

Anomalous conditions in the south-eastern Bering Sea, 1997: nutrients, phytoplankton and zooplankton

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ABSTRACT

Anomalies in the regional weather over the south-eastern Bering Sea during spring and summer of 1997 resulted in significant differences in nutrient availability, phytoplankton species composition, and zooplankton abundance over the continental shelf as compared with measurements in the 1980s. Calm winds and the reduction of cloud cover in spring and summer produced a very shallow mixed layer in which nitrate and silicate were depleted after an April diatom bloom. High submarine light levels allowed subsequent phytoplankton growth below the pycnocline and eventual depletion of nitrate from the water column to depths of 70 m or more. Thus, total new production during 1997 may have exceeded that of previous years when nitrate was not depleted below the pycnocline. A bloom of the coccolithophorid, *Emiliana huxleyi*, was observed in early July in the warm, nutrient-depleted waters over the middle and inner shelf. *Emiliana huxleyi* concentrations reached 4.5×10^6 cells L⁻¹ by September, and the bloom persisted through the autumn. There was evidence for increased abundance of some species of copepods in 1997 as compared with data from the middle domain in June 1981. The abundance of adult and juvenile euphausiids in 1997 was statistically similar to values

measured in 1980 and 1981. However, near-surface swarms were rarely observed on the inner shelf in August–September 1997. Lack of euphausiid availability in the upper water column may partially explain the August–September mass mortality of planktivorous short-tailed shearwaters (*Puffinus tenuirostris*) observed on the inner shelf.

Key words: Bering Sea, coccolithophorids, *Emiliana huxleyi*, nutrients, productivity, zooplankton

INTRODUCTION

Variability in the Bering Sea exists over a range of time scales, resulting from multiple mechanisms (Schumacher and Alexander, 1999). Local and global atmospheric conditions influence ice coverage, wind regimes, and thermal structure that regulate one of the most productive high-latitude continental shelves in the world (NRC, 1996). Concurrent with the 1997 El Niño/Southern Oscillation (ENSO) event at the Equator, anomalous atmospheric conditions were observed over the south-eastern Bering Sea shelf (Overland *et al.*, 2001). Those factors culminated in a bloom of the coccolithophorid, *Emiliana huxleyi* (Lohmann) Hay et Mohler (Sukhanova and Flint, 1998), mass mortality of short-tailed shearwaters (*Puffinus tenuirostris*) (Baduini *et al.*, 2001) and other ecosystem anomalies (Vance *et al.*, 1998; Hunt *et al.*, 1999a,b; Napp and Hunt, 2001; Stabeno *et al.*, 2001). Although *E. huxleyi* is widely distributed in the Pacific Ocean (Okada and Honjo, 1973), large-scale coccolithophorid blooms have not been previously confirmed in the Bering Sea.

Three hydrographic domains (inner, middle, and outer), separated by physical structural fronts or transitional zones, characterize the continental shelf of the south-eastern Bering Sea (Kinder and Coachman, 1978; Coachman, 1986; Schumacher and Stabeno, 1998). The inner front is the transition between the strongly stratified waters of the middle shelf domain and the inner or coastal domain, where a well-mixed water column results when the upper wind-mixed layer overlaps the lower tidally mixed layer. The middle

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shelf and outer shelf domains are separated by a middle transition zone. In most years, the inner front is about 25 km wide and centred over the 50 m isobath (Stabeno *et al.*, 2001). These distinct hydrographic domains have characteristic biological communities and rates of annual production. Sambrotto *et al.* (1986), and Walsh (1983) discussed the interannual differences in phytoplankton abundance within these domains. Cooney and Coyle (1982), Smith and Vidal (1986), and Springer *et al.* (1996) discuss the different zooplankton communities and their rates of secondary production.

A large fraction of the shelf's annual primary production occurs in the late spring, usually from April to May. Ice-edge phytoplankton blooms are common in marginal ice zones (Smith, 1987; Alexander and Niebauer, 1989; Niebauer, 1991), and recent observations suggest that the blooms can begin under the ice before water-column stratification (Stabeno *et al.*, 1998). In the absence of ice, phytoplankton blooms occur in the photic zone as the water column stabilizes. In years when sea ice does not form over the south-eastern Bering Sea shelf, peak phytoplankton biomass usually occurs during mid-May (Sambrotto *et al.*, 1986; Whitledge *et al.*, 1986). This diatom-dominated bloom is the most significant component of the annual production cycle on the shelf. Summer primary production is limited by the absence of nutrients in the upper mixed layer, so summer storms are necessary to mix the water column and re-supply nutrients to the euphotic zone (Sambrotto *et al.*, 1986).

Zooplankton is a trophic link between primary production and apex predators such as seabirds, fish and marine mammals. From 1979 to 1981, the PROBES (Processes and Resources of the Bering Sea Shelf) programme sampled the south-eastern Bering Sea shelf. A substantial proportion of the mesozooplankton (200–2000 μm size) biomass in PROBES samples collected on the inner and middle shelves of the south-eastern Bering Sea was composed of the calanoid copepods *Calanus marshallae* and *Pseudocalanus* spp. (Vidal and Smith, 1986). The euphausiid, *Thysanoessa raschii*, was also a major component of that zooplankton biomass (Vidal and Smith, 1986). Copepods and euphausiids are common in the diets of a number of groundfish, forage fish and seabirds (Livingston, 1991; Hunt *et al.*, 1996; Brodeur *et al.*, 2000; Baduini *et al.*, 2001). Short-tailed shearwaters (*Puffinus tenuirostris*) are an important apex predator on the Bering Sea shelf ecosystem (Baduini *et al.*, 2001), foraging in substantial numbers over the inner shelf and consuming primarily euphausiids (Hunt *et al.*, 1981; Schneider and Hunt, 1982; Schneider *et al.*, 1986). Thus, copepods and

euphausiids are important components of the food web, and any conditions altering their abundance, biomass or the timing of their life-history stages will likely impact apex predators.

Here we report anomalous nutrient, phytoplankton, and zooplankton concentrations and rate processes that occurred in the eastern Bering Sea during 1997. Most, but not all, of these biological observations can be directly attributed to physical oceanographic conditions caused by anomalous local weather during spring and summer (Stabeno *et al.*, 2001).

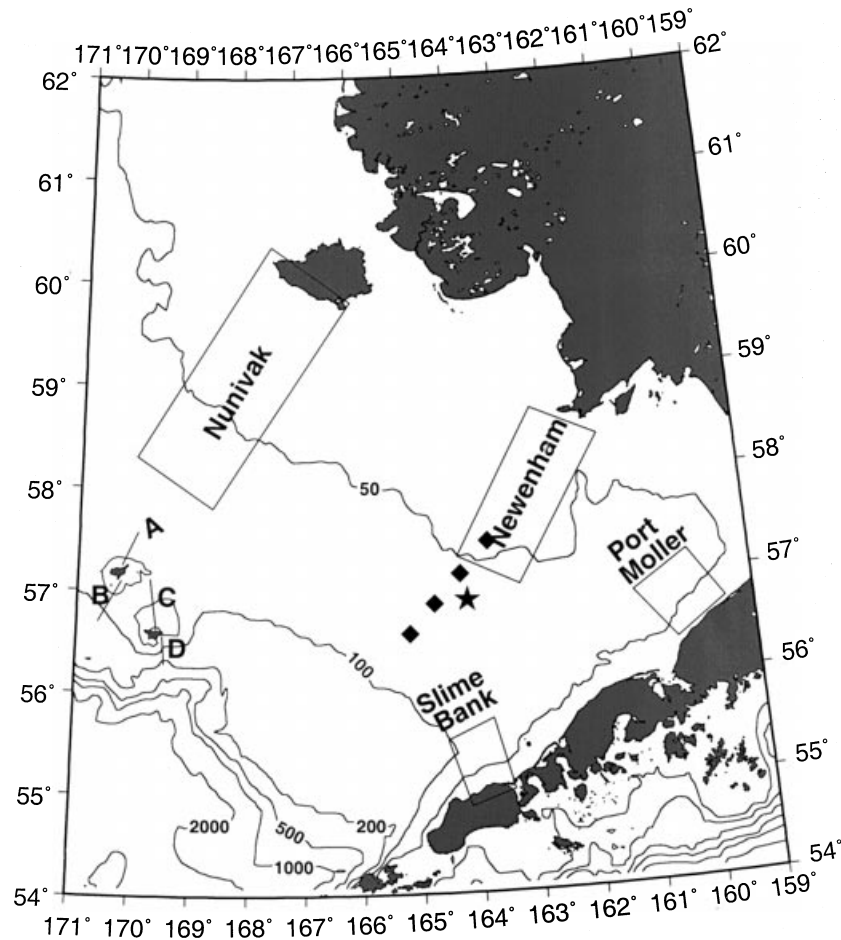
METHODS

This study utilizes data obtained from the NSF-sponsored Inner Front Project (IFP) and the NOAA-sponsored South-east Bering Sea Carrying Capacity (SEBSCC) programme. IFP sampled in and around the inner front in the vicinity of Slime Bank, Port Moller, Cape Newenham and off Nunivak Island during June and August–September, 1997 (Fig. 1). SEBSCC sampled at a biophysical mooring in the middle shelf domain (M2). In addition, SEBSCC data were collected along four sampling transects crossing the frontal zone at the 50 m isobath near the Pribilof Islands (lines A, B, C and D; Fig. 1). SEBSCC Pribilof Island samples were obtained in September (1995–1997).

All water samples were obtained with 5 L or 10 L Niskin bottles mounted on a SeaBird 911+ CTD. Shipboard nutrients (IFP and SEBSCC) were analysed on board using methods modified for small-volume glassware (Whitledge *et al.*, 1981; Whitledge *et al.*, 1986). Approximately 10% (by number) of the nutrient samples were frozen and analysed by the University of Washington Routine Chemistry Lab using the WOCE protocol (WOCE, 1994). Distances in cross-shelf sections of physical and chemical data are from the offshore origin of the IFP transects.

Primary production measurements were made opportunistically at whichever station the ship occupied between 10:00 and 14:00 h. Therefore 'transect' data in Table 1 are a composite from multiple transect lines within one of the sampling grids. Primary productivity rates were estimated using ^{14}C -labelled bicarbonate in triplicate incubations at eight simulated light intensities between 0 and 600 μM photons $\text{m}^{-2} \text{s}^{-1}$ (Zeeman, 1985; Zeeman and Jensen, 1990; Lohrenz, 1993). Photosynthesis vs irradiance data were fitted to a hyperbolic tangent function allowing for photoinhibition using nonlinear least-squares regression techniques (Jassby and Platt, 1976; Platt *et al.*, 1980). Chlorophyll-specific production as a function of light from the incubations plus *in situ* measurements of

Figure 1. Station map showing: Inner Front Project grids on Slime Bank, Port Moller, Cape Newenham and Nunivak Island (rectangles) occupied during 1997. SEBSCC mooring site no. 2 (M2) is shown with star. SEBSCC Pribilof Islands transects A, B, C and D are shown with lines. Diamonds are PROBES stations on the inner and middle shelf. Depth contours are in metres.



irradiance and chlorophyll were used to calculate daily *in situ* production (Zeeman, 1992). Chlorophyll determinations were made using the method of Evans *et al.* (1987).

Water samples were preserved in neutral Lugol's iodine and stored in the dark for enumeration of phytoplankton cells. Samples were settled in 10 mL Utermöhl counting chambers and counted with an inverted microscope.

IFP zooplankton were sampled during June on transects across the inner front near Nunivak Island, Cape Newenham, Port Moller, and Slime Bank and in August/September at Nunivak Island and Slime Bank (Fig. 2). Large zooplankton and micronekton were collected with a 1 m² MOCNESS (Wiebe *et al.*, 1976) with 0.5 mm mesh nets. Most tows were made at night to minimize net avoidance by micronekton. The entire water column was sampled in 10–20 m strata. Small zooplankton were sampled with a 25 cm diameter

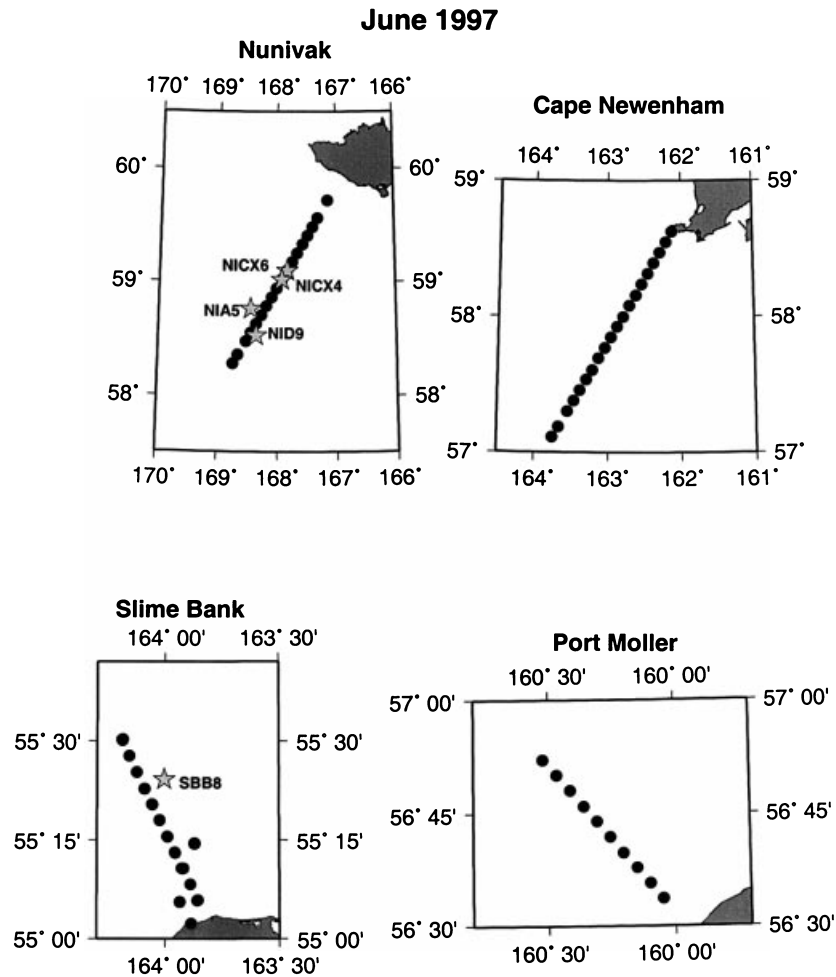
CalVET net (150 µm mesh; Smith *et al.*, 1985) towed vertically from the bottom to the surface at CTD stations (Fig. 2). Volume filtered was estimated with calibrated General Oceanics flow meters in each net. The IFP samples were sorted (at the University of Alaska, Fairbanks) to the lowest taxonomic category possible, staged, enumerated and weighed (formalin-preserved wet weight). Mesozooplankton in the MOCNESS tows were normalized for depth and volume filtered, to produce estimates of the mean, log-transformed, zooplankton concentration (no. m⁻³) by taxon. The abundance of euphausiids was integrated over the water column (no. m⁻²) to facilitate comparison with data collected in 1980 and 1981 (PROBES, 1982, 1983; Smith and Vidal, 1986; Smith, 1991).

SEBSCC zooplankton and micronekton samples were collected along transects radiating from St Paul and St George Islands (Fig. 1). Hydrographic sections

Table 1. Daily primary productivity integrated over the euphotic zone, average light extinction coefficient (k), P_{\max} at surface and chlorophyll maximum, depth of chlorophyll maximum, integrated chlorophyll, and integrated nitrate within Nunivak Island and Slime Bank sampling grids for 1997. Distance is measured from the seaward station presented in the appropriate profiles in Figs 4, 5, 6 and 7. Station NIA24 was 55 km seaward of the outermost station shown in Fig. 5. *, Second value represents a later sampling at this station; -, no sample available.

Cruise	Sample grid	Station	Distance (km)	Productivity (mg C m^{-2} day $^{-1}$)	Avg. k (m^{-1})	P_{\max} (mg C mg Chl a^{-1} h^{-1})	Chlorophyll maximum depth (m)	Integrated chlorophyll (0–30 m) (mg Chl a m^{-2})	Integrated nitrate (0–30 m) (mmol NO_3 m^{-2})
May / June	Nunivak	NICX16	150	4.1	0.221	0.50 / -	28	30.48	8.92
		NICX6	100	296.8	0.018	1.32 / 0.99	38	45.31	3.29
		NIC1	70	71.1	0.149	0.09 / 5.48	22 / 42*	16.95	1.42
		NIA7	40	0.2	0.164	0.32 / 0.34	34	-	-
		NIC12	10	14.0	0.157	0.12 / 0.46	33	18.51	16.50
May / June	Slime Bank	SBC1	50	159.8	0.412	0.30 / 0.30	21	115.65	3.08
		SBD2	45	393.7	0.392	0.40 / 0.60	20	-	-
		SBC4	35	135.5	0.214	1.04 / 0.28	7	90.98	43.10
		SBB4	35	256.8	0.272	0.79 / 0.70	16	107.39	32.47
		SBB8	15	925.1	0.191	10.2 / 1.00	31	-	-
		SBC11	0	4.4	0.166	2.94 / 0.37	29	12.29	33.95
August / September	Nunivak	NIEX12	135	31.6	0.724	0.74 / 1.01	28	113.42	30.21
		NICX10	110	0.1	0.446	- / 0.11	36	76.88	25.66
		NICX4	80	79.2	0.236	3.14 / -	40	57.79	2.34
		NIC3	45	8.6	0.140	0.47 / -	33	28.37	4.92
		NIA5	35	197.7	0.131	1.16 / 1.41	17	20.28	6.78
		NID9	15	792.5	0.158	2.77 / 3.78	17	-	-
		NIC12	5	30.3	0.127	1.96 / 1.26	19	54.20	8.81
		NIA13	0	32.2	0.220	1.69 / 0.47	0	30.42	23.47
		NIA24	-55	23.1	0.155	0.70 / 0.14	24	14.66	68.26
September	Slime Bank	SBE2	55	75.4	0.148	0.84 / -	9	43.69	178.08
		SBA10	15	52.6	0.097	1.43 / -	0	26.71	177.42

Figure 2. CTD and CalVET stations on the C-line (central line of sampling grid shown by circles) of the Nunivak, Cape Newenham, Slime Bank and Port Moller grids in June and August 1997. Stars designate locations of MOCNESS tows.



were used to determine the positions of the seaward and shoreward boundaries of frontal systems near the islands (Brodeur *et al.*, 1997). Discrete-depth samples of zooplankton and micronekton, together with temperature and salinity, were taken with a 1 m² MOCNESS (0.333 mm mesh nets) collecting from \approx 5 m off bottom to the surface. Micronekton and juvenile fish were sampled using a 5 m² Methot trawl with 3 \times 2 mm oval mesh in the body and 1 mm mesh in the codend (Methot, 1986), towed obliquely from 5 m off bottom to the surface. Estimates of euphausiid abundance on the Bering Sea shelf during daytime are significantly lower than during night-time owing to net avoidance (Smith, 1991; Sugisaki *et al.*, 1998). Therefore, MOCNESS and Methot collections were restricted to night in an attempt to minimize net avoidance and allow euphausiids to come off the bottom. All SEBSCC samples were preserved in 5%

buffered formalin:seawater and sent to the Polish Plankton Sorting and Identification Center (Szczecin, Poland) for analysis (Incze *et al.*, 1997).

Estimates of euphausiid concentrations (no. m⁻³) were compared for paired night-time collections made with both the MOCNESS and the Methot net. Samples were collected within several hours of each other at the same location. Estimates of euphausiid concentration between the two gear types did not differ significantly (Wilcoxon signed-rank test, $N = 11$ station pairs, $P = 0.240$). Therefore, we concluded it was valid to use the concentration data from either sampling device for our analyses.

The 1997 IFP CalVET zooplankton data were compared with data collected in 1981 with a 1 m² MOCNESS by PROBES (Smith and Vidal, 1986). The two different nets used the same mesh size but have very different mouth areas. The 1997 data from

each region were separated into two groups: those taken at stations with bottom depth > 50 m and those at stations with bottom depth ≤ 150 m. Because the inner front is ordinarily located along the 50 m isobath, this convention essentially separates samples taken in the middle domain from those taken in inner domain. While the 1997 samples from the Cape Newenham grid are in closest geographical proximity to the location of the 1981 PROBES stations (Fig. 1), the general trend for zooplankton concentration is the same for the Port Moller and Nunivak Island grids as well.

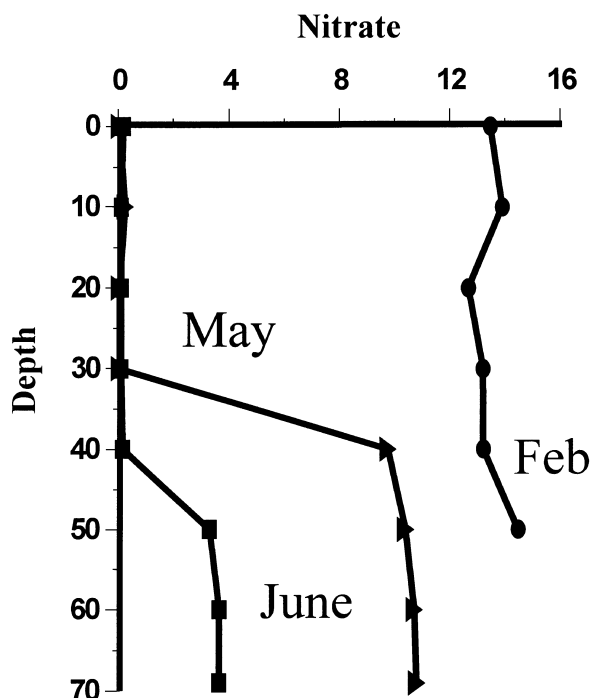
For comparisons of IFP data with those from the PROBES study, we extracted data from the PROBES plankton reports for three stations: 12, 16 and 19 (Fig. 1). Stations 12 and 16 were in > 50 m of water and provide samples from the middle domain close to the outer end of the IFP study grid off Cape Newenham. Station 19 was in about 46 m of water, within the IFP Cape Newenham grid. Mean values and 95% confidence intervals were constructed for log-transformed data. Additionally, we compared by Mann-Whitney U -tests the likelihood that samples from the PROBES stations differed from those obtained in the IFP. In these comparisons, data from PROBES stations 12 and 16 were compared with data from IFP stations having water depths > 50 m in the Port Moller, Cape Newenham and Nunivak Island grids. Similarly, data from PROBES station 19 were compared with data from IFP stations from < 50 m water depth in these three grids. Data from the IFP Slime Bank grid were not used in the comparison because plankton at this grid were oceanic in character, and had little resemblance to the plankton communities at the other grids.

RESULTS

Nutrients and chlorophyll

In 1997, the presence of sea ice and weak wind mixing resulted in an early spring diatom bloom in the middle shelf domain at M2 (Stabeno *et al.*, 2001). By 1 May, phytoplankton biomass was decreasing and nitrate was exhausted from the surface waters (Fig. 3). A reservoir of 6–10 μM nitrate and 15–30 μM silicate, however, was still present in bottom waters, as would be expected after the spring bloom (Whitledge *et al.*, 1986). Nutrient concentrations were further reduced when a storm in late May mixed nutrients from the bottom layers into surface waters, consequently stimulating primary production (Stabeno *et al.*, 2001). After the mixing event, solar heating and weak winds produced a shallow (15–20 m) mixed layer that was not as deep as the euphotic zone (0–32 m). Both net

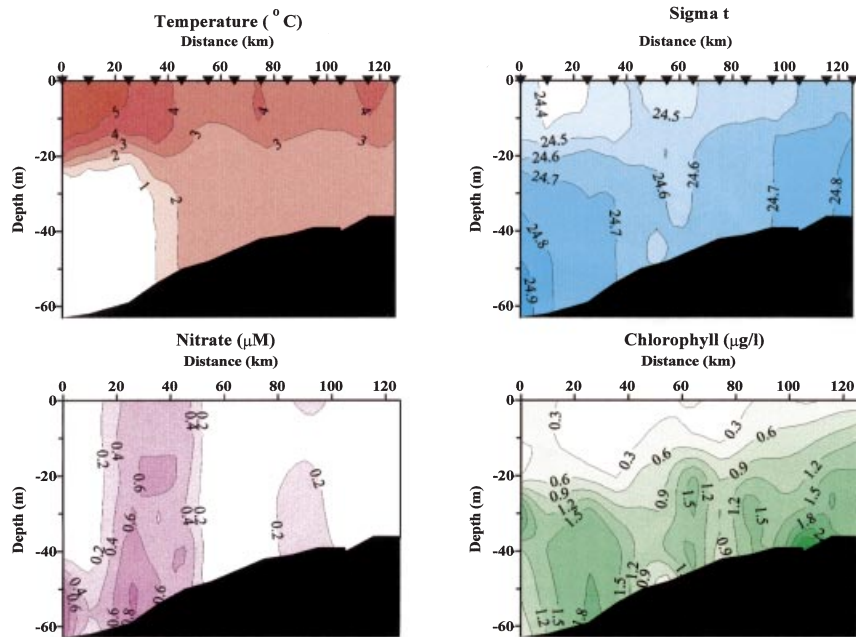
Figure 3. The vertical distribution of nitrate (μM) at SEBSCC mooring site 2 during February, April and June 1997.



photosynthesis and nutrient utilization therefore occurred below the pycnocline. In the lower layer, nitrate concentrations for this early June period were $\approx 4 \mu\text{M}$ (Fig. 3).

Shortly thereafter, during the IFP June cruise, water column stratification between the surface layer and the bottom layer strengthened, and the mixed layer was confined to the upper 20 m (Fig. 4). For the outer 60 km of the transect at Nunivak Island, the chlorophyll maximum was below the mixed layer, with the highest concentrations of chlorophyll in patches near the bottom (see Table 1 for depths of chlorophyll maxima). Within subsurface chlorophyll maxima, primary productivity ranged from 0.1 to 0.9 $\text{mg C m}^{-3} \text{ h}^{-1}$. This relatively deep primary production at the subsurface chlorophyll maximum further reduced nutrient concentrations, which was confirmed by nitrate uptake studies (T. Rho, 2000). Nutrient utilization below the pycnocline in the middle shelf left little nitrate ($< 0.6 \mu\text{M}$) in the bottom water adjacent to the inner front near Nunivak Island. Consequently, vertical mixing at the inner front could provide only very weak nutrient enrichment of surface waters. In addition, owing to anomalously low spring winds, the transition between the two-layered water column and the well-mixed water column

Figure 4. Distributions of temperature ($^{\circ}\text{C}$), sigma-t, nitrate (μM) and chlorophyll *a* ($\mu\text{g Chl } a \text{ L}^{-1}$) along Nunivak Island C-line transect, 21 June 1997. Station locations are indicated by triangles.



(i.e. the inner front) was wider than normal and extended farther inshore than previously observed (Stabeno *et al.*, 2001). In fact, a well-mixed water column was not observed on this transect (Fig. 4).

The inner shelf water column (km 60–120) in June 1997 exhibited very low concentrations ($< 0.2 \mu\text{M}$) of nitrate (Fig. 4).

Figure 5. Distributions of temperature ($^{\circ}\text{C}$), sigma-t, nitrate (μM) and chlorophyll *a* ($\mu\text{g Chl } a \text{ L}^{-1}$) along Nunivak Island C-line transect, 2 September 1997. Station locations are indicated by triangles.

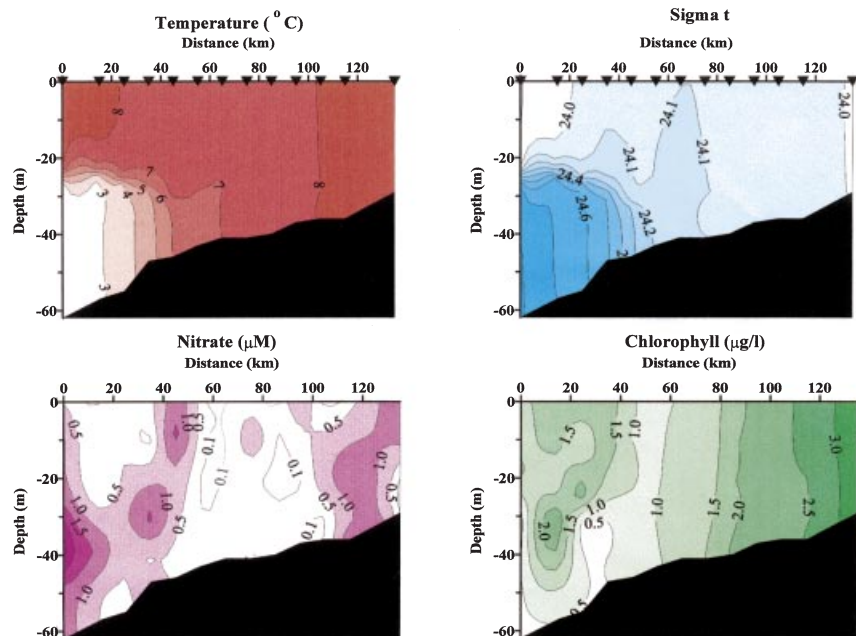
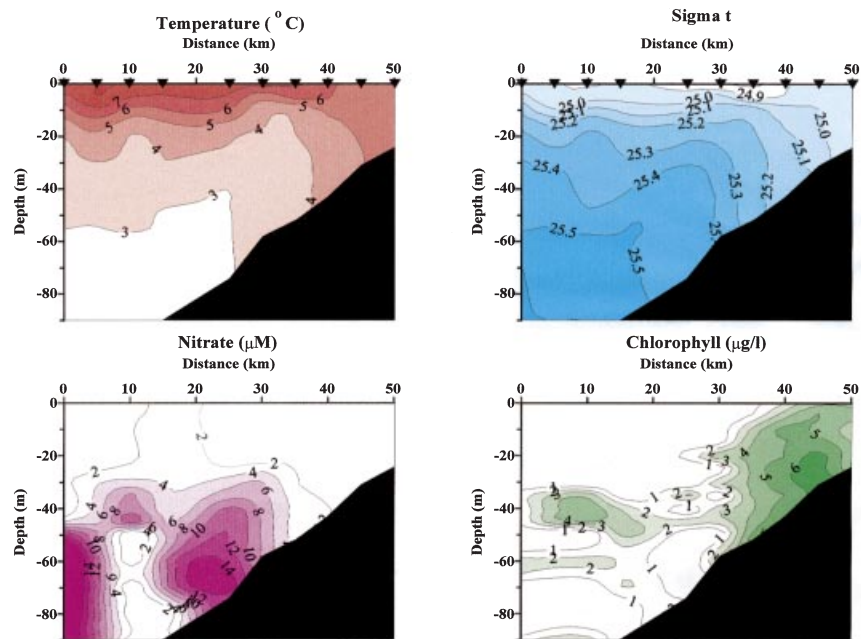


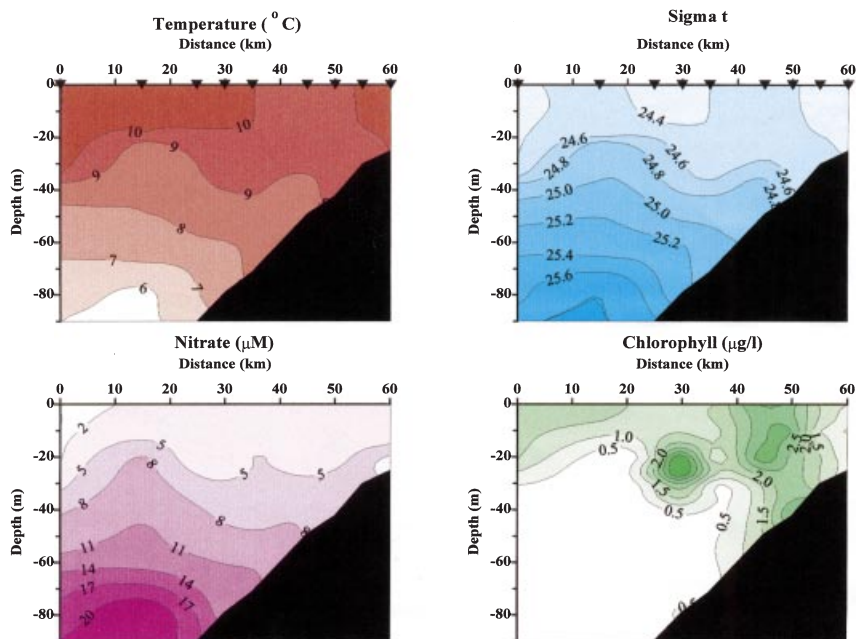
Figure 6. Distributions of temperature ($^{\circ}\text{C}$), sigma-t, nitrate (μM) and chlorophyll *a* ($\mu\text{g Chl } a \text{ L}^{-1}$) along Slime Bank C-line transect, 1–4 June 1997. Station locations are indicated by triangles.



By August/September, the middle-shelf stratification in the Nunivak transect had increased with the intense summer heating of surface waters (km 0–40, Fig. 5). This stable water column contained low con-

centrations of nitrate, $< 0.6 \mu\text{M}$ in the surface and $0.5\text{--}1.5 \mu\text{M}$ in the bottom layer (Fig. 5). The appearance of $1.0 \mu\text{M}$ nitrate at the surface above the front suggests that frontal processes may have been

Figure 7. Distributions of temperature ($^{\circ}\text{C}$), sigma-t, nitrate (μM) and chlorophyll *a* ($\mu\text{g Chl } a \text{ L}^{-1}$) along Slime Bank C-line transect, 10 September 1997. Station locations are indicated by triangles.



facilitating vertical fluxes of nitrate. The increases in nitrate relative to June were most likely the result of remineralization and/or nitrification. Chlorophyll concentrations were relatively uniform ($1\text{--}3.0 \mu\text{g Chl } a \text{ L}^{-1}$) throughout the water column in the inner domain (km 60–130). In the middle domain (km 0–40), higher chlorophyll concentrations ($1\text{--}2.0 \mu\text{g Chl } a \text{ L}^{-1}$) were observed where nitrate concentrations had increased. A small maximum was noted ($2 \mu\text{g Chl } a \text{ L}^{-1}$) below the pycnocline above the 60 m isobath.

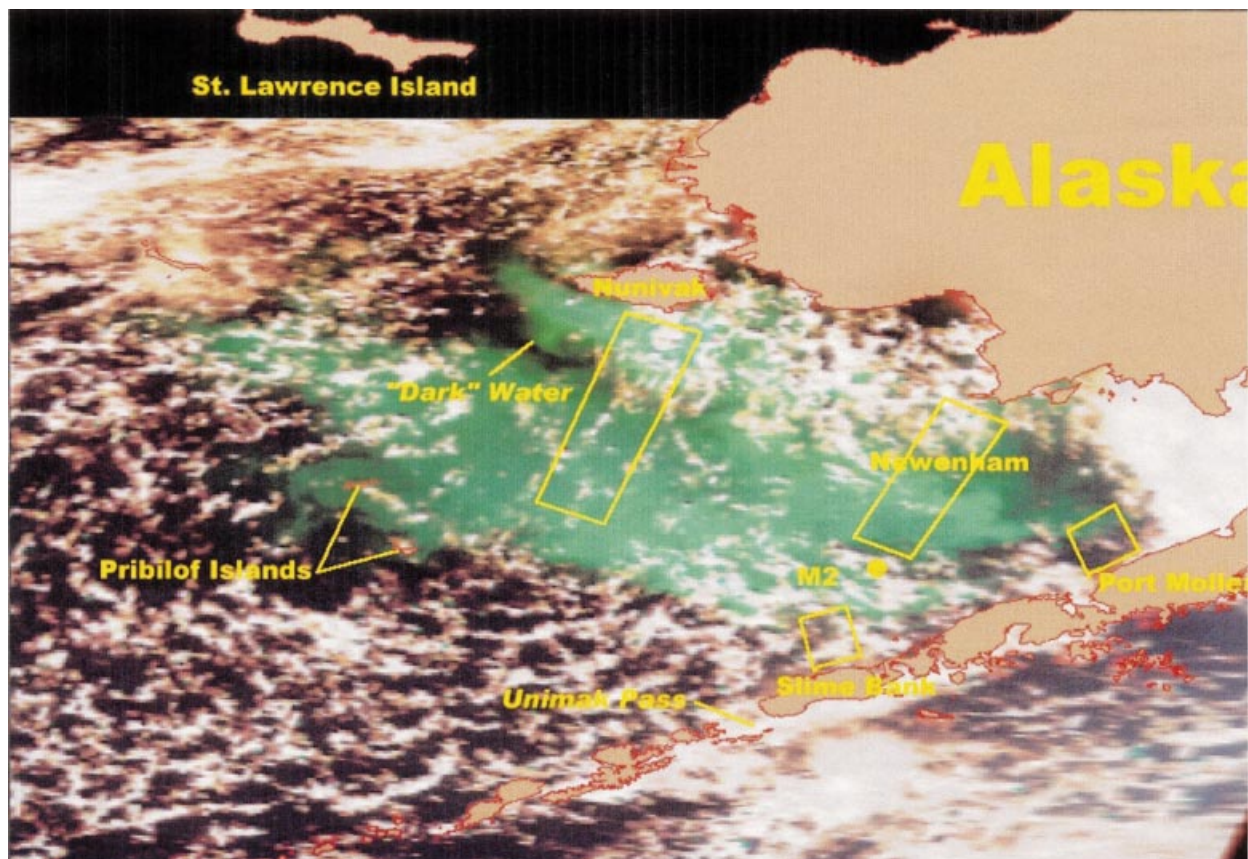
Summer nutrient concentrations were not as depleted on Slime Bank as at Nunivak Island because of Slime Bank's proximity to the shelf edge and Bering Canyon and currents ($\approx 3 \text{ cm s}^{-1}$) in the vicinity of Unimak Pass. The upper water column (i.e. upper 15 m) at Slime Bank in June 1997 (Fig. 6) had low surface nitrate concentrations ($\leq 2 \mu\text{M}$) and elevated chlorophyll biomass inshore of the 60 m isobath. Waters below the pycnocline contained relatively high concentrations of nitrate ($3\text{--}14 \mu\text{M}$) and the

chlorophyll maximum occurred between 30 and 50 m depth offshore, and near the bottom inshore (Fig. 6). Water column stratification at Slime Bank was stronger in September than in June (Fig. 7). Likewise, nitrate concentrations were higher and chlorophyll concentrations were lower in September. Nutrient-rich water, which was likely transported up Bering Canyon, was evident in the lower part of the water column.

Phytoplankton

SeaWiFS satellite imagery revealed the presence of 'chalky', pale green water over much of the southeastern Bering Sea during September 1997 (Fig. 8). Electron micrographs of the cells from the white water confirmed that discoloration was caused by the presence of the coccolithophorid, *Emiliana huxleyi*. Observations using both light and scanning electron microscopy further disclosed that coccolithophorids were already a common component of the phytoplankton assemblage during the June cruise, although

Figure 8. Satellite 'true colour' composite image of the *Emiliana huxleyi* bloom, showing its extensive distribution in the Eastern Bering Sea, 18–25 September 1997.



not in sufficient numbers to be evident to the eye. *Emiliania huxleyi* was the most abundant coccolithophorid observed, although a few cells of *Rhabdosphaera* sp. were also present. Samples from June were a mixture of diatoms ($\approx 19\%$) and coccolithophorids ($\approx 34\%$) by number. Dinoflagellates were 25%, and small unidentified flagellates and monads constituted the remaining 22% of the assemblage. It should be noted that large numbers of *Phaeocystis pouchetii* dominated at the two stations closest to shore at Slime Bank during June. *P. pouchetii* averaged 3.3×10^6 cells L^{-1} and accounted for 92% of the phytoplankton assemblage at these stations, where chlorophyll levels approached $6 \mu g$ Chl *a* L^{-1} . By August/September, typical concentrations of *E. huxleyi* had increased to 2.95×10^5 cells L^{-1} , representing 56% of the community. At this time, chalky-water conditions were prevalent throughout most of Bristol Bay. At Slime Bank, however, *E. huxleyi* accounted for only 17% of the community, and this occurred only at the northern end of the transect that extended into the middle domain. Diatoms dominated cell counts here, with 4.94×10^5 cells L^{-1} ($\approx 55\%$), while chlorophyll concentrations approached $2 \mu g$ Chl *a* L^{-1} .

Given the unusual nutrient conditions and the coccolithophorid bloom, we examined primary productivity inside and outside the bloom in spring and autumn, and found that productivity rates ranged from 0.1 to over 900 mg C m^{-2} day^{-1} during the June and August/September 1997 cruises (Table 1). These rates were highly variable along each transect, especially along the Nunivak Island transects. The high productivity values in August/September near Nunivak Island, at stations NIA5 and NID9 (Fig. 2; Fig. 5, about km 15–35) corresponded roughly to the dark wedge of water visible in the SeaWiFS image to the south and south-west of Nunivak Island (Fig. 8). This appearance of darker water to the south and south-west of Nunivak Island is the result of less coccolith-back-scattered light detected by SeaWiFS, i.e. where the bloom was least dense, the productivity was highest.

At Slime Bank, which was mostly outside the coccolithophorid bloom, the highest rates of productivity were not associated with the frontal zone but occurred offshore of the front. Inshore stations showed relatively high rates of productivity and chlorophyll for both sampling periods. During June, the highest rates of productivity coincided with a pool of high nitrate concentrations at station SBB8 (Fig. 2; Fig. 6, about km 20). High productivity rates offshore coincided with increasing numbers of *E. huxleyi*. Similarly,

the high inshore productivity rates were associated with high concentrations of *P. pouchetii*.

In June at Nunivak Island, P_{max} was highest (1.32 mg C (mg Chl *a*) $^{-1}$ h^{-1}) inshore near the 40 m isobath at station NICX6 (Fig. 2; Fig. 4, km 100). By August/September the offshore values had risen to about 2 mg C (mg Chl *a*) $^{-1}$ h^{-1} , but there was an even higher rate (3.14 mg C (mg Chl *a*) $^{-1}$ h^{-1}) at station NICX4 (Fig. 5, km 80) on the 40 m isobath. At Slime Bank, P_{max} generally increased from near-shore to offshore with a peak (one of two occasions) at a station near the 90 m isobath (Fig. 6) during June.

Zooplankton

Table 2 lists the mean concentrations of calanoid copepods (≤ 50 m and > 50 m isobath) in the four study regions for June 1997 with 95% confidence levels. In most cases, the lower 95% confidence levels for the concentration of *Acartia* spp., *Pseudocalanus* spp., and *Calanus marshallae* in 1997 data were higher than the mean concentrations reported for June 1981, for stations > 50 m water depth (Table 2). Mann-Whitney *U*-tests showed significantly higher 1997 values for *Acartia*, *Pseudocalanus* and *C. marshallae* in the middle domain (all *P*-values < 0.001), and no significant difference for *Oithona* densities between the two studies ($P = 0.696$). In the inner domain, *Acartia* was again significantly more abundant during the IFP ($P < 0.001$), *Pseudocalanus* ($P = 0.053$) was marginally significant, and *C. marshallae* ($P = 0.0810$) and *Oithona* ($P = 0.479$) were not significantly different between 1981 and 1997.

In contrast to the mesozooplankton, the upper 95% confidence levels for the abundance of adult plus juvenile euphausiids in June 1997, in and around the inner front, were similar to estimates from the middle shelf for May and June 1980 and 1981 (Table 3). If the 1981 data are assumed to characterize zooplankton abundance on the inner shelf of the south-eastern Bering Sea, the above results indicate moderately higher calanoid densities and similar euphausiid densities in 1997 relative to 1981. In August/September 1997, adult euphausiids were generally scarce at the Slime Bank and Nunivak Island grid, although juvenile euphausiids, especially *T. inermis*, were more abundant than in June.

Abundance and distribution patterns of adult and juvenile euphausiids, combined, collected in and around the fronts surrounding the Pribilof Islands during September (SEBSCC), showed striking differences among recent years (Table 4). Densities of euphausiids as sampled by the Methot net were similar in 1995 and 1996. However, the densities observed in

Table 2. Comparison of copepod concentrations (no. m⁻³) from the middle and inner shelf domains of the south-eastern Bering Sea. Data from June 1997 are from the Inner Front Project. Data from 1981 are from the PROBES Data Reports. M, geometric mean; L / U, lower and upper 95% confidence levels. PROBES data were taken with a 1 m² MOCNESS with 149 µm mesh nets. Inner Fronts Project data were taken with a CalVET net with 150 µm mesh nets. Data include all copepodid stages. There were four tows at Station 12, five at Station 16 and three at Station 19. Stations 12 and 16, > 50 m water depth; Station 19, < 50 m depth.

A: Inner Front Project data for June 1997											
Taxon and bottom depth (m)	Slime Bank		Nunivak		Cape Newenham		Port Moller				
	M	L / U	M	L / U	M	L / U	M	L / U	M	L / U	L / U
<i>Acartia</i> spp.											
≤ 50	435	137 / 1 385	419	185 / 950	1 349	628 / 2 898	4 587	1 879 / 11 196			
> 50	748	261 / 2 139	443	195 / 1 004	874	329 / 2 319	1 130	410 / 3 118			
<i>Pseudocalanus</i> spp.											
≤ 50	563	196 / 1 617	1 513	739 / 3 099	2 051	915 / 4 594	1 034	461 / 2 271			
> 50	1 178	379 / 3 665	833	340 / 2 045	643	285 / 1 450	743	332 / 1 662			
<i>Calanus marshallae</i>											
≤ 50	22	5 / 98	81	27 / 245	44.7	13.8 / 145	1.3	0.4 / 4.1			
> 50	88	34 / 227	56	21 / 148	33.3	12.8 / 88.1	41.9	14.3 / 123			
<i>Oithona similis</i>											
≤ 50	30	8 / 122	512	233 / 1 127	30.1	9.4 / 95.7	3.4	0.4 / 28.7			
> 50	279	70 / 1 114	625	288 / 1 356	76.5	31 / 189	133	56 / 317			
B: PROBES data for June 1981											
Taxon	Sta 12		Sta 16		Sta 19						
	M	L / U	M	L / U	M	L / U	M	L / U	M	L / U	L / U
<i>Acartia</i> spp.	7	3 / 20	55	20 / 148	80	4 / 1 462					
<i>Pseudocalanus</i> spp.	178	91 / 346	237	181 / 311	313	53 / 1 831					
<i>Calanus marshallae</i>	9	6 / 13	17	13 / 23	37	26 / 52					
<i>Oithona similis</i>	110	64 / 188	242	182 / 323	148	40 / 554					

Table 3. Comparison of euphausiid (adult plus juveniles) abundances (no. m⁻²) from the inner and middle shelf domains of the south-eastern Bering Sea. Data from June 1997 are from the Inner Front Project. Data from May and June 1980 and 1981 are from the PROBES Data Reports. M, geometric mean; L/U, lower and upper 95% confidence levels. PROBES data were taken with a 1m² MOCNESS with 149 µm mesh nets. Inner Front Project data were collected with a 1m² MOCNESS with 500 µm mesh nets. PROBES Stations 12 and 16 were > 50 m deep; Station 19 was < 50 m deep.

PROBES											
1980 Sta 12		Sta 16		1981 Sta 12		Sta 16		Sta 19			
Taxa	M	L/U	M	L/U	M	L/U	M	L/U	M	L/U	
<i>Thysanoessa raschii</i>	9.4	4.4 / 24.4	32.6	0.66 / 678	2.15	0.33 / 6.48	3.72	0 / 93	2.05	0 / 37	
<i>Thysanoessa inermis</i>	0.31	0.28 / 0.37	7.4	4.15 / 13.3	2.36	0.01 / 10.2	1.67	0 / 21	0.73	0 / 8.95	
INNER FRONT 1997											
Bottom depth		Slime Bank		Nunivak		Newenham		Port Moller			
Taxa	(m)	M	L/U	M	L/U	M	L/U	M	L/U	M	L/U
<i>Thysanoessa raschii</i>	≤ 50	75	11 / 458	0.92	0.01 / 61.9	0.66	0.13 / 3.1	0	0 / 0	0	0 / 0
	> 50	27	7.1 / 105	7.72	1.1 / 53.6	0	0 / 0	4.0	0.2 / 74	0	0 / 0
<i>Thysanoessa inermis</i>	≤ 50	1.4	0.13 / 15.1	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0
	> 50	3.6	0.29 / 45.3	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0

Table 4. Geometric means of euphausiid densities (no. m⁻²) collected by Methot trawls along each Pribilof Island transect by year and habitat. A dash indicates no sampling at that habitat / transect combination. Only night tows along each transect were used.

Transect	Year	Habitat		
		Inner	Front	Outer
A	1995	1.15	10.44	19.03
	1996	–	4.82	10.79
	1997	211.27	34.90	71.13
B	1995	0.15	2.26	1.89
	1996	0.10	5.07	17.01
	1997	0.74	12.63	194.73
C	1995	4.72	–	0.48
	1996	1.52	14.49	6.97
	1997	47.86	106.39	164.69
D	1995	2.66	–	39.13
	1996	0.17	35.28	108.12
	1997	11.16	140.89	198.89

1997 were substantially higher than those found in either of the two previous years. In addition, the highest densities on Transect A in 1997 were close to St Paul Island, shoreward of the frontal region, which is the habitat that had the lowest densities in most other year/transect combinations. The species composition also varied among the three years. Along Transect A, the dominant species in all years was *Thysanoessa raschii* (87%, 98%, 62%), but in 1997, *Thysanoessa inermis* was also important (37%). Along Transect C, *T. inermis* dominated in 1995 and 1997 (62%, 72%). Along Transect D, south of St George,

Table 5. *Thysanoessa* species captured with the Methot trawl by year and transect (Fig. 1). Numbers are percentage of total identified euphausiids for the transect.

Year	Species	Transect				Total
		A	B	C	D	
1995	<i>T. inermis</i>	12.6	58.9	62.1	74.5	43.4
	<i>T. raschii</i>	87.4	40.4	37.7	22.8	56.0
	<i>T. spinifera</i>	0.0	0.3	0.2	2.8	0.6
1996	<i>T. inermis</i>	0.9	4.9	20.6	33.4	14.6
	<i>T. raschii</i>	98.1	71.4	74.3	41.7	71.6
	<i>T. spinifera</i>	1.0	23.7	5.1	24.9	13.7
1997	<i>T. inermis</i>	37.1	40.5	71.9	94.5	64.4
	<i>T. raschii</i>	62.4	59.5	27.0	3.8	34.7
	<i>T. spinifera</i>	0.0	0.0	0.8	1.7	0.7

T. raschii was dominant in 1996, whereas *T. inermis* made up the vast majority of the catch in 1997. In general, 1995 was intermediate to the other two years in the relative proportions of euphausiid species (Table 5).

Depth-stratified MOCNESS collections indicated that the maximum night-time abundance on Line A (> 50 m isobath) was usually at or below the base of the mixed layer. In the shallow portion of the same transect (< 50 m isobath), the maximum abundance of euphausiids was observed at the surface.

DISCUSSION

Research during the late 1970s and early 1980s provided an account of nutrient cycling, concentration variability, and phytoplankton growth for the eastern Bering Sea (Sambrotto *et al.*, 1986; Whitledge and Walsh, 1986; Whitledge *et al.*, 1986). The annual nutrient cycle was examined over 4–5 years along a single cross-shelf transect. Major events in the nutrient cycle were replenishment through lateral advection (i.e. basin to shelf) or wind-driven mixing (vertical) and utilization by phytoplankton. Observation of the spring phytoplankton bloom showed that blooms began offshore and slowly progressed inshore, across the shelf. Chlorophyll concentrations typically peaked offshore in mid-April, appearing over the inner domain by early June. Changes in the stability of the water column best explained this pattern. A rapid decline of nitrate in the mixed layer was observed during the spring phytoplankton bloom. During summer, phytoplankton growth was driven by regenerated nitrogen (ammonium), except when episodic wind mixing events replenished nitrate in surface waters (Sambrotto *et al.*, 1986; Whitledge *et al.*, 1986). These events introduced 15–20 mM m⁻² of ‘new nitrate’ into the euphotic zone over the middle shelf domain, resulting in mean nitrate concentrations of ≈ 2 μM. This ‘new nitrate’ was probably essential to maintaining a summer population of diatoms.

During 1997, the southerly extent of sea ice was average, but reached its maximum later than usual and retreated more rapidly than is typical (Stabeno *et al.*, 2001). The year began as a cold spring, but water column stratification began early because there were few storms resulting in a shallow mixed layer (Stabeno *et al.*, 2001). Unusual patterns of nutrient utilization with depth were observed. Normally, uptake of nitrate by phytoplankton is high at the surface, decreasing with depth (Sambrotto *et al.*, 1986). In 1997, however, uptake studies (T. Rho, 2000) clearly indicate that nitrate uptake increased with depth to a maximum

below the pycnocline. This subpycnocline utilization, most likely by diatoms, resulted in depletion of nitrate well below the pycnocline (Fig. 4). Nitrate concentrations in the bottom layer were less than 10–20% of those measured ($6 \mu\text{M}$) in the early 1980s (Hattori and Goering, 1981; Whitley *et al.*, 1986). Low nitrate and silicate concentrations in the bottom waters of the shelf were also attributed to a strong storm in May and a lessening of onshore transport of slope water (Stabeno *et al.*, 2001).

In 1997, a larger portion of the nitrate pool was utilized by phytoplankton production than had been reported for the early 1980s. Preliminary estimates, calculated from nitrate disappearance, revealed that primary productivity in the early 1980s was 10–30% less than in 1997. The effect of this (1997) increased productivity on system's carrying capacity, trophic transfer or amount of the production retained in the water column is not known. Nitrate and silicate depletion plus the anomalously warm water is believed to have contributed to the unusual occurrence of *E. huxleyi*.

Emiliania huxleyi is one of the most abundant and ubiquitous coccolithophorid species in the modern ocean (Okada and Honjo, 1973). This cosmopolitan species can dominate phytoplankton assemblages over a wide range of temperature, salinity and nutrient concentrations (Brand, 1982, 1994). Extensive blooms of *E. huxleyi* commonly occur in both the coastal (Birkenes and Braarud, 1952; Berge, 1962; Holligan *et al.*, 1983; Balch *et al.*, 1991) and oceanic regions of the North Atlantic (Holligan *et al.*, 1993a,b). Within the upper mixed water layer, such blooms typically follow the early spring diatom bloom, which commonly appears to be terminated by the depletion of dissolved silica (Head *et al.*, 1998). Although reflectance algorithms used with NASA's Coastal Zone Color Scanner (CZCS) suggest that localized 'white water' conditions may have occurred between 1978 and 1984 (Brown and Yoder, 1994), the 1997 bloom was the first confirmed report of a large-scale coccolithophorid bloom in the eastern Bering Sea (Sukhanova and Flint, 1998; Vance *et al.*, 1998).

The *E. huxleyi* bloom in late summer had little apparent effect on primary production over the southern shelf. When averaged over both cruises and grids, daily productivity rates ($163 \text{ mg C m}^{-2} \text{ day}^{-1}$), chlorophyll concentrations ($50 \text{ mg Chl } a \text{ m}^{-2}$), and P_{max} ($0.22 \text{ mg C h}^{-1} (\text{mg Chl } a)^{-1}$) were not unusually high for summer values in the Bering Sea. For example, Bering Sea shelf productivity rates averaged about $700 \text{ mg C m}^{-2} \text{ day}^{-1}$ during the summer of 1988 (Zeeman, 1992). During the period

1979–1981, the average rate on the outer and middle shelf was $2.05 \text{ g C m}^{-2} \text{ day}^{-1}$ (Walsh and McRoy, 1986). Productivity rates measured in September during the 1997 coccolithophorid bloom were even less than the relatively low summer rates of 1988. This reduction may be related to strong light attenuation and a shallow euphotic zone (T. Rho, 2000). Estimates of summer productivity may be compared with the $2\text{--}6 \text{ g C m}^{-2} \text{ day}^{-1}$ reported during the spring diatom blooms in 1980 and 1981 (Walsh, 1995), during which the maximum chlorophyll concentration in the region was $750 \text{ mg Chl } a \text{ m}^{-2}$ (Whitley and Walsh, 1986), or about seven times the maximum reported here. In 1997, the low primary productivity rates observed may seem paradoxical in light of the large area covered by the bloom. Nevertheless, low productivity rates have been found within other coccolithophorid blooms (Head *et al.*, 1998), and may result because coccolithophorid blooms generally follow diatom blooms that have depleted nutrients in the water column (Egge and Aksnes, 1992; Rothschild and Squire, 1996).

Of the P_{max} values from the Bering Sea during the summer of 1984, 96% were between 0.8 and $10 \text{ mg C (mg Chl } a)^{-1} \text{ h}^{-1}$ (Zeeman and Jensen, 1990). In 1997, P_{max} ranged from 0.1 to 10.2, showing that there were no obvious changes in photophysiology of bulk phytoplankton (Table 1). In general, there is a paucity of data on photosynthetic P-I parameters for the Bering Sea. The P_{max} values in Table 1 for surface waters averaged 1.57 ± 2.18 and for the chlorophyll max 1.11 ± 1.43 . For comparison, austral summer data from the Weddell–Scotia Sea yielded mean P_{max} values of 1.94 ± 0.79 (Figueiras *et al.*, 1994).

In June at Slime Bank, the water was not yet discoloured by coccoliths, indicating that the coccolithophores were not yet very abundant. Minimal light extinction in June at the northern ends of the Slime Bank transects indicates that the phytoplankton were probably not light limited. Although P_{max} values were high, integrated productivity and chlorophyll were low, which may indicate a rapidly growing population at the onset of exponential growth, or one being cropped rapidly by grazers. Extinction coefficients at Nunivak Island ranged from 0.018 to 0.221 m^{-1} in June and 0.131–0.724 by August/September (Table 1). The high August extinction coefficients were observed at only 2 or 3 stations. At these stations, the 1% light level depth was reduced by 50% or more owing to scattering from the coccoliths of *E. huxleyi*. In general, higher P_{max} stations tended to have relatively low coefficients of light extinction (Table 1),

and surface PAR values were generally more than enough to saturate carbon uptake rates.

In mesocosm studies, Egge and Heimdal (1994) noted that *E. huxleyi* grew faster than *Phaeocystis* sp. at temperatures above 10°C. The presence of both *E. huxleyi* and *P. pouchetii* at Slime Bank during May/June shows that both species were in competition for limited nutrients. As the warm sea surface temperatures increased during summer, the coccolithophorid would have been favoured.

Mesozooplankton abundance in 1997 differed from that measured during 1981 (Smith and Vidal, 1986). In June 1997 in the middle domain, *Acartia* were about 24 times more numerous, *Pseudocalanus* were about 3.5 times as abundant, and *C. marshallae* about 4 times as abundant as in 1981. In 1997 in the inner domain, *Acartia* were about 26 times more abundant than in 1981, *Pseudocalanus* was about 5 times as abundant, and the other species showed little or no difference in abundance between the two years. While the statistical results indicate significant differences in calanoid abundances between 1981 and 1997, the differences may reflect interannual variability rather than a long-term trend. The differences could also be an artefact. A potential source of error in these comparisons was the possibility that clogging of the 149 µm mesh MOCNESS used in PROBES would have caused underestimation of the density of zooplankton. Because the flow meter on the MOCNESS is externally mounted, it measures the distance travelled rather than the volume filtered. The CalVET nets used in the IFP study had flow meters mounted inside the nets, and therefore the amount of water filtered was measured.

In contrast to the copepods, the abundance of adult plus juvenile euphausiids was similar between the two studies, both in the middle domain and in the inner domain. Preliminary reports (Hunt *et al.*, 1999a,b), based on a comparison of 1997 euphausiid densities with those for 1980 reported by Smith (1991, Table 1), suggested that there had been a major reduction in the abundance of euphausiids in 1997. However, as reported here, examination of PROBES data from stations close to those occupied in the IFP and sampled in the same month suggested that no significant reduction of euphausiid numbers in the total water column had occurred in June 1997.

Normally adult euphausiids constitute a major dietary item for short-tailed shearwaters (Hunt *et al.*, 1996). Starvation of shearwaters in August and September 1997 (Baduini *et al.*, 2001) may have been due to low densities of adult euphausiids in August 1997 or to the unavailability of euphausiids. Euphausiids may have reduced either their daytime mating or their

foraging activities in near-surface waters owing to unusually high surface temperatures over much of the middle and inner shelf (Hanamura *et al.*, 1989; Stabeno *et al.*, 2001). Because shearwaters can quickly search large geographical regions for prey, their starvation suggests that low euphausiid availability in surface waters was a general feature of the inner and middle shelf in August.

Near the Pribilof Islands on the middle and outer shelf domains, concentrations of euphausiids in September 1997 were high, as compared with 1995 and 1996. The high concentrations of euphausiids in 1997 determined by net tows agreed with concurrent results from acoustic surveys around the Pribilof Islands: high backscatter at 120 kHz was observed in 1997 relative to 1995 and 1996 (Swartzman *et al.*, 1999). These acoustic traces show that euphausiids migrated well up into the water column at night. Neither the acoustic data nor the MOCNESS stratified tows indicated night-time avoidance of the warm surface layers (9°C) by adult and juvenile euphausiids. However, these surface temperatures were comparable to those that caused cessation of daytime near-surface swarming by *Thysanoessa inermis* off Japan (Hanamura *et al.*, 1989).

It is unclear why euphausiid densities in 1997 were so much higher near the Pribilof Islands than in surveys earlier in the 1990s. They may have suffered lower mortality owing to lower densities of predatory fish such as juvenile walleye pollock (*Theragra chalcogramma*) (Brodeur and Wilson, 1999). In addition, elevated sea surface temperatures in 1997 may have accelerated larval development, resulting in higher densities of juvenile euphausiids that year than in 1995 or 1996.

In spite of higher densities of euphausiids around the Pribilof Islands in 1997 than in most of the IFP grids, significant mortality of short-tailed shearwaters occurred near these islands (Baduini *et al.*, 2001). Availability, rather than concentration, may be the relevant issue. Daytime surface swarms of adult euphausiids were not observed in September, and euphausiid distribution during daytime tended to be deep in the water column. Water clarity at stations dominated by coccolithophorids was lower than at stations unaffected by the bloom, and the turbid waters extended to the bottom at some stations. This may have made it difficult for short-tailed shearwaters to locate prey patches (Lovvorn *et al.*, 2001) and few birds were observed foraging around the Pribilof Islands in September 1997 (G.L. Hunt, unpublished data).

In 1997, atmospheric forcing strongly perturbed the south-eastern Bering Sea ecosystem. The unusual climate as reported by Overland *et al.* (2001) and the

resultant physical conditions (Stabeno *et al.*, 2001) influenced production and species composition of the phytoplankton in the south-eastern Bering Sea. Relatively calm, sunny spring and summer conditions (Overland *et al.*, 2001; Stabeno *et al.*, 2001) resulted in a warm, shallow mixed layer and the complete utilization of water column nutrients by phytoplankton. While the inner frontal region has been proposed to enhance nutrient availability and prolong phytoplankton production during summer (Hunt *et al.*, 1996), the anomalous weather conditions and nutrient depletion of frontal source waters resulted in a broad, diffuse front with meagre nutrient enrichment. Despite this weakness, the inner front appeared to have facilitated upward flux of nutrients at Nunivak Island in both June and August 1997. New production, estimated from nutrient depletion, was 10–30% higher than that measured in the past, while summer productivity rates were not markedly different. In summer, the first documented coccolithophorid bloom for the Bering Sea began in the anomalously warm, nutrient-depleted, shallow upper mixed layer. By autumn, the bloom covered most of the south-eastern Bering Sea shelf and sometimes extended to the bottom in waters up to 80 m deep. The unusual climatic conditions were accompanied by elevated abundance of copepods on the inner portion of the middle domain and in the inner domain, and increased abundance of euphausiids near the Pribilof Islands. The apparent alterations in zooplankton densities, relative to the early 1980s, observed in 1997 – along with high mortality of shearwaters, marked declines in the salmon fishery (Kruse, 1998), and altered cetacean distributions (Tynan, 1999) – are possible indications of the impact of long-term warming on trophic relationships on the Bering Sea shelf. It is unclear how these observations relate to the observed changes in physical forcing, or to each other. However, it is clear that the Bering Sea ecosystem rapidly responds to atmospheric/climatic perturbations (Napp and Hunt, 2001).

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