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Zooplankton species composition, abundance and biomass on the eastern Bering Sea shelf during summer: The potential role of water-column stability and nutrients in structuring the zooplankton community

Kenneth O. Coyle^{d,*}, Alexei I. Pinchuk^a, Lisa B. Eisner^b, Jeffrey M. Napp^c^a Seward Marine Center, PO Box 730, University of Alaska, Seward, AK 99664, USA^b Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 11305 Glacier Highway, Juneau, AK, 99801, USA^c NOAA, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA^d Institute of Marine Science, University of Alaska, Fairbanks 99775-7220, USA

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ABSTRACT

The southeastern Bering Sea sustains one of the largest fisheries in the United States, as well as wildlife resources that support valuable tourist and subsistence economies. The fish and wildlife populations in turn are sustained by a food web linking primary producers to apex predators through the zooplankton community. Recent shifts in climate toward warmer conditions may threaten these resources by altering productivity and trophic relationships in the ecosystem on the southeastern Bering Sea shelf. We examined the zooplankton community near the Pribilof Islands and on the middle shelf of the southeastern Bering Sea in summer of 1999 and 2004 to document differences and similarities in species composition, abundance and biomass by region and year. Between August 1999 and August 2004, the summer zooplankton community of the middle shelf shifted from large to small species. Significant declines were observed in the biomass of large scyphozoans (*Chrysaora melanaster*), large copepods (*Calanus marshallae*), arrow worms (*Sagitta elegans*) and euphausiids (*Thysanoessa raschii*, *T. inermis*) between 1999 and 2004. In contrast, significantly higher densities of the small copepods (*Pseudocalanus* spp., *Oithona similis*) and small hydromedusae (*Euphysa flammea*) were observed in 2004 relative to 1999. Stomach analyses of young-of-the-year (age 0) pollock (*Theragra chalcogramma*) from the middle shelf indicated a dietary shift from large to small copepods in 2004 relative to 1999. The shift in the zooplankton community was accompanied by a 3-fold increase in water-column stability in 2004 relative to 1999, primarily due to warmer water above the thermocline, with a mean temperature of 7.3 °C in 1999 and 12.6 °C in 2004. The elevated water-column stability and warmer conditions may have influenced the zooplankton composition by lowering summer primary production and selecting for species more tolerant of a warm, oligotrophic environment. A time series of temperature from the middle shelf indicates that the warmer conditions in 2004 are part of a trend rather than an expression of interannual variability. These results suggest that if climate on the Bering Sea shelf continues to warm, the zooplankton community may shift from large to small taxa which could strongly impact apex predators and the economies they support.

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1. Introduction

A major goal of oceanographic research is to understand the ecological response to physical forcing. Knowledge of this response is critical to assessment of the potential impacts of global climate change on marine ecosystems. Water-column stability is one of the mechanisms linking the ecosystem to physical forcing. The influence of water-column stability on

vertical mixing and nutrient flux to the euphotic zone has a profound effect on the intensity and magnitude of primary production, which in turn provides the energy driving pelagic and benthic ecosystems. While the influence of water-column stability on ecosystem response is generally accepted (Mann and Lazier, 1991; Gargett, 1997; Edwards et al., 2000), application of the theory to specific ecosystems requires some quantitative measure of water-column stability relative to measurable ecosystem responses.

Recent climate-related influences on the Bering Sea ecosystem have demonstrated the sensitivity of the region to potential impacts from climate change (Hunt et al., 2002; Schumacher et al.,

* Corresponding author. Tel.: +19074747705; fax: +19074747204.

E-mail address: coyle@ims.uaf.edu (K.O. Coyle).

2003). The evidence of long-term climate change includes gradual increases in atmospheric temperature, decreases in the area influenced by permafrost on the land masses near the Bering Sea coast, the retreat of Alaskan glaciers, and declines in the thickness and extent of Bering Sea and Arctic Ocean sea-ice cover (Chapman and Walsh, 1993; Osterkamp, 1994; Wadhams, 1995, 2000; Overland and Stabeno, 2004). The potential sensitivity of the southeastern Bering Sea ecosystem to climatic influences is indicated by a number of unusual occurrences in recent years, including an intense coccolithophorid bloom (Sukhanova and Flint, 1998; Stockwell et al., 2001), a high mortality of short-tailed shearwaters (Baduini et al., 2001), and Pacific salmon returns far below predicted numbers (Napp and Hunt, 2001). The potential impacts of climate change on the southeastern Bering Sea have generated concern because of the large amounts of fish and wildlife resources of importance to the commercial, tourist and subsistence economies (NRC (National Research Council), 1996). These concerns have prompted a number of research efforts to document temporal change in fishery and wildlife resources and to understand the mechanisms driving those changes (Macklin et al., 2002).

These studies included two that provided data for this investigation. The first was a National Science Foundation funded program to study the Inner Front of the southeastern Bering Sea (Macklin et al., 2002) and the second was a multidisciplinary research effort in summer of 2004 to study the cross-shelf distribution of oceanographic properties in the Pribilof Islands region and near a long-term oceanographic mooring site (M2) on the middle shelf off Cape Newenham. These studies have permitted us to examine the possible response of the Bering Sea ecosystem to climate-related shifts in water-column stability. The Inner Front and Pribilof studies provided an opportunity to compare shelf zooplankton and micronekton populations during summer of 1999, a relatively cold year, and 2004, a warm year. Using data from these two projects, we compared the abundance and biomass of major zooplankton taxa on the middle shelf off Cape Newenham in August, 1999 and 2004, relative to water-column stability as measured by a stability coefficient. Data from the Inner Front and Pribilof studies provide an initial measure of the magnitude and range of shifts in water-column stability, and an indication of the potential changes in zooplankton species composition and food web relationships that may result from climate-related shifts in stability on the Bering Sea shelf during summer. Additional conductivity–temperature–depth (CTD), nutrient and zooplankton data from the North Pacific Anadromous Fish Commission's BASIS program (Bering Aleutian Salmon International Survey) aided in placing the 2004 observations off Cape Newenham and near the Pribilof Islands in a broader geographic context of the eastern Bering Sea shelf between the Alaska Peninsula and St Lawrence Island. Since 2000 the US component of BASIS has collected hydrographic, fluorescence, chlorophyll, nutrient, zooplankton and pelagic fish data during August–September over a grid of approximately 150 stations on the eastern Bering Sea shelf from 55° to 64°N latitude.

1.1. Site description

The southeast Bering Sea shelf is more than 500 km wide (Stabeno et al., 1999) and uniformly level, with an average slope of about 1 m per 3 km (McDonald et al., 1981). During spring, summer and fall, fronts divide the Bering Sea shelf into three distinct hydrographic regions: the inner, middle and outer domains (Coachman, 1986). The shallower inner domain is unstratified due to mixing of the upper and lower water columns by wind and tides, respectively. The inner front, usually located

near the 50 m isobath (Stabeno et al., 2001), separates the inner and middle domains. The middle domain is a two-layered system, with an upper mixed layer separated from the deeper layer by a seasonal pycnocline at 15–40 m depth. The outer domain, from 100 to 200 m depth, consists of a wind-mixed surface layer and a tidally mixed bottom layer, separated by a transition zone. The middle and shelf-break fronts separate the middle domain and outer domain from outer shelf and slope waters, respectively (Coachman, 1986). Production in the middle domain occurs primarily as a spring bloom in April–May, followed by a series of post-bloom production events driven by mixing from storms (Sambrotto et al., 1986; Bond and Overland, 2005). Nutrients for production in the middle domain come mainly from onshore advection of oceanic water in winter and early spring, and by nutrient regeneration in summer (Whitledge et al., 1986; Rho et al., 2005). Summer new production in the middle domain is therefore dependent on the nutrient reservoir isolated from the euphotic zone by thermal stratification. Nutrients are generally absent from the inner domain during summer following the spring bloom (Whitledge et al., 1986; Kachel et al., 2002).

2. Methods

Samples were collected between 26 July and 19 August 2004 on 10 transects around the Pribilof Islands, one transect across the outer shelf to the south of the islands and a grid around the NOAA/PMEL M2 mooring in the middle of the southeastern Bering Sea shelf to the southwest of Cape Newenham (Fig. 1). CTD and fluorescence profiles were taken with a Seabird model 911 Plus¹ with conductivity, temperature and fluorescence sensors. The small zooplankters were sampled with a 25-cm diameter CalVET system (CalCOFI Vertical Egg Tow; Smith et al., 1985) having 150 µm mesh nets. Each net was equipped with General Oceanics flowmeters in the mouth of the net to monitor the volume filtered. The flowmeters were attached to the net frame with an elastic cord to keep the flowmeter inside the nets during descent. The nets were fished vertically during the day from 100 m depth to the surface or from the bottom to the surface at depths less than 100 m. Large zooplankton and micronekton were collected with a 1-m² MOCNESS (Wiebe et al., 1976) with 500 µm-mesh nets. The MOCNESS was equipped with a flowmeter positioned outside the mouth of the net and with Seabird conductivity and temperature sensors. The net was fished at night and oblique samples were collected in 20-m increments from 100-m depth to the surface or from the bottom to the surface at shallower depths. All samples were preserved in 10% formalin: seawater for later sorting.

The zooplankton samples were processed as follows: each sample was poured into a sorting tray and large organisms, primarily shrimp and jellyfish, were removed and enumerated. The sample then was split sequentially using a Folsom splitter until the smallest subsample contained about 100 specimens of the most abundant taxa. The most abundant taxa were identified, staged, enumerated and weighed in both MOCNESS and CalVET samples. Each larger subsample was examined to identify, enumerate and weigh the larger, less abundant taxa. Blotted, preserved wet weights of all specimens of each taxa and stage initially were taken on each sample, and the coefficient of variation in average wet weight was computed. If, as subsequent samples were analyzed, the coefficient of variation for any given taxa and stage changed by less than 5%, wet weights were no longer measured for that taxon for that cruise, and the wet weight

¹ Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

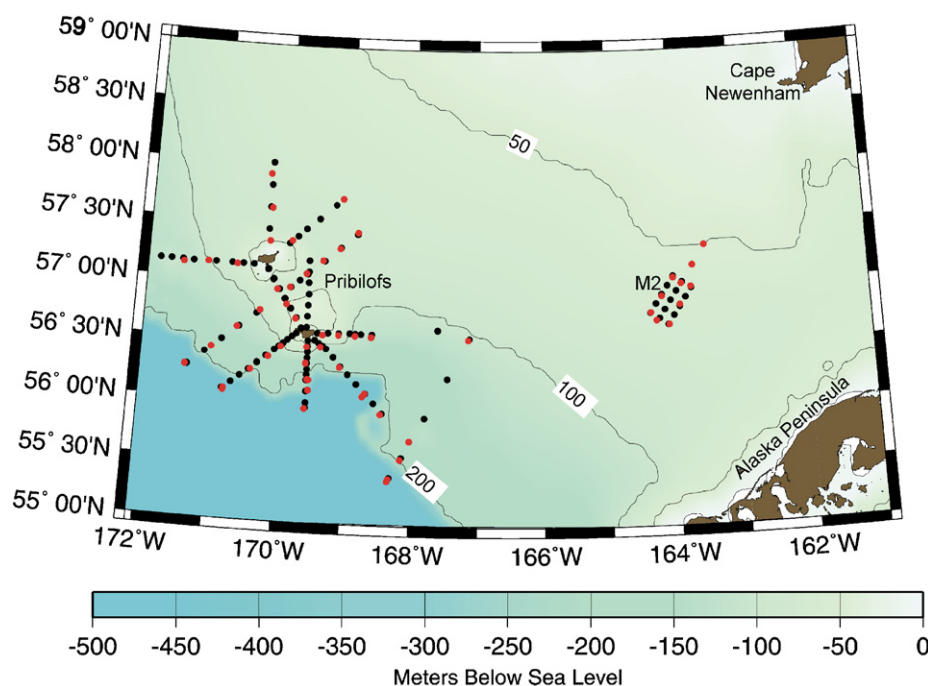


Fig. 1. Station locations for the Pribilof Project in the southeastern Bering Sea, July–August 2004. Dots indicate CalVET and CTD stations. Red dots = locations where MOCNESS tows were also taken.

biomass was estimated by multiplying the specimen count by the mean wet weight. In practice, only calanoid copepods had consistent wet weights after weighing each taxa and stage in about 10–15 samples. Therefore, wet weights on euphausiids, shrimp and other larger taxa were measured and recorded individually for each sample. Wet weight measurements were done on a Cahn Electrobalance or Mettler top loading balance, depending on the size of the animal. All animals in the samples were identified to the lowest taxonomic category possible. Copepodid stages were identified and recorded. The wet weight and counts of all pollock were taken as part of the sample processing procedures described above.

Only adult and occasionally stage V *Acartia* were identified to species. Earlier copepodids were identified as *Acartia* spp. The specimens identified to species were *A. longiremis* and *A. hudsonica*. *Pseudocalanus* were not identified to species but referred to as *Pseudocalanus* spp. Species likely to occur in Alaskan waters include *P. minutus*, *P. moultoni*, *P. newmani*, *P. acuspes* and *P. mimus*. Copepodid stages IV through VI of the *Neocalanus plumchris* – *N. flemingeri* species complex were routinely identified to species. Earlier stages were referred to as *Neocalanus plumchris*–*flemingeri*. The two species were pooled for statistical analyses.

The data were uploaded to a Microsoft Access database, and analysis was done with standard statistics software. Physical properties influencing zooplankton distribution were analyzed as follows. The depth of the thermocline at each station was computed from 1-m bin-averaged vertical temperature profiles by locating the depth where dT/dZ was maximum (T = temperature, °C; Z = depth, m). The mean water-column temperature and salinity above and below the thermocline were then computed. In addition, the stratification parameter, the energy required to redistribute the water-column mass by complete vertical mixing ($J\,m^{-3}$) was computed (Simpson et al., 1977; Fiedler et al., 1998). The zooplankton abundance was power transformed to stabilize the variance. All copepodid stages of individual taxa were pooled for canonical correlation analysis.

Canonical correlation was run on abundance data to look for relationships between the physical properties and abundance of the major zooplankton taxa.

A subsample of 10 formalin-preserved pollock from the MOCNESS tows was measured and weighed from two stations near M2 and three stations near the Pribilof Islands in 2004, and from four stations near M2 in 1999. The fish were measured to the nearest millimeter (fork length), the alimentary tract between the esophagus and pyloric caeca was removed, and the contents were identified to the lowest taxonomic level possible. The weight of each prey item was obtained from zooplankton wet weights measured as outlined above. An index of relative importance (IRI; see Brodeur and Pearcy, 1990) was calculated to compare prey items within stomachs. The IRI was computed for each prey taxon using the equation $IRI = \%F(\%N + \%W)$, where $\%F$, $\%N$ and $\%W$ are the percent frequency of occurrence, the percentage relative to the total number of prey in the stomachs, and the percentage relative to the total weight of prey in the stomachs, respectively, for each prey taxon. The IRI for each prey taxon was converted to percentage of the total IRI for graphing.

Samples taken in August 1999 near M2 were examined for differences in water-column properties and zooplankton abundance and biomass between 1999 and 2004. Sampling techniques were identical to those outlined above (see Coyle and Pinchuk, 2002a,b). Supplemental material collected by BASIS in August–September 2004 was used to provide additional information on the geographic distribution of *Calanus marshallae*, nutrients and physical properties. The BASIS zooplankton data were collected with a 60-cm bongo net equipped with General Oceanics flowmeters and 505- μm nets. Double oblique tows were done from the surface to near the bottom. Samples were preserved in 5% formalin: seawater and sorted at the Morski Instytut Rybacki Plankton and Identification Center (Szczecin, Poland) to the lowest taxonomic level and developmental stage possible. The physical data were collected with a Seabird model 25 CTD. Nutrient samples were immediately frozen after collection and analyzed within 6 months. Analyses were conducted by the

University of Washington Marine Chemistry Laboratory with a Technicon auto analyzer following standard colorimetry protocols (UNESCO, 1994).

3. Results

3.1. Cross shelf distribution in 2004

Canonical correlation revealed significant relationships among the abundance of the major species in the CalVET and MOCNESS samples and physical variables (Tables 1 and 2). The correlations were 0.92 and 0.96, the explained variance was 49% and 81%, and the probabilities were <0.0001 for the CalVET and MOCNESS samples, respectively. Negative correlations occurred between the abundance of shelf copepods and positive correlations between oceanic copepods relative to salinity and water-column stability (Tables 1 and 2). The stations were divided into two groups at 0.7 on a plot of the CalVET canonical scores (Fig. 2). A map of the stations by group revealed that stations above 0.7 occurred in the Outer Domain beyond the 100-m isobath (Group 1) and stations below 0.7 occurred in shallower locations of the middle domain (Fig. 3). The 32.4 isohaline of mean salinity below the thermocline formed a boundary separating Group 1 from the rest of the stations (Fig. 4). To examine differences between geographic locations in the middle domain, the rest of the stations were divided into two groups: those near the Pribilof Islands (Group 2) and those near M2 (Group 3) (Fig. 3). ANOVA analysis revealed significant differences between the mean abundance of the major copepod species by group (Table 3). Oceanic species (*Neocalanus plumchrus-flemingeri*, *Neocalanus cristatus*, *Metridia* spp., *Eucalanus bungii*) were absent from the M2 region, present at very low abundance around the Pribilofs, and common in the outer domain. *Calanus marshallae*, which usually occurs over the shelf, was virtually absent from the M2 and Pribilof regions, but common in the outer domain (Table 3). *Pseudocalanus* spp. were significantly more abundant near M2 than near the Pribilofs, but

the remaining taxa (*Acartia* spp., calanoid nauplii) showed no significant differences between the M2 and the Pribilof area, but were significantly less abundant in the outer domain than among the station groups in the middle domain. The MOCNESS samples were stratified into the same three groups (Fig. 5), and the copepod taxa showed similar distributions (Table 4). Oceanic taxa were virtually absent from the middle domain (Groups 2 and 3). *C. marshallae* was common in the outer domain, but present at much lower abundance in the middle domain, both near the Pribilofs and near M2. Pollock occurred mainly in the middle domain, and hydromedusae, dominated by *Catablema* spp. and *Euphysa flammea*, were more abundant near M2 than near the Pribilofs.

3.2. Climate-related interannual differences between 1999 and 2004

A number of differences were observed in the water-column properties and the shelf zooplankton community in the eastern Bering Sea in 2004 relative to 1999. These physical and biological differences are outlined below.

3.2.1. Differences in temperature, salinity and water-column stability

Significant differences were observed in physical variables between August 1999 and 2004. Mean temperature above the thermocline was higher in 2004 than in 1999 by about 5 °C, but mean temperature below the thermocline was higher in 2004 relative to 1999 by less than 2 °C (Table 5). The larger difference in both temperature and salinity above and below the thermocline in 2004 relative to 1999 resulted in much greater water-column stability in 2004 (Table 5). The mean stability parameter was about 2.5 times higher in 2004, suggesting that an additional 63 J m⁻³ would be required to mix the water column in 2004 relative to 1999. Mean salinity above and below the thermocline was significantly different between years, but the differences were marginal. The geographic extent of the warm, stable water in 2004 is characterized by a grid of CTD data from the eastern Bering Sea (Fig. 6A and B). The warm surface layer was present in the inner

Table 1
Correlation coefficients relating physical parameters and jellyfish to abundance of major shelf zooplankton taxa in CalVET samples from the southeastern Bering Sea, July–August 2004

Physical parameter	<i>Oithona similis</i>	<i>Pseudocalanus</i> spp.	<i>Acartia</i> spp.	Calanoid nauplii
Upper mixed temperature	−0.033	0.160	−0.154	−0.386
Lower mixed temperature	0.160	−0.132	0.220	0.338
Stability parameter	−0.142	−0.208	−0.572	−0.455
Upper mixed salinity	−0.102	−0.219	−0.313	−0.071
Lower mixed salinity	−0.351	−0.454	−0.657	−0.280
Jellyfish biomass	0.064	0.097	0.207	0.084
Integrated fluorescence	0.181	−0.011	−0.015	0.083

Canonical $R = 0.92$, $P < 0.0001$, explained variance = 49%.

Table 2
Correlation coefficients relating physical parameters and jellyfish to abundance of major oceanic zooplankton taxa in MOCNESS samples from the southeast Bering Sea, July–August 2004

Physical parameter	<i>Neocalanus plumchrus</i>	<i>Neocalanus cristatus</i>	<i>Metridia</i> spp.	<i>Eucalanus bungii</i>	<i>Calanus marshallae</i>
Upper mixed temperature	−0.282	−0.293	−0.216	−0.474	−0.258
Lower mixed temperature	−0.282	−0.450	−0.451	−0.287	−0.388
Stability parameter	0.513	0.448	0.457	0.334	0.303
Upper mixed salinity	0.684	0.785	0.754	0.697	0.162
Lower mixed salinity	0.861	0.903	0.887	0.849	0.419
Jellyfish biomass	−0.746	−0.707	−0.600	−0.642	−0.604
Integrated fluorescence	0.456	0.570	0.511	0.483	0.045

Canonical $R = 0.96$, $P < 0.0001$, explained variance = 81%.

domain along the entire coast. The inner front dividing the inner domain from the stratified middle domain is illustrated by the distinct discontinuity in water-column stability and bottom water temperature at about the 50-m depth contour (Figs. 1 and 6A and B). The warm surface layer stretched across the shelf to the shelf break in the eastern Bering Sea; however, a pool of stable water was present in the middle domain from Nunivak Island south to the Alaska Peninsula between the inner front and the shelf break (Fig. 6A).

3.2.2. Differences in zooplankton abundance and biomass

The observed differences in physical parameters between 1999 and 2004 were accompanied by significant differences in the zooplankton community. Comparisons were made between stations taken in the vicinity of M2 during August 1999 and August 2004 (Fig. 7). Mean abundance of the small copepods *Oithona* spp. and *Pseudocalanus* spp. was higher by over 3–5 times in 2004 relative to 1999 (Table 5). In contrast, abundance of the larger zooplankton species, *Calanus marshallae*, *Thysanoessa* spp. and *Sagitta elegans*, had declined substantially by 2004 and *C. marshallae* had virtually disappeared from the M2 region (Table 6). The mean biomass of all copepods as measured by CalVET tows at

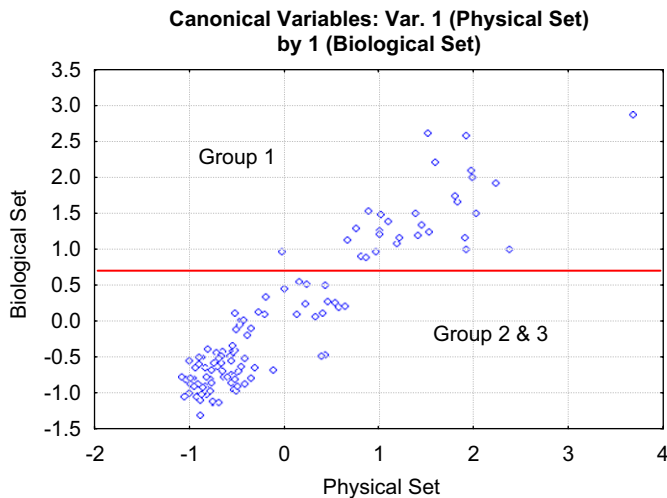


Fig. 2. Canonical scores of physical variables versus abundance of major calanoid species (Tables 1 and 2) from CalVET tows taken on the southeastern Bering Sea shelf in July–August 2004. The 0.7 line (red line) divides shelf stations from oceanic stations. Shelf stations are divided into those near the Pribilofs (Group 2) and those near Mooring 2 (Group 3).

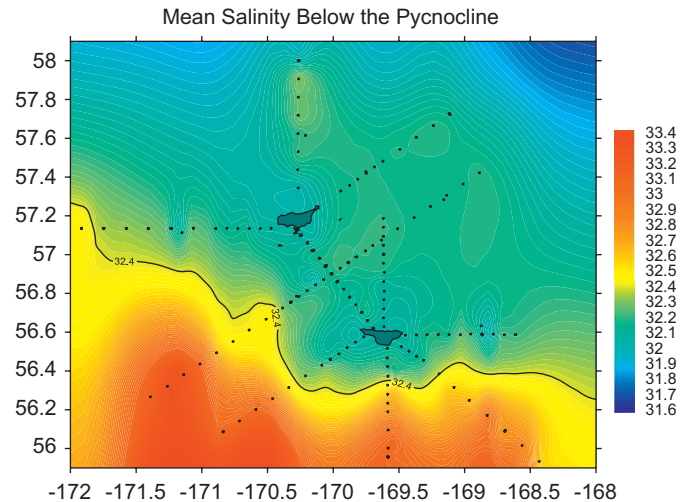


Fig. 4. Mean salinity below the thermocline, showing the 32.4 isohaline dividing the shelf and oceanic zooplankton communities near the Pribilof Islands, July–August 2004. Dots indicate CTD station locations.

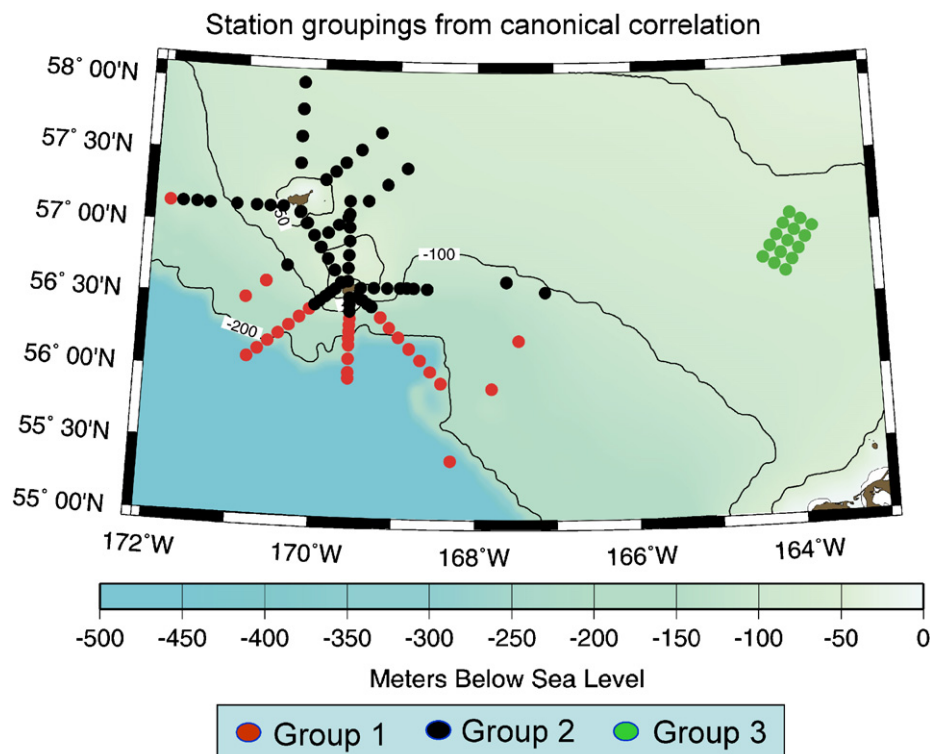
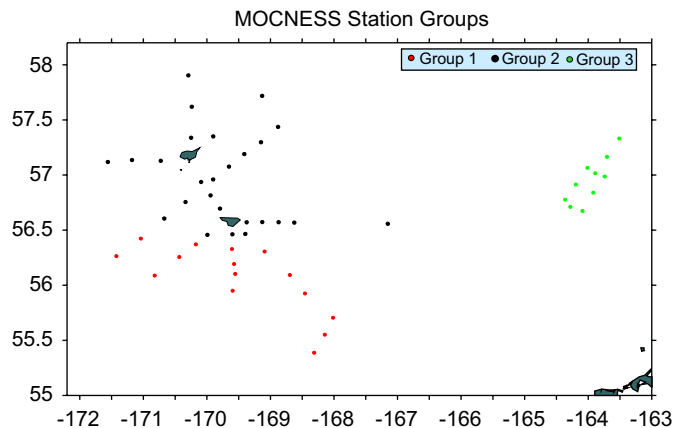


Fig. 3. Distribution of CalVET station groups separated by canonical correlation comparing physical oceanographic variables with abundance of the major zooplankton taxa on the southeastern Bering Sea shelf, July–August 2004.

Table 3Mean abundance (No. m⁻³) of major zooplankton taxa from CalVET tows in the southeastern Bering Sea (July–August 2004) by group (Fig. 3)

Species	Group 1	Group 2	Group 3	P value	Bonferroni
<i>Oithona similis</i>	649	2049	1633	0	2 = 3 > 1
<i>Pseudocalanus</i> spp.	98	325	1211	0	All different
<i>N. plumchrus</i> and <i>N. flemingeri</i>	2.7	2.4E–07	0	0	2 = 3 < 1
<i>Neocalanus cristatus</i>	0.28	9.26E–12	0	0	2 = 3 < 1
<i>Metridia</i> spp.	9.2	2.0E–03	0	0	2 = 3 < 1
<i>Eucalanus bungii</i>	23	0.04	2.26E–09	0	All different
<i>Calanus marshallae</i>	3.0	0.015	8.13E–04	0	2 = 3 < 1
<i>Acartia</i> spp.	8.1	375	507	0	2 = 3 > 1
Calanoid nauplii	1.12	128	2.7	0	1 = 3 < 2

**Fig. 5.** Distribution of MOCNESS station groups from the southeastern Bering Sea, July–August 2004.

M2 was 149 mg m⁻³ in 1999 but only 51 mg m⁻³ ($P = 0.0003$) in 2004. The mean biomass of *Pseudocalanus* spp. increased from 16 to 41 mg m⁻³ ($P = 0.0006$), *O. similis* biomass increased from 2 to 10 mg m⁻³ ($P = 7E-5$), while the biomass of *C. marshallae* declined from 60 to 6.7×10^{-4} mg m⁻³ ($P = 4E-6$), indicating a major shift in production from the large to small copepod assemblage. In 1999, *C. marshallae* was the dominant mesozooplankton particle-grazer in the middle domain on the stratified side of the inner front beyond 150 km (Fig. 8), where patches with abundances as high as 3000 m⁻³ were observed. Mean abundance of hydromedusae was significantly higher in 2004 relative to 1999 (Table 6). Biomass changes followed the abundance changes (Table 7). *C. marshallae* biomass had declined by almost 99%, while the biomass of *S. elegans* and *Thysanoessa* spp. had declined by 98% and 93%, respectively. *Chrysaora melanaster*, a large scyphozoan, had a mean biomass of over 3 g m⁻³ in 1999, but its biomass had declined by about 97%, to under 0.07 g m⁻³ in 2004. In contrast, mean biomass of the smaller hydromedusae had been below 10⁻⁸ g m⁻³ in 1999, but was over 0.05 g m⁻³ in 2004 (Table 7).

3.2.3. Differences in pollock size and diet

Mean abundance of age-0 pollock near M2 was lower in 2004 relative to 1999 by about 80%; however, the biomass was over 2.5 times greater in 2004. The higher biomass in 2004 was due to the overall greater size of pollock from the M2 region in 2004 relative to the same period in 1999 (Figs. 9 and 10). The M2 fish in 2004 were 50–60 mm standard length (SL), while the 1999 fish were 25–35 mm long. The size of pollock from the Pribilof region in 2004 was not significantly different from those near M2 in 1999 ($P = 0.09$). Although pollock were larger in 2004 than in 1999, they were eating small copepods in 2004 (primarily *Pseudocalanus* spp. with a mean individual wet weight of about 0.1 mg; Figs. 9

and 11). In contrast, pollock diets near M2 in 1999 contained substantial amounts of larger prey items (*C. marshallae* copepodid stage V weighing about 1.5 mg wet weight and pagurid crab zoea weighing 3.6 mg). Pollock near the Pribilof Islands in 2004 were eating primarily the smaller copepods, but juvenile euphausiids (about 6 mg wet weight) and very small juvenile *Limacina helicina* (0.003 mg wet weight) were also ingested.

3.3. Spatial distribution of *Calanus marshallae*, nitrogenous nutrients and salinity

The information outlined above clearly demonstrates a significant shift between 1999 and 2004 in the abundance and biomass of major zooplankton taxa near M2 in the middle domain of the southeastern Bering Sea. These detailed comparisons are restricted to a fairly narrow region on the shelf; however, a broader geographic coverage of information on the abundance of *Calanus marshallae*, temperature, salinity and concentrations of nitrogen nutrients in 2004 was provided by the BASIS program (Figs. 12–15).

In August–September 2004, *Calanus marshallae* occurred predominantly in the southwest corner of the sampling grid to the north of Unimak Island (Fig. 12). High concentrations also were observed on the northwest corner of the grid near St. Lawrence Island and in the coastal zone on the southeast corner of the grid. *C. marshallae* occurred at very low densities or was absent from the remaining locations on the shelf. Elevated *C. marshallae* populations off Unimak and St. Lawrence Islands were associated with elevated concentration of nitrate above and below the thermocline (Fig. 13). Elevated nitrate concentrations above the thermocline were confined to the southwestern region off Unimak Island. Most of the shelf north of the Pribilof Islands had little or no nitrate either above or below the thermocline. Elevated ammonium concentrations were observed below the thermocline on the shelf around St. Matthew Island, south to the Pribilof Islands, across the middle of the grid between 57° and 59°N and in a small area on the north side of the Alaska Peninsula (163°W) (Fig. 14). Little or no ammonium was observed above the thermocline.

Mean salinity above and below the thermocline was lower on the northern shelf between St. Matthew and St. Lawrence Islands than on the southeastern shelf (Fig. 15). Salinity distributions indicate a penetration of low-salinity inner domain water westward across the northern shelf in 2004. Westward penetration of inner domain water was not observed on the southeastern shelf.

4. Discussion

The observed differences in zooplankton community composition at M2 between 1999 and 2004 appear to be much larger than

Table 4Mean abundance (No. m⁻³) of major zooplankton taxa from MOCNESS tows in the southeastern Bering Sea (July–August 2004) by group (Fig. 4)

Taxa	Group 1	Group 2	Group 3	P value	Bonferroni
<i>N. plumchrus</i> and <i>N. flemingeri</i>	4.66	7.94E–04	0	0	All different
<i>Neocalanus cristatus</i>	2.26	4.43E–05	0	0	2 = 3 < 1
<i>Metridia</i> spp.	37.78	3.29E–03	1.08E–06	0	2 = 3 < 1
<i>Eucalanus bungii</i>	17.66	0.449	3.84E–06	0	All different
<i>Calanus marshallae</i>	3.27	0.69	0.11	0.00017	2 = 3 < 1
<i>Thysanoessa</i> spp.	3.70	1.49	0.05	0	1 = 2 > 3
Hydromedusae	6.82E–07	6.22E–02	0.11	0	2 = 3 > 1
<i>Theragra chalcogramma</i>	2.07E–05	3.52E–02	1.67E–02	0	2 = 3 > 1

Table 5Mean physical properties and abundance (No. m⁻³) of major copepod taxa in CalVET tows from the M2 region of the southeastern Bering Sea in 1999 and 2004

Data type	1999	2004	P value
UpperMixedTemp	7.0	12.6	0
LowerMixedTemp	2.0	3.2	0
Stability parameter (J m ⁻³)	34.9	98.4	0
UpperMixedSal	31.6	31.8	0
LowerMixedSal	31.7	32.0	0
<i>Oithona similis</i>	348	1633	0
<i>Pseudocalanus</i> spp.	404	1211	0
Calanoid nauplii	161	2.69	0.015
<i>Acartia</i> spp.	277	507	0.264
<i>Calanus marshallae</i>	44	8.13E–04	0
<i>Centropages abdominalis</i>	0	2.69E–03	0.177

UpperMixedTemp = mean temperature above the thermocline (°C), LowerMixedTemp = mean temperature below the thermocline (°C), UpperMixedSal = mean salinity above the thermocline, LowerMixedSal = mean salinity below the thermocline.

the interannual variability observed within past research programs such as PROBES (Processes and Resources of the Bering Sea Shelf; Smith and Vidal, 1986), SEBSCC (Southeast Bering Sea Carrying Capacity; Napp et al., 2002) or Inner Front (Coyle and Pinchuk, 2002a). These differences between the 2 years may have a number of causes: changes in circulation altering the cross-shelf distribution of zooplankton communities, changes in phytoplankton production or water temperature. In the following discussion, we examine the potential causes for the observed changes, and review the literature on the abundance, biomass and distribution of the affected species to place our observations within the context of zooplankton measurements made on the southeastern Bering Sea shelf during the last half of the 20th century. In addition, the distribution of nutrients, water-column properties and *C. marshallae* on the eastern Bering Sea shelf south of St. Lawrence Island is discussed to place the observations at M2 into a broader geographic context.

4.1. Cross-shelf distribution

Regional separation of zooplankton communities on the southeastern Bering Sea shelf has been recognized for about 50 years. Based on cross-shelf transects in TINRO plankton surveys from 1958 to 1965, Meshcheryakova (1964, 1970a,b) identified the oceanic and shelf zooplankton communities divided by a front where bottom water salinities were about 32‰. She further noted that during colder years, the front dividing the communities was confined to the shelf-break region by cold, winter-remnant bottom water (cold pool) on the middle shelf, but penetrated much further inshore during warmer years when the cold pool was absent or less developed (see Coyle et al. (1996) for English

summary). These Soviet observations were further refined by detailed studies in the late 1970s and early 1980s (Cooney and Coyle, 1982; Smith and Vidal, 1986; Vidal and Smith, 1986), when the boundary salinity was set at about 32.5 and an additional front between the middle shelf and coastal waters was described. During a warm, stormy spring of 1998, in the absence of cold bottom water, oceanic zooplankton were observed as close to shore as the 50 m depth contour, where they dominated zooplankton biomass in June 1998, but had almost completely disappeared from the region by August (Coyle and Pinchuk, 2002a). During July–August 2004, oceanic zooplankton were not observed around the Pribilof Islands or on the shelf near M2, but were confined to the shelf break where bottom salinities exceeded 32.4. Therefore there was no evidence to support the hypothesis that observed changes in zooplankton communities in 2004 were due to changes in cross-shelf circulation.

4.2. Zooplankton community differences (1999 and 2004)

While the 32.4 isohaline boundary separating oceanic and shelf zooplankton communities is expected, the marked changes in the shelf zooplankton community between 1999 and 2004 seemed unusual. These changes included large reductions in the abundance of euphausiids, chaetognaths, scyphozoans and *Calanus marshallae* from the shelf regions accompanied by increases in populations of *Oithona similis* and *Pseudocalanus* spp. along with increases in the biomass of hydromedusae (Tables 5–7). The changes in zooplankton abundance and biomass will be discussed by taxon in the following subsections, to place the observations in a temporal context.

4.2.1. *Calanus marshallae*

Calanus marshallae has been a dominant zooplankton grazer on the southeastern Bering Sea shelf since at least the mid 20th century. It dominated the zooplankton in August 1961–1965, where it averaged up to 79% of the copepod populations (Meshcheryakova, 1970b) and reached maximum populations of 169 ind.m⁻³. Mean abundances of *C. marshallae* in the middle domain in April–June 1980–1981 ranged from 9 to 76 ind.m⁻³ (Smith and Vidal, 1986; Stockwell et al., 2001). The mean abundance in CalVET tows was about 44 ind.m⁻³ for August 1999 (Table 5), not particularly high by earlier standards. Mean abundance of *C. marshallae* in MOCNESS tows for all locations sampled in the middle domain near the Inner Front in 1999 (Coyle and Pinchuk, 2002a) was 21 and 38 ind.m⁻³ for June and August, respectively. The mean abundance in MOCNESS tows near M2 in August 1999 was 300 ind.m⁻³ with a maximum of 3000 ind.m⁻³. Additional measurements of *C. marshallae* populations in the middle domain ranged from about 2 to 1200 ind.m⁻³ between 1995 and 1999, depending on the month sampled (Baier and

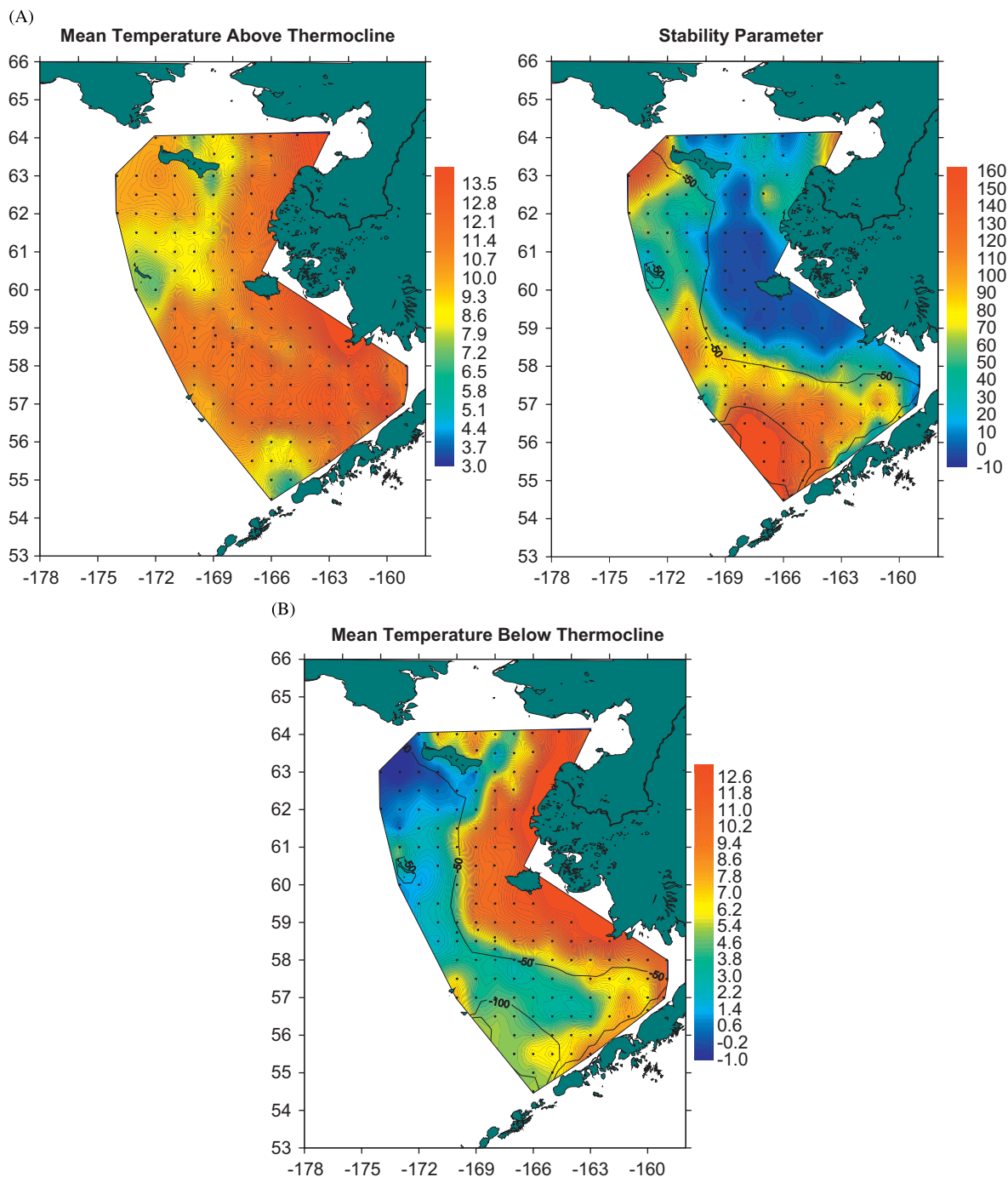


Fig. 6. (A) Mean temperature above the pycnocline ($^{\circ}\text{C}$) and water-column stability (J m^{-3}) in the eastern Bering Sea in August–September 2004. Black dots indicate station locations; lines indicate 50, 100 and 200 m isobaths (BASIS data). (B) Mean temperature below the pycnocline ($^{\circ}\text{C}$) in the eastern Bering Sea in August–September 2004. Black dots indicate station locations; lines indicate 50, 100 and 200 m isobaths (BASIS data).

Napp, 2003), with mean abundance of $120\text{--}150 \text{ ind. m}^{-3}$ in 1998 and 1999. These data indicate that *C. marshallae* occasionally attained very high biomass in the middle domain between 1995 and 1999.

The presence of dense patches of *Calanus marshallae* on the southeastern Bering Sea shelf during the last half of the 1990s is consistent with the presence of foraging baleen whales in the region (Tynan et al., 2001; Moore et al., 2002; Tynan, 2004). Bioenergetic models suggest that right whales require copepod prey densities of at least $4.7 \times 10^3\text{--}1.5 \times 10^6 \text{ ind. m}^{-3}$ in very thin

layers to meet daily energy requirements (Kenney et al., 1986; Baumgartner and Mate, 2003). Thus, our maximum density estimate of 3000 ind. m^{-3} near M2 in August 1999 is not unreasonable, given the presence of right whales in the area. The presence of right whales in the M2 region during 1999 (and their absence during the 2004 cruise; G. Hunt, pers. comm.) is therefore additional evidence of the magnitude of *C. marshallae* densities in the region. The normal cross-shelf distribution of *C. marshallae* was reversed in 2004, with maximum densities occurring in oceanic waters and very low densities in shelf waters,

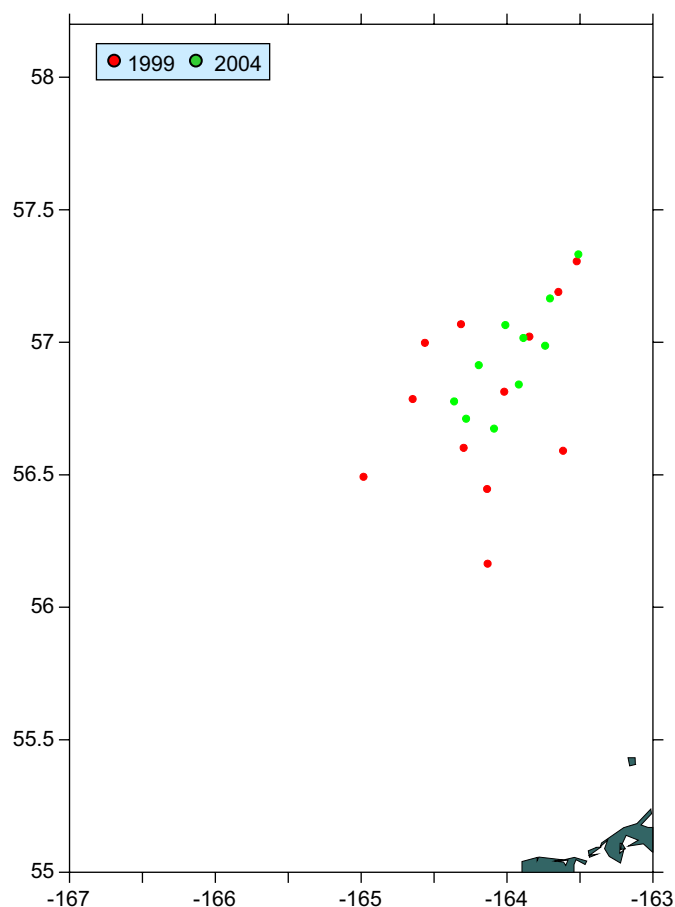


Fig. 7. Locations of MOCNESS tows taken in August 1999 and 2004 on the southeastern Bering Sea shelf near M2.

Table 6

ANOVA comparing mean abundance (No. m^{-3}) of major taxa from MOCNESS tows in the M2 region of the southeastern Bering Sea in 1999 and 2004

Taxa	1999	2004	P value
<i>Calanus marshallae</i>	300	0.114	0
<i>Thysanoessa</i> spp.	0.33	0.051	0.031
Hydromedusae	3.86E-07	0.11	0
<i>Sagitta elegans</i>	14.3	1.13	0
<i>Theragra chalcogramma</i>	0.091	0.017	0.0018

both near the Pribilof Islands and in the middle domain near M2. Mean abundance of *C. marshallae* was 1 ind. m^{-3} in 2004, unusually low by historical standards. The above observations therefore indicate a major shift in the abundance and biomass of *C. marshallae* between 1999 and 2004.

Although a fairly long history of zooplankton sampling has clearly documented the presence of *Calanus marshallae* in the middle domain of the southeastern Bering Sea shelf during summer and fall (Meshcheryakova, 1964, 1970a,b; Cooney and Coyle, 1982; Smith and Vidal, 1986; Vidal and Smith, 1986; Coyle and Pinchuk, 2002a), less is known about its concentration on the shelf north of the Pribilof Islands. *C. marshallae* was present in substantial numbers near St. Matthew Island in September 1960 (Meshcheryakova, 1970b). In addition, auklets foraging off St. Matthew Island in the 1980s were taking *C. marshallae*, and a mean abundance for *C. marshallae* of $50.9 \text{ animals m}^{-3} \pm 12$ (standard error) was reported from vertical tows in August,

1985 (Obst et al., 1995). The available data therefore indicate that high populations of *C. marshallae* occurred on the northern shelf during late summer in the 1980s and during summer in the 1960s.

4.2.2. Small copepods

Abundance of *Pseudocalanus* spp. in 1961–1965 ranged from 78 to 964 ind. m^{-3} , with numbers increasing from May through September–October (Meshcheryakova, 1970b). Highest *Pseudocalanus* spp. abundance in 1980–1981 (5032 ind. m^{-3}) occurred in October 1981 (Smith and Vidal, 1986), consistent with the trend toward higher abundances in fall. The higher abundances in the early 1980s relative to the early 1960s may be due to differences in gear type rather than a secular trend in *Pseudocalanus* spp. abundance, as the Russian collections were done with a 36-cm diameter Juday net with 168- μm mesh rather than a 1- m^2 MOCNESS with 149- μm mesh. Mean *Pseudocalanus* abundance during spring was significantly greater in 1994–1998 relative to 1980–1981 (Stockwell et al., 2001; Napp et al., 2002). Note, however, that mean abundances in 1994–1998 were well within the range of values reported for 1980–1981 at some stations during October (5032 ind. m^{-3} in October 1981 compared to a mean of about 2500 ind. m^{-3} in 1996). Nevertheless, the greater mean *Pseudocalanus* spp. and *Oithona similis* abundances in 2004 relative to 1999 (Table 5) were highly significant and cannot be attributed to differences in gear type or sampling season since both were identical between the two periods. *Pseudocalanus* spp. are predominantly shelf species in Alaskan waters; they tend to be positively correlated to temperature and attain highest populations in summer (Coyle and Pinchuk, 2002a, 2003, 2005; Coyle, 2005; Napp et al., 2005). *Pseudocalanus* spp. were much more abundant near the Pribilof Islands during a warm year (1998) than during a cold year (1999) (Schabetsberger et al., 2003). *Oithona similis* tends to be more wide spread, occurring in both oceanic and shelf habitats, but also tends to be positively correlated to temperature and most abundant in summer (Coyle and Pinchuk, 2002a, 2005; Coyle, 2005). The higher abundances of *Pseudocalanus* spp. and *O. similis* in 2004 relative to earlier measurements therefore are consistent with the warmer surface waters observed on the southeastern Bering Sea shelf in August 2004 (Table 5).

4.2.3. Hydromedusae

The prolate (bell-shaped) anthomedusae *Catablema* spp. and *Euphysa flammea* were the most common hydrozoan species at M2 in 2004, but were virtually absent from the area in 1999. Anthomedusae are characterized by a prolate (bell-shaped) body facilitating motion, and they therefore are thought to be ambush-foraging predators, often preying on planktonic crustaceans including small copepods (Costello and Colin, 2002; Colin et al., 2003). Because growth of hydrozoans depends on temperature and food availability (e.g., Matsakis, 1993), the high abundance of small copepods and warm temperature observed at M2 in 2004 appear to be ideally suited for successful development of these jellyfish. Scyphozoans are potential predators of hydromedusae (Costello and Colin, 1994; Sullivan et al., 1994). Therefore, the low numbers of scyphozoans observed in 2004 might have contributed to the success of hydromedusae by relieving predation pressure. The observed trends in the population of hydromedusae are consistent with warming on the southeastern Bering Sea shelf.

4.2.4. Euphausiids

Euphausiids of the genus *Thysanoessa* are common constituents of the zooplankton on the southeastern Bering Sea shelf (Cooney, 1981; Vidal and Smith, 1986; Smith, 1991) and important

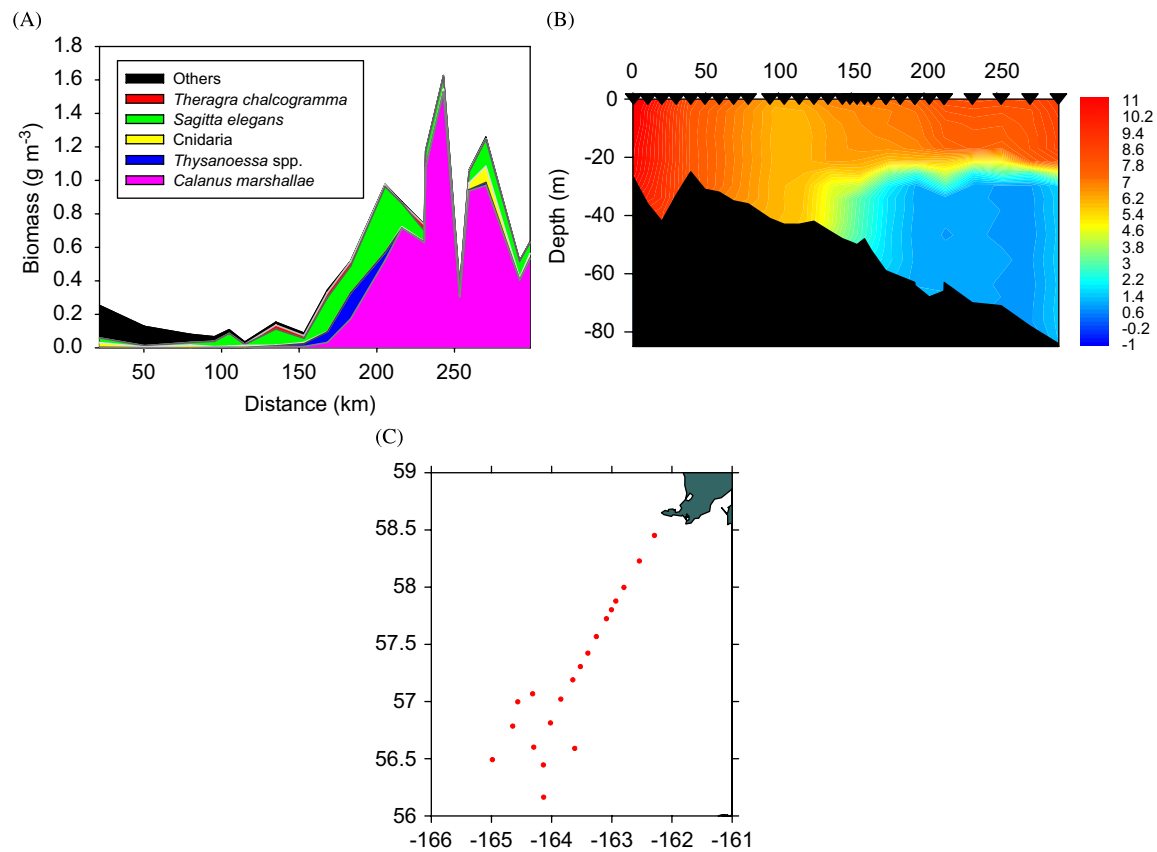


Fig. 8. Biomass of major zooplankton taxa in MOCNESS tows and temperature profile along the Cape Newenham transect on the southeastern Bering Sea shelf in August 1999. Distance is from just north of the northern most station. “Others” indicates all other taxa except *Chysaora melanaster*: (A) zooplankton biomass, (B) temperature (°C), (C) station locations.

Table 7
ANOVA comparing mean biomass (g m⁻³) of major taxa from MOCNESS tows in the M2 region of the southeastern Bering Sea in 1999 and 2004

Taxa	1999	2004	<i>P</i> value
<i>Calanus marshallae</i>	0.51	9.63E-05	0
<i>Thysanoessa</i> spp.	6.30E-03	4.67E-04	0.007
<i>Sagitta elegans</i>	0.11	2.20E-03	0
Hydromedusae	3.08E-09	5.43E-02	0
<i>Theragra chalcogramma</i>	5.29E-03	1.44E-02	0.090
<i>Chrysaora</i> spp.	3.08	6.95E-02	0.001

components in the diets of a number of fish, birds and mammals (Ogi et al., 1980; Schabetsberger et al., 2003; Tynan, 2004). The mass mortality of short-tailed shearwaters on the inner shelf of the southeastern Bering Sea in 1997 was attributed to their inability to locate euphausiid prey (Baduini et al., 2001; Lovvorn et al., 2001), apparently due to reduced water clarity caused by a coccolithophorid bloom (Sukhanova and Flint, 1998; Stockwell et al., 2001). Acoustic measurements and net data indicated that euphausiid densities in the middle and inner domains had not changed substantially between 1980–1981 and 1997–1998 (Stockwell et al., 2001; Coyle and Pinchuk, 2002b). The very low euphausiid concentrations observed near M2 during 2004 may indicate a shift in the distribution and abundance of euphausiids on the southeastern Bering Sea shelf. A shift to low euphausiid abundance on the shelf may impact fish, birds and mammals that forage on these species in the middle domain.

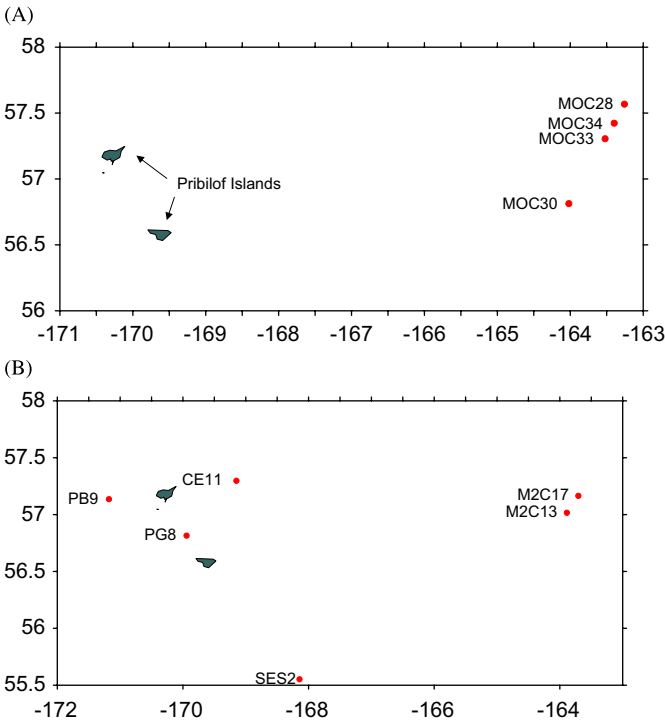


Fig. 9. Location of fish sampling stations on the southeastern Bering Sea shelf in July–August. (A) 1999; (B) 2004.

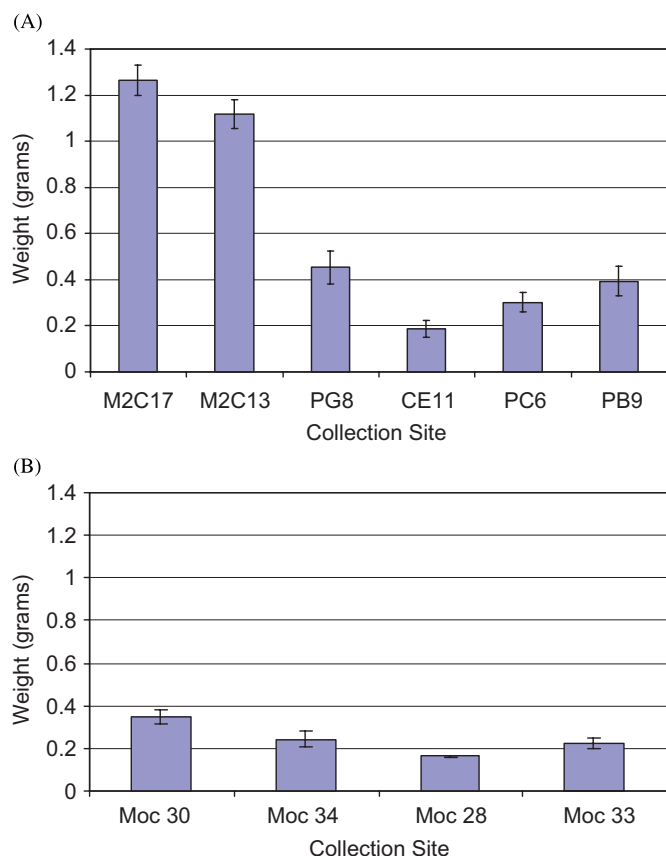


Fig. 10. Pollock wet weight at selected stations near the Pribilof Islands (PG8, CE11, PC6, PB9) and near M2 (M2C17, M2C13) in August 2004 (A); near M2 in August 1999 (B).

4.3. Shifts in zooplanktivorous predators relative to prey

Age-0 pollock and the scyphozoan *Chrysaora melanaster* are major planktivores of the southeastern Bering Sea shelf (Brodeur et al., 1999, 2002; Ciannelli et al., 2004; Winter et al., 2005). Therefore, shifts in the size, diet or biomass of these species may indicate a substantial shift in energy flow through the ecosystem. In this section we outline our observations relative to literature information on scyphozoans and pollock diets.

4.3.1. Shift in pollock size and diet

The shift in size and diet of age-0 pollock on the Bering Sea shelf in 2004 relative to 1999 may have a variety of causes and implications. Comparison of the relative size of pollock in the catches at M2 in 1999 and 2004 indicate that fish taken in 2004 were significantly larger than individuals collected in 1999, and the fish from 1999 near M2 were similar in size to those near the Pribilofs taken during 2004 (Figs. 9 and 10). Fish near M2 in August 2004 may have been from an earlier hatching than fish at M2 in 1999, or their growth rates may have been accelerated by warmer temperatures. Despite the smaller size of pollock at M2 in 1999, substantially more large prey were contributing to their diet relative to that of the larger fish in 2004 (Fig. 11). This difference is clearly related to prey availability, since the dietary data from both 1999 near M2 and from the Pribilofs in 2004, as well as literature sources (Schabetsberger et al., 2003; Ciannelli et al., 2004), indicate that pollock between 30 and 60 mm SL are capable of selecting larger prey. Euphausiids become an increasingly important prey as the pollock exceed 50 mm SL (Schabetsberger

et al., 2000; Ciannelli et al., 2004). Therefore, the lack of large prey in the middle shelf in 2004 may have resulted in food limitation for the age-0 pollock as their size increased beyond that at which they can acquire their nutritional needs from a small copepod diet alone. There is at least some evidence that the condition of age-0 pollock in late fall may determine their winter survival and the overall year-class strength when they recruit to the fishery (Sogard and Olla, 2000). The observed shifts in size and diet of the age-0 pollock therefore have the potential to impact the fishery as well as energy flow to other apex predators in the ecosystem.

4.3.2. Shift in scyphozoan biomass relative to potential prey (1999 and 2004)

Scyphozoans are an important component of the zooplankton biomass on the Bering Sea shelf (Brodeur et al., 1999, 2002), and a major shift in scyphozoan biomass is indicative of a substantial change in energy flow through the pelagic ecosystem. The biomass of the dominant scyphozoan, *Chrysaora melanaster*, increased dramatically on the southeastern Bering Sea shelf during the 1990s (Brodeur et al., 1999, 2002). The cause of the increase is uncertain, but two hypotheses have been suggested: (1) a regime shift in 1989 that altered production on the shelf (Brodeur et al., 1999); (2) a release from competitive control by declines in populations of fin-fish competitors (Brodeur et al., 2002). The second hypothesis cannot be addressed without detailed information on forage fish densities on the Bering Sea shelf during the 1980s and 1990s. The first hypothesis is consistent with the observed trends in scyphozoan and zooplankton biomass.

Comparison of the biomass of scyphozoans and their potential zooplankton prey revealed a consistent trend in scyphozoan biomass relative to prey biomass. The significantly lower biomass of *C. melanaster* in 2004 relative to 1999 was accompanied by substantially lower biomass of potential prey for *C. melanaster* at the M2 site (Table 7). To compare our scyphozoan biomass estimates with those of Brodeur et al. (2002), the *C. melanaster* wet weight biomass was converted to carbon, assuming that dry weight is 3.3% wet weight (Shenker, 1985) and carbon biomass (g m^{-2}) is 7.22% of dry weight (Larson, 1986). The remaining zooplankton biomass, excluding scyphozoans, was converted to carbon according to Wiebe (1988). The mean zooplankton biomass in the M2 region declined from 7.2 g C m^{-2} in 1999 to 1 g C m^{-2} in 2004. During the same period, the scyphozoan biomass declined from 0.5 to 0.08 g C m^{-2} . During both periods, the scyphozoan carbon biomass was 7–8% of the zooplankton carbon biomass. The mean zooplankton and scyphozoan biomass for August 1999 at all middle domain stations with depth greater than 50 m was 5.4 and 0.48 g C m^{-2} , respectively; values for June 1999 were 0.62 and 0.11 g C m^{-2} . These values compare with 2.8 and 0.3 g m^{-2} for zooplankton and scyphozoan biomass respectively, reported by Brodeur et al. (2002) for the middle domain. The above numbers suggest that the high scyphozoan biomass in 1999 was sustained by unusually high zooplankton biomass that accumulated sometime between June and August of that year. *Calanus marshallae* was the dominant component of zooplankton biomass observed in the M2 region and therefore the species most likely responsible for the observed changes in scyphozoan biomass.

4.4. Factors influencing the biomass of *Calanus marshallae*

Two factors may be responsible for the observed changes in the summer biomass of *Calanus marshallae*: (1) recruitment of copepodids from reproduction of the previous year's cohort

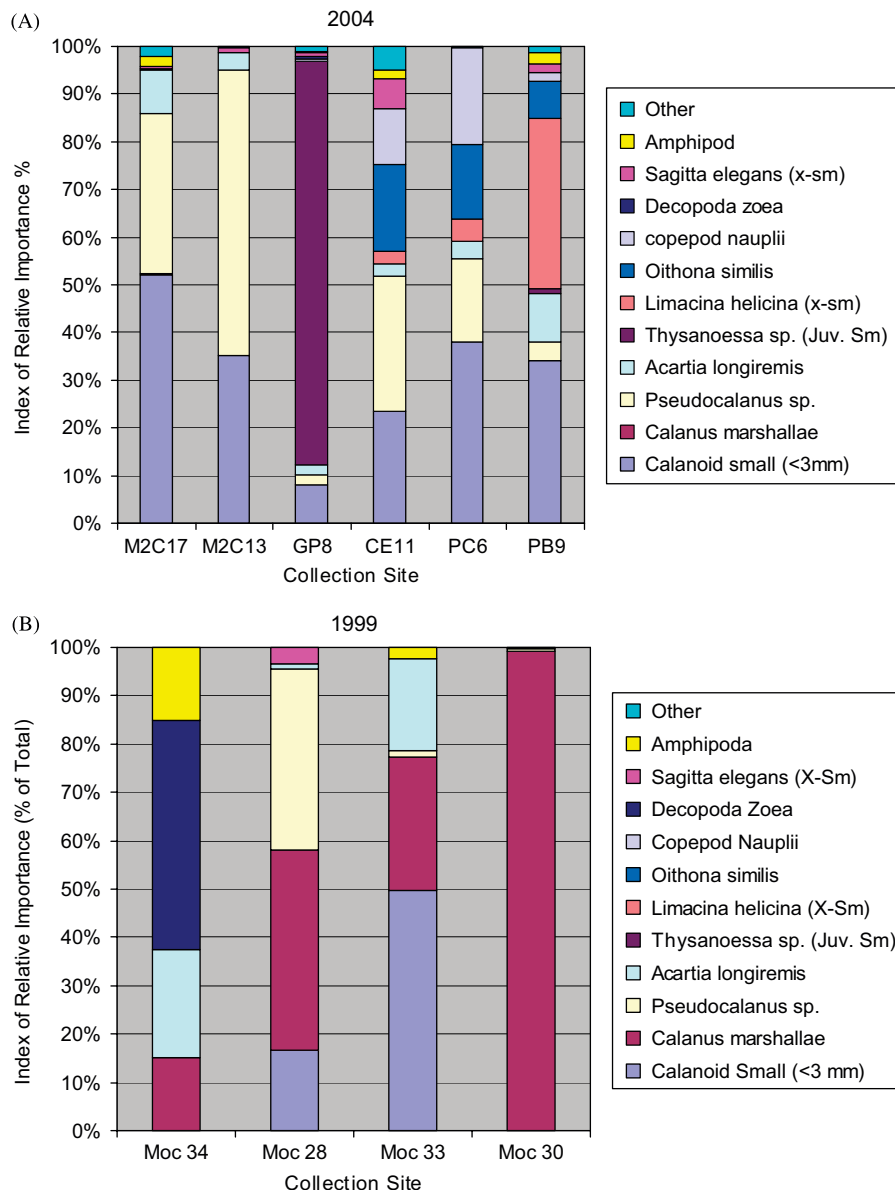


Fig. 11. Major prey items of pollock expressed as index of relative importance (Brodeur and Pearcy, 1990) from (A) the M2 region in 2004 (M2C17, M2C13), from near the Pribilof Islands in 2004 (GP8, CE11, PC6, PB9) and (B) from near M2 during 1999.

during early spring; (2) summertime growth and survival of the cohort produced during spring. Life-history studies indicate that recruitment of *C. marshallae* copepodids occurs in May, with highest recruitment during years when ice extends further southward (Baier and Napp, 2003). High abundance of *C. marshallae* at M2 in 1999 is therefore consistent with the observed ice conditions. Between June and August 1999, *Calanus marshallae* populations in the middle domain grew from predominantly copepodid stages I–III to stages IV–VI, with a biomass accumulation of about 2.7 g C m^{-2} in the 1–1.5 months between early June and August (Table 8). High amounts of primary production must have occurred in June, July and early August to support this growth. High production also implies the presence of a substantial nutrient reservoir in the middle domain to fuel the production.

Nutrients fueling production in the middle domain undergo a strong seasonal cycle. Most of the nutrients driving production are transported to the middle domain of the southeastern Bering Sea from the shelf break by cross-shelf advection during winter (Stabeno et al., 2002). Nitrate and ammonium are depleted from

the euphotic zone in late May to early June and post-bloom production is fueled by summer storms, which disrupt the thermocline and mix nutrients into the euphotic zone (Whitledge et al., 1986; Rho et al., 2005). In the early 1980s, post-bloom wind events every 5–7 days generated approximately 37% of the total annual production (Sambrotto et al., 1986). The presence of high amounts of post-bloom production in 1999 is indicated by the accumulation of organic matter in sediment traps at the M2 site during summer (Smith et al., 2002). Apparently, high zooplankton biomass in the middle domain during the late 1990s must have been sustained by substantial amounts of post-bloom production resulting from injection of nitrogenous nutrients into the euphotic zone by storms.

4.5. The optimum stability hypothesis

The amount of post-bloom production available for zooplankton in the middle domain depends on the presences of nutrients

below the pycnocline, the water-column stability, the intensity and frequency of wind events, and water-column temperature, which not only influences stability, but also the metabolic rates and energy requirements of the zooplankton. If stability is too low, phytoplankton are easily mixed below the compensation depth and are unable to grow. If stability is too high, the nutrient reservoir on the shelf is trapped below the thermocline away from

the euphotic zone, thus limiting production. If water temperatures are warm, the metabolic requirements of the zooplankton may exceed the available energy from primary production, resulting in overall lower zooplankton biomass. As long as a nutrient reservoir is present below the pycnocline on the shelf, zooplankton production during summer will be elevated by disruption of the pycnocline resulting in elevated phytoplankton production from mixing of nutrients into the euphotic zone.

These observations suggest that in the presence of a nutrient reservoir below the thermocline, an optimum stability window exists for summer production and zooplankton growth on the Bering Sea shelf, similar to that proposed for the Gulf of Alaska (Gargett, 1997). Based on the high zooplankton biomass, high scyphozoan biomass and the presence of foraging cetaceans in the middle domain of the southeastern Bering Sea shelf in the late 1990s (Tynan, 2004), and on the stability measurements for the middle domain (Table 5), we propose that the optimal stability for zooplankton production during summer is on the order of $30\text{--}40\text{Jm}^{-3}$. We further posit that as stability increases, post-bloom production on the middle shelf declines. With mean stabilities somewhere between the optimum of $30\text{--}40\text{Jm}^{-3}$ in 1999 and the mean of 90Jm^{-3} in 2004, post-bloom production becomes too low to support large grazers on the shelf and the trophic structure of the shelf reorganizes. Euphausiids and large copepods become confined to the shelf break region, and mesozooplankton grazers in the middle domain become dominated by small copepods. Large predators such as scyphozoans and cetaceans are replaced by small gelatinous zooplankton, and age-0 pollock diets narrow to small copepods. Apparently, the region of elevated stability in August 2004 was spread across the middle domain of the southeastern Bering Sea shelf north to about 58°N latitude (Fig. 6).

Application of the optimum stability hypothesis is limited to regions where a nutrient reservoir is present below the pycnocline. Although stability was substantially lower on the northern Bering Sea shelf between 60°N and St. Lawrence Island relative to the southeastern shelf in fall of 2004 (Fig. 6), nitrate and ammonium concentrations were also low throughout the water column on the northern shelf (Figs. 13 and 14), suggesting that

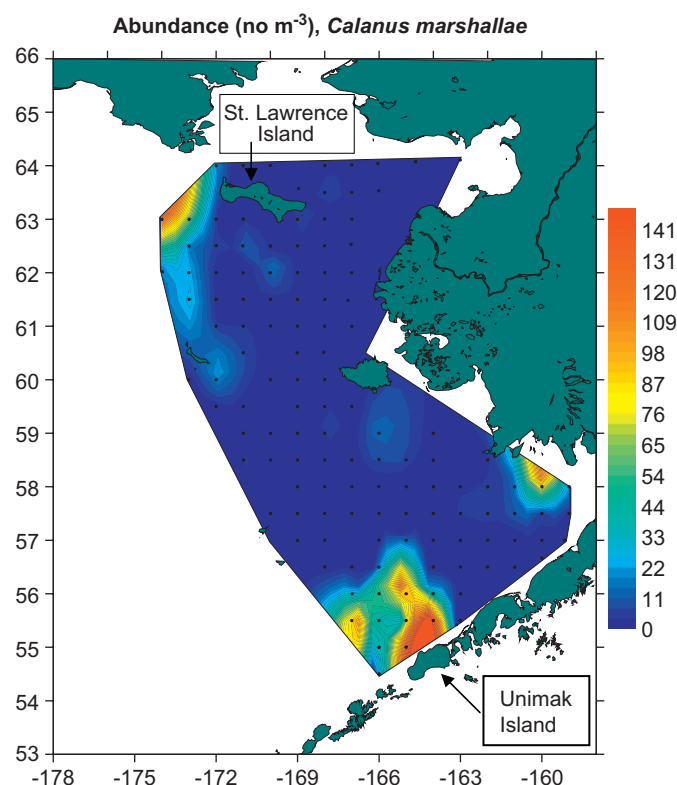


Fig. 12. Abundance of *Calanus marshallae* on the eastern Bering Sea shelf in September, 2004. Black dots indicate station locations (BASIS data).

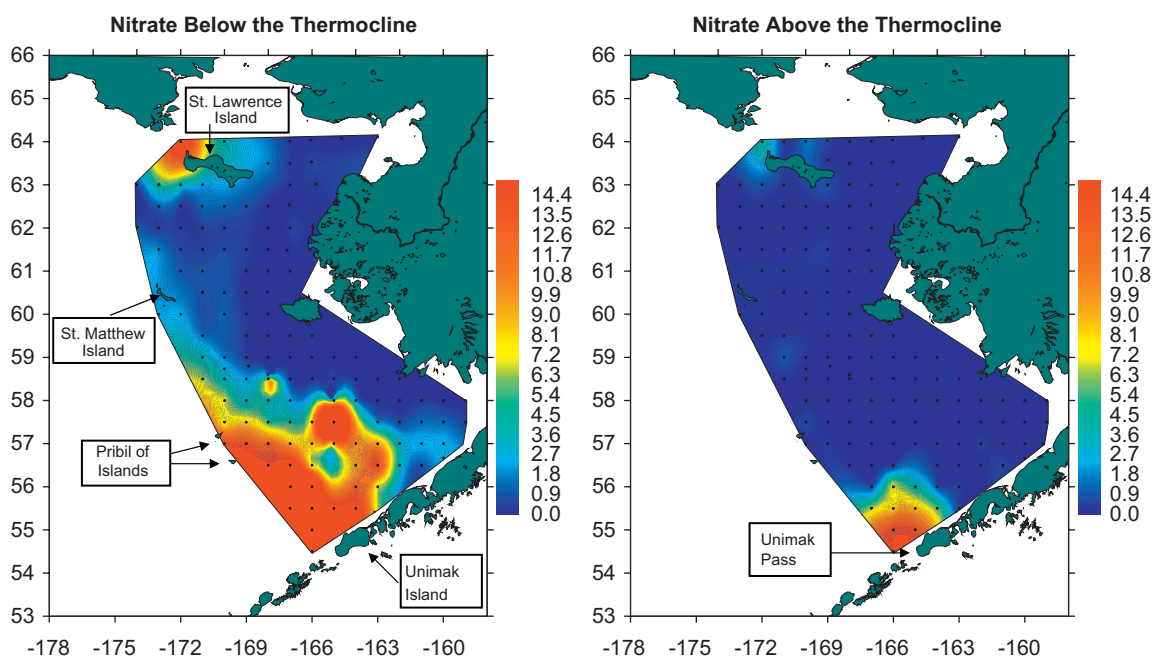


Fig. 13. Nitrate concentration (μM) on the eastern Bering Sea shelf in August–September 2004. Black dots indicate station locations (BASIS data).

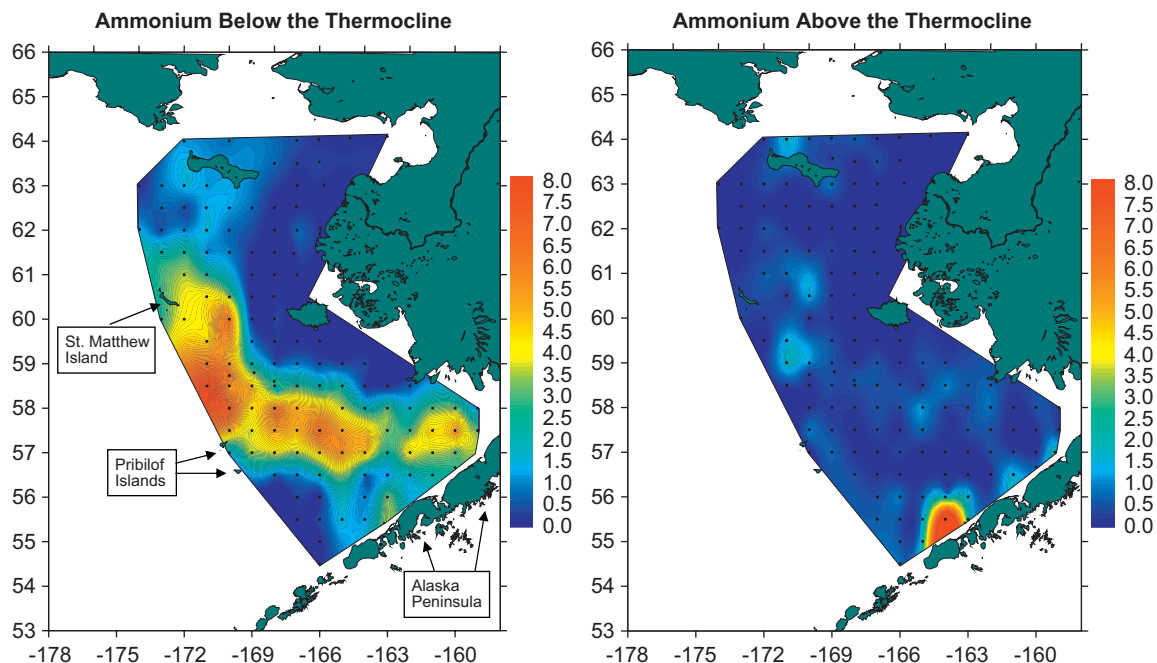


Fig. 14. Ammonium concentration (μM) on the eastern Bering Sea shelf in August–September 2004. Black dots indicate station locations (BASIS data).

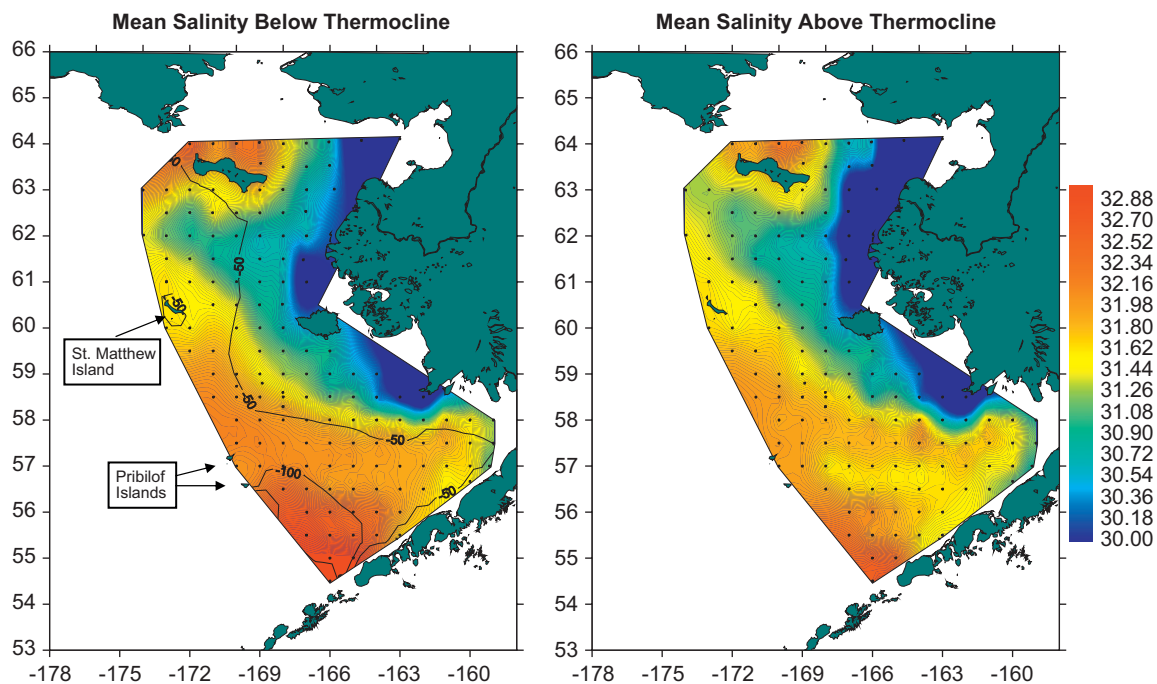


Fig. 15. Mean salinity above and below the thermocline on the eastern Bering Sea shelf in August–September 2004. Black dots indicate station locations; lines indicate 50, 100 and 200-m isobaths (BASIS data).

post-bloom production on the northern shelf may have been limited by lack of nutrients in the entire water column rather than stability. Nutrients may have been lower on the northern shelf due to penetration of low-nutrient, low-salinity inner domain water westward beyond the 50 m isobath (Fig. 15). *Calanus marshallae* abundance was low on the northern shelf (Fig. 12), except near the western end of St. Lawrence Island, where nutrient-rich Anadyr water moves northward through Anadyr Strait (Walsh et al., 1989). Thus a consistent pattern of distribution of *Calanus* abundance relative to nutrient availability for post-bloom production was observed. While the data indicate that nutrient limitation

of post-bloom production was probably occurring across the entire eastern Bering Sea shelf in 2004, elevated stability sequestering nutrients below the pycnocline was the limiting mechanism primarily in the middle domain of the southeastern Bering Sea.

4.6. Decadal temporal context

Long-term mooring deployments at M2 indicate that during the last decade, the Bering Sea has undergone a warming on the

Table 8
Abundance (No. m⁻³) and biomass (mg C m⁻²) of *Calanus marshallae* by stage on the southeastern Bering Sea shelf in 1999

Stage	June		August	
	Abundance	Biomass	Abundance	Biomass
I	1664	3.4	3	0.002
II	1954	12.7	85	0.3
III	1188	20.3	174	2.1
IV	475	20.4	2749	145
V	64	4.1	12599	2630
VI female	44	4.8	140	25.2
VI male	14	0.9	11	0.9

order of 3 °C (Stabeno et al., 2007). A major contributor to this shift has been a warm air mass over the Bering Sea, especially between 2001 and 2005. The warmer conditions are associated with stronger Aleutian low pressure systems that push warmer maritime air northward over the Bering Sea. The overall warmer conditions have resulted in a shorter ice season on the southeastern Bering Sea shelf, particularly from 2002 to 2005, and the shorter ice season seems to be due in part to a feedback mechanism whereby warmer sea conditions result in a delayed transition to the ice-covered winter oceanographic regime. In addition, a strong Aleutian low can result in an earlier transition to the ice-free summer regime or a spring when ice is completely absent. Coldest summer sea-surface temperatures during the mooring record occurred in 1999, which had a late ice retreat. The warmest sea-surface temperatures occurred in 2004, when an early ice retreat occurred. Depth-averaged temperatures at M2 for the last 10 years revealed a warming trend, in which temperatures from 2001 through 2005 were warmer than the 10-year mean. The warm conditions in 2004 therefore appear to be part of a long-term warming trend rather than an anomaly.

4.7. Conclusion

The observations above can be summarized as follows:

(1) Comparison of copepod distributions and water mass types indicates that the observed shift from large to small zooplankton taxa on the Bering Sea shelf between 1999 and 2004 did not appear to be caused by major shifts in circulation and water masses. (2) Literature data indicate that *C. marshallae*, *Thysanoessa* spp. and *C. melanaster* are commonly present on the shelf in high numbers and biomass, so the low abundance and biomass of these species in 2004 appears to be unusual. (3) The elevated concentrations of small copepods and hydromedusae are consistent with the elevated temperatures and greater water-column stability observed on the southeast shelf in 2004. (4) The shift in diet of age-0 pollock suggests that the observed changes in zooplankton abundance and biomass may impact higher trophic levels. (5) Post-bloom production in the middle domain of the southeastern shelf was apparently limited by high water-column stability. Although stability on the northern shelf was lower than on the southern shelf, a lack of nutrients in the water column may have limited post-bloom production on the northern shelf, rather than elevated stability. (6) Based on stability measurements during 1999 when large zooplankton were abundant, and 2004 when large zooplankton were rare or absent on the southeast Bering Sea shelf, we postulate that optimum stability for production of large zooplankton is about 30–40 J m⁻³. With stability somewhere between 40 and 90 J m⁻³, nutrients become trapped below the pycnocline, post-bloom production declines and the shelf zooplankton community reorganizes from a large to a small zooplankton assemblage.

Confirmation and clarification of the role of stability and nutrient concentrations in determining the structure of the zooplankton community on the Bering Sea shelf during summer will require a multiyear sampling effort. The research must document water-column properties in addition to primary production and zooplankton species composition, abundance and biomass over a broad geographic area for an extended time period. The magnitude of the ecosystem response will probably depend on the timing and rate at which stability is established, in addition to the magnitude of the stability at any given time. Presumably, warmer, calmer conditions in spring will result in earlier and more rapid development of stability of sufficient intensity to sequester nutrients below the pycnocline, thus prolonging the period of nutrient limitation of summer production and maximizing the ecosystem response relative to colder, stormier summer conditions. Therefore, any program to test the ecosystem response to stability will have to document the timing of thermocline formation, as well as the magnitude of the stability and the duration of high stability, to more fully understand the mechanistic links between climate and the ecosystem on the Bering Sea shelf. Nevertheless, the current information suggests that if the warming documented in recent years (Overland and Stabeno, 2004; Stabeno et al., 2007), were to continue and intensify, the size composition of zooplankton taxa on the Bering Sea shelf will be altered, thus changing trophic relationships among zooplankton consumers, with the potential for substantial impacts on commercial and wildlife resources with trophic links to the zooplankton community.

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