indicator of the composition of the associated water. For example, oceanic copepods were found east of St. Lawrence I. in Shpanberg Strait on both cruises in 1985, but on none of the cruises in 1986, suggesting that a measureable change occurred between the two years in the circulation pattern of Anadyr Water entering the study area. Cross-sections of salinity and nitrate in Anadyr and Shpanberg straits during mid-July of 1985 and 1986 confirmed the change in the flow regime between the two years. Anadyr Water apparently occupied a greater proportion of Anadyr Strait in 1985 than in 1986, particularly on the eastern side, where it extended virtually to the coast of St. Lawrence I. Moreover, in 1985 a portion of Anadyr Water split off of the main body and travelled around the south side of the island, carrying oceanic zooplankton into the study area through western Shpanberg Strait. In contrast, during the same interval in 1986, all of the Anadyr Water, and oceanic zooplankton, entered through Anadyr Strait.

North of St. Lawrence Island, the cross-shelf distribution of zooplankton was further affected by lateral spreading and layering. Anadyr Water tended to be held to the west by Bering Shelf Water and Alaskan Coastal Water, which restricted the eastern limit of the oceanic community, particularly south of Bering Strait. Still, in July and September 1986 oceanic copepods were common in water with salinities between 32.0 ppt and 32.5 ppt, thus documenting the areal extent of Anadyr Water that was not apparent from physical characteristics alone. Turbulence in Bering Strait and the prominent downstream, eastward loop in the trajectory of the current led to a broad mixing zone between the three water masses in the southern Chukchi Sea and an eastward extension of the range of the oceanic species, again in water with intermediate physical characteristics. The layering of Bering Shelf and Alaskan Coastal water westward over Anadyr Water similarly expanded the range of Calanus marshallae.

Primary production induced by the nutrients carried in Anadyr Water is uncontrolled by the herbivores on average, and provides for rich benthic food webs, while the constant supply of zooplankton biomass advected in the flow accounts for the abundant marine avifauna on islands in the Bering Strait region. East of the area influenced by Anadyr Water, flagellates succeed diatoms following the spring bloom, annual primary producton is low because of nutrient limitation, and zooplankton communities of smaller shelf and coastal species replace the oceanic one. The availability of energy to higher trophic levels in pelagic food webs is consequently less, and the number and diversity of coastal avian populations is low (Springer et al. 1987).

There was little difference between years in the abundance of oceanic copepods in Anadyr Water. Some of the variability was apparently related to fluctuations in the amount of water transported through Bering Strait, and in the proportion of the total contributed by the three sources. In contrast, the abundance of *Calanus marshallae* was significantly lower during summer in 1986 than 1985, in connection with notable changes in the hydrography between years. It is questionable if such a decline was important to planktivores on the northern shelf because of the surplus of oceanic species, but in as much as zooplankton stocks in the north may be indicative of conditions elsewhere, fishes and birds over the middle shelf farther south might have been affected by the drop in the abundance of important prey (Springer et al. 1986). Moreover, the grazing stress on phytoplankton probably would have decreased by a similar amount between years, which could have led to a proportional increase in the benthic carbon flux.

Like *Calanus marshallae*, the numbers and biomass of *Sagitta* elegans were significantly lower east of 32.4 ppt in 1986 than in 1985. There was no difference west of 32.4 ppt. Thus, the principal species of herbivore and carnivore of the shelf community both exhibited large interannual variability in abundance and biomass that contrasts with the apparent stability of the same taxa in the oceanic community.

Most of the zooplankton entrained in the Bering Slope Current are probably returned to the Bering Sea with the larger fork which turns south near Cape Navarin on the Siberian coast (Coachman et al. 1975). In spite of that, the transport of oceanic species in Anadyr Water creates a plume of uncharacteristically high biomass on a shallow continental shelf. The annual flux is large compared to production estimates of the community at its source and to standing stock estimates of endemic zooplankton in the sink, and should be considered when calculating carbon budgets for the Bering and Chukchi seas.

CHAPTER 3

Food Habits of Planktivorous Seabirds in the Bering Sea

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INTRODUCTION

A series of three physical fronts in the southeastern Bering Sea divides the continental shelf area into three hydrographic domains; a fourth domain lies over deep water seaward of the shelf break (see reviews by Iverson et al. 1979; Kinder and Schumacher 1981a). The inner front is located at approximately the 50 m isobath (Schumacher et al. 1979); the middle front at the 100 m isobath (Coachman and Charnell 1979), and the shelf break front at the 200 m isobath (Kinder and Coachman 1978). The fronts derive variously from interactions between tidal mixing, wind mixing and stratification. Interfrontal domains are characterized physically by patterns of vertical structure, temperature and salinity.

Characteristic assemblages of organisms and food webs are found within each domain (Iverson et al. 1979). For example, the middle front limits the cross-shelf distribution of zooplankton, particularly copepods (Cooney 1981, Smith and Vidal 1984) which are key elements in the transfer of energy between primary producers and higher trophic levels in regional pelagic food webs (Walsh and McRoy 1986; Smith and Vidal 1984). Large herbivorous copepods, *Neocalanus cristatus*, *N. plumchrus* and *Eucalanus bungii*, which are restricted to the oceanic and outer shelf domains, account for a greater shunt of carbon through pelagic food webs than do the smaller, less efficient grazers such as *Pseudocalanus* spp., *Calanus marshallae* and *Acartia* spp., which predominate in the middle shelf domain (Cooney and Coyle 1982). The most recent estimates of carbon flux from phytoplankton to zooplankton in the southeastern Bering Sea suggest that there is a more than two-fold difference in transfer rates between domains, i.e., 68 g C m^{-2} yr^{-1} in the outer shelf domain and 26 gC m^{-2} yr^{-1} in the middle shelf domain (Walsh and McRoy 1986). Thus, the outer shelf domain is dominated by a pelagic food web including walleye pollock (Theragra chalcogramma), which now supports the largest single-species fishery in the north Pacific Ocean (Bakkala and Traynor 1984). The middle domain is dominated by benthic food webs supporting large standing stocks of epifaunal invertebrates (Jewett and Feder 1981) and the commercially important yellow-finned sole (Limanda aspera) (Iverson et al. 1979).

Large-scale patterns of copepod distribution corresponding to the outer and middle shelf domains might be expected to influence the distribution of planktivores other than fishes. Least auklets (Aethia pusilla) nest only on offshore islands in the Bering Sea (Sowls et al. 1978) and, during the breeding season, they feed primarily on large calanoid copepods (Bedard 1969b; Searing 1977; Hunt et al. 1981a). In this chapter, I examine the hypothesis that the location of the insular breeding colonies relative to the large hydrographic domains determines the numbers and distribution of least auklet populations, and an alternative hypothesis that invokes interspecific competition and physical processes other than those maintaining hydrographic domains as the more important factors in the biogeography of least auklets in the Bering Sea. I present food habits data of these birds from St. Matthew I. and St. Lawrence I., compare them to similar data from St. Lawrence I. and the Pribilof Is. from other studies, and examine the distribution of least auklets in relation to: 1) the biological domains of the Bering Sea, 2) the distribution of other members of copepod-based food webs in the Bering Sea, and 3) oceanographic features that may act to concentrate prey biomass in the vicinity of breeding colonies.

METHODS

Least auklet food samples were obtained on St. Lawrence I. in 1981 and on St. Matthew I. in 1982-83 (Fig. 52). Adult birds were collected during the chick period (late July to mid-August) while returning to the colonies from feeding, or they were trapped at the colonies as they arrived. The contents of the sublingual pouches were removed after collection; trapped birds regurgitated spontaneously. Auklets carry food to chicks in the sublingual pouch, and because it is some distance from the intestinal tract, little digestion takes place between the time the prey are captured and the time they are fed to the chicks. Accurate determinations of the numbers and identities of the various prey taxa consumed are therefore possible.

Prey items were stored in 70% ethanol in the field and were later identified in the laboratory using preserved reference material and standard taxonomic keys. Prey were measured and assigned to size categories according to Bedard (1969a), who determined volume indices (number of individuals of a given taxon per ml) for the principal zooplankton taxa in each size category in auklet diets during his study. The categories are I., 0.0-7.0mm; II., 7.1-15.0mm; and III.,

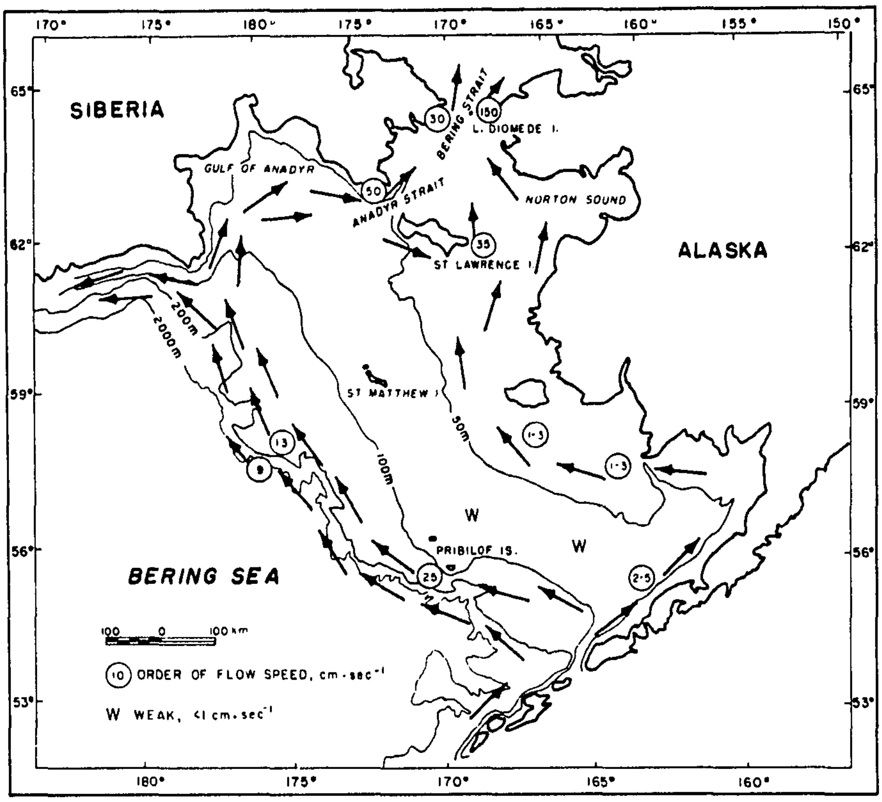


Figure 52. Locations of principal least auklet colonies in the eastern Bering Sea. Generalized circulation patterns are from Kinder et al. (1975), Kinder and Schumacher (1981b).

>15.1mm. Bedard did not report a volume index for Neocalanus plumchrus so we used his value for Calanus marshallae, a species of similar size. The volume index and number of individuals of each taxon were used to estimate their respective biomass contributions to the total diet.

In order to compare my results on a biomass basis with the previous studies, I applied the volume indices to food habits data from St. Lawrence I. in 1964-66 and 1976 using information on prey numbers and sizes reported by Bedard (1969a) and Searing (1977), respectively. Hunt et al. (1981a) reported relative numbers (percentages) of the various prey taxa of auklets on the Pribilofs during 1975-1978, but did not report any sizes. Therefore, I estimated the proportions of each taxon in the three size categories on the Pribilof Is. using the mean proportions obtained on St. Matthew I. in 1982-83 and then applied the appropriate volumetric index value to the resulting numbers.

RESULTS AND DISCUSSION

Food habits

Prey of least auklets from St. Matthew I. and St. Lawrence I. are listed in Table 6 and Table 7, respectively. Table 7 also contains data from St. Lawrence I. for 1964-1966 (from Bedard 1969a) and for 1976 (from Searing 1977). Auklet prey from the Pribilof Is. in 1975-78 (from Hunt et al. 1981a) are listed in Table 8.

Copepods contributed by far the greatest biomass to auklet

Table 6. Prey of least auklets on St. Matthew I.

	1982 (n=29)		1983 (n=40)	
Taxon	Number	Volume (%)	Number	Volume (%)
Calanus marshallae	18,658	89	17,668	84
N. plumchrus	0	0	1	<0.1
Hyperiidae	150	5	59	3
Gammaridae	216	4	209	9
Decapod zoea	187	1	460	3
Thysanoessa spp.	10	<0.1	8	1
Limacina helicina	73	<0.1	8	<0.1
Other	1	<0.1	1	(0.1

Table 7. Prey of least auklets on St. Lawrence I. Data for 1964-66 are from Bedard (1969a); data for 1976 are from Searing (1977).

	1964-66 (n=124)		1976 (n=12)		1981 (n=24)	
Taxon	Number	Volume (%)	Number	Volume (%)	Number	Volume (%)
Calanus marshallae	77,908	65	344	3	3,132	26
N. plumchrus	0	0	9,047	90	6,205	50
N. cristatus	1,444	8	32	2	197	11
Eucalanus bungii	169	<1	9	<1	0	0
Hyperiidae	2,102	9	57	1	32	<1
Gammaridean	533	3	9	<1	21	<1
Decapod zoea	2,808	3	47	<1	643	7
Thysanoessa spp.	2,325	7	2	<1	1	<1
Limacina helicina	6	<1	34	<1	3	<1
Other	311	1	31	<1	0	0

Table 8. Prey of least auklets on the Pribilof Is., 1975-78. Numbers (%) are from Hunt et al. (1981a); volume (%) is according to text; N=258.

Taxon	Number (%)	Volume (%)
Calanus marshallae	65	30
N. plumchrus	11	5
N. cristatus	24	48
Hyperiidae	2	9
Gammaridae	2	5
Decapod zoea	0	0
Thysanoessa spp.	<1	2
Limacina helicina	0	0
Other	0	0

diets on all three islands in all years, ranging from about 74% on St. Lawrence I. in 1964-1966 to about 95% on St. Lawrence I. in 1976. No other taxon contributed more than about 9% to prey biomass in any year. *Calanus marshallae* was essentially the only species of copepod taken by auklets on St. Matthew I.; one individual of *Neocalanus plumchrus* was identified. *Calanus marshallae*, *Neocalanus cristatus* and *N. plumchrus* all contributed importantly to auklet diets on St. Lawrence I. and on the Pribilofs.

Relations to hydrographic domains

St. Matthew I. lies near the center of the middle shelf domain (Fig. 52). The nearly exclusive occurrence of *Calanus marshallae* in auklet diets is consistent with the distributional data on copepods in the southeastern Bering Sea, which show that this species is characteristic of the middle shelf domain but not of the outer shelf or oceanic domains (Cooney 1981; Smith and Vidal 1984). Least auklets on St. Matthew I. apparently do not fly as far as the outer shelf domain to feed, a distance of about 40-50 km.

The Pribilof Is. are geographically within the middle shelf domain, but they lie near the middle front. Although *Calanus marshallae* was numerically dominant in least auklet diets on the Pribilofs, the outer shelf copepods contributed nearly twice as much biomass to auklet diets there, with the most important species being *Neocalanus cristatus*, the largest of the calanoid copepods in the Bering Sea.

Prey of least auklets on St. Lawrence I. include species characteristic of both the outer and middle shelf domains as on the Pribilofs. However, St. Lawrence I. lies in shallow water less than 50 m deep; the 50 m isobath generally delimits the position of the inner front separating the coastal and middle shelf domains in the southeastern Bering Sea. This apparent inconsistency can be explained by an examination of the flow regime of the Bering Sea, which consists of strong currents across the northern shelf, but which originates far to the south.

Circulation over most of the Bering Sea shelf is characterized by a coastal current and a pattern of transport oriented from southeast to northwest in the middle and outer shelf domains (Fig. 52). Currents are weak except along the shelf break and slope where the Bering Slope Current flows at mean speeds of about 10-25 cm sec^{-1}; net transport in the Bering Slope Current is about 5 Sv to the northwest (Kinder et al. 1975). A portion of the flow is entrained in a strong, northward barotropic current passing through Bering Strait (Coachman et al. 1975). The total volume transport averages about 1 Sv and consists of three distinct water masses as defined by three temperature-salinity (T-S) envelopes. Alaskan Coastal Water, originating in Norton Sound, is a warm, low-salinity water mass similar to coastal domain water in the southeastern Bering Sea. Bering Shelf Water and Anadyr Water are both cold, high-salinity water masses originating in the basin of the Bering Sea. Anadyr Water is composed of approximately 80-90% Bering Sea water cooled by the admixture of cold water from the central Gulf of Anadyr during its transit of the outer Gulf; likewise Bering Shelf Water is thought to be water from the Bering Sea that is modified on the middle shelf (Coachman et al. 1975).

The hydrographic structure of the northern shelf is maintained by density differences between adjoining water masses, which lead to the formation of fronts. In contrast, boundary processes lead to front formation in the southeastern Bering Sea, which then allows the development of distinctive interfrontal hydrographic domains (Iverson et al. 1979; Kinder and Schumacher 1981a). Thus, the physical processes on the northern shelf are fundamentally different than those in the southeastern Bering Sea.

The consequences of the flow regime for the ecology of the northern shelf are profound. Because a major fraction of Anadyr Water apparently remains beneath the pycnocline in summer, i.e., below the euphotic zone, nitrate levels remain high during the transit across the shelf. In the vicinity of Bering Strait, nitrate levels of 20-30 ug-at l^{-1} have been recorded during summer (Husby and Hufford 1971; McRoy et al. 1972; Sambrotto et al. 1984; Chapter 1). Shoaling depths and a narrowing of the channel in Anadyr and Bering straits constrict the flow and accelerate the currents leading to vertical eddy coefficients as high as 10 cm^2 sec^{-1} in the Bering Strait region (Coachman et al. 1975). The turbulence is sufficient to raise the nutrient-rich water through the pycnocline into the euphotic zone, creating a functional upwelling system (Fig. 53). Consequently, primary production in the flow field is prolific throughout the summer, making this one of the most productive regions in the world (McRoy et al. 1972; Sambrotto et al. 1984; Walsh et al. 1988; Chapter 1).

Figure 53. Water mass distribution in the Bering Strait region. Turbulence raises cold Anadyr Water (light shading) to the surface northwest of St. Lawrence I. and through Bering Strait: upwelling of Anadyr Water along the southwest coast of St. Lawrence I. is also pronouced. Warm Alaskan Coastal Water follows the mainland from Norton Sound (obscured by clouds) through the eastern Chukchi Sea. NOAA 4 infrared imagery; temperature enhancement scale is -1° to 12°C.

In comparison, primary production in the outer and middle shelf domains is estimated at only 166 and 162 g C m^{-2} yr^{-1}, respectively (Walsh and McRoy 1986). Annual production in both domains results primarily from a typical bloom period in spring after the water column has stabilized, and interannual variation in total carbon fixation is a function of the frequency and intensity of summer storms that can disrupt the pycnocline and resupply nutrients to the euphotic zone (Sambrotto and Goering 1983). As in the case of the physical processes, the primary production regimes of the southeastern shelf and the northern shelf are fundamentally different.

Besides fertilizing the northern shelf waters with nutrients, the flow also seeds the region with zooplankton, as indicated by the composition of auklet prey on St. Lawrence I. Endemic Bering Sea zooplankters, including copepods characteristic of the outer shelf domain, have been found far downstream in the eastern Chukchi Sea (Johnson 1956). Zooplankton grazers cannot control the growth of phytoplankton, however, which leads to a major benthic flux of carbon and explains the high standing stocks of benthic invertebrate macrofauna on the Bering-Chukchi shelf reported by Stoker (1981). In this regard the northern shelf is similar to the middle shelf, where nearly 80% of the annual primary production enters the detritus pool (Walsh and McRoy 1986).

Interspecific competition for copepods

Walleye pollock reach their greatest density in the outer shelf domain, although some, principally one-year-old fish, range well onto the middle shelf (Smith 1981). Spawning occurs predominantly along the southeast outer shelf and 0 age-class juveniles have been found in large numbers in the vicinity of the Pribilof Is. (Smith 1981). The diet of the larvae consists mainly of copepod nauplii, changing to larger copepodids, adult copepods and other zooplankton during the first year (Clarke 1978; Smith 1981; Nishiyama in prep). Whales, primarily fin whales (*Balaenoptera physalus*), are common in the southeastern Bering Sea and along the shelf break (Nasu 1974), where they also feed on copepods as well as other zooplankters (Nemoto 1957, 1959). Pollock and whales are, therefore, direct competitors with auklets for copepod biomass. Smith and Vidal (1984) suggested that declines in numbers of *Neocalanus cristatus* and *N. plumchrus* from the outer shelf domain during spring represent losses to vertebrate predators. A decline of about 80% in survivorship of these copepods occurred during April-May, predating the onset of egg-laying by auklets at the colonies and possibly affecting the size of the population.

Pollock are rarely found on the northern shelf, where they are replaced by Arctic cod (*Boreogadus saida*) and saffron cod (*Eleginus gracilis*) (Wolotira et al. 1979; Frost and Lowry 1981a). Probably because of harsher environmental conditions, populations of these cods, as well as of other fishes, are small compared to those in the southeastern Bering Sea as indicated by test fishery data (Wolotira et al. 1979) and by the absence of a commercial fishery on the northern shelf. In summer the baleen whales are represented by the grey whale (Eschrichtius robustus) which feeds primarily on benthic amphipods (Frost and Lowry 1981a). Thus, competition among auklets, whales and fishes for copepods is probably low compared to that in the outer shelf domain.

Pollock is the largest contributor of biomass to diets of piscivorous seabirds on the Pribilof Is. (Hunt et al. 1981a) and St. Matthew I. (Springer et al. 1986). On St. Lawrence I., piscivorous seabirds feed on a variety of fishes including Arctic cod, sand lance (Ammodytes hexapterus) and capelin (Mallotus villosus) (Springer et al. 1987). The ratio of the numbers of murres (Uria spp.), the numerically dominant avian piscivores at Bering Sea breeding colonies, to the numbers of least auklets (Fig. 54) indicates a shift in the proportions of available fish and copepod biomass from predominantly fish in the southeast to predominantly copepods in the north. This trend is consistent with the reported distribution of pollock, and with the inferred competition for copepods in the southeastern Bering Sea.

Local physical features

Areas of cold, upwelled water surrounding the Pribilofs and St. Matthew I. are common features in summer (Figs. 55 & 56). Kinder et al. (1983) found the edge of this zone around St. Paul I. (Pribilof Is.) to correspond to a front approximately at the 50 m isobath. The density of feeding murres was significantly higher at the front surrounding St. Paul I. than in nearby waters on either side of it. Auklets showed no association with the front but were all within the

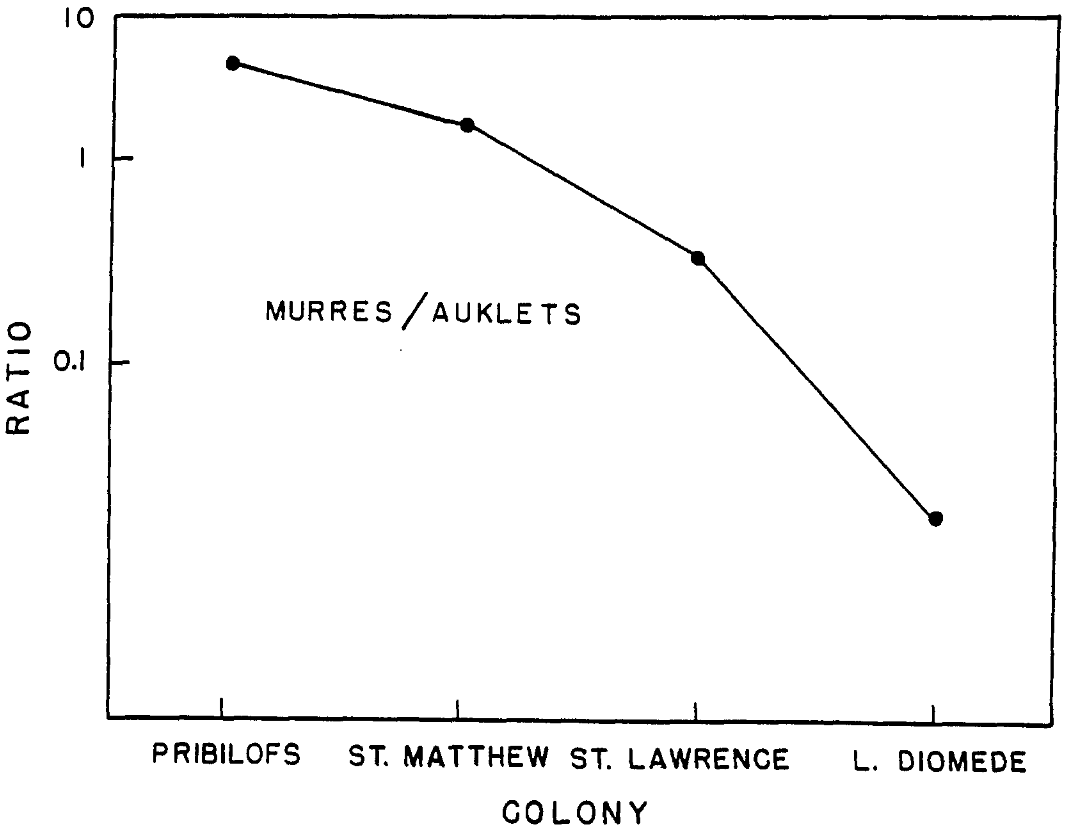
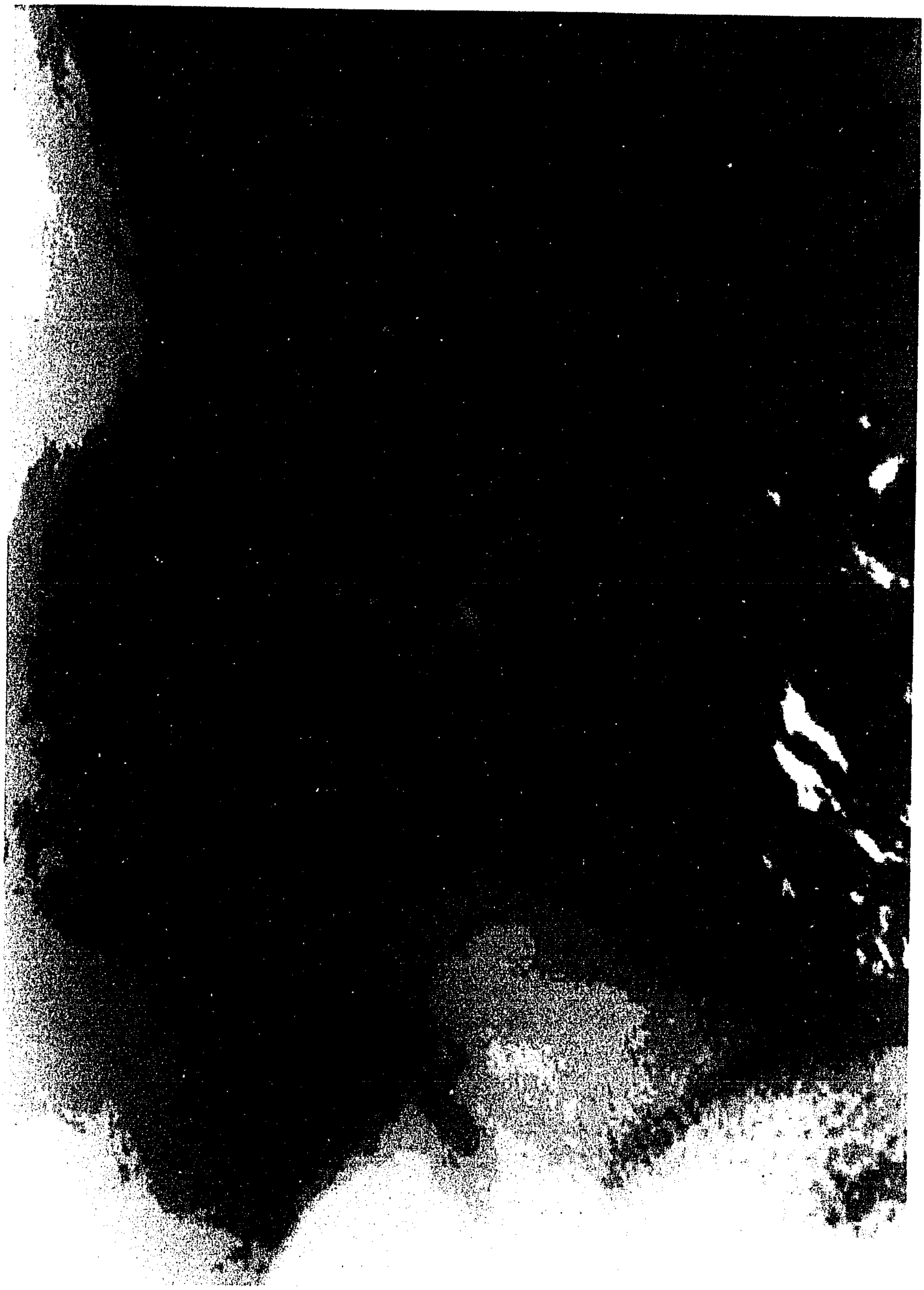


Figure 54. Relative numbers of murres and least auklets at colonies in the Bering Sea, from Sowls et al. (1978) and Roseneau et al. (1985).

Figure 55. Upwelling around the Pribilof Is. Shading, source and enhancement as in Figure 53.

Figure 56. Upwelling around St. Matthew I. Shading, source and enhancement as in Figure 53.



area of well-mixed water between the front and the island. Such observations indicate that zooplankton and possibly fishes are also relatively more abundant within the mixed zone and in the front, a conclusion supported by numerous examples of the enhancement of productivity and biomass in similar situations elsewhere (e.g., Owen 1981). During early August 1983 on St. Matthew I., southerly winds apparently caused strong, localized upwelling along the northeastern coastline as indicated by a shift in the feeding areas of least auklets from offshore north and northeast of the island to a zone within 10 m to about 1 km of shore. The majority of least auklets nesting on the northeastern side of the island fed in this zone during that time. Horizontal plankton tows taken in the upper 10 m of the water column nearshore during the upwelling episode contained primarily <u>Pseudocalanus</u> spp., <u>Acartia</u> spp. and <u>Calanus marshallae</u> in densities in the order of 10^4 m^{-3}, 400 m^{-3} and 200 m^{-3}, respectively.

Upwelling at the edge of St. Lawrence I. (Fig. 53) is also common. It occurs during periods of strong northeasterly winds that establish Ekman transport offshore on the west side of the island, and possibly under other conditions as well. Bedard (1969a) first pointed out the effect that this process has on feeding auklets on St. Lawrence I.; during upwelling the birds fed intensively along the western shoreline, while at other times they fed over a broad area offshore. In 1981 we saw a similar episode when auklets shifted their feeding from generally north of the island in Anadyr Strait to the western coast line within 12 hours after the onset of strong northeast winds. Growth rates of least auklet chicks during upwelling were significantly greater than when the birds fed elsewhere (Roseneau et al. 1985). The prey taken near shore was similar to that from Anadyr Strait, consisting primarily of the outer self *Neocalanus plumchrus* (Table 9). In contrast, the smaller number of auklets that fed south of the island, apparently outside of the area affected by upwelling, fed mainly on the middle shelf *Calanus marshallae*.

CONCLUSIONS

The physical and biological characteristics of the continental shelf of southeastern Bering Sea are fundamentally different than those on the northern shelf. The formation of fronts over the southeastern shelf leads to the development of distinctive domains by restricting cross-shelf advective and diffusive processes governing the distribution of nutrients and biota. In contrast, on the northern shelf the juxtaposition of water masses with differing physical properties creates fronts between them, and the role of advection is paramount in creating a domain with prolific primary production and a well-developed copepod-based food web.

The location of the offshore islands in the Bering Sea relative to the major hydrographic domains apparently is a criterion determining the numbers of least auklets at breeding colonies. The distribution of the principal copepod prey species, however, is a less important factor than is the distribution of copepod biomass. Copepod biomass could be affected by predation and by physical features that act to concentrate the animals in the vicinity of the island colonies.

Table 9. Comparison of copepod prey of least auklets feeding in three areas near St. Lawrence I. Number of individuals (% volume).

	Prey		
Area	*C. marshallae*	*N. plumchrus*	*N. cristatus*
Anadyr Strait	266 (6)	3,210 (74)	130 (20)
SW of island	2,576 (81)	600 (19)	0
Nearshore, W coast	185 (6)	2,395 (79)	67 (15)

Examples of such physical mechanisms are insular upwelling and associated local frontal systems like those around the Pribilof Is. and St. Matthew I., and the presence of the Bering Slope Current that sweeps oceanic zooplankton onto the northern shelf.

The relation between numbers of piscivorous murres and planktivorous auklets at breeding colonies in the Bering Sea suggests a gradient in the relative proportions of fish and copepod biomass available to avian consumers: there are relatively more murres in the southern Bering and more auklets in the northern Bering. Competition among vertebrate consumers of copepods in the outer shelf domain could limit the number of auklets there, while the absence of competition on the northwest shelf might explain, in part, the immense auklet populations in the Bering Strait region. Differences in the relative proportions of nesting habitat available to auklets and murres on the islands (talus for auklets and cliffs for murres) might contribute to the differences in species composition, although the effect is probably secondary to that of differential prey abundance.

If pollock act to enhance populations of piscivores and depress populations of other planktivores, declines in the abundance of pollock in the past decade (Bakkala and Traynor 1984) could account for recent patterns in the reproductive success and numerical tends in seabird populations in the Bering Sea. Between 1969 and 1973 the catch per unit effort (CPUE) of the commercial pollock fishery in the southeastern Bering fell by about 70%, suggesting a significant decline of the pollock population. The CPUE has not recovered since then. The reproductive success of black-legged kittiwakes (Rissa tridactyla), a piscivorous gull that also feeds on pollock, on the Pribilof Is. during the late 1970s (Hunt et al. 1981b) was relatively low compared to other colonies in Alaska during the same time (Springer et al. 1985). Kittiwakes on the Pribilof Is. and St. Matthew I. have had very low reproductive success since 1981 (Springer et al. 1986; V. Byrd unpubl. data). In contrast, the least auklet population on St. Lawrence I. might have doubled between 1966 and 1976 (Searing 1977), and between 1976 and 1982 least auklets on the Pribilof Is. may have increased also (Craighead and Oppenheim 1985). Similar multi-species interactions have been reported elsewhere and often signal changes in ecosystems of major proportions (May et al. 1979; Vesin et al. 1981).

CHAPTER 4

Food Habits of Piscivorous Seabirds in the Northern Bering Sea

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INTRODUCTION

The marine environment of the Bering Strait region of the northern Bering Sea leads to one of the most highly productive ecosystems in the N Pacific Ocean, with primary productivity reaching 2-4 g C m^{-2} d^{-1} during much of the summer (McRoy et al. 1972; Sambrotto et al. 1984). Such rates result from the interaction of distinct water masses (Chapter 1) flowing north from the Bering Sea, through Bering Strait and into the Chukchi Sea (Fig. 57). Bering Strait provides the only connection between the Pacific and Arctic oceans and the transport of water through the strait may be important to the global marine CO_2 budget (Walsh et al. 1988).

Anadyr Water, on the northwestern shelf, originates as a bifurcation of the Bering Slope current that traverses the Bering Sea along the continental shelf break (Coachman et al. 1975; Kinder et al. 1975). It is cold, 0 - 2° C, and saline, 32.7 - 33.0 ppt, and, because it originates at depth in the Bering Sea and remains sequestered beneath the euphotic zone during its transit of the northern shelf, it has very high nutrient levels, e.g., 25 ug at NO_3 l^{-1}, throughout summer (Husby and Hufford 1969; McRoy et al. 1972; Chapter 1). This nitrate is primarily responsible for the prolific phytoplankton growth over the shelves of the northern Bering and southern Chukchi seas. Also, because of its origin, Anadyr Water carries a considerable biomass of zooplankton onto the northern shelf, including the large oceanic copepods _Eucalanus bungii_, _Neocalanus plumchrus_, _N. cristatus_ and _Metridia pacifica_ (Chapter 2; Springer

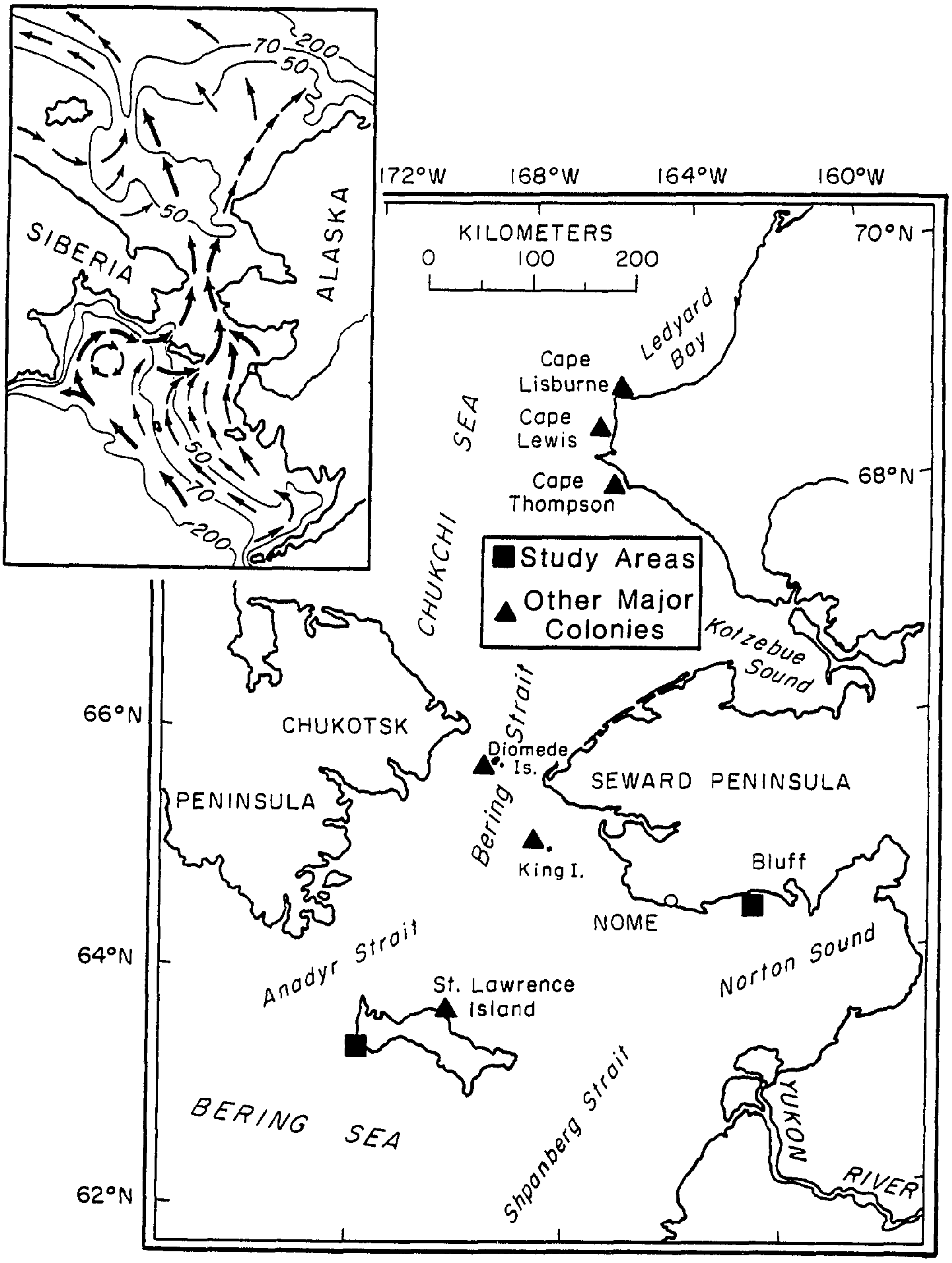

Figure 57. The Bering-Chukchi shelf and generalized circulation patterns from Coachman et al. (1975).

and Roseneau 1985), species that are otherwise restricted to the outer shelf and oceanic domains of the Bering Sea (Cooney 1981; Smith and Vidal 1984).

In contrast to Anadyr Water, Alaskan Coastal Water on the northeastern shelf is a low-salinity, seasonally warm water mass composed of coastal water from the southeastern Bering Sea. It is augmented considerably in Norton Sound by the Yukon River. Primary production is low during most of the summer following a spring bloom (Chapter 1), and the zooplankton community is typical of the coastal zone farther south, being composed of small-bodied grazers such as *Acartia clausi*, *Centropages abdominalis* and *Tortanus discaudatus*, as well as the cladocerans *Podon spp.* and *Evadne spp.* and various taxa of meroplankton (Neimark 1979; Cooney 1981; Chapter 2).

The physical and biological differences between the water masses on the northern shelf could be expected to lead to characteristic pathways of energy flow to upper trophic levels, and to characteristic communities of vertebrate consumers. Most of the carbon fixed over the northern shelf enters benthic food webs and supports very large populations of invertebrate macrofauna (Stoker 1981), which in turn support important numbers of the walrus (*Odobenus rosmarus*) and gray whale (*Eschrichtius robustus*) populations of the Pacific Ocean (Frost and Lowry 1981a; Fay 1982). There are, additionally, well-developed pelagic food webs, and the transport of zooplankton in Anadyr Water probably accounts for the immense breeding populations of planktivorous auklets (*Aethia spp.*) on St. Lawrence I. and other islands in the Bering Strait region (Springer and Roseneau

1985). These auklets do not nest on islands in or near Norton Sound, i.e., entirely within the influence of Alaskan Coastal Water, probably because of inadequate food availability. Similarly, the thick-billed murre (Uria lomvia) is an uncommon breeding species in Norton Sound (Drury et al. 1981), while on St. Lawrence I. it numbers in the order of 0.25 x 10^6 birds (Roseneau et al. 1985). In fact, of the 13 seabird species known to breed in the Bering Strait region (Sowls et al. 1978), only two, the common murre (U. aalge) and black-legged kittiwake (Rissa tridactyla) nest in substantial numbers (ca. 2-3 x 10^4) in Norton Sound (Springer et al. 1985; Murphy et al. 1986), as well as at all of the other regional colonies. Such an uneven breeding distribution of seabirds across the northern shelf suggests an uneven distribution of seabird food webs.

Seabirds nest at many colonies in the Bering Strait region, including other sites on the mainland coast and on other islands (Sowls et al. 1978). During the breeding season they are the most numerous, conspicuous and accessible of the higher trophic level vertebrates, and are, therefore, appropriate subjects for use in studying food webs and patterns of energy flow in ecosystems. Several studies have described the regional colonies and numerous aspects of the breeding biology of the seabirds at them (Swartz 1966; Drury et al. 1981; Roseneau et al. 1985; Springer and Roseneau 1985; Springer et al. 1984, 1985; Murphy et al. 1986). In this chapter, I compare the diets of common murres and kittiwakes from Norton Sound with those from St. Lawrence I., and I compare the diets of these species at both locations with the diets of thick-billed murres on St. Lawrence I.

The diversity of marine environmental conditions near and around St. Lawrence I. should lead to a variety of food webs supporting seabirds, while in Norton Sound, the small number and low diversity of seabirds there might result from an impoverished prey base which depends on the maintenance of a warm, low-salinity environment throughout summer.

METHODS

Murres and kittiwakes were collected at Bluff, the largest colony in Norton Sound, and at the western end of St. Lawrence I. as they returned to the colonies from feeding. These collections were made from a raft at least 2-3 km from the colonies. Two additional samples of thick-billed murres were collected from St. Lawrence I., one of 6 birds while they fed within about 1 km of shore on the north coast, and another of 12 birds from shore as they flew over the beach during a period of inclement weather when boating was impossible. A sample of 4 common murres was also collected from the beach. Kittiwake chicks were collected at Bluff in 1983, but not adult kittiwakes or murres.

The stomach contents were preserved in 70% ethanol within 1-2 hours of collection. Fish prey were counted and identified on the basis of otoliths, dense bones of the inner ear that resist digestion and have species-specific configurations. Because otoliths grow with the fishes, the biomass of prey in the diets can be estimated by using regression equations relating otolith length to fish length and fish length to fish weight. Details of this type of analysis and discussions of its limitations, as well as the regression equations, can be found in Springer et al. (1984, 1986), except that the equation relating the length and weight of sand lance (*Ammodytes hexapterus*) is:

log weight (g) = -6.45 + 3.47 x log length (mm); from D. Schmidt and P. Craig, unpubl. data.

Invertebrates generally were too fragmented to allow accurate counting, and we have indicated their importance only by their frequency of occurrence, i.e., presence or absence.

Repeated observations were made from several locations along the north shore of Norton Sound and from around the northern and western half of St. Lawrence I. of the directions murres and kittiwakes were flying when going to and coming from feeding areas. These observations provide a general indication of the locations of important feeding areas and are helpful to understanding relationships between environmental conditions and seabird food webs.

Throughout this chapter I use published and unpublished data to describe various aspects of the physical and chemical environment, primary production and zooplankton communities of the Bering - Chukchi shelf. The unpublished data have been acquired as part of ISHTAR (Inner Shelf Transfer and Recycling), a larger, interdisciplinary study of this region administered by the University of Alaska.

RESULTS

Food habits

Saffron cod (Eleginus gracilis), including young-of-year cods that presumably were saffron cod, and sand lance were overall the most important prey of both common murres and kittiwakes at Bluff (Tables 10 & 11). Young-of-year flatfish (Pleuronectidae) was the only other taxon contributing appreciably to diets of common murres, and then only in 1982, while Arctic cod (Boreogadus saida) was the only other species that might have been important to kittiwakes, during mid-summer. Invertebrates were encountered much less frequently than fishes, occurring in common murres in only one year and in kittiwakes in only two years.

The estimated biomass of fish in murre diets at Bluff was variable but not significantly different (Kruskal Wallis $p < 0.05$) between years (Table 12). In 1984, four collections were made between 10-17 July, during which time fish biomass increased by over an order of magnitude (Fig. 58). The change was due to increasing numbers of saffron cod through 16 July and to more sand lance in the 17 July collection; 4 of 6 murres collected on 17 July had eaten sand lance compared to only 1 of 25 collected between 10-16 July ($x^2 = 14.0$, $v = 1$, $P < 0.005$). The increase in fish biomass occurred during a period of rapid warming of the coastal zone when the water temperature rose 8^0 C in 7 days. Fish biomass in kittiwake diets was also variable (Table 13), but not significantly different between years.

Arctic cod contributed by far the greatest biomass to the

Table 10. Occurrence of major taxa in diets of common murres at Bluff.

	1978 (9-12 Aug)		1980 (22 Jul)		1981 (11-21 Jul)		1982 (16 Jul)		1984 (10-17 Jul)	
	n	%[1]	n	%[1]	n	%[1]	n	%[1]	n	%[1]
Number examined	22	(100)	12	(100)	19	(100)	5	(100)	31	(100)
Number empty	0	(0)	1	(8)	0	(0)	0	(0)	2	(6)
Frequency of invertebrates	0	0	0	0	0	0	1	20	4	14
Frequency of fishes	22	100	11	100	19	100	5	100	29	100
A. Frequency of Occurrence										
Saffron cod	13	59	8	73	8	42	4	80	19	66
Arctic cod	0	0	0	0	0	0	0	0	0	0
Walleye pollock	0	0	0	0	0	0	0	0	3	10
Cods	0	0	0	0	1	5	0	0	0	0
Y-O-Y cods	4	18	0	0	8	42	3	60	7	24
Sculpins	0	0	6	55	1	5	1	20	8	28
Y-O-Y sculpins	0	0	1	9	0	0	0	0	7	24
Sand lance	8	36	5	45	14	74	0	0	5	17
Capelin	0	0	0	0	1	5	0	0	1	3
Y-O-Y flatfishes	0	0	0	0	2	11	2	40	2	7
Unidentified fishes	9	41	2	18	0	0	1	20	1	3
Shrimps	0	0	0	0	0	0	0	0	1	3
Mysids	0	0	0	0	0	0	0	0	2	7
Crustaceans	0	0	0	0	0	0	0	0	2	7
B. Numbers of Individuals										
Saffron cod	62	2	30	50	16	4	11	4	48	10
Arctic cod	0	0	0	0	0	0	0	0	0	0
Walleye pollock	0	0	0	0	0	0	0	0	5	1
Cods	0	0	0	0	1	<1	0	0	0	0
Y-O-Y cods	104	39	0	0	14	3	175	7	193	41
Sculpins	0	0	8	13	3	<1	1	<1	8	2
Y-O-Y sculpins	0	0	2	3	0	0	0	0	12	3
Sand lance	91	34	18	30	401	90	0	0	188	40
Capelin	0	0	0	0	1	<1	0	0	11	2
Y-O-Y flatfishes	0	0	0	0	8	2	58	24	9	2
Unidentified fishes	13	5	2	3	0	0	0	0	1	<1
C. Estimated Wet Weight (g)										
Saffron cod	582	47	1,606	90	289	15	172	60	1,481	37
Arctic cod	0	0	0	0	8	<1	0	0	0	0
Walleye pollock	0	0	0	0	0	0	0	0	90	2
Cods[2]	0	0	0	0	0	0	0	0	0	0
Y-O-Y cods	112	9	0	0	7	<1	89	31	97	2
Sculpins	0	0	31	2	5	<1	3	1	35	<1
Y-O-Y sculpins	0	0	1	<1	0	0	0	0	6	<1
Sand lance	530	42	135	8	1,626	84	0	0	2,163	55
Capelin	0	0	0	0	2	<1	0	0	24	1
Y-O-Y flatfishes	0	0	0	0	4	<1	30	10	5	<1
Unidentified fishes[3]	26	2	4	<1	0	0	0	0	2	<1

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[1] Values in parentheses represent the frequency among the total number of birds examined. Values not in parentheses represent the percent frequency, numbers, or weight, respectively, among birds containing identifiable prey remains.

[2] Weight = weight of saffron cod.

[3] Weight = 2 g/fish.

Table 11. Occurrence of major taxa in diets of black-legged kittiwakes at Bluff.

	1978 (9-12 Aug)		1980 (22 Jul)		1981 (11-21 Jul)		1982 (16 Jul)		1983[1] (17 Aug)		1984 (10-17 Jul)	
	n	%[2]	n	%[2]	n	%[2]	n	%[2]	n	%[2]	n	%[2]
Number examined	7	(100)	7	(100)	17	(100)	15	(100)	6	(100)	6	(100)
Number empty	1	(14)	0	(0)	1	(6)	1	(7)	1	(17)	2	(33)
Frequency of invertebrates	0	0	0	0	0	0	4	29	0	0	1	25
Frequency of fishes	6	100	7	100	16	100	11	79	5	100	4	100
A. <u>Frequency of Occurrence</u>												
Saffron cod	2	33	2	29	3	19	4	29	3	60	2	50
Arctic cod	0	0	0	0	1	6	0	0	2	40	0	0
Walleye pollock	0	0	0	0	0	0	0	0	0	0	0	0
Cods	0	0	0	0	0	0	0	0	0	0	0	0
Y-O-Y cods	1	17	0	0	1	6	1	7	0	0	0	0
Sand lance	4	66	5	71	11	69	7	50	2	40	2	50
Y-O-Y flatfishes	0	0	0	0	0	0	0	0	2	40	0	0
Unidentified fishes	0	0	0	0	0	0	2	14	1	20	1	25
Crustaceans	0	0	0	0	0	0	2	14	0	0	0	0
Polychaetes	0	0	0	0	0	0	1	7	0	0	0	0
Insects	0	0	0	0	0	0	0	0	0	0	1	25
B. <u>Numbers of Individuals</u>												
Saffron cod	4	9	3	13	3	4	6	10	6	27	2	11
Arctic cod	0	0	0	0	3	4	0	0	2	9	0	0
Walleye pollock	0	0	0	0	0	0	0	0	0	0	0	0
Cods	0	0	0	0	0	0	1	1	0	0	0	0
Y-O-Y cods	1	2	0	0	1	1	0	0	0	0	0	0
Sand lance	40	89	21	87	62	90	53	87	11	50	15	83
Y-O-Y flatfishes	0	0	0	0	0	0	0	0	2	9	0	0
Unidentified fishes	0	0	0	0	0	0	2	3	1	5	1	6
C. <u>Estimated Wet Weight (g)</u>												
Saffron cod	127	29	212	50	231	48	169	32	86	59	22	30
Arctic cod	0	0	0	0	102	21	0	0	19	13	0	0
Walleye pollock	0	0	0	0	0	0	0	0	0	0	0	0
Cods[3]	0	0	0	0	0	0	1	<1	0	0	0	0
Y-O-Y cods	1	<1	0	0	1	<1	0	0	0	0	0	0
Sand lance	317	71	211	50	147	31	362	68	40	27	50	68
Y-O-Y flatfishes	0	0	0	0	0	0	0	0	1	<1	0	0
Unidentified fishes[4]	0	0	0	0	0	0	4	1	2	1	2	3

[1] Chick regurgitations.

[2] Values in parentheses represent the frequency among the total number of birds examined. Values not in parentheses represent the percent frequency, numbers, or weight, respectively, among birds containing identifiable prey remains.

[3] Weight = weight of saffron cod.

[4] Weight = 2 g / bird.

Table 12. Estimated wet weight (g) of fishes in diets of common murres at Bluff. Geometric mean (range ± 1 SD); ND = no data.

Year	10-13 Jul	16-17 Jul	21-22 Jul	9-12 Aug
1984	11 (2-65) n = 18	78 (18-340) n = 13	ND	ND
1982	ND	33 (7-170) n = 4	ND	ND
1981	23 (3-170) n = 9	ND	34 (6-200) n = 9	ND
1980	ND	ND	48 (6-360) n = 12	ND
1978	ND	ND	ND	24 (5-120) n = 22

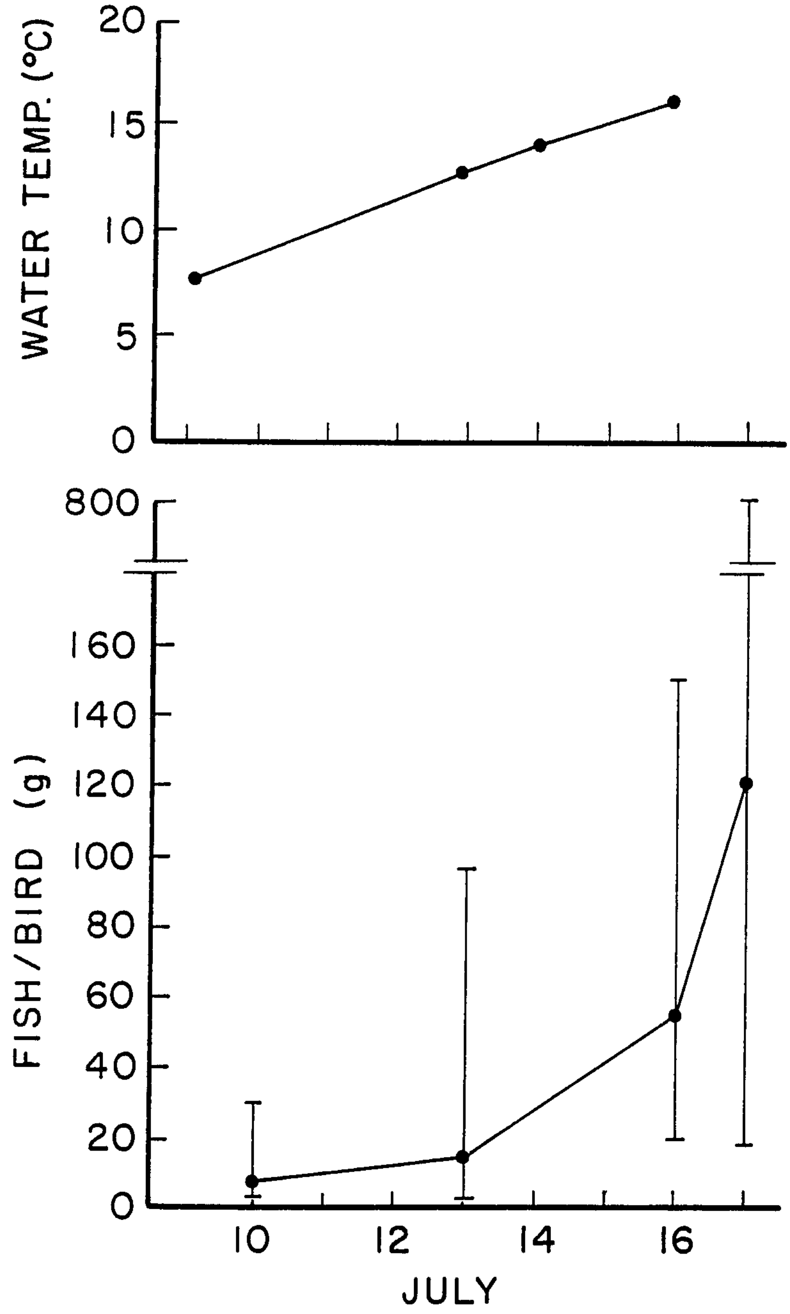

Figure 58. Weight of fish in diets of Common Murres at Bluff, and nearshore water temperature in July 1984. Geometric mean weight (g) with a range of ± 1 SD.

Table 13. Estimated wet weight (g) of fishes in diets of black-legged kittiwakes at Bluff. Geometric mean (range ± 1 SD); ND = no data.

Year	11-12 Jul	13-17 Jul	16 Jul	16-21 Jul	21-22 Jul	9-12 Aug
1984	ND	7 (2-30) n = 5	ND	ND	ND	ND
1982	ND	ND	13 (2-81) n = 9	ND	9 (1-81) n = 6	ND
1981	10 (2-60) n = 12	ND	ND	11 (3-41) n = 5	ND	ND
1980	ND	ND	ND	ND	38 (12-120) n = 7	ND
1978	ND	ND	ND	ND	ND	32 (6-170) n = 7

diets of common murres on St. Lawrence I. (Table 14). Arctic cod were not taken by common murres at Bluff, nor were walleye pollock (Theragra chalcogramma) or capelin (Mallotus villosus), as they were at St. Lawrence I., while saffron cod were taken at both colonies. Kittiwakes at St. Lawrence I. took sand lance almost exclusively (Table 14). As at Bluff, invertebrates were infrequently found in either species, particularly common murres.

Arctic cod was also the most important of the fishes to thick-billed murres on St. Lawrence I., although none of the other species of cods was present in their diets (Table 14). Thick-billed murres fed more often on sculpins (Cottidae) and invertebrates than did common murres. Invertebrates were much more frequent in the birds collected while feeding near the north shore on 19 July (83%, n = 6) than in birds collected when returning from feeding offshore northwest of the island between 21 July - 3 August (29%, n = 14). Gammaridean amphipods were present in 75% and euphausiids in 50% of the northshore samples. Also, sculpins and sand lance were the only fishes eaten by thick-billed murres in the coastal collection, while Arctic cod was eaten by 71% of those that fed offshore to the north.

Common murres contained an estimated average biomass of fish prey of 92 g (geometric mean; range, + 1 SD = 31-270 g; n = 14). There was no difference (Kruskal Wallis $p < 0.05$) between the biomass of fish in birds collected flying over the beach and those collected from the raft, nor between these and any of the samples from Bluff. There was, however, a difference (Kruskal Wallis $p < 0.01$) between the amount of fish in thick-billed murres collected on the north shore and

Table 14. Occurrence of major taxa in diets of thick-billed murres (TBMU), common murres (COMU), and black-legged kittiwakes (BLKI) on western St. Lawrence I., 19 July - 3 August 1981.

	TBMU		COMU		BLKI	
	n	%[1]	n	%[1]	n	%[1]
Number examined	32	(100)	14	(100)	19	(100)
Number empty	2	(6)	0	(0)	4	(21)
Frequency of invertebrates	10	33	1	7	8	53
Frequency of fishes	27	90	14	100	11	73
A. <u>Frequency of Occurrence</u>						
Saffron cod	0	0	1	7	0	0
Arctic cod	15	56	9	64	0	0
Walleye pollock	0	0	1	7	0	0
Cods	1	4	2	14	0	0
Y-O-Y cods	0	0	1	7	0	0
Sculpins	4	15	1	7	0	0
Y-O-Y sculpins	5	19	1	7	0	0
Sand lance	6	22	5	36	8	67
Capelin	0	0	3	21	1	8
Y-O-Y flatfishes	1	4	0	0	0	0
Unidentified fishes	0	0	0	0	0	0
Shrimps	3	11	0	0	0	0
Gammaridea	4	15	0	0	2	17
Mysids	0	0	0	0	1	1
Parathemisto spp.	1	4	0	0	1	8
Euphausiids	4	15	0	0	0	0
Mysids	1	4	1	7	0	0
Polychaetes	1	4	0	0	2	17
B. <u>Numbers of Individuals</u>						
Saffron cod	0	0	2	2	0	0
Arctic cod	54	48	38	33	0	0
Walleye pollock	0	0	6	5	0	0
Cods	4	4	3	3	0	0
Y-O-Y cods	0	0	1	1	0	0
Sculpins	9	8	2	2	0	0
Y-O-Y sculpins	26	23	16	14	0	0
Sand lance	18	16	43	37	78	99
Capelin	0	0	5	4	1	1
Y-O-Y flatfishes	1	1	0	0	0	0
Unidentified fishes	0	0	0	0	0	0
C. <u>Estimated Wet Weight (g)</u>						
Saffron cod	0	0	40	2	0	0
Arctic cod	2,585	86	1,452	77	0	0
Walleye pollock	0	0	148	8	0	0
Cods	99	3	39	2	0	0
Y-O-Y cods	0	0	1	<1	0	0
Sculpins	195	7	19	1	0	0
Y-O-Y sculpins	13	<1	4	<1	0	0
Sand lance	107	4	115	6	183	95
Capelin	0	0	65	3	10	5
Y-O-Y flatfishes	1	<1	0	0	0	0
Unidentified fishes	0	0	0	0	0	0

[1] Values in parentheses represent the frequency among the total number of birds examined. Values not in parentheses represent the percent frequency, numbers, or weight, respectively, among birds containing identifiable prey remains.

flying over the beach, which were equal, and the amount in birds collected from the raft, which was larger (N shore, x = 3 g, range = 1 - 10 g, n = 6; beach, x = 7, range = 1 - 60, n = 12; returning, x = 80, range = 10 - 420, n = 14).

Feeding areas

There was no direction consistently taken by murres or kittiwakes departing the Bluff colony to feed, nor was there any direction from which they tended to return. Most birds appeared to feed offshore except when sand lance were abundant along the coast.

Approximately half of the murres breeding on St. Lawrence I. nest on the northcentral coast and the other half nest on the southwestern coast (Roseneau et al. 1985). During July and August 1981, the majority of birds from both of these areas fed northwest of the island. Comparatively small numbers of murres fed near shore around the western half of the island and offshore south of it. Kittiwakes, in contrast to murres, fed mainly near shore, particularly along the north and south coasts.

DISCUSSION

Distribution of seabirds and their prey

Three species of fishes constituted the majority of the biomass of all fishes in the diets of murres and kittiwakes - saffron cod and sand lance in Norton Sound, and Arctic cod and sand lance on St. Lawrence I. Indeed, gadids and sand lance are important prey of these and other piscivorous seabirds at large colonies elsewhere in northern Alaska: walleye pollock, a gadid, appears to be the single most important species offshore on the Pribilof Is. and St. Matthew I. (Hunt et al. 1981a; Springer et al. 1986); sand lance are similarly important at Cape Peirce, a mainland colony in Bristol Bay in the southeastern Bering Sea (Lloyd 1985); and Arctic cod, saffron cod and sand lance are all important at Cape Thompson and Cape Lisburne in the eastern Chukchi Sea (Swartz 1966; Springer et al. 1984).

The differential occurrence of Arctic cod on the northwestern shelf and saffron cod in Norton Sound fits with other data on the distribution of these two species (Wolotira et al. 1979; Frost and Lowry 1981b). Arctic cod are most abundant in Arctic Ocean waters, such as the Chukchi and Beaufort seas, and generally do not range very far south of St. Lawrence I., where they are replaced by pollock and Pacific cod (Gadus macrocephalus). Saffron cod, on the other hand, are found in the greatest numbers in Norton Sound, and are common in the eastern Chukchi and western Beaufort seas (Wolotira et al. 1979; Craig and Haldorson 1981; Springer et al. 1984), apparently because of the warm coastal jet. Although infrequent, the occurrence of saffron cod and walleye pollock, in addition to Arctic cod, in common murre diets on St. Lawrence I. is not surprising considering the diversity of environmental conditions in the surrounding waters.

The differences in prey taken by thick-billed and common murres on St. Lawrence I. were similar to differences that have been found in other mixed-species colonies on St. Matthew I. and in the eastern Chukchi Sea (Swartz 1966; Springer et al. 1984, 1986), i.e., thick-billed murres take more sculpins and benthic invertebrates, while common murres generally take more of the pelagic species such as sand lance and capelin. In the eastern Chukchi Sea, both species of murres feed on Arctic cod and saffron cod, but common murres generally take a greater proportion of saffron cod than do thick-billed murres (Springer et al. unpubl. data). The absence of thick-billed murres in Norton Sound, therefore, might indicate the lack of a sufficiently productive and suitable community of benthic prey to supplement the primarily pelagic prey of young age classes of cods. This possibility is supported by fisheries surveys that found sculpins more abundant by a factor of about 2-4 on the northern shelf outside of Norton Sound than inside of it (Wolotira et al. 1979), and invertebrate surveys that have found a much lower benthic macrofauna biomass in Norton Sound, 5-10 g C m^{-2}, compared to the region north of St. Lawrence I., 20-30 g C m^{-2} (Stoker 1981; Grebmeier 1987).

Carbon budget

Because the feeding distribution of seabirds from the colonies on St. Lawrence I. and in Norton Sound are not well known, that is, we do not know the extent of the feeding areas even though we know the general locations - it is difficult to estimate the relationship between production at lower trophic levels and carbon transfer to the birds in an areal budget. This is complicated by the strongly advective nature of both regions, particularly on the northwestern shelf, and the role of food web organisms transported from the south in the economy of upper level consumers. Such transport is clearly important to the planktivorous auklets on St. Lawrence I. (Springer and Roseneau 1985), and might also increase overall prey availability to the piscivores there, as suggested by the occurrence of pollock among the prey of common murres.

Nevertheless, we can get some perspective on the levels of carbon transfer through the food webs in the different regimes by simply estimating the absolute daily carbon requirements of the birds. For example, in the order of 0.5 x 10^6 murres, roughly equal numbers of the two species, nest on St. Lawrence I., and most of them feed in the same general area (Roseneau et al. 1985). Using an average body weight for murres of 1 kg and a conservative daily food requirement of 30% of their body weight (Wiens and Scott 1975), they consume about 1.5 x 10^8 g (wet weight) d^{-1}, or 1.5 x 10^7 g C d^{-1}. The kittiwakes, which number about 0.1 x 10^6 and weigh about 450 g, consume about 1.4 x 10^6 g C d^{-1}. In addition, the planktivores remove approximately 8 x 10^6 g C d^{-1} of zooplankton biomass, assuming populations (Sowls et al. 1978) of 1 x 10^6 least auklets (Aethia pusilla) that weigh about 100 g and 0.5 x 10^6 crested auklets (A. cristatella) that weigh about 300 g. Thus, the combined carbon requirement of the principal species of seabirds on St. Lawrence I. is in the order of 2.4 x 10^7 g C d^{-1}. In contrast, the major species at Bluff, about 3 x 10^4 murres and 2 x 10^4 kittiwakes (Murphy et al. 1986, MS), consume a total of only 1.2 x 10^6 g C d^{-1}.

The murres and kittiwakes at Bluff appear to feed generally over a broad area offshore of the colony. If we assume that they feed generally within a radius of 40 km, as they do on the Pribilof I.

(Wiens 1984), and that they are consolidated around the colony for 120 days each year, then the areal carbon requirement would be 40 mg C m^{-2} yr^{-1}. Using the same feeding radius for kittiwakes, their consumption would be 12 mg C m^{-2} yr^{-1}.

Cooney (1981) estimated that the annual secondary production of zooplankton on the inner shelf of the southeastern Bering was about 4 g C m^{-2} yr^{-1}. A similar level of production in Norton Sound, where annual primary productivity may be in the order of 50 g C m^{-2} yr^{-1} (Walsh et al. 1988), would imply a flux of less than 10% of the annual phytoplankton production through the pelagic food web, with greater than 90% going to the benthos. If we further assume an ecological efficiency of 10% between the zooplankton and planktivorous fishes, fish production would be in the order of 400 mg C m^{-2} yr^{-1}, or a factor of about 8 greater than the requirement of the birds.

Food webs and the environment

Fish abundance in Norton Sound apparently varies considerably between years, as indicated by large fluctuations in the reproductive success of murres and kittiwakes at Bluff (Murphy et al. 1986, MS). There is a strong correlation between seabird productivity and environmental temperature, with warm years being good and cold years being poor (Springer et al. 1985; Murphy et al. 1986). An analysis of seabird prey in the coastal zone of the eastern Chukchi Sea over several years indicated that warm years were also generally favorable for certain fishes, particularly sand lance, which were larger by age class and were much more abundant in warm years than in cold years

(Springer et al. 1984).

The connection between water temperature and fish abundance might be direct, that is, water temperature might affect the distribution and growth rates (i.e., metabolism) of various fishes having given thermal preferences, or it might be indirect, by affecting the development of zooplankton prey populations that support the fishes. For example, in the coastal eastern Chukchi downstream of Norton Sound in summer 1983, a cold year north of Bering Strait, the five most numerous taxa of prey consumed by sand lance that year were not abundant in the water column until late summer, at the same time that sand lance began to be caught by seabirds (Fig. 59). The seasonal increases in zooplankton and sand lance abundance followed by about two weeks a significant rise in water temperature. In comparison, the rapid increase in fish biomass in murre diets during the warming period in Norton Sound in 1984 demonstrates possibly a direct response of the fishes to temperature, such as seeking out favorable, i.e., warm, areas. In 1976, also a cold year in Norton Sound, sand lance were generally scarce, but they were found concentrated in Golovin Bay (Barton 1977), a shallow, well-protected bay in Norton Sound that undoubtedly warms early.

The coastal zooplankton community not only tolerates the characteristically large annual fluctuations in both temperature and salinity, but many taxa probably depend on the seasonal warming for successful reproduction (Neimark 1979; Cooney 1981). The same apparently applies to certain fishes, such as sand lance. Thus, the anomolous eastward excursion of Anadyr-Bering Shelf water across the

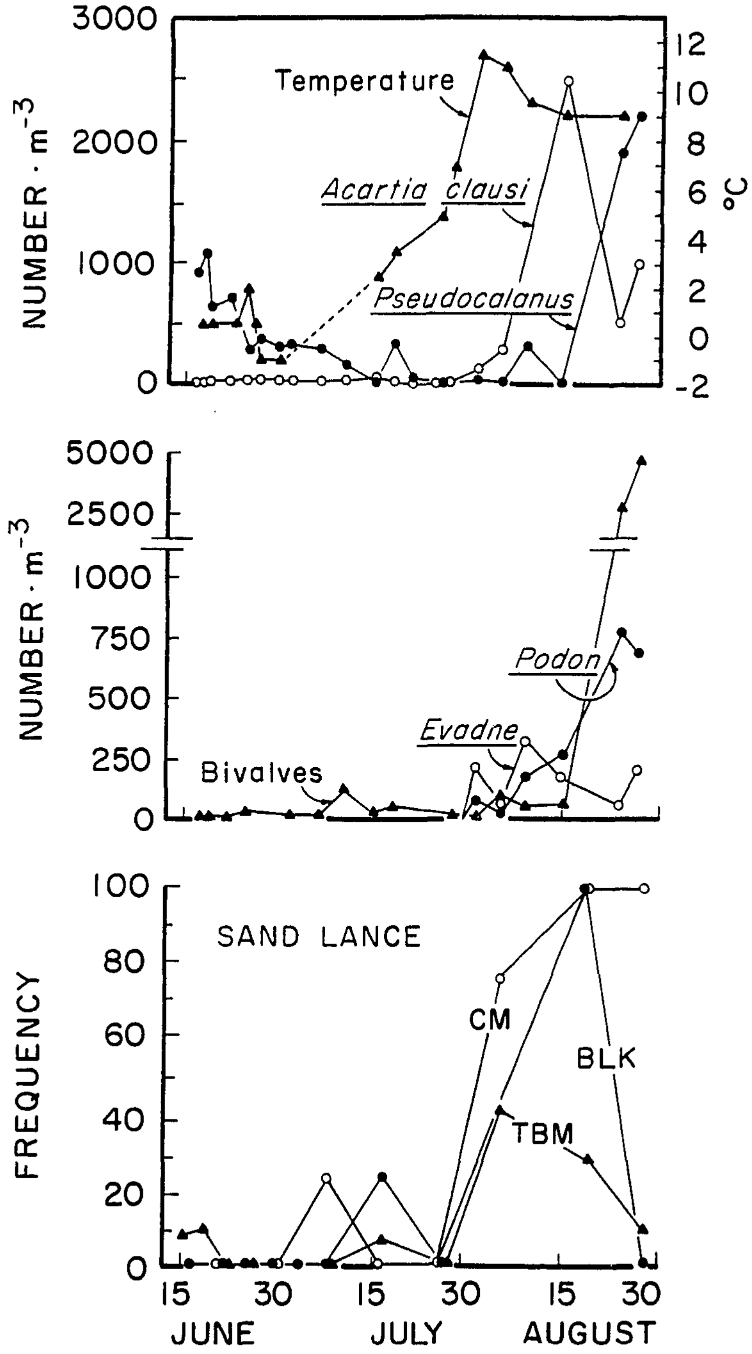

Figure 59. Water temperature, water column concentrations of zooplankton prey of sand lance, and the frequency of occurrence of sand lance in diets of murres and kittiwakes at Cape Lisburne in 1983.

northern shelf and into Norton Sound during summer 1984 (Fig. 60), rather than possibly stimulating productivity by infusing nutrients, phytoplankton and zooplankton, disrupted the food web to the point that murres and kittiwakes suffered the poorest breeding season in at least a decade and some adult kittiwakes even starved to death (Murphy et al. MS).

The environment of the northwestern shelf influenced by the flow of cold Anadyr Water tends to be more thermally and chemically stable than that in Norton Sound during summer, and the animals that live there do not have to adjust to such a large seasonal range of temperature and salinity. How much difference this makes to their population stability is not known. Clearly, much depends on the abundance of zooplankton in the flow, which presumably is determined by physical and biological factors far to the south. The prolific primary production and the rich supply of zooplankton should certainly enhance *in situ* production at the higher trophic levels.

Besides this oceanic-based food web, a second pelagic system like that in Norton Sound can develop in summer in the coastal zone around St. Lawrence I., and includes sand lance and their prey, which is probably similar to that along the mainland coast, i.e., *Pseudocalanus* spp. and other small zooplankters. In 1981, a warm year, sand lance were so abundant near the island that the growth rates of kittiwake chicks were the highest we have recorded in northern Alaska (Roseneau et al. 1985), where growth rates are often much higher than elsewhere in the species' range. Interestingly, such a trophic pathway apparently is poorly developed around the Pribilof

Figure 60a. NOAA 7 infrared image of the northern Bering Sea shelf showing the typical distribution of cold Anadyr Water (lighter shading) northwest of St. Lawrence I. and warm Alaskan Coastal Water (darker shading) in Norton Sound and downstream in the eastern Chukchi Sea, 18 July 1982.

Figure 60b. Imagery showing the extent of anomolous circulation across the northern shelf from late June through mid-August 1984, i.e., cold Anadyr and Bering Shelf water from the west extending eastward and deeply into Norton Sound, 16 July 1984.

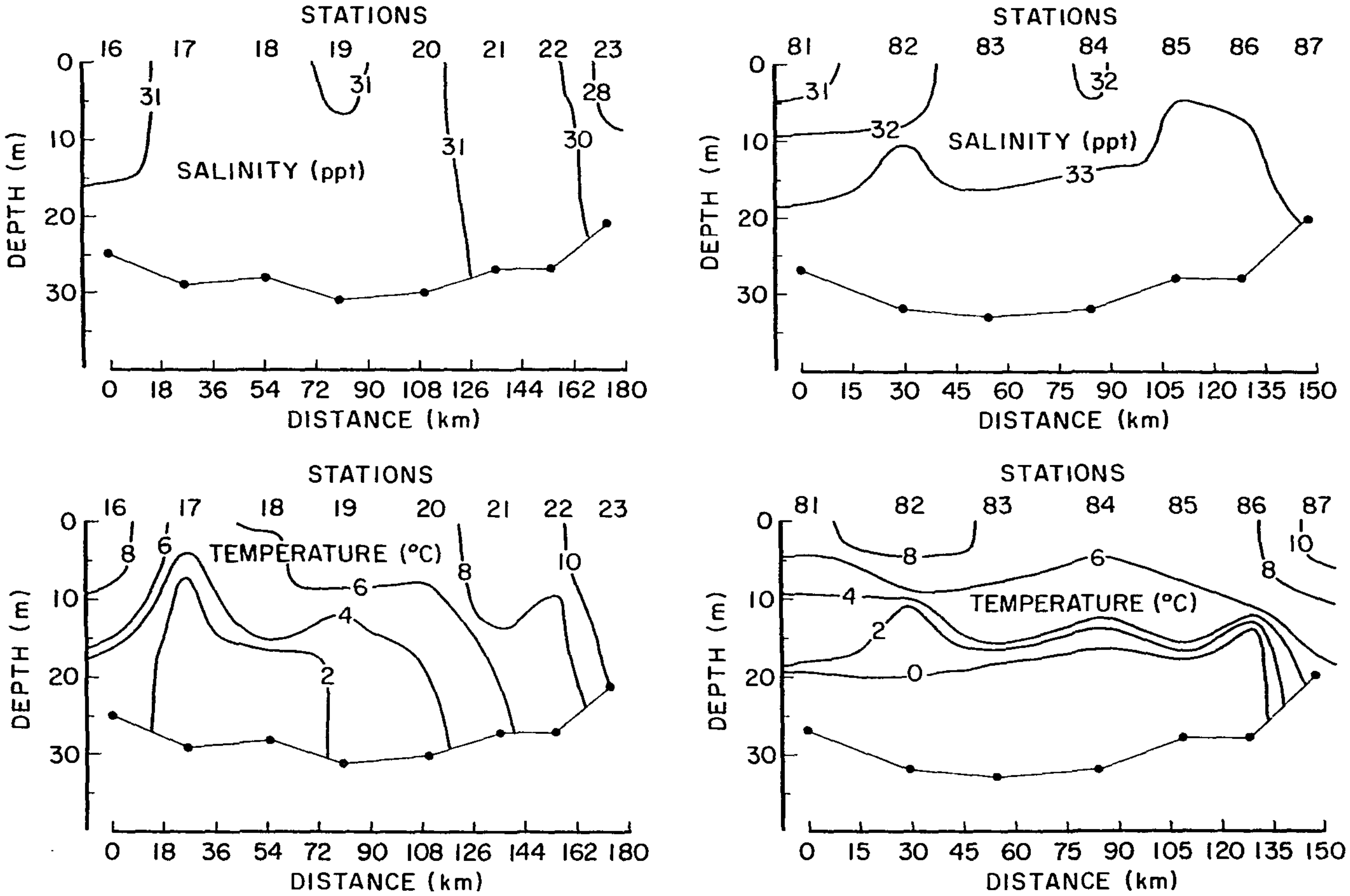

Figure 60 (c). Hydrographic cross section from eastern St. Lawrence I. to the Yukon River delta showing the typical condition, 17-18 August 1983 (left). (d). Hydrographic cross sections from eastern St. Lawrence I. to Nome confirming the anomoly shown in (b) above, 1 July 1984 (right) (from J. Grebmeier, unpubl. data).

Is. or St. Matthew I. to the south, judging from the infrequent occurrence of sand lance in seabird diets there (Hunt et al. 1981a; Springer et al. 1986, unpubl. data).

As along the mainland coast, sand lance around St. Lawrence I. are not available each summer. Sand lance availability was apparently low in 1976 and 1984, as it was elsewhere in northern Alaska in those years (Springer et al. 1984). Both summers were environmentally cold, and kittiwakes throughout the northern Bering and eastern Chukchi had very poor reproductive success.

CONCLUSIONS

Murres and black-legged kittiwakes, with circumarctic distributions, are among the most abundant and widespread of all seabirds. They are found throughout Alaska wherever suitable nesting habitat, i.e., sea cliffs, occurs (Sowls et al. 1978). The distribution of the two species of murres is not uniform, however. Common murres are much more numerous than thick-billed murres at coastal colonies in the Gulf of Alaska and the Bering Sea, while thick-billed murres predominate at offshore insular colonies such as the Pribilof Islands. Auklets, which are unique to the North Pacific, nest only on offshore islands with ready access to large-bodied taxa of zooplankton, particularly copepods and euphausiids characteristic of oceanic waters.

On the basis of the location of St. Lawrence I., that is, on the inner shelf within shallow waters less than 50 m deep, one would not expect to find large populations of thick-billed murres and auklets that are typically associated with more oceanic food webs. Yet the numbers of these species on St. Lawrence I. and other islands near Bering Strait, e.g., the Diomede Islands and King Island, are among the largest known in Alaska. Indeed, least auklets (Aethia pusilla) and crested auklets (A. cristatella) probably attain their greatest numbers there, even though the islands are geographically within the coastal zone (Iverson et al. 1979). This apparent paradox is a result of the transport of waters of the Bering Sea into the Chukchi Sea through Bering Strait, and more particularly, of Anadyr Water, which originates in the oceanic domain along the continental shelf break and constitutes an important part of the northward flow. It transforms the otherwise coastal oceanographic nature of much of the Bering - Chukchi shelf into one characterized by sustained, high levels of primary production commonly associated with upwelling areas, large standing stocks of zooplankton, a diversity of forage fishes and spectacular populations of marine birds and mammals.

In contrast to this system, a typically coastal environment is found nearshore around St. Lawrence and within the domain of Alaskan Coastal Water, including Norton Sound. In Norton Sound, primary and secondary production are both relatively low, oceanic zooplankton are absent, suitable species of forage fishes are few and the seabird populations are small. The transfer of energy through the coastal food web to higher trophic levels is apparently dependent on seasonal warming and the effect it has on the biology of zooplankton and fishes. Thus, in the northern Bering Sea, marine food webs, and hence seabird populations, are related as much to the advective oceanographic regime as to the apparent geographical setting in relation to hydrographic and biological domains existing farther south.

CHAPTER 5

Food Habits of Piscivorous Seabirds in the Eastern Chukchi Sea

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INTRODUCTION

Two breeding colonies in the eastern Chukchi Sea, Cape Thompson and Cape Lisburne, support about 500,000 piscivorous seabirds, of which approximately 90% are murres (*Uria* spp.), and 9% are Black-legged Kittiwakes (*Rissa tridactyla*) (Swartz 1966; Springer et al. 1985b). In 1976 the reproductive success of the kittiwakes was extremely low at both colonies. Symptoms of the breeding failure were characteristic of season-long food shortage: few birds developed brood patches , copulation was seldom seen, few eggs were laid, egg laying occurred late in the breeding season, and most of the few chicks that hatched died, apparently of starvation. Reproductive success improved incrementally between 1977 and 1979 and remained relatively high in 1980 (Springer et al. 1985b). The recovery was typified by progressively earlier laying dates, larger clutch and brood sizes, and fewer empty nests. Growth rates of kittiwake chicks were high in most years after 1976, indicating good late-season food availability in those summers.

These changes, and similar changes in the breeding biology of murres (Springer et al. 1985b), signal variability of comparable magnitude in regional food webs. In this chapter, I show that the diets of murres and kittiwakes varied within breeding seasons and between years, variations that corresponded in time to interannual changes in water temperature and sea ice cover. I review recent and long-term climatic variability in northern Alaska and discuss possible interactions between climate, oceanography, and the fish populations supporting marine birds in the eastern Chukchi Sea.

METHODS

Field work was conducted during portions of each summer of 1976-1979 at Cape Thompson and 1976-1980 at Cape Lisburne (Fig. 61). Except in 1976 at Cape Lisburne, murres and kittiwakes were collected at intervals during each breeding season as they returned to the colonies from offshore feeding areas. Most birds fed at considerable distances from both colonies and to visit those areas to collect specimens was not practical . The stomach contents and the lining of the proventriculus of each bird were removed and stored in 70% ethanol and the prey remains were identified in the laboratory using taxonomic keys and preserved reference material.

Because food items were usually in an advanced stage of digestion when the birds returned to the colonies, invertebrate prey were often identified from parts such as rostra, jaws, uropoda. and eyes, and fishes were identified from otoliths. Sculpins (Cottidae) were counted and identified using preopercular bones as well as otoliths.

The sizes of most fish prey recovered from murres and kittiwakes were reconstructed from regressions of fish length on otolith length, and from fish weight on fish length (Table 15). Sculpins were often not identifiable to species or genera, and for analytical purposes regression equations for *Myoxocephalus quadricornis* were used to estimate their size. *M. quadricornis* was

Figure 61. Map of the study area in northwestern Alaska.

Table 15. Regression equations for estimating lengths and weight of fish identified in prey remains of murres and kittiwakes.

Fish	Equation	N	r	Source
Arctic cod	Fish lng. (cm) = 2.198			
	x otolith lng. (mm) + 1.588	202	0.981	Frost and Lowry 1981b
	log wt. (g) = -5.196 + 3.031 log lng. (mm)	277	0.98	Craig et al. 1982
Saffron cod	Otoliths > 8.5 mm			
	Fish lng. (cm) = 2.323			
	x otolith lng. (mm) - 4.839	110	0.963	Frost and Lowry 1981b
	Otoliths < 8.5 mm			
	Fish lng. (cm) = 1.740			
	x otolith lng. (mm) - 0.090	36	0.932	Frost and Lowry 1981b
	log wt. (g) = -5.610 + 3.233 log lgn. (mm)	180	0.94	Craig and Haldorson 1981
Sculpins[A]	Fish lng. (cm) = 4.009			K. Frost and L. Lowry,
	x otolith lng. (mm) - 4.364			unpubl. data
	log wt. (g) = -6.016			
	+ 3.46 log lng. (mm)	272	0.98	Craig and Haldorson 1981
Sand lance	Fish lng. (mm) = 4.01			
	x otolith lng. (units)[B]+ 19	31	0.91	This study
Capelin	Fish lng. (mm) = 3.42			
	x otolith lng. (units)[B]+ 29	12	0.99	This study

[A] Equations were derived from specimens of *Myoxocephalus quadricornis*.

[B] 12.5 units mm^{-1}.

the only species of sculpin in the eastern Chukchi Sea for which size data were available.

Intact sand lance (Ammodytes hexapterus) and capelin (Mallotus villosus), from which otolith length - fish length regression equations were derived, were found on beaches near the colonies after storms or after they were dropped by birds. They were generally partially desiccated, making their wet weights unreliable. Based on the average weight and length of 14 relatively fresh sand lance (mean weight = 3.0 g, s = 1.9: mean length = 88 mm, s = 16) collected at Cape Lisburne in 1978, and the mean length of all colony/year samples, we estimated the average weight of individual sand lance consumed by seabirds by colony and year.

Most of the capelin collected by us were adult fish and were much larger than those taken by murres and kittiwakes. In 1978 at Cape Lisburne, two specimens in the smaller size class were obtained (mean weight = 4.0, s = 3.0; mean length = 94 mm, s = 16). We used these values to estimate the average weight of individual capelin in each colony/year sample in the same way as for sand lance. The values (grams) we used for mean individual wet weights are as follows:

		Cape Lisburne	Cape Thompson
Sand lance	1977	3	2
	1978	3	3
	1979	3	4
	1980	4	-

Capelin	1977	-	2
	1979	2	3
	1980	3	-

Righteye flounders (Pleuronectidae) were generally young-of-year fish and were assigned an average weight of 1.0 g, based on the weight of one intact specimen. A variety of taxa, including snailfishes (Cyclopteridae, especially *Liparis* spp.), pricklebacks (Stichaeidae, especially *Stichaeus punctatus* and *Chirolophus* spp.), and herring (*Clupea harengus*), were categorized as "other fishes." They were generally small: the weight of three pricklebacks and one herring averaged 2 g each (s = 1.8).

Many otoliths were broken and could not be accurately measured, even though they could be identified and the number of fish they represented could be determined. Therefore, weights of the various taxa of fishes in individual birds were estimated by multiplying the number of a given taxon in each bird by the average weight of all individuals of that taxon in that year. The average weight of a taxon was estimated by measuring a subsample of all intact otoliths and using the appropriate equations (Table 15), or it was based on the above weight estimates.

Cod otoliths could not always be identified to species. In such cases, the unidentified cod were apportioned to the two species (Arctic cod, *Boreogadus saida*, and saffron cod, *Eleginus gracilis*) according to the proportions of Arctic and saffron cod that were identified in all specimens collected in a given interval, e.g. 1-20

July 1977, Cape Lisburne.

Sand lance were aged by counting opaque and hyaline zones of otoliths (Reay 1972). Arctic cod, saffron cod, and sculpins were aged by comparing the calculated body lengths with length distributions of known-aged fishes reported by Craig and Haldorson (1981). Capelin were aged on the basis of similar data provided by Pitt (1958a).

Intact invertebrates were measured and average weights were used to estimate weights of certain groups. The average weight of 13 amphipods (Amphipoda) was 0.2 g (s = 0.15 g); of 10 mysids (Neomysis spp. and Mysis spp.) it was 0.2 g (pooled sample); of 20 euphausiids (Thysanoessa spp.), 0.1 g (pooled sample); of 17 shrimps (predominantly Pandalus spp. and Eualus spp.), 0.5 g (s = 0.3 g); and of 2 polychaetes (Nereis spp.), 1 g (s = 0.2 g). "Other invertebrates," including hermit crabs (Labidochirus splendescens), squids (Cephalopoda), and snails (Gastropoda), were assigned an average weight of 1 g; no intact specimens in this group were recovered.

Information on murre and kittiwake feeding areas was obtained by land-based observations of directions taken by birds as they flew to and from the colonies, and by similar boat-based observations along the coastline up to 60 km from the colonies. In 1978 an aircraft was used to supplement the land- and boat-based observations during 25 - 29 July and 18 - 19 August. Transects were flown offshore up to 130 km from the colonies.

In analyzing differences in the lengths and biomass of fishes in seabird diets between colony/year samples, I first conducted

Kruskal-Wallis tests. If the test result was significant ($p < 0.05$), I then used a multiple comparisons procedure (Conover 1980) to determine which samples differed from one another. I have used the notation K-W/MCP, $p < 0.05$ to indicate when these tests revealed significant differences between mean values.

Limitations

A general limitation of this study, and one common to most food habits studies, is the problem of accurately determining the number and size of prey organisms consumed by the birds. Birds were collected as they returned to the colonies from feeding; however, differences between individuals in the time spent feeding and time since feeding are unknown. This problem is complicated by differential digestibility of fish and invertebrate prey. Bradstreet (1980) concluded that the number of fish otoliths in murre stomachs provided a satisfactory index of the number of fishes recently ingested. Also, as I have done, he attempted to reduce bias by using invertebrate parts to estimate the number and size of the various taxa consumed by murres.

A related question is whether invertebrates found in bird stomachs were eaten by the birds directly, or indirectly after they were first eaten by fishes that subsequently became prey. With the exception of cumaceans, larval crustaceans, and copepods, I have assumed that all invertebrates in a bird stomach were intentionally consumed.

A specific limitation of this study is the use of weight estimates of sand lance, capelin, flatfishes, and "other fishes" based on small numbers of specimens. While the values I used can be improved upon with additional data, I applied the estimates in a uniform manner that should provide indices of the relative importance of these taxa in seabird diets within and between years. Likewise, the following data should provide indices for assessing other changes in diets, such as in the total biomass consumed, although the values I report probably underestimate the actual consumption when it is calculated on the basis of the energy requirements of seabirds (Wiens and Scott 1975).

RESULTS

Food habits

The food habits of murres and kittiwakes during all years combined were similar at the two colonies (Tables 16 and 17) and were similar to those reported previously for Cape Thompson (Swartz 1966). A notable difference between the colonies was the near absence of mysids and euphausiids in diets at Cape Thompson. The two species of murres fed on similar kinds of fishes, although common murres (*Uria aalge*) took many fewer sculpins, flatfishes, and other fishes, but more sand lance and capelin, than did thick-billed murres (*U. lomvia*). Thick-billed murres took a greater number of invertebrates than did common murres. Kittiwakes rarely fed on sculpins of flatfishes, benthic taxa that would generally not be available to them because they feed only on prey that are at or near the surface. Polychaetes

Table 16. Occurrence of major taxa in diets of thick-billed murres (TBMU), common murres (COMU), and black-legged kittiwakes (BLKI) at Cape Thompson, 1976-79.

	TBMU		COMU		BLKI	
	n	%[1]	n	%[1]	n	%[1]
Number examined	246	(100)	62	(100)	116	(100)
Number empty	33	(13)	13	(21)	11	(9)
Frequency of invertebrates	115	54	6	12	20	19
Frequency of fishes	182	85	45	92	91	87
A. <u>Frequency of Occurrence</u>						
Cods	85	40	29	59	55	52
Sculpins	87	41	14	29	0	0
Sand lance	45	21	20	41	32	30
Capelin	26	12	12	24	17	16
Flatfishes	19	9	3	6	0	0
Other fishes	28	13	3	6	3	3
Shrimps	69	32	3	6	4	4
Amphipods	29	14	3	6	0	0
Mysids	0	0	0	0	1	1
Euphausiids	1	<1	0	0	0	0
Polychaetes	18	8	0	0	12	11
Other invertebrates	36	17	1	2	7	7
B. <u>Numbers of Individuals</u>						
Cods	350	8	203	26	241	27
Sculpins	835	25	137	17	0	0
Sand lance	213	6	271	34	325	36
Capelin	199	6	138	18	146	16
Flatfishes	180	5	4	<1	0	0
Other fishes	271	8	16	2	6	<1
Shrimps	244	7	4	<1	34	4
Amphipods	910	27	12	2	0	0
Mysids	0	0	0	0	2	<1
Euphausiids	1	<1	0	0	0	0
Polychaetes	36	1	0	0	137	15
Other invertebrates	73	2	1	<1	14	2
C. <u>Estimated Wet Weight (g)</u>						
Cods	2574	43	2210	59	2626	63
Sculpins	1555	26	414	11	0	0
Sand lance	497	8	694	19	975	23
Capelin	595	10	383	10	415	10
Flatfishes	180	3	4	<1	0	0
Other fishes	130	2	32	<1	12	<1
Shrimps	122	2	2	<1	17	<1
Amphipods	312	5	2	<1	0	0
Mysids	0	0	0	0	1	<1
Euphausiids	1	<1	0	0	0	0
Polychaetes	36	<1	0	0	137	3
Other invertebrates	73	1	1	<1	14	<1

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[1] Values in parentheses represent the frequency among the total number of birds examined. Values not in parentheses represent the percent frequency, numbers, or weight, respectively, among birds containing identifiable prey remains.

Table 17. Occurrence of major taxa in diets of thick-billed murres (TBMU), common murres (COMU), and black-legged kittiwakes (BLKI) at Cape Lisburne, 1977-80.

	TBMU		COMU		BLKI	
	n	%[1]	n	%[1]	n	%[1]
Number examined	198	(100)	48	(100)	71	(100)
Number empty	16	(8)	3	(6)	4	(6)
Frequency of invertebrates	85	47	9	20	22	33
Frequency of fishes	173	95	45	100	60	90
A. <u>Frequency of Occurrence</u>						
Cods	99	54	35	78	28	42
Sculpins	89	49	10	22	4	6
Sand lance	75	41	25	56	29	43
Capelin	13	7	2	4	7	10
Flatfishes	15	8	7	16	0	0
Other fishes	8	4	1	2	5	7
Shrimps	39	21	1	2	1	1
Amphipods	48	26	2	4	4	6
Mysids	19	10	3	7	0	0
Euphausiids	15	8	1	2	8	12
Polychaetes	12	7	0	0	13	19
Other invertebrates	11	6	1	2	2	3
B. <u>Numbers of Individuals</u>						
Cods	660	13	202	31	158	5
Sculpins	529	10	17	3	5	<1
Sand lance	838	16	255	39	263	8
Capelin	55	1	60	9	29	<1
Flatfishes	123	2	83	13	0	0
Other fishes	22	<1	6	<1	7	<1
Shrimps	165	3	5	<1	1	<1
Amphipods	985	19	4	<1	1318	42
Mysids	295	6	9	1	0	0
Euphausiids	1544	29	6	<1	1626	51
Polychaetes	8	<1	0	0	51	2
Other invertebrates	25	<1	3	<1	2	<1
C. <u>Estimated Wet Weight (g)</u>						
Cods	5028	51	1034	53	912	36
Sculpins	1135	12	18	1	30	1
Sand lance	2703	27	669	34	830	33
Capelin	132	1	122	6	87	3
Flatfishes	123	1	83	4	0	0
Other fishes	44	<1	12	<1	14	<1
Shrimps	83	<1	3	<1	1	<1
Amphipods	197	2	<1	<1	264	10
Mysids	59	<1	2	<1	0	0
Euphausiids	155	2	<1	<1	163	7
Polychaetes	8	<1	0	0	52	2
Other invertebrates	25	<1	3	<1	2	<1

[1] Values in parentheses represent the frequency among the total number of birds examined. Values not in parentheses represent the percent frequency, numbers, or weight, respectively, among birds containing identifiable prey remains.

were taken more frequently by kittiwakes than by murres at both colonies, as were euphausiids at Cape Lisburne. Polychaetes are usually members of the benthic infauna, but they spawn in the water column (Johnson 1943) and the heteronereis worms become available to seabirds at that time. The apparently large contribution of amphipods to the diets of the kittiwakes at Cape Lisburne is misleading, since all but eight were recovered from a single bird.

Temporal changes in diets

Throughout the summer of 1976 at Cape Thompson, thick-billed murres fed on cods, sculpins, and other fishes (Fig. 62), while common murres and kittiwakes fed almost entirely on cods alone (Fig. 63). Sand lance were uncommon and capelin and flatfishes were absent in the birds' diets. Sand lance and capelin comprised an increasingly larger proportion of prey from one interval to the next in the summer of 1977, and they were important summer-long in 1979. The same pattern was apparent at Cape Lisburne (Figs. 62 and 63): sand lance and capelin became progressively more important in murre and kittiwake diets later in the summer of all years, and they became more important earlier in the summer in successive years. Flatfishes occurred in the diets of thick-billed murres only in 1978-1979 at Cape Thompson and in 1979-1980 at Cape Lisburne.

Besides the changes in the proportions of various fish taxa in seabird diets, there is an indication that the absolute quantity of prey in thick-billed murre diets also changed. With only one exception, both the number of fishes (Table 18) and the estimated

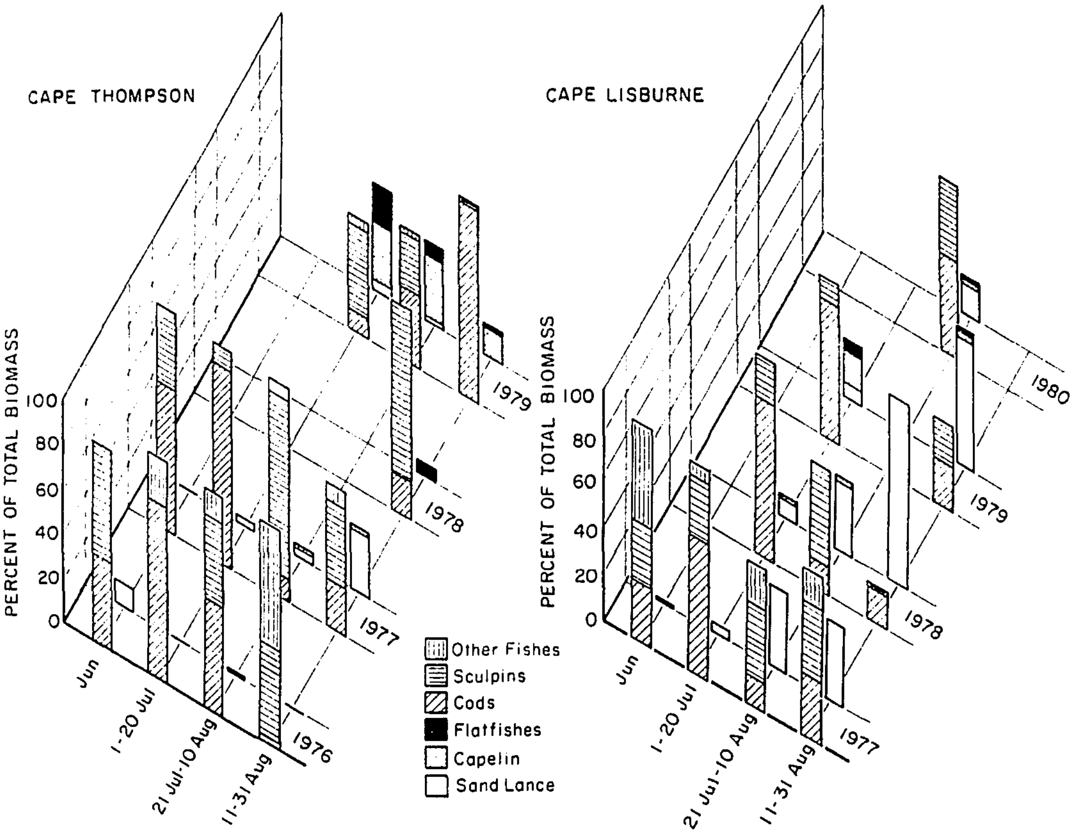


Figure 62. Percent contribution of various taxa to the total biomass of fishes in diets of thick-billed murres at Cape Thompson and Cape Lisburne.

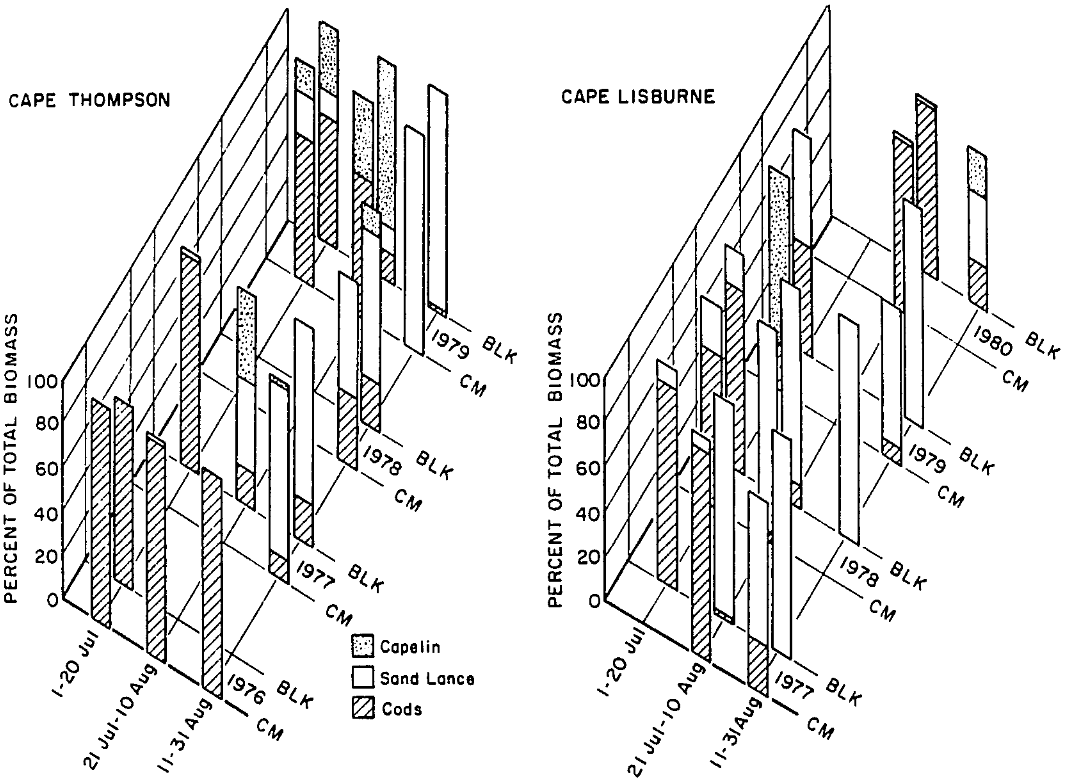


Figure 63. Percent contribution of various taxa to the total biomass of fishes in diets of common murres and black-legged kittiwakes at Cape Thompson and Cape Lisburne.

Table 18. Numbers of fishes in diets of thick-billed murres (arithmetic mean number per bird). ND = no data.

	Jun			1-20 Jul			21 Jul-10 Aug			11-31 Aug		
	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s
Cape Thompson												
1976	11	1.2	0.6	8	1.4[A]	1.4	15	1.1[B]	1.6	11	6.4	11
1977	32	1.0	2.6	9	6.4	8.1	20	25	54	45	8.7	14
1978		ND			ND			ND		14	10	15
1979		ND		26	15	3.7	34	7	8	8	7	7
Cape Lisburne												
1977	6	5	7	22	5.6	7.8	15	6.6	8.7	9	9	12
1978		ND		17	8	14	29	20[C]	20	10	15	13
1979		ND		17	12	14		ND		19	23	25
1980		ND			ND		32	6.2	8.4		ND	

[A] Value is less than in 1-20 Jul 1979 (K-W/MCP, $p < 0.05$).

[B] Value is less than in 21 Jul-10 Aug 1977 and 1979.

[C] Value is greater than in 21 Jul-10 Aug 1977 and 1980.

biomass of those fishes (Table 19) in the diets of the birds from Cape Lisburne increased between years in each of the three intervals for which we have multi-year data. Although few of the differences were significant due to the large variability among birds in the amount of prey in their stomachs, there is the appearance of a trend of increasing consumption of fishes in successive years. Such a trend is less apparent in the data from Cape Thompson except that fish numbers and biomass in 1976 were generally lower than they were in later years.

Invertebrates constituted a small proportion of prey biomass compared with that of fishes in the diets of all three species of birds. However, the apparent importance of invertebrates to thick-billed murres changed within and between years (Fig. 64). Invertebrates were least important in late summer of most years at both colonies, and they were less important summer-long in successive years. The decline in the consumption of invertebrates between years corresponded to the apparent trend of increasing consumption of fishes.

Characteristics of prey populations

The average size of most of the principal taxa of fishes eaten by murres and kittiwakes in the eastern Chukchi Sea increased between most years (Fig. 65). Although the annual contribution of various age classes to the total take of individual taxa undoubtedly changed, many of the differences between years apparently can be accounted for by changes in size-at-age of the fishes.

Table 19. Weight of fishes in diets of thick-billed murres (arithmetic mean wet weight (g) per bird). ND = no data.

	Jun			1-20 Jul			21 Jul-10 Aug			11-31 Aug		
	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s
Cape Thompson												
1976	11	11	17	8	34	40	15	15[A]	28	11	11	21
1977	32	3.8	8.3	9	44	54	20	30	32	45	18	30
1978		ND			ND			ND		14	17	16
1979		ND		26	24	29	34	25	26	8	61[B]	66
Cape Lisburne												
1977	6	10	13	22	19[C]	29	15	14[D]	18	9	23	36
1978		ND		17	23	44	29	43	70	10	53	55
1979		ND		17	64	81		ND		19	57	67
1980		ND			ND		32	54	84		ND	

[A] Value is less than in 21 Jul-10 Aug 1977 and 1979 (K-W/MCP, $p < 0.05$).

[B] Value is greater than in 11-31 Aug 1976-1978.

[C] Value is less than in 1-20 July 1979.

[D] Value is less than in 21 Jul-10 Aug 1978 and 1980.

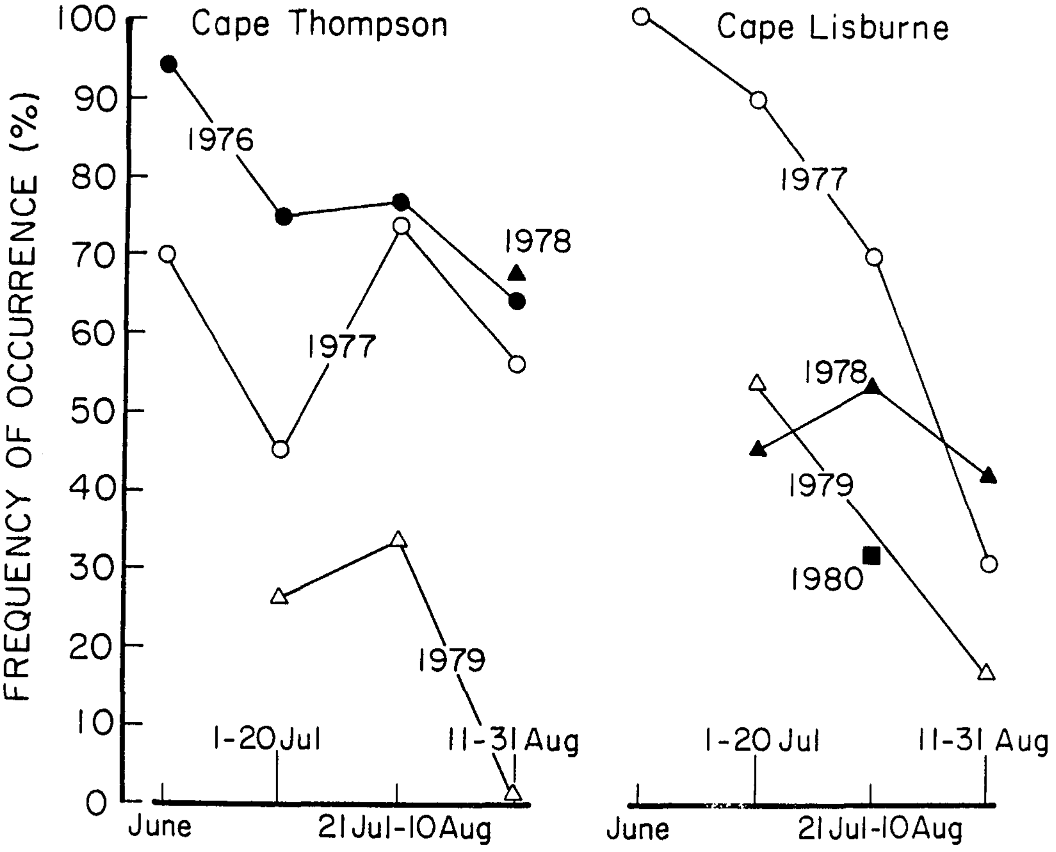


Figure 64. Frequency of occurrence of invertebrates in diets of individual thick-billed murres.

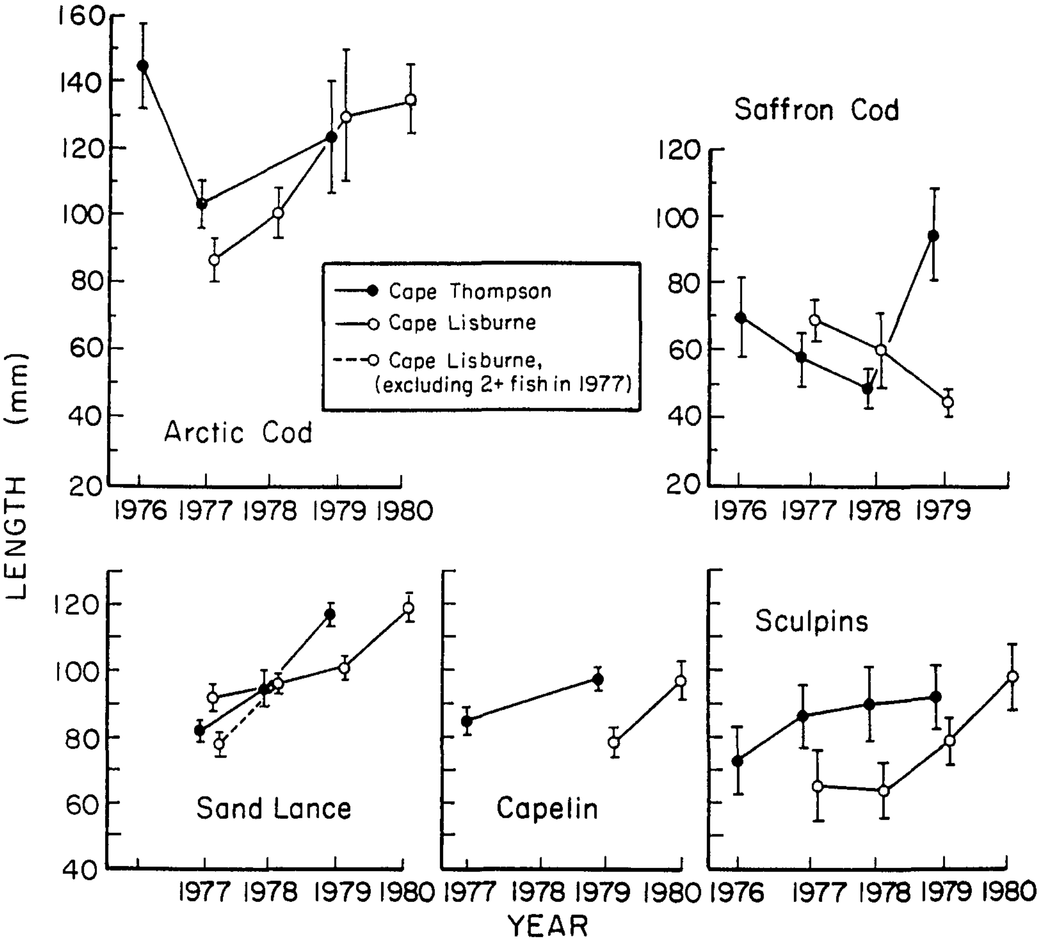


Figure 65. Average length of fishes eaten by murres and kittiwakes in the eastern Chukchi Sea. Bars indicate the 95% confidence interval.

The average length of sand lance was longer each successive year between 1977 and 1980 at both colonies (K-W/MCP, $P < 0.05$). Capelin were larger in 1979 than in 1977 at Cape Thompson and were larger in 1980 than in 1979 at Cape Lisburne. Most sand lance were age class 1+, with a few age class 0+ individuals; sand lance older than age class 1+ were uncommon except at Cape Lisburne in 1977 when age class 2+ fish accounted for an unusual bimodal size distribution that year. Andriyashev (1954) noted that sand lance in the coastal zone of Murmansk also were predominantly age class 1+. Capelin were predominantly age class 1+ juveniles, although remains of a few larger adults were recovered. The adult capelin were spawning as shown by developing reproductive products in both males and females.

Arctic cod at Cape Lisburne exhibited the same trend of increasing average size in later years, and the differences between 1977-78 and 1978-79 were significant. Size distributions of Arctic cod tended to be bimodal: smaller fish were predominantly age class 1 and larger fish were predominantly age class 3. The annual increases in average size of Arctic cod at Cape Lisburne resulted from changes in relative numbers of the two age classes between years, as well as from apparent increases in average sizes of age class 1 fish. Craig and Haldorson (1981) reported that the sizes of age classes 1-5 Arctic cod in Simpson Lagoon (northeast of Cape Lisburne in the Beaufort Sea) were all larger in 1978 than in 1977, and the difference was significant for age class 2 fish, which averaged 15 mm longer in 1978 ($P < 0.001$). At Cape Thompson the average size of Arctic cod decreased between 1976 and 1977, because of a large change in proportions of age classes. However, the average sizes of individual age classes appeared to increase between years, especially between 1977 and 1979, as they did at Cape Lisburne and Simpson Lagoon.

The majority of sculpins in all years were age classes 0-2, and the average length increased between most years at both Cape Thompson and Cape Lisburne. The increases were significant between 1976 and 1977 at Cape Thompson and between 1978 and 1980 at Cape Lisburne.

Saffron cod were considerably smaller than Arctic cod (Fig. 65), and most were age class 0 fish with a few age class 1 fish. Unlike the other species, saffron cod were smaller in successive years at both colonies, except between 1978 and 1979 at Cape Thompson. A change in age class strength probably explains the difference in size of saffron cod between 1978 and 1979 at Cape Thompson.

The sizes of sand lance, capelin, sculpins, and Arctic cod tended to increase with decreasing latitude. Within all years that samples were collected at both Cape Thompson and Cape Lisburne, sculpins and capelin were always significantly larger at Cape Thompson. Sand lance also tended to be larger at Cape Thompson than at Cape Lisburne, significantly so in 1979.

Arctic cod were significantly larger at Cape Thompson than at Cape Lisburne in 1977. Increasing size with decreasing latitude has been reported by Andriyashev (1954) for sand lance in the Barents Sea, and by Lowry and Frost (1981), who showed that Arctic cod in the Bering Sea were larger than in the Chukchi and Beaufort seas. In contrast, saffron cod tended to be larger at Cape Lisburne that at

Cape Thompson. Wolotira et al. (1979) found a similar north to south decline in size-at-age of saffron cod in the Bering and Chukchi seas in 1976.

Feeding areas

The majority of murres from Cape Thompson fed south of the colony in all years during June and most of July. In 1976, flight directions shifted somewhat to the west in August, but few murres were ever seen flying north. A clear shift to the north occurred in late July of 1977 and by early August nearly all murres from Cape Thompson fed north of the colony. A similar shift occurred in 1978, although there was somewhat less distinction between early and late season feeding areas. We observed a few murres during aerial surveys offshore of Cape Thompson in 1978 and there was no obvious pattern of distribution at sea. In 1979, murres fed over a broader area throughout the summer than during previous years; flight directions were widely scattered between south and west in early July. About half of the murres shifted to the west and north by early August, and thereafter murres could be seen flying to and from nearly all offshore directions.

Few murres were seen on the water between Cape Thompson and Cape Lisburne, except in the immediate vicinity of a colony at Cape Lewis, during any of our aerial surveys or during numerous flights we made when going between field camps. Therefore, when murres from Cape Thompson fed north of the colony, they probably mingled with birds from Cape Lisburne. In August of 1978 we intercepted several flocks of southbound murres west of Cape Lisburne and followed them to Point Hope in our survey aircraft. At Point Hope we watched other flocks arriving from the same direction and subsequently confirmed that they were returning to Cape Thompson.

Murres at Cape Lisburne fed northeast of the colony in Ledyard Bay during June and most of July in 1977-79. By early August they foraged generally north of the colony, and gradually shifted more to the northwest by late August. Early-season observations were not made in 1976; however, in late August murres were flying in directions more to the west than in any subsequent year. Observations made during aerial transects flown in July 1978 indicated that murres were feeding nearshore and in the center of Ledyard Bay near the interface of two water masses.

Kittiwake feeding areas tended to be closer to the colonies, but generally lay in the same direction as those of murres in June and July. Beginning sometime between mid-July and early August of all years except 1976, kittiwakes concentrated along the coastline north and south of Cape Thompson and east of Cape Lisburne. The shift to coastal feeding occurred when sand lance or capelin arrived near shore east of Cape Lisburne and north of Cape Thompson, and it occurred earlier in summer in later years. In 1976 when sand lance and capelin were absent, kittiwakes foraged widely offshore throughout the summer.

DISCUSSION

The patterns of change in the diets of murres and kittiwakes at Cape Thompson and Cape Lisburne between 1976 and 1980, i.e., an apparent increase in fish biomass in diets of thick-billed murres concurrent with a decrease in the importance of invertebrates and an increase in the proportions of sand lance and capelin in diets of murres and kittiwakes, are consistent with an hypothesis that the availability of fish biomass to seabirds in the eastern Chukchi Sea was relatively low in 1976, but increased in successive years. The annual increases in the average size of several of the fishes support this view and suggest that differences in fish availability between years could have been related to environmental conditions that affect fish growth, reproduction, and distribution. Sea ice and seawater temperature, important elements of the highly variable environment of northern Alaska, fluctuated considerably during the past decade and the fluctuations could have caused changes in regional food webs and hence in seabird breeding biology.

Regional physical processes

The southern extent of winter ice in the Bering Sea characteristically varies considerably between years, a consequence of changing weather patterns (Walsh and Johnson 1979; Johnson 1980; Niebauer 1980). Beginning in 1973, anomalous atmospheric circulation resulted in the progressive cooling of the Bering Sea and led to large negative deviations from normal sea-surface temperature and shelf bottom water temperature and a large positive deviation from normal ice cover by 1976 (Dickson and Namias 1979; Niebauer 1980). Between fall 1976 and spring 1979 the trend reversed: sea-surface temperature, which was 1.4° C below normal in 1975, rose 0.7-0.8° C yr^{-1}. Sea ice, which reached its maximum southern extent in the winter of 1975-76, decreased about 10% yr^{-1} from 1977 through 1979 (Niebauer 1980). Annual changes in ice cover and sea-surface temperatures were not confined to the Bering Sea, but were also pronounced in the eastern Chukchi Sea (Fig. 66).

The eastern Chukchi Sea is dominated year-round by a strong barotropic current flowing north out of the Bering Sea (Coachman et al. 1975; Coachman and Aagaard 1981). Water velocity of 150 cm s^{-1} through Bering Strait is common and mean volume transport is in the order of 1-2 Sv. In summer the total flow is composed of three distinct water masses, Anadyr Water, Bering Shelf Water, and Alaskan Coastal Water. Anadyr Water and Bering Shelf Water are cold, high-salinity water masses. Alaskan Coastal Water, in contrast, is a warm, low-salinity water mass found in the northeastern Bering and eastern Chukchi seas. Alaskan Coastal Water tends to follow the 40-m isobath north of Bering Strait, which takes it eastward toward the Cape Thompson-Point Hope region. North of Point Hope the current tends to follow the Alaskan coast, flowing northeast around Cape Lisburne and into the Beaufort Sea east of Barrow (Fleming and Heggarty 1966; Hufford 1973; Coachman et al. 1975).

Alaskan Coastal Water develops annually on the shallow shelf of the northeastern Bering Sea (Fig. 67) from cold, relatively saline

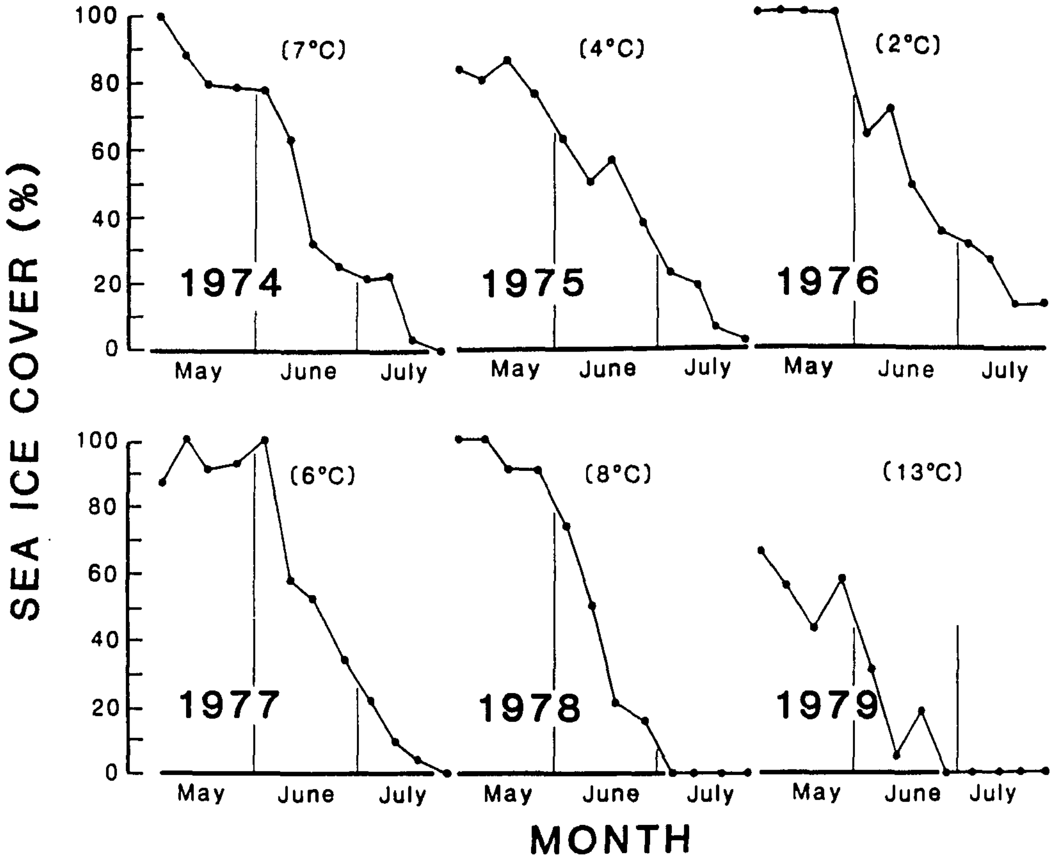


Figure 66. Percent ice cover over the northern Bering Sea and eastern Chukchi Sea. Numbers in parentheses are sea-surface temperatures measured near Cape Lisburne (mean date = 16 July, s = 3 d). Water temperatures were measured directly or from infrared imagery.

Figure 67a. Alaskan Coastal Water development. Warm Alaskan Coastal Water (darker shading) from Norton Sound and the Yukon River intrudes into the ice-covered Chukchi Sea, 7 June 1980. NOAA 4 infrared imagery with a temperature enhancement scale of -3° to 12°C.

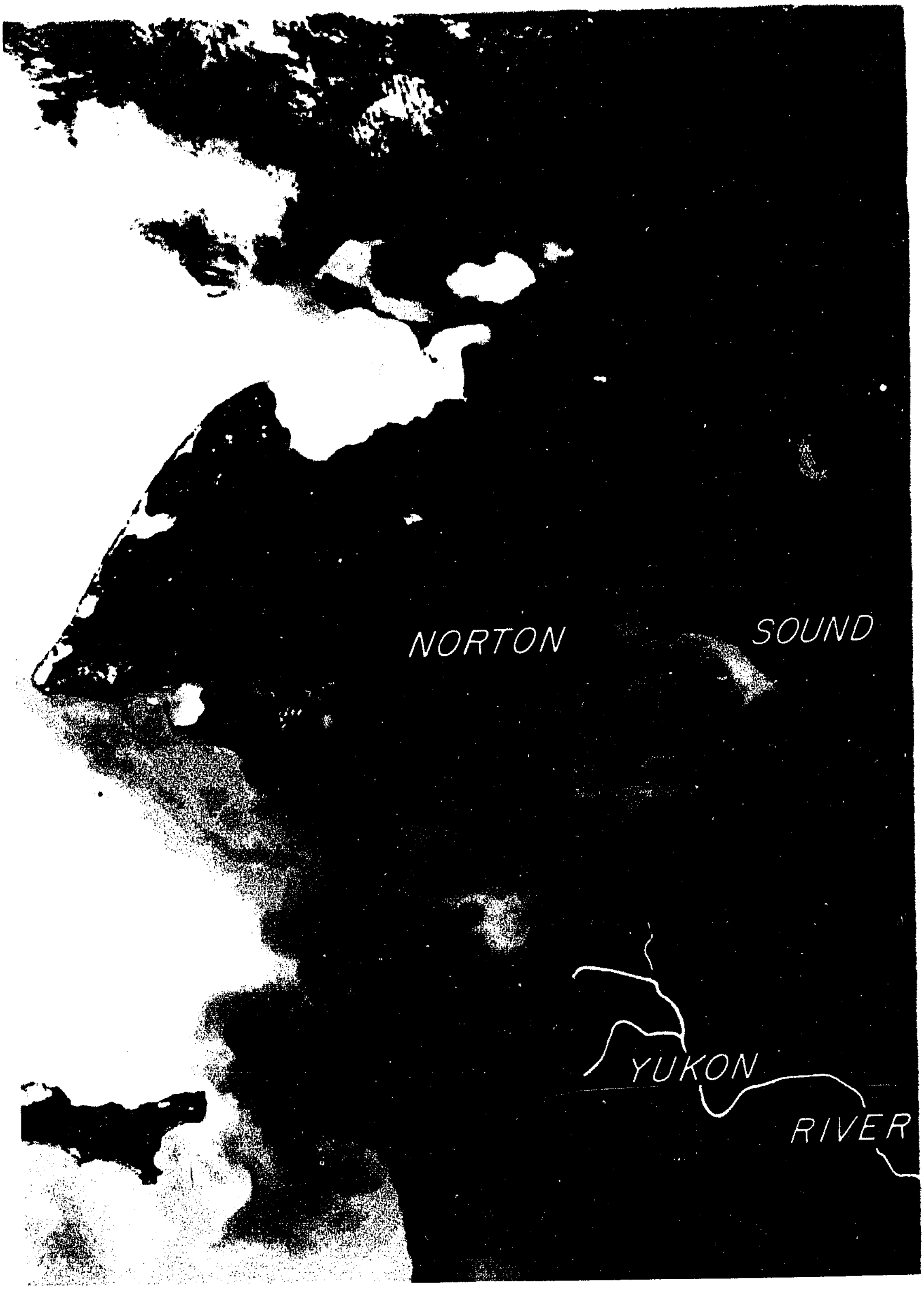
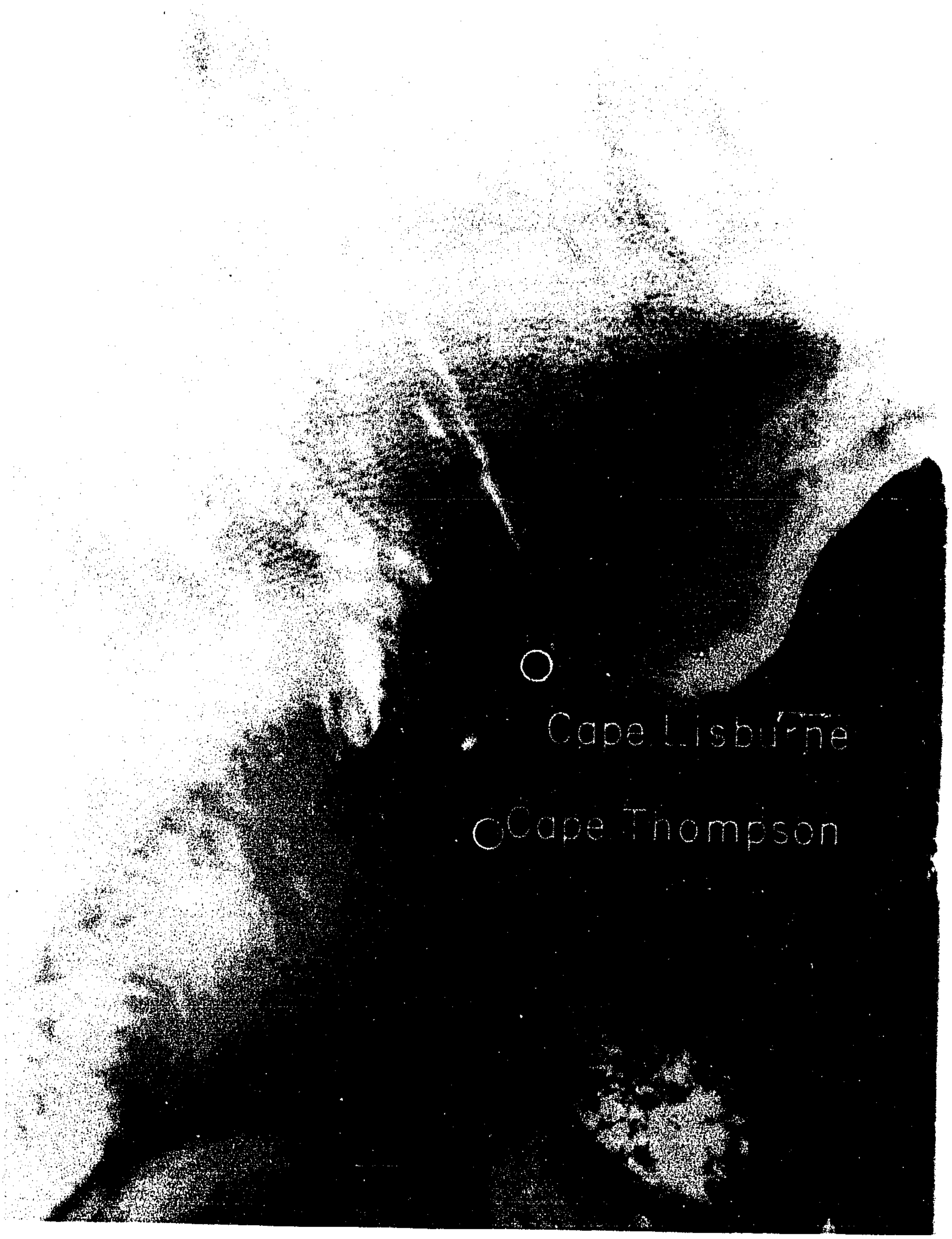

NORTON
SOUND
YUKON
RIVER

Figure 67b. With the dissipation of sea ice, the warm coastal jet flows through the eastern Chukchi Sea past Cape Lisburne, 29 July 1980. Shading, source and enhancement as in (a).


Cape Lisburne
Cape Thompson

water that is diluted by melting ice and river input, primarily from the Yukon River, and rapidly heated by insolation (Coachman et al. 1975). The temperature of coastal water flowing through Bering Strait may rise from near 0 to 10° C during the first month following dissipation of sea ice (Bloom 1964; Ingraham 1981). The seasonal development of the Alaskan Coastal Water mass, therefore, apparently depends on the winter extent of ice into the Bering Sea and its rate of retreat in spring.

Seabird food webs

The Bering Sea shelf shoreward of about the 100 m isobath has high levels of primary productivity, about 166 g C m^{-2} yr^{-1} (Walsh and McRoy 1986). Poor coupling to pelagic herbivores, however, results in a relatively inefficient system, with a major fraction of the annual production being lost to endemic pelagic food webs (Cooney and Coyle 1982). High nitrate concentrations in Anadyr Water (Husby and Hufford 1969; Sambrotto et al. 1984) promote primary production rates as high as 4 g C m^{-2} d^{-1}, rates comparable to those in the major upwelling areas of the world (McRoy et al. 1972). The only limitation to the total yearly phytoplankton growth in the western strait area appears to be the length of time suitable water column light and stability conditions prevail (Chapter 1). Because of the volume and speed of water transported through Bering Strait, a significant portion of the carbon fixed there during summer is swept downstream. Particulate organic matter advected from the northern Bering Sea shelf, plus that originating in the southern Chukchi Sea, could be important to the annual carbon budgets of the food webs of seabirds at Cape Thompson and Cape Lisburne.

The flow of water also plays an important role in determining the composition and abundance of zooplankton assemblages on the Bering-Chukchi shelf. Endemic Bering Sea copepods, including *Neocalanus cristatus*, *N. plumchrus*, *Eucalanus bungii* and *Metridia pacifica* are advected into the Chukchi Sea during summer, and contribute significantly to the diversity and standing stock of zooplankton (Johnson 1956; Redburn 1974; Chapter 2). The intrusion of warm Alaskan Coastal Water creates a temperature regime favorable for the rapid development of zooplankton, and as a result zooplankton biomass is about an order of magnitude greater than in the colder central Arctic Ocean (Redburn 1974).

Sand lance are seasonal predators of the nearshore zooplankters and are considered to be a coastal, shallow-water species except in winter when they move into deeper water and spawn (Andriyashev 1954; Macy et al. 1978; Rogers et al. 1979). Shoaling year class 1+ fish run onshore in summer in northern Alaska (pers. obs.) and in the Barents Sea (Andriyashev 1954), presumably in response to the abundance of prey. Sand lance in the eastern Chukchi Sea feed on the coastal copepods *Acartia* spp. and *Pseudocalanus* spp., the cladocerans *Podon* spp. and *Evadne* spp., and meroplankton, particularly bivalve larvae (Springer et al. 1987). In the Barents Sea, sand lance feed on *Calanus finmarchicus* and larvae of barnacles, euphausiids and amphipods during early summer, and shift to small copepods, particularly *Microsetella* spp., *Acartia* spp. and *Oithona* spp., towards late summer (Andriyashev 1954). Sand lance in the northern Gulf of Alaska feed predominantly on calanoid copepods and barnacle larvae (Rogers et al. 1979; Blackburn et al. 1981). The abundance of several species of coastal zooplankton in Norton Sound and the eastern Chukchi Sea is well correlated with warming water temperature (Niemark 1979; Springer et al. 1987), and temporal patterns of distribution of barnacle larvae in the eastern Chukchi Sea near Barrow, Alaska, are strongly influenced by the dynamic hydrographic regime imposed by the seasonal intrusion of Alaskan Coastal Water (Redburn 1974). Therefore, the occurrence of sand lance earlier in the summer each year after 1976 and concurrent increases in their abundance could have been functions of the rate of development of prey populations, a rate that apparently depends on the pattern of spring warming of the coastal zone.

Smaller average sizes of sand lance in colder years in the eastern Chukchi Sea, as reported for sand lance on the Grand Bank(Winters 1981), could have resulted from poor coupling to seasonal prey because of delayed development of prey populations. Also, sand lance size might be influenced directly by the effect of water temperature on the fish. For example, the emergence of sand lance (*A. marinus*) in spring from the sand where they overwinter is related to warming water temperatures (Winslade 1974), and the incubation time of sand lance eggs increases from 13 d at 16° C to 33 d at 6° C (Inoue et al. 1967). Delays in emergence dates and prolonged incubation times of eggs in colder years could shorten the growing season for sand lance and aggravate the effects of relatively low prey availability.

Annual differences in seasonal water temperatures in the eastern Chukchi Sea could likewise account for the annual differences in abundance and size of capelin. Pitt (1958b) reported that capelin on the Grand Bank will spawn in a rather broad range of water temperatures, but spawning and embryonic development are delayed in colder years. Although adult capelin do not feed while spawning, juveniles feed intensively throughout the summer, predominantly on copepods (Vesin et al. 1981). Therefore, the presence or absence of juvenile capelin near Cape Thompson and Cape Lisburne in summer could be related to the presence or absence of seasonally abundant food, as proposed in the case of sand lance. Pitt (1958b) also showed that growth rates of capelin were slower in colder years than in warmer years and suggested that the difference was a factor of water temperature and food conditions.

The most abundant and widespread fishes in the eastern Chukchi Sea are Arctic cod and sculpins (Alverson and Wilimovsky 1966; Craig and Haldorson 1981; Craig et al. 1982). Arctic cod feed on copepods, amphipods, and mysids (Lowry and Frost 1981; Craig et al. 1982). Small sculpins feed mainly on mysids, amphipods, and isopods (Craig and Haldorson 1981). The degree to which these food webs might be affected by seasonal warming patterns or subsidized by particulate carbon imported from the Bering Sea is unknown. If there is a positive effect, then it should be greater in warmer years when the annual production cycle begins relatively early in summer, and it should be greatest near Bering Strait where the particulate load would be highest. Increasing sizes of Arctic cod and sculpins between 1976 and 1980, and from north to south, suggest such effects.

Unlike other fishes, saffron cod apparently decreased in size from 1976 to 1978 at Cape Thompson and from 1977 to 1979 at Cape Lisburne, in spite of improving environmental conditions. Saffron cod are found in greatest numbers in summer in the northern Bering Sea and southern Chukchi Sea (Lowry and Frost 1981) and are the most abundant species in Norton Sound (Wolotira et al. 1979). Saffron cod are also found along the coast of the Beaufort Sea as far east as the Mackenzie Delta and Tuktoyaktuk Peninsula, but are not generally numerous (Craig and Haldorson 1981). They were the more common of the two species of cods taken by the birds in late summer in the eastern Chukchi Sea, comprising 67% of 312 individual cods identified to the species level in the 11-31 August interval of all years combined. In contrast, Arctic cod comprised 84% of 391 cods in the combined intervals from June to 10 August.

Neimark (1979) found that 80% of the diet of saffron cod in Norton Sound consisted of copepods and 20% consisted of cladocerans. Copepods and cladocerans are also important food of sand lance and capelin, and because sand lance, capelin, and saffron cod are all found nearshore in summer, competition among them for prey could occur. Vesin et al. (1981) suggested that declines in numbers of capelin in the northeast Newfoundland-Labrador area could have increased copepod availability sufficiently to influence growth and development of other zooplankton consumers. They cited recent dramatic increases in the abundance of Arctic cod and short-finned squid (_Illex illecebrosus_) as evidence of such a relationship. In the eastern Chukchi Sea, the numbers and sizes of capelin and sand lance increased during the years that saffron cod declined in size, suggesting similar competitive interactions among these coastal zooplanktivores.

Finally, the absence of flatfishes in the diets of thick-billed murres in the earlier, colder years of this study also could have been a function of water temperature. Pruter and Alverson (1962) believe that the spawning of *Hippoglossoides robustus* and *Limanda aspera*, the two most abundant pleuronectids in the Chukchi Sea, is generally unsuccessful because of the harsh temperatures offshore and because the coastal jet would sweep the pelagic eggs and larvae north into an even more severe environment. They suggested that the presence of these two species of flatfishes in the Chukchi Sea depends instead on the transport of eggs, larvae, and juveniles from the Bering Sea. The abundance of flatfishes, which is very low throughout the Chukchi Sea compared with the Bering Sea (Pruter and Alverson 1962), could be expected to be greater in warmer years, however, when the Alaskan Coastal Water mass develops early in the summer.

Biology of murres and kittiwakes

Summer foraging patterns of murres and kittiwakes and differences in those patterns between years could have been related to changes in the physical environment and the effects I suggest these changes had on food webs and prey availability. The case of kittiwakes appears relatively simple. During early summer of all years, kittiwakes foraged widely offshore. When sand lance or capelin arrived nearshore, kittiwakes shifted their feeding accordingly. The shift occurred between early July and mid-August, depending on the year; it was earlier in warmer years and later in colder years. In the very cold summer of 1976 when neither sand lance nor capelin were present, kittiwakes fed offshore throughout the summer.

Changes in murre foraging areas during the summer and between years are not as straightforward as those of kittiwakes. In June and early July of all years, murres from Cape Thompson fed south of the colony toward Bering Strait where energy levels are higher than in the Chukchi Sea. However, zooplankton, for example copepods, which are abundant in the northern Bering Sea and Bering Strait region as eggs, nauplii, and copepodids in early summer, are carried north into the eastern Chukchi Sea. The northward movement of an assemblage of organisms, including zooplankton and their fish predators, could lead to the shift in murre feeding areas at Cape Thompson from south to west to north during summer. By mid-August of most years, the center of murre prey abundance appeared to be situated north and west of Cape Lisburne, since large numbers of murres from both colonies fed there. Wing (1974) showed that copepod biomass and diversity in the eastern Chukchi Sea were greatest in a region of relatively warm water northwest of Cape Lisburne in September-October 1970. The occurrence of a variety of fish species was also higher there at that time than in the surrounding waters (Ingham et al. 1972). Annual variations in foraging patterns of murres at Cape Thompson could be explained by differences in the timing of annual production cycles in the northern

Bering Sea-Bering Strait region, and consequently the timing and rate of export of food web organisms.

The feeding distribution of murres offshore of Cape Lisburne in July 1978 coincided with the position of a frontal zone between warm Alaskan Coastal Water and cold Arctic Ocean water. Such fronts often have significant biological effects by mechanically concentrating organisms and enhancing productivity (Owen 1981). A front between Alaskan Coastal Water and Arctic Ocean water is apparently a regular physical feature in summer that could account for the regular use of Ledyard Bay by feeding seabirds. The position of the front might vary depending on the season and the year, explaining the variability of feeding patterns of murres from the Cape Lisburne colony.

Changes in the breeding biology of murres and kittiwakes between 1976 and 1980 and the corresponding changes in prey populations represent adjustments to the large-scale environmental fluctuations that occurred during that period. Although many details are lacking, effects of the climatic oscillation during the 1970's were apparently manifested in at least two different food webs: arctic benthic and demersal food webs that include Arctic cod, sculpins, and flatfishes and boreal pelagic food webs that include sand lance and capelin. Furthermore, environmental effects on seabirds and their food webs in northern Alaska were not restricted to Cape Thompson and Cape Lisburne. The same pattern of breeding failure followed by recovery in kittiwakes and common murres at Bluff in Norton Sound was documented between 1975 and 1980 (Drury et al. 1981; Springer et al.

1985). Food availability at Bluff also seemed to be the most important factor in determining annual levels of reproductive success. Apparent food shortages likewise led to a poor breeding season for murres and kittiwakes on St. Lawrence Island in 1976 (Searing 1977). Murres and kittiwakes in Norton Sound feed primarily on sand lance and saffron cod, and on St. Lawrence Island they feed on cods, sand lance, and capelin (Springer et al. 1987). St. Lawrence Island and Norton Sound are located in the headwaters of the current that flows out of the Bering Sea and into the Chukchi Sea. Breeding seabirds throughout the northern Bering Sea-eastern Chukchi Sea region may be related, therefore, by common food web dependencies that are influenced by similar physical processes.

If energy flow through food webs in northern Alaskan waters waxes and wanes in response to patterns of environmental change during intervals of a few years, as it apparently did in the 1970′s, it might also adjust to longer term fluctuations in the environment (Cushing and Dickson 1976; Walsh 1978). For example, between the late 1940′s and mid-1960′s, sea-surface temperature over the bulk of the northern Pacific Ocean (15-60° N and 130° E - 110° W) was generally normal or above; only three years in the mid-1950′s were slightly below normal (Namias and Cayan 1981). Since 1964, however, sea-surface temperature has been above normal in only three years. Such differences in the physical environment might alter energy budgets in northern Alaska sufficiently to account for the large declines in numbers of murres that we have documented at Bluff and at Cape Thompson (Springer et al. 1985). Below-average temperatures for many years could have resulted in relatively less energy available to murres, relatively low levels of natality, and the recent numerical decline as recruitment fell below adult mortality. At Cape Thompson, murre numbers were highest in 1960, a time when water temperatures had been above normal for several preceding years. However, relatively cold temperatures prevailed from the mid-1960's until 1976. A simulation analysis predicted that murre numbers at Bluff would increase beginning in 1983 (Springer et al. 1985), a consequence of improved reproductive success associated with the recent warming trend, if the population decline resulted from climatic fluctuations and not other causes.

SUMMARY

SUMMARY

Hydrography

The exceptionally broad continental shelf of the Bering Sea is divided by a series of three fronts generated by the interaction of wind mixing and tidal pumping. Once established in spring, the fronts restrict cross-shelf diffusion and advection and allow the development of distinct hydrographic domains. Advection is strong along-shelf, however, with the Bering Slope Current flowing northwest along the shelf break and a coastal current following the mainland north. Anadyr Water, a northern branch of the Bering Slope Current, converges with Alaskan Coastal Water, the coastal flow, and with Bering Shelf Water between St. Lawrence Island and Bering Strait. Density fronts separate these water masses, creating three hydrographic domains with distinct physical and chemical characteristics within a small geographic area. Current velocities are high on the northern shelf, and the primarily northward flow patterns are determined by the interaction of atmospheric pressure gradients, wind forcing and topographic steering. Lighter Bering Shelf Water and Alaskan Coastal Water tend to override the denser Anadyr Water, providing vertical stability to an often turbulent water column.

Because of its origin on the shallow inner shelf, Alaskan Coastal Water tends to warm rapidly in spring following the dissipation of sea ice. The rate of retreat of sea ice from the Bering Sea, which exhibits pronounced interannual variability, is related to the rate of warming of the coastal water, such that seasonal temperature patterns also vary greatly between years.

Production regimes

Annual primary production is not especially high in the outer and middle shelf domains of the Bering Sea, and is low in the inner domain. The production derives primarily from a spring bloom subsequently augmented by smaller scale events induced by wind mixing below the nutricline, except in the shallow inner domain, where nutrients are stripped from the entire water column during the bloom. The feature that makes the outer domain particularly productive at higher trophic levels in pelagic food webs appears to be the efficient use made of the diatom bloom by herbivorous oceanic zooplankton. Such tight coupling between the primary producers and primary consumers may serve as a model for the nature of energy transfer throughout pelagic food webs. The large grazers are restricted to deeper water primarily because of the middle front, and in the middle and inner domains the zooplankton communities are unable to harvest the spring bloom efficiently . This leads to a proportionally high benthic flux of phytoplankton and large benthic biomass in the middle domain, while primary production in the inner domain is so low that neither benthic nor pelagic biomass is large.

Were it not for Bering Strait, the northern Bering and southern Chukchi seas probably would be typical of the inner shelf elsewhere, with low annual production because of nutrient limitation. However, the advective, virtually inexhaustable supply of nutrients to the Bering - Chukchi shelf via the "river" of Anadyr Water changes all that by promoting a eutrophic, high-production regime in the shallow waters of a large part of the region. Phytoplankton grow profusely summer-long in a plume running generally south to north through the western Bering Strait area along the interface between Anadyr Water and Bering Shelf Water. The vertical stability provided by horizontal layering of the water masses apparently satisfies the critical depth criterion for net phytoplankton growth.

Anadyr Water also carries with it oceanic zooplankton that are key links in the transfer of energy to higher trophic levels in the pelagic food web. Because zooplankton are continuously supplied to the northern shelf during summer, several vertebrate species at higher trophic levels have prospered, particularly planktivorous marine birds. On average, the oceanic zooplankton cannot control the diatom population in the high-production region, as they apparently do over the outer shelf, and most of the phytoplankton production in the plume sinks and is converted into rich benthic communities. The flux of phytodetritus is apparently so large near the center of the high-production zone in the southern Chukchi Sea that invertebrates are largely eliminated, apparently because microbial activity leads to anoxia near bottom.

Planktivores in the Bering Strait region seem to have little effect on the overall abundance of zooplankton, just as the zooplankton do not control the diatoms. This uncoupled pelagic food web contrasts with that in the outer domain of the Bering Sea, where it is thought that the zooplankton efficiently graze the annual phytoplankton production and are themselves controlled by higher trophic levels.

Adjacent to this highly productive ecosystem, but sharply separated from it, is an impoverished, nutrient-limited one typical of most of the inner domain farther south. Following the spring diatom bloom, production by the successional phytoflagellate community in the inner domain, although efficient, is nevertheless low. The high, post-bloom growth efficiency of the primary producers is probably mirrored in tightly coupled pelagic food webs, including microheterotrophs and small herbivorous and omnivorous zooplankton. Oceanic zooplankton are excluded, and higher trophic level populations are small. Planktivorous seabirds are absent, and the piscivorous species often experience severe interruptions in energy availabilty that are apparently related to interannual variation in water temperature and its effects on food web organisms.

The food webs

Carbon is fixed in the high production plume on the Bering - Chukchi shelf primarily by large silicious diatoms in the genera *Chaetoceros* and *Thalassiosira* spp., which are common in the Bering Sea. The successional development of the floral community is arrested because of the heavy nutrient load of Anadyr Water. The dominant herbivores are the imported oceanic copepods *Neocalanus cristatus*, *N. plumchrus*, *Eucalanus bungii* and *Metridia Pacifica*. Depending on the season and year, zooplankton biomass is augmented to varying degrees by the oceanic larvacean *Oikopleura labradoriensis* and by resident shelf species, particularly *Calanus marshallae*.

Neocalanus cristatus, *N. plumchrus* and *Calanus marshallae* are the most important prey of planktivorous least auklets, the most abundant seabird breeding in the Bering Strait region. Crested auklets, the second most abundant seabird, also feed on copepods, as well as on other taxa. Other marine birds, particularly murres, are by far the most numerous of the piscivorous pelagic consumers. Seabirds are also the most diverse group, with nine primarily piscivorous species breeding in the northern Bering and eastern Chukchi seas. Murres that feed in waters influenced by the Anadyr stream consume chiefly Arctic cod, and supplement their diets with saffron cod, capelin, sand lance, sculpins and pollock. Like the large copepods, pollock also are expatriates from the south.

Contrasting with the highly productive, oceanic-based food web associated with the flow of Anadyr Water is that found in the environmentally inner shelf region to the east. The depletion of nutrients by diatoms in spring leads to the development of a successional flora, with flagellates dominating the phytoplankton community during most of the productive season. The herbivores are mainly *Calanus marshallae* and small copepods, particularly *Pseudocalanus* spp. and *Acartia longiremis*. Arctic cod are replaced in the warm coastal environment by saffron cod, which attain their greatest biomass in Norton Sound. Young age classes of saffron cod are likely important consumers of zooplankton during summer. In some years, juvenile sand lance occur in very large numbers near shore, where they also feed on zooplankton.

Fishes are essentially the only vertebrate planktivores near shore in the northern Bering Sea and eastern Chukchi Sea, since the auklets seldom venture far from the bounty to the west. The number and diversity of the piscivorous seabirds in the coastal zone is generally low, with primarily only three species populating the small colonies in Norton Sound and Kotzebue Sound. Saffron cod and sand lance are the most important prey of murres and kittiwakes in Norton Sound. The avifauna is larger and more diverse at Cape Thompson and Cape Lisburne in the eastern Chukchi Sea than at coastal colonies farther south, possibly because the birds have access to feeding areas influenced by the Anadyr stream.

Unanswered questions

Many questions about the production regime on the Bering - Chukchi shelf remain unanswered. Foremost among them is why phytoplankton do not bloom wherever Anadyr Water provides nutrients to the euphotic zone. The principal hypothesis is that of the requirement for vertical stability in a turbulent water column. The stability can be provided by layering of coastal water from the western Bering Sea, Bering Shelf Water or Alaskan Coastal Water over Anadyr Water. The role of the oceanic zooplankton in affecting the areal extent of the plume also is questionable. On average the grazers are unable to control the bloom, but they might be able to limit the size of the area of high phytoplankton biomass.

Another major question is what becomes of all of the nitrate exported from the Bering Sea in Anadyr Water. Is it fully utilized by phytoplankton in the Chukchi Sea? Unfortunately, physics and politics so far have combined to prevent us from solving this problem. That is, because of international politics we have been unable to sample west of the U.S. - U.S.S.R. convention line, where the bulk of Anadyr Water apparently flows north of Bering Strait. The answer is particularly important in assessing the role of primary production on the Bering - Chukchi shelf in the global carbon budget.

There is as yet little information on the level of interannual variability in primary production within the plume on the northern shelf. Differences between years in production are probably related to meteorological effects on the total transport of Anadyr Water through the area, as well as on the trajectory of the water through Anadyr Strait and on the pattern of vertical stability. Unless it is of unexpected proportions, such variability in carbon fixation will likely have little significance to higher trophic levels in pelagic food webs, since a high rate of phytoplankton growth is maintained throughout summer in most years. Variability in primary production could have a much greater effect on benthic food webs, which depend on the rain of phytoplankton to support their dense populations.

Of potentially greater importance to pelagic organisms could be fluctuations in the supply rate of oceanic copepods to the region. Differences between years could have two sources, one being fluctuations in the transport of Anadyr Water, and the other being interannual changes in secondary production in the oceanic region of the Bering Sea. The continual replenishment of zooplankton through advection, however, would tend to damp food web effects that might otherwise result from fluctuations in the abundance of zooplankton off the shelf where they originate. Small-scale physical features, such as localized upwelling around islands and fronts that concentrate zooplankton, probably are more important to upper trophic levels, particularly planktivorous seabirds, than is the annual primary and secondary production.

Little is known also about variability in annual primary production in the shelf area outside the boundaries of the plume. Because water depths are shallow and the spring bloom apparently removes from the water column essentially all of the nitrate regenerated over winter, there is no source for resupply during summer, the Yukon River not withstanding. Therefore, it seems likely that differences between years in primary production are small.

The small taxa of phytoflagellates are probably grazed efficiently by microheterotrophs and zooplankton. Still, in situ secondary production is necessarily low, and is subject to destabilizing effects of fluctuations in water temperature, which are extreme in the coastal zone of the northern Bering Sea and eastern Chukchi Sea between seasons and years. Breakdowns in energy transfer to higher trophic levels, particularly seabirds, do occur, apparently in response to fluctuations in water temperature, but it is not yet known which trophic levels get decoupled or why. Water temperature affects the production of the small coastal zooplankton, which in turn are the food of fishes that support many seabirds. Water temperature can also have a direct effect on the productivity and growth of the fishes themselves, and may be responsible for interannual differences in their distribution, hence availability to predators, if not in their absolute numbers. The ultimate breeding performance of kittiwakes throughout the region, for example, appears to be dependent on the availability of sand lance, a fish that may be both directly and indirectly influenced by water temperature.

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