Available online at www.sciencedirect.com
ScienceDirect
Deep-Sea Research II 54 (2007) 2885–2905
DEEP-SEA RESEARCH
PART II
www.elsevier.com/locate/dsr2

Potential effects of temperature on the benthic infaunal community on the southeastern Bering Sea shelf: Possible impacts of climate change

K.O. Coyle[a,*], B. Konar[a], A. Blanchard[a], R.C. Highsmith[b], J. Carroll[c], M. Carroll[c], S.G. Denisenko[d], B.I. Sirenko[d]

[a]*Institute of Marine Science, University of Alaska, Fairbanks, AK 99775, USA*
[b]*National Institute for Undersea Science and Technology, University of Mississippi, MS 38677-7685, USA*
[c]*Akvaplan Niva, Tromso, Norway*
[d]*Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russian Federation*

Received in revised form 12 April 2007; accepted 14 August 2007
Available online 24 October 2007

Abstract

In the late 1950s, Soviet researchers collected benthic infaunal samples from the southeastern Bering Sea shelf. Approximately 17 years later, researchers at University of Alaska Fairbanks also sampled the region to assess infaunal biomass and abundance. Here, the two data sets were examined to document patterns and reveal any consistent differences in infaunal biomass among major feeding groups between the two time periods. No significant differences in the geometric mean biomass of all taxa pooled were indicated between the two study periods (1958–1959 = 49.1 $g\,m^{-2}$; 1975–1976 = 60.8 $g\,m^{-2}$; $P = 0.14$); however, significant differences were observed for specific functional groups, namely carnivores, omnivores and surface detritivores. Of the 64 families identified from both data sets from all functional groups, 21 showed statistically significant ($P \leqslant 0.05$) differences in mean biomass. Of the 21 families showing significant differences, 19 (91%) of the families had higher mean biomass in the 1975–1976 data set. The above differences suggest a trend toward higher overall infaunal biomass for specific functional groups during mid 1970s compared with the late 1950s. Temperature measurements and literature data indicate that the mid-1970s was an unusually cold period relative to the period before and after, suggesting a mechanistic link between temperature changes and infaunal biomass. Food-web relationships and ecosystem dynamics in the southeastern Bering Sea indicate that during cold periods, infaunal biomass will be elevated relative to warm periods due to elevated carbon flux to the benthos and exclusion of benthic predators on infaunal invertebrates by the cold bottom water on the shelf. As long-term observations of temperature and sea-ice cover indicate a secular warming trend on the Bering Sea shelf, the potential changes in food-web relationships could markedly alter trophic structure and energy flow to apex consumers, potentially impacting the commercial, tourist and subsistence economies.
© 2007 Elsevier Ltd. All rights reserved.

Keywords: Benthos; Infauna; Biomass; Temperature; Bering Sea; Bristol Bay

*Corresponding author. Tel.: +1 907 474 7705; fax: +1 907 474 7204.
E-mail addresses: coyle@ims.uaf.edu (K.O. Coyle), bkonar@guru.uaf.edu (B. Konar), arnyb@ims.uaf.edu (A. Blanchard), ray@olemiss.edu (R.C. Highsmith), jolynn.carroll@akvaplan.niva.no (J. Carroll), michael.carroll@akvaplan.niva.no (M. Carroll), dest@zin.ru (S.G. Denisenko), marine@zin.ru (B.I. Sirenko).

0967-0645/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.dsr2.2007.08.025

1. Introduction

A combination of the timing and magnitude of energy fluxes to the benthos, biotic interactions and physical influences control benthic community structure. Energy fluxes may include carbon fixation by benthic micro and macroalgae, carbon fixation by benthic autotrophic or chemotrophic bacteria or sinking of organic detritus or phytoplankton cells to the benthos. Species composition at any given time and place reflects the integrated sum of the above factors, which vary in their relative and overall level of influence on the community. In some areas, the key factor is energetics, including food production, seasonal availability, distribution and consumption (Grebmeier et al., 1988; Highsmith and Coyle, 1990, 1992; Grebmeier, 1993; Feder et al., 1994a). In other areas, benthic community structure is controlled more by biotic factors such as competition, predation and recruitment success (Eckman, 1996; Iken et al., 2001; Bolam et al., 2002; Dunstan and Johnson, 2003; Coyle et al., 2007). At mid-Arctic latitudes, especially where more southerly adapted species are interacting with Arctic species, community composition tends to reflect the outcome of interactions between species or populations (Nirini and Oliver, 1983; Thomson and Martin, 1986; Coyle and Highsmith, 1994). However, even though the composition and character of benthic communities at certain times and locations can be a result of the direct influence of energetic considerations or biotic interactions, over longer spatial and temporal scales, physical factors are of predominant importance because they establish the regulatory framework for biotic interactions (Zenkevich, 1927; Dahle et al., 1998; Smith et al., 1999).

One of the major physical factors influencing ecosystems is climate, and the potential effects of global climate change on ecosystems is an ongoing concern (Galbraith et al., 2002; Graham et al., 2002; Williamson et al., 2002; Clarke and Harris, 2003; Pearson and Dawson, 2003; and others). Climate can influence marine subarctic ecosystems by changing annual cycles of water temperature, thus impacting the species composition and diversity of marine communities; by changing the amount and duration of ice cover, thus influencing the timing and magnitude of primary production; and by altering trophic relationships, thus impacting the relative biomass of species at a variety of trophic levels. Several temporal scales of climate variability are known to exist. Examples range from interannual shifts (Dement'ev, 1991; Rabouille et al., 2001; Parkinson, 1991; Bertram et al., 2001; Constable et al., 2003; Callaghan et al., 1998; Suyker et al., 2003) to oscillations extending from decades to centuries (Dickson et al., 1988; Ebbesmeyer et al., 1990; Carroll and Carroll, 2003). In the Bering Sea, climate change from the El Niño-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) occur at time scales of 3–10 years (Stabeno et al., 2001). Superimposed over the short-term oscillations is a long-term warming trend in Alaska as indicated by 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 ice cover (Chapman and Walsh, 1993; Osterkamp, 1994; Wadhams, 2000). As climate models predict that global warming will be most pronounced at higher latitudes (Cattle and Crossley, 1995; IPCC, 1998, 2001; Weller and Lange, 1999; Hassol, 2004), the warming trends are likely to have their greatest impact on Arctic and subarctic ecosystems, including the Bering Sea (Overland and Stabeno, 2004).

The sensitivity of the Bering Sea ecosystem to climate perturbations has been demonstrated by anomalous conditions related to the recent ENSO events and PDO anomalies (Overland et al., 2001). The physical oceanographic anomalies involved both unusual water temperatures and alterations in the position and intensity of the frontal systems dividing water masses on the inner shelf (Stabeno et al., 2001; Kachel et al., 2002). Since oceanographic conditions associated with the fronts and water masses strongly influence energy flow through the system (Walsh and McRoy, 1986), climate-related changes in the oceanographic conditions can influence both the pelagic and benthic communities.

In this paper, we compare estimates of benthic biomass in the southeast Bering Sea generated from material collected by Soviet researchers in the late 1950s with similar estimates generated by Alaskan researchers in the mid-1970s. A subset of the Soviet samples collected from 1958 to 1961 were analyzed by Neyman (1963) and Semenov (1964). These analyses emphasized the spatial distribution in biomass of benthic infaunal species in the diets of commercially important fish. Haflinger (1978, 1981)

analyzed the Alaskan data using cluster analysis to identify species groups by region. In contrast, our analysis focused on potential differences in biomass of families in major trophic groups between the two sampling periods.

Information on the biomass and taxonomic composition of benthic infauna from before 1980 provides an important baseline for evaluating climate-related impacts on the benthic community in the southeast Bering Sea. As this region contains abundant wildlife and fisheries resources of substantial importance to indigenous communities, as well as commercial and tourist economies (Napp and Hunt, 2001), information facilitating evaluation of climate-related environmental impacts on the southeastern Bering Sea has economical as well as scientific value.

1.1. Site description

The southeast Bering Sea shelf is more than 500 km broad (Hunt et al., 2002) and uniformly level, with an average slope of about 1 m per 3 km (McDonald et al., 1981). During summer, 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 at about 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). Sediments in the Middle Domain consist primarily of sand and silt; gravel occurs in some near-shore areas of the Inner Domain (Burrell et al., 1981). From 50% to over 70% of the sediment material in the Middle and Outer domains consist of silt particles (0.01–0.1 mm diameter), with the remainder consisting primarily of fine sand grains (0.1–0.25 mm diameter). In some regions, with a strong tidal influence, sand particles can predominate to water depths of 60–90 m (Greshanovich, 1964).

2. Methods

2.1. Sample collection

The samples were collected on the southeastern Bering Sea shelf during two sampling periods: 1958–1959 (period 1) and 1975–1976 (period 2) (Fig. 1). Samples from period 1 (referred to as the 1958–1959 data in the text) were collected by Soviet fisheries research expeditions (Neyman, 1963; Semenov, 1964), and the data were provided by the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia. Sampling was done from the trawl vessels Zhemchug in July and August 1958 and Pervenets in 1959 (dates not given). Single replicates were taken with a 0.25 m^2 Okean-50 benthic grab at each station. The sample set consisted of 95 stations from 1958 and 120 stations from 1959. The samples were sieved on a 1-mm screen and preserved in 4% formalin. Sample processing was done at the VNIRO laboratory. Species identifications and wet weights were done on not less than 90% of the total biomass. Families and species identified from the samples are listed in Neyman (1963). Particular emphasis was placed on those taxa comprising the food base for commercial fish species. Samples from period 2 were collected by the Institute of Marine Science, University of Alaska Fairbanks (Haflinger, 1981) and are referred to as the 1975–1976 data set. Sampling was done with 0.1 m^2 VanVeen grabs at 65 stations in May, June and August 1975 and 34 stations in April and May 1976. Five replicate samples were taken at each stations, sieved through a 1.0-mm mesh screen, and preserved in 10% buffered formalin for later sorting and identification. The material was identified to the lowest taxonomic level possible, and blotted wet weights were obtained on each taxon. The material in this study therefore consisted primarily of infaunal organisms. The whole animal with shell was weighed in both studies.

2.2. Standardization of taxonomic designations

The taxonomic designations were standardized before analysis to ensure that observed differences were not due to synonymies. Comparisons were done at the family level to minimize potential error due to inconsistencies in species identifications. National Oceaongraphic Data Center codes (NODC codes) were added to each data record to

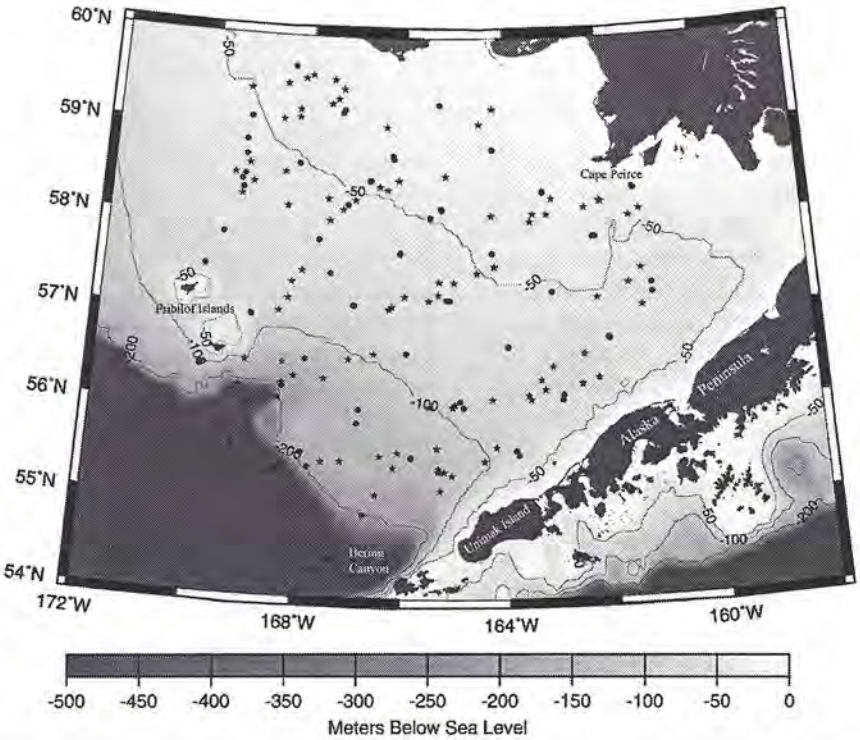

Fig. 1. Station distribution on the southeastern Bering Sea shelf. Stars indicate 1958–1959 stations, dots indicate 1975–1976 stations.

facilitate sorting by taxonomic categories. The large, predatory gastropods of the family Neptuneidae are normally not thought of as infauna, but the biomass of this family (presumably consisting of juveniles and smaller species in the samples) is included here, as neptuneids are an important component of the shelf ecosystem (e.g., Feder et al., 1994b).

2.3. Temperature records

Bottom-water temperatures for each station during period 1 were measured when the Russian benthic collections were taken. Bottom-water temperatures for period 2 (1975 and 1976) were provided from separate cruises to the southeast Bering Sea shelf in 1975 and 1976 by the Pacific Marine Environmental Laboratory (PMEL). Sample locations for both periods are plotted in Fig. 2. Samples for period 2 were collected in May, August and September in 1975 and June, August, September and early October 1976. A total of 569 measurements were used to characterize the bottom temperatures during the summers of 1975 and 1976.

2.4. Data analysis

The data were loaded into an ACCESS database for analysis. The analysis was designed to detect significant differences in biomass of the major functional and taxonomic groups between the two sampling periods. The data were sorted by family and the families were grouped into feeding categories consisting of carnivores, subsurface detritivores, suspension feeders, omnivores and surface detritivores. The aggregate biomass (wet weight, $g\,m^{-2}$) for all taxa belonging to each family or functional group was the main metric for comparison between periods. Only data between 54° and 60°N and 160° and 170°W were analyzed. The above precautions ensured maximum overlap between the 1958–1959 and 1975–1976 data sets.

The data sets for spatial statistical analysis consisted of the latitude and longitude of each station and the biomass for the family or functional group selected. The east–west and north–south distances (x and y distances) from the lower left corner of the sampling grid were computed for each station. The spatial relationships of biomass were determined by computing the semivariogram

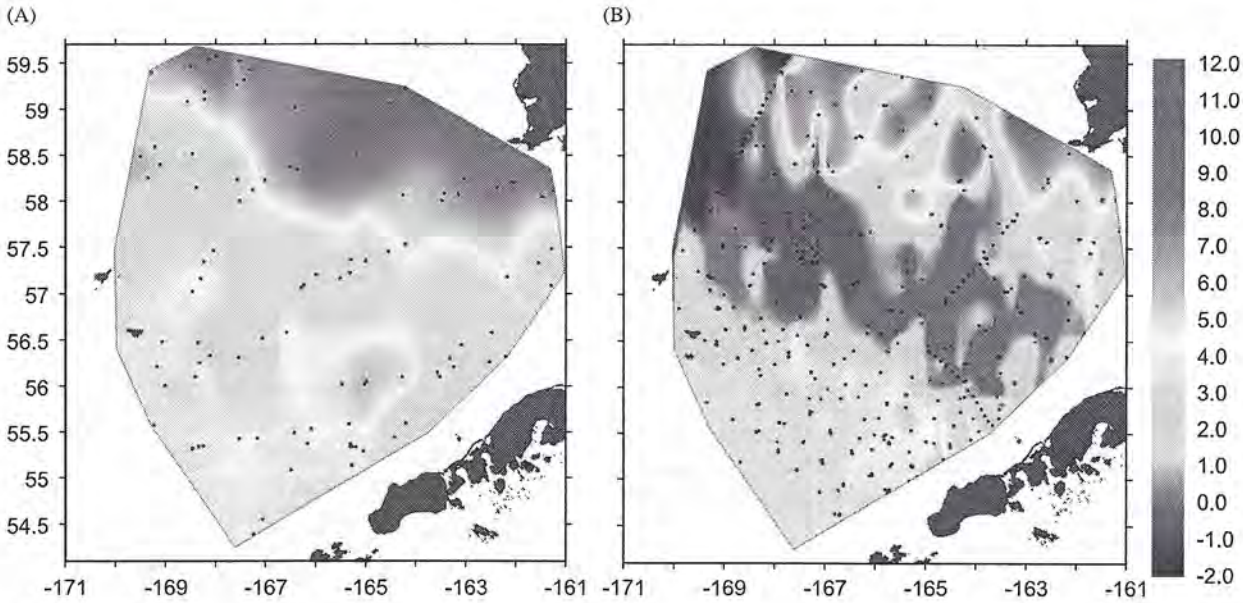

Fig. 2. Bottom water temperature (°C) on the southeastern Bering Sea shelf, (A) 1958–1959 (Zoological Institute data); (B) 1975–1976 (PMEL).

function $\gamma(h)$:

$$\gamma(h) = \frac{1}{2|N(h)|}\sum_{N(h)}(z_i - z_j)^2,$$

where $N(h)$ is the set of all paired distances h between sample locations, $|N(h)|$ is the number of distinct pairs in $N(h)$ and z_i and z_j are the data points. The semivariogram was plotted and fit to standard geostatistical models. In practice, the spherical model

$$\gamma(h) = \begin{cases} 1.5\dfrac{h}{r} - 0.5\left(\dfrac{h}{r}\right)^3 & \text{for } h \leqslant r, \\ 1 & \text{for other values} \end{cases}$$

consistently provided the best fit to the data (r is the range of influence defined below). In some cases, a locally weighted regression smoother was used to more accurately fit the semivariogram model. In addition, the robust variogram estimator was also occasionally employed (as defined by Cressie and Hawkins, 1980):

$$\bar{\gamma}(h) = \frac{\left[1/(2|N(h)|)\sum_{N(h)}|z_i - z_j|^{1/2}\right]^4}{0.457 + 0.494/|N(h)|}.$$

Anisostropy refers to directional variations in the spatial correlations of the data. When present, directional variograms were generated to correct for anisotropy in the data. In practice, anisotropy was rarely observed. The semivariogram was used to generate estimates of the sill (the random variance defined as $\lim_{h\to\infty}\gamma(h)$), the nugget effect (the value of $\gamma(h)$ for $h = 0$) and the range of influence (the shortest distance at which the data are no longer autocorrelated).

If the semivariogram indicated spatial correlation in the distribution of the selected taxon, then spatial statistics were used to look for differences in mean biomass. The application of spatial statistics ensured that any spatial correlations in the data were accounted for, thus avoiding potential errors in the confidence intervals due to pseudoreplication (Hurlbert, 1984).

The nugget, sill and range of influence obtained as outlined above were used in an ordinary block kriging algorithm to obtain estimates of the predicted value and upper and lower 95% confidence intervals for a 40×40 grid covering the box outlined by the latitude and longitude limits. The block kriging mean was computed using a moving window estimator (Kern and Coyle, 2000). Formal tests comparing the null hypothesis of equal means in biomass between sampling periods were done using the Z statistic computed from the mean-square prediction error as outlined in Kern and Coyle (2000). The Z statistic was compared with the standard normal distribution to obtain the

significance level. This approach provides for rigorous statistical inferences by minimizing pseudoreplication due to spatial correlations in the data.

All taxa, for which spatial correlations were not detected, were analyzed using standard parametric techniques. Analysis of variance was used to detect statistically significant differences in mean biomass between the 1958–1959 and 1975–1976 data sets. Differences were considered significant at $P \leqslant 0.05$. P values are listed only for families that were present in both 1958–1959 and 1975–1976 data sets. Mean biomass for all families reported in each data set are tabulated for completeness.

3. Results

3.1. Temperature differences

Minimum and maximum bottom temperatures in 1958–1959 were 0.5 and 11.3 °C, respectively. A contour plot indicated that the warmest temperatures occurred on the northern boundary of the sample regions, coldest water occurred in isolated patches in the Middle Domain between about 50 and 100 m depth along a band running southeast through the study site (Fig. 2A). Minimum and maximum temperatures in 1975–1976 were −1.7 and 9.8 °C, respectively. Subzero temperatures occurred in a band between 50 and 100 m depth (Fig. 2B). Mean bottom temperatures in the middle domain for 1958–1959 and 1975–1976 were 2.7 and 0.9 °C, respectively. Temperatures in the Inner Domain where the water is less than 50 m depth, were more variable, reflecting the greater seasonal influence of summer climate on bottom-water temperatures.

3.2. Differences by functional group

Generally, total benthic biomass was higher in the southeastern Bering Sea in 1975–1976 relative to 1958–1959 (Fig. 3), with an overall mean of 60.8 g m^{-2} in 1975–1976 compared with 49.1 g m^{-2} in 1958–1959. However, confidence intervals (95%) overlapped in all areas except the northeastern edge of the study site. Global block kriging indicated no significant differences in the geometric mean biomass between the two study periods (Table 1). Analysis by individual functional feeding groups revealed significantly higher mean biomass during 1975–1976 relative to 1958–1959 for carnivores, surface detritivores and omnivores (Table 1). Differences in carnivore biomass occurred in the northwestern and central areas (Fig. 4), differences in omnivore biomass were observed in the southern and central regions (Fig. 5), and differences in surface detritivores were observed primarily in the eastern region (Fig. 6), where higher biomass occurred in the 1975–1976 data. Although overall mean biomass of subsurface detritivores was not

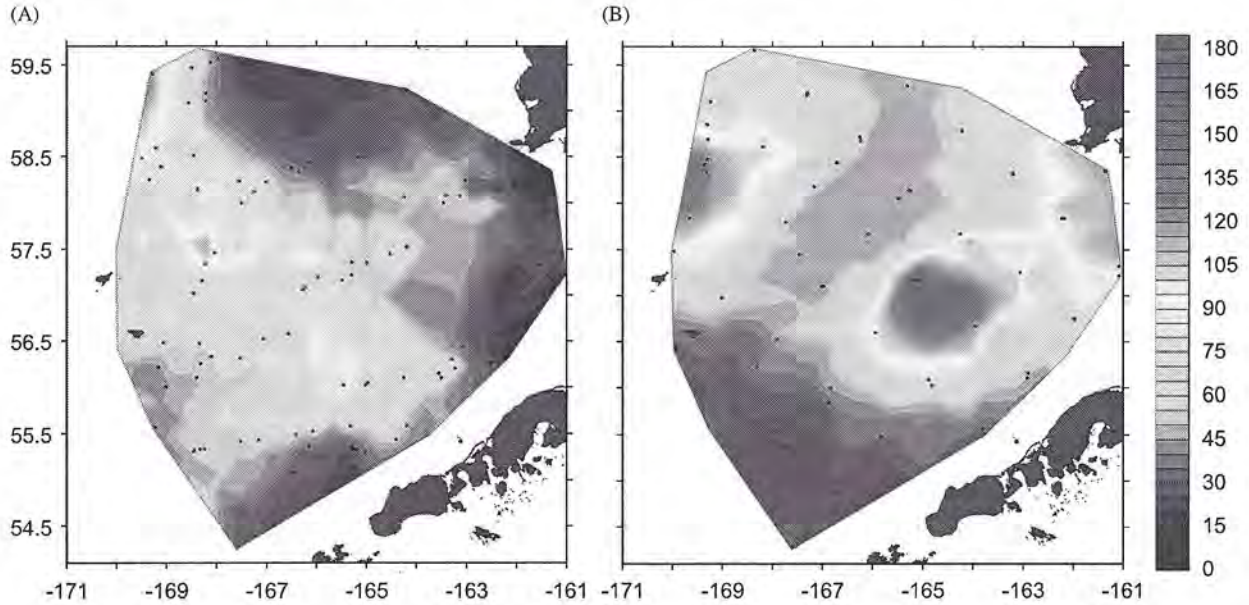

Fig. 3. Distribution of benthic infaunal biomass (g m^{-2}) on the southeastern Bering Sea shelf: (A) 1958–1959 and (B) 1975–1976.

Table 1
Geometric mean biomass and 95% confidence interval of the major feeding groups in the southeastern Bering Sea

Group	1958–1959		1975–1976		*P*-value
	Mean biomass ($g\,m^{-2}$)	95% Con. inter.	Mean biomass ($g\,m^{-2}$)	95% Con. inter.	
All Taxa	49.1	14.6	60.8	10.9	0.14
Carnivores	3.9	1.1	8.2	2.1	**0.0001**
Omnivores	0.84	0.26	1.5	0.32	**0.0054**
Suspension feeders	3.1	0.23	3.5	1.43	0.33
Subsurface detritivores	8.0	2.19	8.9	2.13	0.315
Surface detritivores	10.5	0.78	16.3	5.41	**0.014**

The bold font indicates that the *P*-value <0.05.
P-values were computed from the *Z*-statistic using global block kriging.

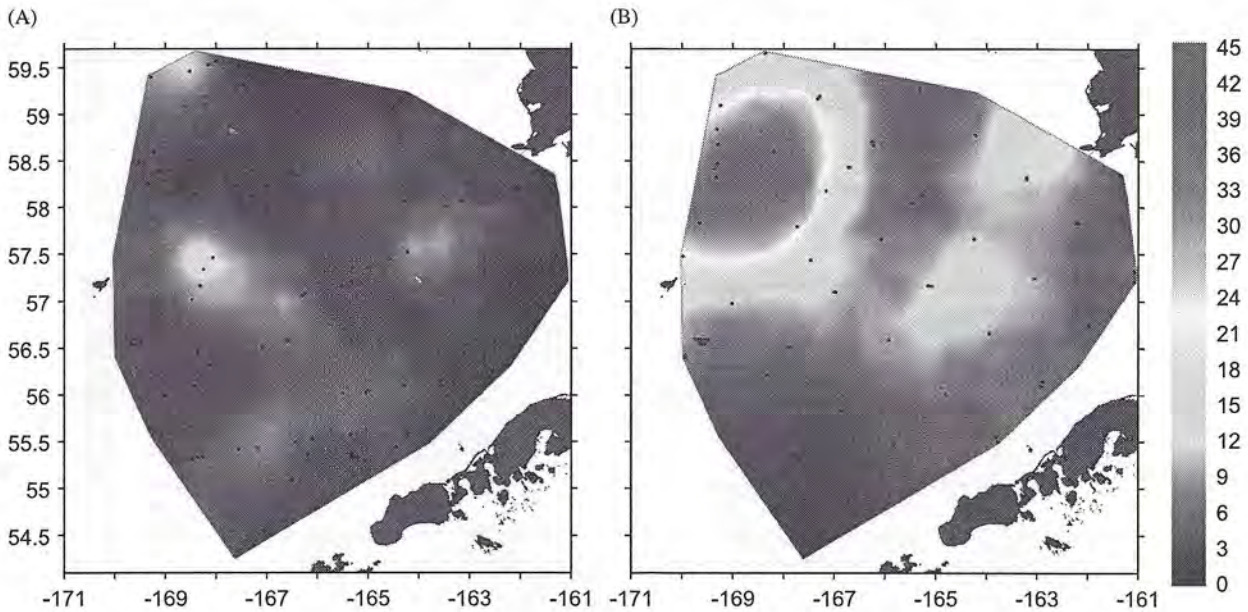

Fig. 4. Biomass of benthic infaunal carnivores ($g\,m^{-2}$) on the southeastern Bering Sea shelf: (A) 1958–1959 and (B) 1975–1976.

different between periods, biomass in the central region was higher in the 1975–1976 data relative to the 1958–1959 data (Fig. 7). Suspension feeders in the 1958–1959 data tended to concentrate in the eastern sector of the study regions, but were scattered at discrete sites across the study area in the 1975–1976 data (Fig. 8).

Analysis of each feeding group by family follows. Major families present are listed alphabetically in Table 2 by phylum or class. In tables listing the biomass by family and trophic category (Tables 3–7), the families are listed in order of descending biomass. The results below are presented by major trophic group, and deal primarily with those species showing significant differences between the 1958–1959 and 1975–1976 data sets. The results are generally presented in order of decreasing biomass.

3.2.1. Carnivores

Of the 27 families classified as carnivores, 14 were reported from the 1975–1976 data but did not occur in the 1958–1959 data (Table 3). Only 1 family (Aphroditidae) occurred in the 1958–1959 data but not in 1975–1976 data. If families not reported in the 1958–1959 data are subtracted from the 1975–1976 data, then the mean biomass of carnivores in the two data sets is almost identical. Of

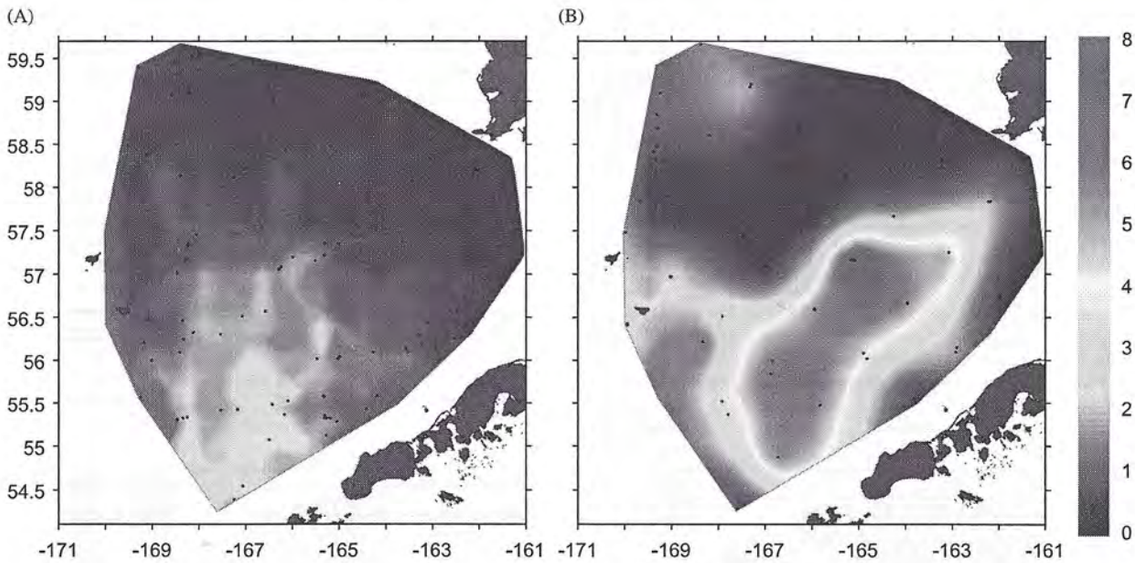

Fig. 5. Biomass of benthic infaunal ominvores ($g\,m^{-2}$) on the southeastern Bering Sea shelf: (A) 1958–1959 and (B) 1975–1976.

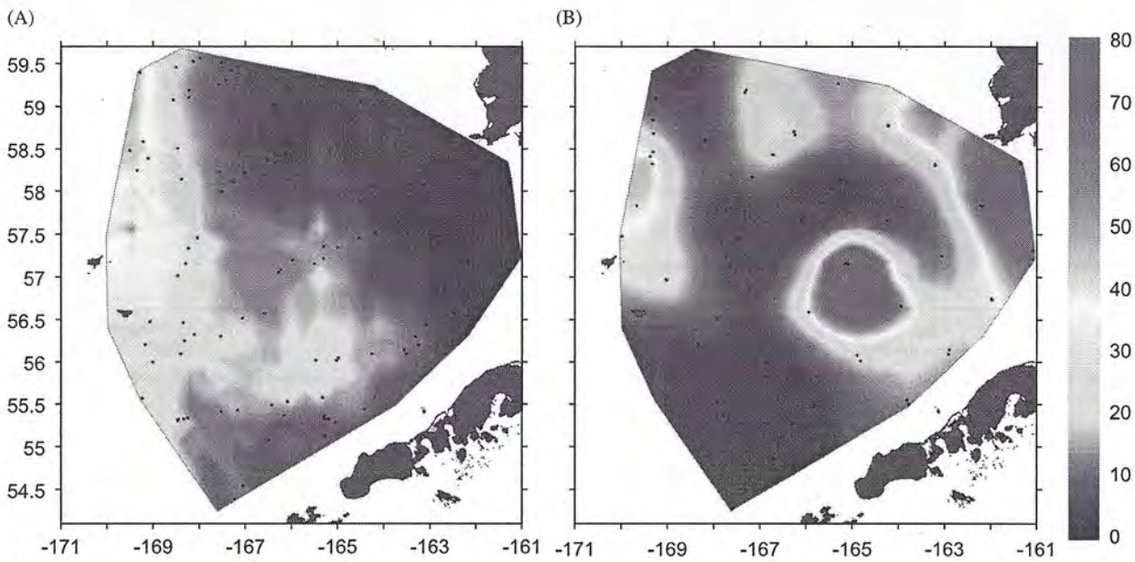

Fig. 6. Biomass of benthic infaunal surface detritivores ($g\,m^{-2}$) on the southeastern Bering Sea shelf: (A) 1958–1959 and (B) 1975–1976.

families absent from the 1958–1959 data, the Neptuneidae comprised about 40% of the biomass in the 1975–1976 data. The neptuneids consisted of 8 species (*Colus hypolispus*, *Plicifusus virens*, *Mohnia*, *Neptunea heros*, *Neptunea lyrata*, *Neptunea communis* and *Neptunea ventricosa*), found at nine stations. The genus *Neptunea* made up 99% of the total neptuneid biomass, and consisted of 28 specimens found at 6 stations. It is unclear if neptuneids were not collected by the Russian sampling gear, or were not counted during sample processing. The remaining families not found in the 1958–1959 data made up about 7% of the total biomass in the 1975–1976 samples.

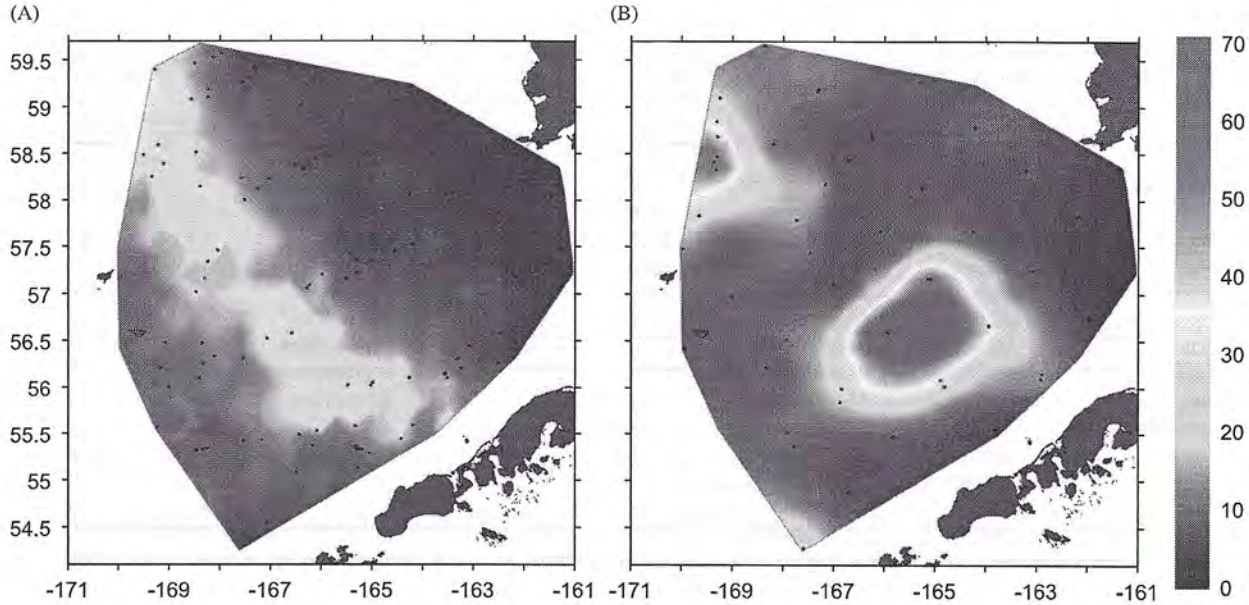

Fig. 7. Biomass of benthic infaunal subsurface detritivores ($g\,m^{-2}$) on the southeastern Bering Sea shelf: (A) 1958–1959 and (B) 1975–1976.

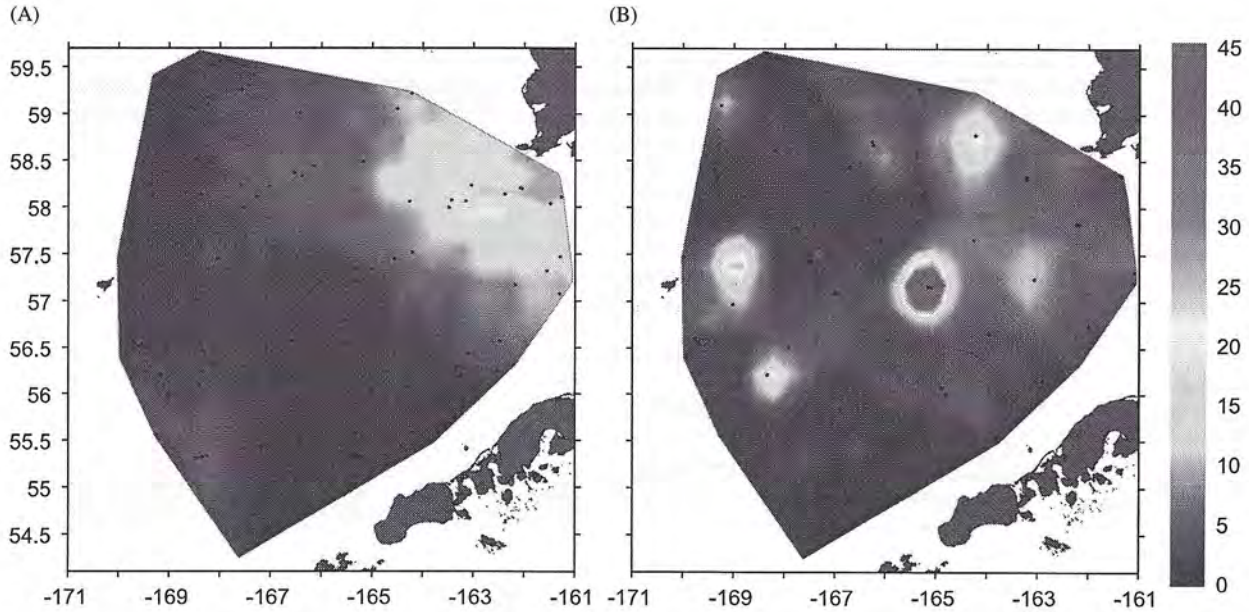

Fig. 8. Biomass of benthic infaunal suspension feeders ($g\,m^{-2}$) on the southeastern Bering Sea shelf: (A) 1958–1959 and (B) 1975–1976.

Four carnivore families found in both data sets had significantly different mean biomass: Nephtyidae, Naticidae, Cylichnidae and Phyllodocidae (Table 3). The nephtyids and phyllodocids are polychaets; the cylichnids and naticids are gastropods (Table 2). The nephtyids occupied the northwestern and central part of the study area. The species were identified as *Nephtys caeca*, *Nephtys ciliata*, *Nephtys cornuta*, *Nephtys ferruginea*, *Nephtys longosetosa*, *Nephtys paradoxa*, *Nephtys punctata*, *Nephtys rickettsi*, and *Aglaophamus rubella*. *N. paradoxa* was reported in 1958–1959 but not

Table 2
Families reported from the 1958–1959 and 1975–1976 benthic infaunal data from the southeastern Bering Sea, listed by phylum or class

Polychaeta	Gastropoda	Bivalves	Crustacea	Echinodermata	Ascideacea
Ampharetidae	Buccinidae	Astartidae	Acanthonoto-zomatidae	Amphiuridae	Ascidiacea
Amphictenidae	Cancellaridae	Bivalvia	Aegidae	Echinarachniidae	Molgulidae
Aphroditidae	Cylichnidae	Cardiidae	Ampeliscidae	Echinoidea	Styelidae
Apistobranchidae	Diaphanidae	Carditidae	Amphipoda	Goniopectinidae	
Arabellidae	Epitoniidae	Cuspidaridae	Anthuridae	Ophiacanthidae	
Capitellidae	Gastropoda	Hiatellidae	Aoridae	Ophiactidae	
Chaetopteridae	Muricidae	Lyonsiidae	Arcturidae	Ophiuridae	
Cirratulidae	Naticidae	Mactridae	Argissidae	Ophiuroidea	
Cossuridae	Neptuneidae	Montacutidae	Campylaspidae	Schizasteridae	
Eunicidae	Pyramidellidae	Myidae	Caprellidae	Strongylocentrotidae	
Flabelligeridae	Retusidae	Mytilidae	Copepoda		
Glyceridae	Rissoidae	Nuculanidae	Corophidae		
Goniadidae	Trichotropidae	Nuculidae	Cumacea		
Hesionidae	Trochidae	Pandoridae	Diastylidae		
Lumbrineridae	Turridae	Periplomatidae	Eusiridae		
Magelonidae	Turritellidae	Solenidae	Gammaridae		
Maldanidae		Tellinidae	Gammaridea		
Nephtyidae		Thraciidae	Gnathiidae		
Nereidae		Thyasiridae	Haustoriidae		
Onuphidae		Ungulinidae	Idotheidae		
Opheliidae		Veneridae	Isaeidae		
Orbiniidae			Ischyroceridae		
Oweniidae			Isopoda		
Paraonidae			Lampropidae		
Phyllodocidae			Leuconidae		
Pilargidae			Lysianassidae		
Polychaeta			Munnidae		
Polynoidae			Nannastacidae		
Polyodontidae			Oedicertidae		
Sabellaridae			Paranthuridae		
Sabellidae			Pardaliscidae		
Scalibregmidae			Phoxocephalidae		
Serpulidae			Pleustidae		
Sigalionidae			Podoceridae		
Sphaerodoridae			Pseudocumidae		
Spionidae			Stenothoidae		
Sternaspidae					
Syllidae					
Terebellidae					
Trichobranchidae					
Trochochaetidae					

in 1975–1976. *A. rubella*, *N. cornuta*, *N. ferruginea*, *N. punctata* and *N. rickettsi* appeared in 1975–1976 but not in 1958–1959. The remaining species were present in both data sets. The species unique to 1975–1976 or 1958–1959 were not common, occurring at only 1–3 stations. The Naticidae were represented by three species: *Lunatia pallida*, *Natica clausa* and *Polinices nanus*. The 1958–1959 data had only the genus *Natica*, which occurred at six of the stations, primarily on the eastern half of the study area. Naticidae occurred in the central and eastern half of the study region in 1975–1976. The Cylichnidae consisted of 2 species, *Cylichna occulta* and *Cylichna alba*. *Cylichna* in the 1958–1959 data were identified only to the genus level. *Cylichna* in 1975–1976 occurred in three large patches (in the northern and southern central shelf regions, and near the Pribilof Islands), but were confined primarily to the eastern region in 1958–1959. The phyllodocids were represented by *Eteone californica*, *Eteone longa*, *Eteone pacifica*, *Eteone tuberculata*, *Mysta* sp., *Phyllodoce groenlandica*, *Phyllodoce*

Table 3
Arithmetic mean biomass for carnivores in the southeastern Bering Sea

Family	1958–1959		1975–1976		P-value
	Mean biomass ($g\,m^{-2}$)	Percent of stations with taxon	Mean biomass ($g\,m^{-2}$)	Percent of stations with taxon	
Nephtyidae	4.55	69	8.61	100	**0.00**[a]
Muricidae	1.38	1	0.15	3	0.86
Naticidae	0.099	5	0.42	56	**0.03**[a]
Cylichnidae	0.084	6	0.37	77	**0.00**[a]
Buccinidae	0.75	1	0.017	2	0.56
Turridae	0.59	5	0.13	36	0.67
Aphroditidae	0.58	43	0	0	–
Phoxocephalidae	0.53	42	0.21	97	0.26
Eunicidae	0.22	6	0.024	3	0.18
Glyceridae	0.2	23	0.065	20	0.08
Phyllodocidae	0.12	15	0.25	79	**0.02**
Retusidae	0.017	3	0.011	32	0.83
Cuspidaridae	0.0043	2	0.022	2	0.40
Neptuneidae	0	0	7.98	14	–
Polynoidae	0	0	0.47	56	–
Lineidae	0	0	0.35	2	–
Sigalionidae	0	0	0.2	86	–
Goniadidae	0	0	0.1	68	–
Chaetodermatidae	0	0	0.062	23	–
Arabellidae	0	0	0.027	18	–
Polyodontidae	0	0	0.011	2	–
Pardaliscidae	0	0	0.0033	8	–
Stenothoidae	0	0	0.0010	12	–
Diaphanidae	0	0	0.00085	5	–
Pilargidae	0	0	0.00068	2	–
Hesionidae	0	0	0.00033	5	–
Anthuridae	0	0	0.000061	2	–
Total biomass	9.12		19.48		
1975–1976 only			9.21		

The bold font indicates that the P-value <0.05.
1975–1976 Only: summed biomass of families present in the 1975–1976 data but absent from the 1958–1959 data.
[a]Global block kriging values.

maculata and *Phyllodoce mucosa*. *P. groenlandica* and *Eteone* occurred in both data sets, but the latter were identified to species in the 1975–1976 data only. *E. californica* and *E. pacifica* occurred at only 1 station each, *E. tuberculata* occurred at two stations and the *Mysta* species occurred at 4 stations. Phyllodocids occurred primarily near the shelf break in 1958–1959 and near the central and eastern regions in 1975–1976.

The Aphroditidae were present in the 1958–1959 data but absent in the 1975–1976 data, while the Polynoidae were present in the 1975–1976 data and absent in the 1958–1959 data. This discrepancy

Table 4
Arithmetic mean biomass for subsurface detritivores in the southeastern Bering Sea

Family	1958–1959		1975–1976		P-value
	Mean biomass ($g\,m^{-2}$)	Percent of stations with taxon	Mean biomass ($g\,m^{-2}$)	Percent of stations with taxon	
Nuculanidae	6.25	62	6.06	76	0.46[a]
Maldanidae	5.57	67	4.42	95	0.27[a]
Sternaspidae	1.92	19	1.84	30	0.50
Opheliidae	1.6	52	0.99	62	0.27
Nuculidae	1.52	49	3.24	77	0.06
Goniopectinidae	1.40	4	0.3	5	0.94
Orbiniidae	0.91	68	0.98	91	0.23[a]
Cirratulidae	0.27	17	0.12	82	0.80
Amphictenidae	0.21	15	1.07	48	**0.04**
Scalibregmidae	0.19	22	0.18	32	0.63
Flabelligeridae	0.1	8	0.0463	38	0.60
Capitellidae	0.056	5	0.2	74	**0.00**
Thyasiridae	0.031	12	0.36	67	**0.00**
Cossuridae	0.00049	1	0.00030	3	0.78
Sphaerodoridae	0	0	0.000071	5	–
Total biomass	20.03		19.81		
1975–1976 only			0.000071		

The bold font indicates that the P-value <0.05.
1975–1976 Only: summed biomass of families present in the 1975–1976 data but absent from the 1958–1959 data.
[a]Global block kriging values.

probably resulted from taxonomic confusion since both families occur in the superfamily Aphroditacea. The biomass and percentage of stations occupied by the superfamily were similar in both data sets (Table 3). The Aphroditidae in the 1958–1959 data were identified only to family level at all stations but one, where the genus *Aphrodita* was recorded. The Sigalionidae and Goniadidae occurred in over two-thirds of the 1975–1976 stations but were absent from the 1958–1959 data (Table 3). The Sigalionidae were represented by *Pholoe minuta*, a widely distributed Arctic boreal species, which reaches about 25 mm length (Pettibone, 1963). This family also belongs to the Aphroditacea and it may be included in the Aphroditidae in the 1958–1959 data. The Goniadidae were represented by *Glycinde armigera*, *Glycinde picta* and *Goniada annulata*. The Goniadidae belong to the superfamily Glyceracea, and may be represented in the 1958–1959 data by the family Glyceridae, which were identified only to the family level by the 1958–1959 taxonomists. The aplacophoran mollusk family Chaetodermatidae included

Table 5
Arithmetic mean biomass for suspension feeders in the southeastern Bering Sea

Family	1958–1959		1975–1976		P-value
	Mean biomass ($g\,m^{-2}$)	Percent of stations with taxon	Mean biomass ($g\,m^{-2}$)	Percent of stations with taxon	
Carditidae	11.58	23	35.01	32	0.18[a]
Ampeliscidae	1.23	55	0.58	83	0.06[a]
Mytilidae	0.68	15	0.84	33	0.97
Mactridae	0.57	12	0.047	20	0.10
Astartidae	0.45	12	0.17	14	0.5
Sabellidae	0.34	22	0.56	62	0.53
Hiatellidae	0.22	5	0.0085	5	0.45
Haustoriidae	0.18	16	0.084	58	0.51
Serpulidae	0.029	1	0.025	2	0.95
Myidae	0.0069	2	0.035	9	0.09
Pandoridae	0.0029	1	0	0	–
Lyonsiidae	0.00049	1	0.24	21	**0.00**
Molgulidae	0	0	0.51	8	–
Solenidae	0	0	0.11	6	–
Veneridae	0	0	0.094	14	–
Periplomatidae	0	0	0.094	3	–
Montacutidae	0	0	0.058	65	–
Styelidae	0	0	0.03	5	–
Caprellidae	0	0	0.0026	17	–
Aoridae	0	0	0.00023	2	–
Total biomass	15.29		38.50		
1975–1976 only			0.9		

The bold font indicates that the P-value <0.05.
1975–1976 Only: summed biomass of families present in the 1975–1976 data but absent from the 1958–1959 data.
[a]Global block kriging values.

Table 6
Arithmetic mean biomass for omnivores in the southeastern Bering Sea

Family	1958–1959		1975–1976		P-value
	Mean biomass ($g\,m^{-2}$)	Percent of stations with taxon	Mean biomass ($g\,m^{-2}$)	Percent of stations with taxon	
Lumbrineridae	1.1	25	1.44	33	0.25
Trochidae	0.51	25	0.38	73	0.65
Nereidae	0.069	3	0.0032	5	0.31
Onuphidae	0.016	2	0.11	23	0.06
Priapulida	0.0029	2	0.15	23	**0.00**
Epitoniidae	0	0	0.13	2	–
Trichotropidae	0	0	0.098	2	–
Cancellaridae	0	0	0.03	15	–
Syllidae	0	0	0.0034	23	–
Total biomass	1.7		2.34		
1975–1976 only			0.26		

The bold font indicates that the P-value <0.05.
1975–1976 Only: summed biomass of families present in the 1975–1976 data but absent from the 1958–1959 data.

a single chiton species, *Chaetoderma robusta* (Table 3). Chaetodermatidae were not listed in the 1958–1959 data. The Arabillidae were represented primarily by 1 species, *Drilonereis falcate*. The Arabillidae are related to the Lumbrineridae, which was classified as an omnivore in this work. The remaining families classified as carnivores present in the 1975–1976 data but absent in the 1958–1959 data comprised a small percentage of the total carnivore biomass and occurred at a small percentage of the stations.

3.2.2. Subsurface detritivores

Subsurface detritivores comprised 15 families, 3 of which had significantly different biomass between sampling periods (Table 4). The Amphictenidae (Pectinariidae) consisted of *Pectinaria auricoma*, *Pectinaria belgica*, *Pectinaria brevicoma*, *Pectinaria granulata* and *Pectinaria hyperborea*. *P. hyperborea* occurred in 1958–1959 at one station; other specimens were identified to the genus level at other stations. The other species occurred in the 1975–1976 data only. *Pectinaria* occurred primarily in the northwestern area of the study site in 1958–1959, but occurred in the central area in the 1975–1976 data. High 1975–1976 biomass in the central area was due to a high value for *P. granulata* at one station ($50\,g\,m^{-2}$). All other values were below $10.4\,g\,m^{-2}$. The Capitellidae were concentrated primarily in the southwestern region in 1975–1976, but occurred in the center of the study area in 1958–1959. The species composition consisted of *Capitella capitata*, *Heteromastus filiformis* and *Notomastus lineatus*. 1958–1959 identifications were made to the family level only. The Thyasiridae species included *Axinopsida orbiculata*, *Axinopsida serricata*, and *Thyasira flexuosa*; *A. serricata* occurred at only 1 station and all 1958–1959 identifications were to the genus *Axinopsida* only. These bivalves occurred primarily in the southern part of the study area in 1958–1959 and in the central part in 1975–1976. The Sphaerodoridae, identified as *Sphaerodoropsis minuta* and *Sphaerodoropsis sphaerulifer*, occurred at only 3 stations in 1975–1976.

The mean biomass of the Nuculanidae, Maldanidae and Orbiniidae were not significantly different overall; kriging indicated an overall temporal and

Table 7
Arithmetic mean biomass for surface detritivores in the southeastern Bering Sea

Family	1958–1959		1975–1976		*P*-value
	Mean biomass ($g\,m^{-2}$)	Percent of stations with taxon	Mean biomass ($g\,m^{-2}$)	Percent of stations with taxon	
Ophiuridae	15.17	31	2.45	27	**0.00**[a]
Cardiidae	7.46	18	23.83	41	**0.04**[a]
Tellinidae	6.4	59	15.12	83	**0.00**[a]
Echinarachniidae	1.76	17	6.28	26	**0.00**[a]
Spionidae	1.21	36	0.49	83	0.48
Trichobranchidae	1	25	0.34	29	0.28
Terebellidae	0.96	17	3.67	58	**0.05**[a]
Amphiuridae	0.96	29	0.69	45	0.65
Sabellaridae	0.77	2	0.0019	2	0.41
Ampharetidae	0.52	33	0.43	76	1
Schizasteridae	0.39	1	0	0	–
Dentaliidae	0.36	11	0.14	14	0.41
Aegidae	0.32	4	0.0073	2	0.19
Isaeidae	0.31	23	0.48	76	**0.03**
Ophiacanthidae	0.3	1	0	0	0.42
Lysianassidae	0.29	22	0.53	79	**0.02**
Turritellidae	0.26	15	0.77	33	**0.01**
Ungulinidae	0.23	38	0.0029	6	**0.00**
Gammaridae	0.13	3	0.071	21	0.72
Corophidae	0.084	4	0.029	30	0.82
Strongylocentrotidae	0.069	2	0	0	–
Magelonidae	0.056	13	0.21	73	**0.00**
Ophiactidae	0.039	2	0.00079	2	0.27
Oweniidae	0.033	11	0.12	47	**0.01**
Oedocerotidae	0.029	6	0.12	71	**0.00**
Chaetopteridae	0.0039	1	0	0	–
Thraciidae	0	0	0.18	14	–
Leuconidae	0	0	0.12	94	–
Golfingiidae	0	0	0.061	17	–
Diastylidae	0	0	0.058	35	–
Ischyroceridae	0	0	0.021	48	–
Paraonidae	0	0	0.018	29	–
Echiuridae	0	0	0.017	2	–
Apistobranchidae	0	0	0.0075	8	–
Pyramidellidae	0	0	0.0069	9	–
Pleustidae	0	0	0.0030	23	–
Idotheidae	0	0	0.0017	5	–
Podoceridae	0	0	0.0014	8	–
Argissidae	0	0	0.0013	14	–
Lampropidae	0	0	0.0012	12	–
Munnidae	0	0	0.00061	6	–
Trochochaetidae	0	0	0.00059	5	–
Campylaspidae	0	0	0.00029	6	–
Gnathiidae	0	0	0.00017	5	–
Arcturidae	0	0	0.00017	5	–
Pseudocumidae	0	0	0.00015	3	–
Paranthuridae	0	0	0.000061	2	–
Acanthonotozomatidae	0	0	0.000061	2	–
Eusiridae	0	0	0.000030	2	–
Nannastacidae	0	0	0.000022	2	–
Total biomass	39.11		56.28		
1975–1976 only			0.5		

The bold font indicates that the *P*-value <0.05.
1975–1976 Only: summed biomass of families present in the 1975–1976 data but absent from the 1958–1959.
[a]Global block kriging values.

spatial patchiness in the subsurface detritivore biomass.

3.2.3. Suspension feeders

Suspension feeders included 21 families, 8 of which were observed only in the 1975–1976 data (Table 5). Of the families observed in both 1958–1959 and 1975–1976, only the Lyonsiidae had significantly different biomass. The Lyonsiidae, consisting of *Lyonsia arenosa* and *Lyonsia norvegica*, occurred at 21% of the sites in 1975–1976 but at only one site in 1958–1959. *Pandora* was found at one site in 1958–1959. The Montacutidae were observed at two-thirds of the 1975–1976 stations but did not appear in 1958–1959. The species included *Mysella beringensis*, *Mysella planate*, *Odontogena borealis*, *Rochefortia compressa* and *Rochefortia tumida*. These species are common in the Bering Sea (Abbott, 1974), and their absence from the 1958–1959 data may reflect taxonomic confusion or a conscious decision to exclude them during sample processing.

3.2.4. Omnivores

Omnivores included 9 families of which 4 appeared only in the 1975–1976 data. Of the taxa appearing in both data sets, only the biomass of Priapulidae was significantly different (Table 6). Priapulidae from 1975 to 1976 were identified to *Priapulus caudatus*; those from 1958 to 1959 were left at the phylum level. The only other taxon with significantly different biomass was Cancellariidae, which appeared in 15% of the 1975–1976 stations but not in 1958–1959; they were identified to the species *Admete viridula*.

3.2.5. Surface detritivores

Surface detritivores had the highest number of taxa, consisting of 51 families, of which 23 occurred in the 1975–1976 data only. Of the families occurring in both data sets, 10 had significantly different biomass between sampling periods (Table 7). Cardiidae were common during both sampling periods and consisted of *Cardium* sp. (1958–1959 only), *Clinocardium californiense* (3 stations in 1975–1976), *Clinocardium ciliatum*, *Serripes groenlandicus* and *Serripes laperousi* (1 station, 1975–1976). Cardiidae biomass in 1975–1976 was higher in the western, central and eastern regions of the study grid, with greatest differences in the central regions, where the biomass of *C. ciliatum* was over 1 $kg\,m^{-2}$ in 1975–1976; highest biomass in the 1958–1959 data was 643 $g\,m^{-2}$. Tellinidae were also common in both data sets; species included *Macoma brota* (1 Station, 1975–1976), *Macoma calcarea*, *Macoma lama* (1 station, 1975–1976), *Macoma moesta* (1975–1976 only) and *Tellina lutea* (1975–1976 only). Animals at a number of 1958–1959 stations were identified to family or genus *Tellina* only. The Tellinidae occurred primarily in the northern region of the study grid in 1958–1959, and in the eastern region in 1975–1976. Overall biomass was higher in 1975–1976, with greatest differences in distribution between periods in the northern and eastern areas. Echinarachniidae were confined primarily to the eastern edge of the study site in 1975–1976 and to the northern and central region in 1958–1959. Significant differences in biomass of the Echinarachniidae were observed in different regions. The family consisted entirely of the sand dollar *Echinarachnius parma*. The Terebellidae consisted primarily of *Artacama coniferi* and *Artacama proboscidea* (identified only to genus in the 1958–1959 data), several species of *Pista*, and a number of specimens identified only to family. The 1975–1976 data contained an additional 8 genera and 13 species not listed in the 1958–1959 data. The terebellids showed differences in distribution, with concentrations in the northwestern and central regions in 1975–1976, and in the southern region in 1958–1959.

Widespread taxa also showing significant differences included the Isaeidae, Lysianassidae, Magelonidae, Oweniidae and Oedicerotidae (Table 7). The Iaeidae consisted primarily of *Photis* and *Protomedeia*; 1958–1959 data contained only the latter. Lysianassids consisted of 8 genera, of which 2 occurred in both data sets (*Orchomene* and *Anonyx*). Magelonidae consisted of 3 species of *Magelona*; 1958–1959 reported only *Magelona pacifica*. The Oweniids were represented by 4 species, *Galathowenia oculata* (occurring only in the 1958–1959 data), *Myriochele heeri* (identified to genus only in the 1958–1959 data), *Owenia fusiformis* and *Owenia lobopigida* (1 station, 1958–1959). Oedicerotids consisted of 4 genera and 10 species. *Arrhis luthkei* occurred only in the 1958–1959 data, *Bathymedon* was observed in both data sets, *Monoculodes*, *Monocolopsis* and *Pontocrates* occurred only in the 1975–1976 data, and *Westwoodilla* was represented by *Westwoodilla caecula* and *Westwoodilla abyssalis*, the latter occurring at one station in 1958–1959. Global block kriging revealed significant differences in the biomass of Ophiuridae,

probably due to differences in their spatial distribution. Ophiurids consisted of 3 species of *Ophiura* found in both data sets. The turritellids were observed at no more than 33% of the sites and consisted of *Tachyrhynchus erosus* in the 1975–1976 data and *Turritella* in the 1958–1959 data.

Of the taxa occurring only in the 1975–1976 data, the widespread families included Leuconidae, Ischyroceridae and Diastylidae. Their absence from the 1958–1959 data suggests that specimens of these pericarids may have been present during the earlier sampling period but not identified to the family level. These taxa and others occurring only in the 1975–1976 data were a small portion of the total biomass and did not appear to contribute substantially to overall differences in biomass of surface detritivores between periods.

3.3. Summary of results

Of the 121 families identified from the data sets, 51 were identified only from the 1975–1976 data, 6 occurred only in the 1958–1959 data and 64 were present in both data sets. Of the 121 total families, 45 had significantly different biomass between sampling periods, but 24 of those families were totally absent from the 1958–1959 data. Of the 64 families identified from both data sets, 36 had higher biomass in the 1958–1959 data, but only 2 of those differences were statistically significant. Of the 21 families identified from both data sets and with significant biomass differences between data sets, 90% had higher biomass in the 1975–1976 data. Thus, the observations suggest a trend toward higher biomass in the 1975–1976 period relative to 1958–1959.

4. Discussion

4.1. Potential sources of bias

Comparison of data collected by different institutions and research programs is complicated by the potential biases introduced by differences in sampling gear and sample processing protocols. In this study, 1958–1959 samples were collected by a 0.25-m^2 Okean type grab, one replicate was collected at each station and identification of individual taxa emphasized species comprising the food base for commercial fish. The 1975–1976 samples were collected with a smaller 0.1-m^2 VanVeen grab, five replicates were taken and all species retained in the 1-mm sieve were identified to the lowest taxonomic level possible. The absence of some taxa from the 1958–1959 data that were present in the 1975–1976 data is probably related to the above differences in both the sampling gear and the sample processing protocol. While the Okean grab is larger than the VanVeen, only one replicate per station was taken during the Russian survey. Given that the 1975–1976 researchers took five replicates with the smaller grab, they probably on average sampled about twice as much material per station as the Russian survey. The 1975–1976 data are therefore more likely to contain the rarer species. In addition, taxa not consumed by commercial fish were not necessarily identified to species by the Russian taxonomists. These differences are the most likely reasons for more species listed in the 1975–1976 data than in the 1958–1959 data. Direct comparison of biomass by taxa is also complicated by possible differences in species identification. The potential biases introduced by the above differences in field and laboratory techniques were minimized by grouping samples by family and by documenting which comparisons involved those families, which occurred in both the 1958–1959 and 1975–1976 data sets. Since at least 90% of the biomass in the Russian samples was identified (Neyman, 1963), biases in biomass between 1975–1976 and 1958–1959 data due to differences in processing protocol are not likely to exceed 10%.

Assessment of the potential error resulting from differences in sample protocol and gear type used by Russian and other international researchers was undertaken by Denisenko et al (2005). Parallel samples were taken in the Pechora Sea using 0.1- and 0.25-m^2 grabs according to Russian and Norwegian protocols. The proportion of species in different systematic groups was similar in both sample sets. Nevertheless, some smaller species were absent from Russian samples in 2 out of 17 stations. These differences were attributed to either patchiness or differences in sampling efficiency by the larger grab relative to sediment type.

Finally, differences in station distribution and sample density are a potential source of error when comparing the 1958–1959 and 1975–1976 data. Errors resulting from differences in sampling design were minimized by restricting our analysis to the region where spatial overlap of stations from both data sets was greatest. In addition, the use of kriging where spatial autocorrelations were observed provided statistically rigorous tests of differences in

mean biomass, even though station locations within the study area differ spatially between sampling periods. Therefore, while some of the differences in biomass between the 1958–1959 and 1975–1976 observations may reflect biases introduced by different sampling protocols, the statistically significant higher biomass consistently observed in 1975–1976 relative to 1958–1959 suggests the presence of a temporal trend that may reflect environmental changes impacting the benthic community.

4.2. Temperature and climate effects

The trend toward higher biomass in the 1970s relative to the late 1950s appears to be associated with temperature differences between the two periods. Mean sea-surface temperature anomalies were strongly negative in 1975 and 1976 (Bond and Adams, 2002), with ice covering much of the southeast Bering Sea shelf for over a month (Wyllie-Echeverria and Wooster, 1998; Stabeno et al., 2001). In contrast, temperature anomalies were about 0 in 1959 (Bond and Adams, 2002). The fluctuations in the southeast Bering Sea climate appear to be related to shifts in the Arctic Oscillation (AO) and the Pacific Decadal Oscillation (PDO). The PDO underwent a strong transition and the AO underwent a moderate transition in the winter of 1976–1977, resulting in an abrupt shift from periods of high ice cover to periods of low ice cover on the southeast Bering Sea shelf (Stabeno et al. 2001; Hunt et al., 2002). The evidence suggests that 1958–1959 was a period of average temperatures, while 1975–1976 was a period of unusually cold temperatures.

A continuous band of subzero water known as the cold pool was observed in the Middle Domain south to approximately 56°N latitude during 1976 (Kinder and Schumacher, 1981). Kinder and Schumacher (1981) reported summer bottom-water temperatures in the Middle Domain between −1 and 3 °C. In contrast, mean bottom-water temperature in the Middle Domain during 1958 and 1959 was 2.7 °C, with a temperature range between 0.5 and 5.3 °C; subzero temperatures were not observed in this region in 1958–1959. The cold pool is generated by sea-ice melt during spring; in years without ice the coldest bottom-water temperatures are about 4 °C (Stabeno et al., 2001). The geographic extent of ice penetration southeastward on the shelf and the area subsequently occupied by the resulting cold pool is determined by winds influenced by the position and intensity of the Aleutian Low, particularly in April (Wyllie-Echeverria and Wooster, 1998). When winds are predominantly from the Pacific (maritime), the ice is blown northward and warmer temperatures promote faster ice melt, resulting in reduced ice cover and a smaller cold pool. When winds are predominantly from the north (continental), temperatures are colder, ice is pushed farther southeastward and the cold pool occupies a greater portion of the southeastern Bering Sea shelf during summer.

The temperature measurements for 1975 and 1976 from PMEL were taken immediately before and after the benthic surveys in 1975 and before the survey in 1976. They covered the entire sampling region (Fig. 2) and provide a fairly complete characterization of bottom-water temperatures in the Middle and Outer Domains at depths greater than 50 m. Bottom temperatures in these deeper regions are fairly constant during summer due to insulation from seasonal warming by the strong seasonal thermocline, which develops during summer (Coachman, 1986). The patchy bottom-water temperatures in the Inner Domain reflect actual differences relative to the dates that samples at a particular location were taken. Since the shallower Inner Domain is unstratified, mixed by tides from below and winds from above (Stabeno et al., 2001), bottom-water temperatures can have a strong seasonal component. Therefore, temperature measurements taken during the month before or after the benthic sampling cruise may be either colder or warmer than those actually experienced by the animals at the time of sampling. However, the overall average as reflected in the composite figure (Fig. 2) is probably the best mean characterization of the thermal environment experienced by the benthic community during the summers of 1975 and 1976. In late fall and early winter, strong winds erode the pycnocline and mix the water column, erasing the cold pool. Therefore, if it is present in summer, it is an indication of ice cover during the previous spring.

The amount of organic carbon transferred to the benthic community is strongly influenced by oceanographic conditions on the southeastern Bering Sea shelf. Weak cross-shelf circulation between the Outer and Middle Domains confines much of the zooplankton biomass during the spring bloom to the outer shelf (Cooney and Coyle, 1982; Smith and Vidal, 1986; Vidal and Smith, 1986). As a result, a higher proportion of the annual primary production

sinks ungrazed to the benthic environment in the Middle Domain relative to the Outer Domain. Walsh and McRoy (1986) estimated primary production in the Outer and Middle Domains of approximately 164 g C m^{-2} yr^{-1}. On the outer shelf, approximately 42% of the production goes through the pelagic food web, and the remaining 58% goes to the benthos; in the Middle Domain only about 16% goes to the plankton and 84% goes to the benthos (Walsh and McRoy, 1986). Thermal stratification leads to rapid depletion of nutrients in the euphotic zone and an end to the spring bloom by late May or early June (Whitledge et al., 1986). The remaining production during summer results primarily from storms, which mix nutrients into the euphotic zone and stimulate brief episodes of phytoplankton production (Sambrotto et al., 1986). Production in the Inner Domain is confined primarily to the spring bloom, because nutrients are depleted from the entire water column by the end of May (Stockwell et al., 2001). Since much of the annual primary production across the entire shelf occurs during the spring bloom, the magnitude of the biomass and grazing rate of herbivorous zooplankton during spring can markedly influence the amount of carbon shunted to the benthic food web.

Sea ice is a major factor influencing the timing and intensity of the spring bloom, and the fate of the resulting production. If ice is present during April and May, ice melt results in early stratification of the water column and an ice-related bloom (Niebauer et al., 1990, 1995). Production occurs in cold water as a rapid pulse. Low temperatures suppress zooplankton metabolism, leading to low grazing and growth rates by zooplankton consumers. Grazing measurements and growth rate estimates indicate that zooplankton could remove less than 2% of the estimated daily production during an ice-edge bloom on the southeast Bering Sea shelf (Coyle and Cooney, 1988), and zooplankton production was only about 3–4% of that during spring bloom periods without ice (Coyle and Pinchuk, 2002). The ungrazed phytoplankton production presumably sinks to the benthos.

In the absence of ice, the water column remains unstratified until winter winds have ceased and thermal stratification stabilizes the water column. If storms are frequent, vertical mixing renews the nutrient supply to the euphotic zone, prolonging the bloom (Hunt et al., 2002). Zooplankton are exposed to longer periods of phytoplankton production under warmer conditions, and are thus able to remove a larger percentage of the total annual carbon production. The above scenario is supported by long-term trends in the biomass of gelatinous zooplankton in the Middle Domain (Brodeur et al., 1999). Following a shift to a low-ice regime in the late 1970s, the gelatinous zooplankton biomass began a gradual increase, reaching values of over 10 times those measured in 1979. This increase in jellyfish biomass is most likely the result of increases in the amount of carbon transferred through the pelagic food web relative to the benthos. Consequently, although long-term observations indicate a constant nutrient supply to the southeast Bering Sea shelf (Rho et al., 2005) and a relatively constant total annual carbon production (Hunt et al., 2002), more of the available production apparently reaches the benthos during a cold year with extensive ice cover, relative to a warm year without ice. This difference in carbon flux to benthic food webs in a cold year with heavy ice cover, relative to warmer conditions with little or no ice cover, is one possible explanation of the observed trend toward high biomass in mid-1970s relative to the late 1950s.

4.3. Predators on infauna

In addition to higher overall carbon input, higher benthic biomass also may be promoted by low densities of ground fish during periods of low temperature; many flatfish species avoid the subzero waters of the cold pool (Moiseev, 1964). In contrast, during the warm period in the late 1970s and 1980s, the total biomass of benthic infaunal consumers on the southeastern Bering Sea shelf increased (Livingston et al., 1999), particularly the yellowfin sole (*Limanda aspera*), rock sole (*Lepidopsetta bilineata*) and flathead sole (*Hippoglossoides elassodon*). The mean bottom temperatures between 1969 and 1993 showed a distinct minimum between 1971 and 1976, reflecting a period of unusually cold temperatures on the shelf (Livingston et al., 1999). In contrast to the above fish species, high recruitment of king crab (*Paralithodes camtschatica*) occurred in the early 1970s (Zheng and Kruse, 2000) when mean bottom temperatures were low. Low king crab recruitment was observed in the late 1970s and early 1980s, when temperatures were high (Zheng and Kruse, 2000). These trends suggest that temperature can markedly influence the abundance of predators on infaunal invertebrates. Thus, warmer temperatures not only could lead to lower

overall carbon flux to the benthic infaunal community on the southeastern Bering Sea shelf, but also may result in higher overall abundance, and by extension, predation by vertebrate infaunal consumers. The evidence suggests that warming conditions on the Bering Sea shelf could substantially alter energy flow and food web relationships in the benthic infaunal community, leading to overall declines in infaunal biomass.

Benthic infaunal communities in cold bottom water with high carbon flux to the benthos on the Bering Sea shelf can have high production and generate unusually high biomass (Highsmith and Coyle, 1990; Coyle and Highsmith, 1994). The high production rate is due to the accumulation of high biomass in the larger animals (Highsmith and Coyle, 1991). Although the production–biomass (*PB*) ratio is lower in cold arctic conditions, apparently due to lower overall metabolic rates, the cold environment apparently promotes the accumulation of biomass in large individuals, thus compensating for the lower *PB* ratios observed in benthic amphipod communities (Highsmith and Coyle, 1991). The combination of elevated carbon flux to the benthos and high biomass of infaunal suspension feeders results in a short, very efficient food chain linking primary production to marine mammal predators such as gray whales (Highsmith and Coyle, 1992).

The response of a benthic community to climate variation is also influenced by the generation times of the organisms relative to the duration of the climate cycle. The generation times of infaunal benthos can be extremely variable, from months for small crustaceans and worms, to decades for large bivalves (Sainte-Marie, 1991; Feder et al., 1979). In addition, animals with meroplanktonic larvae may be introduced in high numbers from regions outside of the study area. It is therefore difficult to make generalizations about the response time of the community to a climatic or physical disturbance. Disturbance studies in the Barents Sea indicate response times for some communities on the order of 4 years (Denisenko, 2001); however, these times are likely to be highly variable from region to region and community to community and cannot be readily generalized. Benthic communities may also be influenced by trawling, particularly the shallow infaunal taxa. Determination of the actual response time of a benthic community to a disturbance requires long-term monitoring of the community.

5. Conclusion

As concern about the impacts of global climate change on the environment grows, historical data become increasingly valuable as base lines for evaluating climate-related shifts in species composition and biomass. Nevertheless, comparison of data from different institutions, taken at different times is often complicated by potential biases due to different sampling designs and processing protocols. The potential biases in this study were minimized by using only infaunal samples washed on 1-mm screens, including only those regions where station overlap was greatest, restricting biomass comparisons of taxonomic groups to the family level where both families were present in the data, and application of spatial statistics where spatial correlations were observed in the data. In this study, of the 21 benthic infaunal families present in both data sets and showing significant biomass differences between the warmer period of the late 1950s, and the unusually cold period of the mid-1970s, 19 had higher biomass during the cold period. The above observations are consistent with a climate-change scenario generating lower carbon flux to the benthic community and elevated intensity of fish predation on infaual invertebrates during warmer periods. Comparisons in this study were complicated by differences in sampling gear, a lack of replication in the Russian data, and some differences in station distribution and sample processing protocols. However, these difficulties do not preclude description of trends in the data using accepted statistical methods nor comparison of these trends to those expected in a climate change scenario as outlined above.

While the biomass trends outlined in this paper are suggestive of a climate effect, the benthic infaunal community may be influenced by additional disturbances such as trawling or pollution. The actual response of any community to a disturbance requires long-term data before and after the disturbance, to document the initial impact and the community response. Since climate influences are likely to operate at time scales of decades to centuries, the 1- and 2-year studies common in the scientific literature are insufficient to definitively document climate impacts. Nevertheless, the data from the 1958–1959 and 1975–1976 studies provide critical base line information against which to evaluate future changes in the southeastern Bering Sea benthic community.

Acknowledgments

We express our gratitude to the following individuals who participated in the planning, organization and execution of various aspects of this research effort: Sabine Cochrane, Howard Feder, Tom Pearson, Andrey Proshutensky and Tatiana Savinova; A.A. Neyman (Russian Federal Research Institute of Fisheries and Oceanography) participated in the collection, processing and identification of the Russian material. This research was funded by National Science Foundation Office of Polar Programs award number OPP-0002239 through the International Arctic Research Center. This paper was first presented in the GLOBEC-ESSAS Symposium on Effects of climate variability on sub-arctic marine ecosystems, hosted by PICES in Victoria, BC, May 2005.

References

Abbott, R.T., 1974. American Seashells: The Marine Mollusca of the Atlantic and Pacific Coasts of North America. Van Nostrand Reinfold Co., New York, 663pp.

Bertram, D.F., Mackas, D.L., McKinnell, S.M., 2001. The seasonal cycle revisited: interannual variation and ecosystem consequences. Progress in Oceanography 49 (1–4), 283–307.

Bolam, S.G., Fernandez, T.F., Huxham, M., 2002. Diversity, biomass, and ecosystem processes in the marine benthos. Ecological Monographs 72 (4), 599–615.

Bond, N.A., Adams, J.M., 2002. Atmospheric forcing of the southeast Bering Sea shelf during 1995–99 in the context of a 40-year historical record. Deep-Sea Research II 40, 5869–5887.

Brodeur, R.D., Mills, C.E., Overland, J.E., Shumacher, J.D., 1999. Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. Fisheries Oceanography 8 (4), 296–306.

Burrell, D.C., Tommos, K., Naidu, A.S., Hoskin, C.M., 1981. Some geochemical characteristics of Bering Sea sediments. In: Hood, D.W., Calder, J.A. (Eds.), The Eastern Bering Sea Oceanography and Resources. Office of Marine Pollution Assessment, NOAA, University of Washington Press, Seattle, pp. 305–319.

Callaghan, T.V., Press, M.C., Lee, J.A., Robinson, D.L., Anderson, C.W., 1998. Spatial and temporal variability in the responses of Arctic terrestrial ecosystems to environmental change. Proceedings of the International Symposium on Polar Aspects of Global Change. Polar Research 18 (2), 191–197.

Carroll, M.L., Carroll, J., 2003. The Arctic Seas. In: Black, K., Shimmield, G. (Eds.), Biogeochemistry of Marine Systems. Blackwell Publishing Ltd., Oxford, UK, pp. 127–156.

Cattle, H., Crossley, J., 1995. Modeling Arctic climate change. Philisophical Transactions of the Royal Society, London A 352, 201–213.

Chapman, W.L., Walsh, J.E., 1993. Recent variation of sea ice and air temperatures in high latitudes. Bulletin of the American Meteorological Society 74, 33–47.

Clarke, A., Harris, C.M., 2003. Polar marine ecosystems: major threats and future change. Environmental Conservation 30, 1–25.

Coachman, L.K., 1986. Circulation, water masses, and fluxes on the southeastern Bering Sea shelf. Continental Shelf Research 5 (1–2), 23–108.

Constable, A.J., Nicol, S., Strutton, P.G., 2003. Southern Ocean productivity in relation to spatial and temporal variation in the physical environment. Journal of Geophysical Research (C Oceans) 108 (C4 (np)).

Cooney, R.T., Coyle, K.O., 1982. Trophic implications of cross-shelf copepod distributions in the southeastern Bering Sea. Marine Biology 70, 187–196.

Coyle, K.O., Cooney, R.T., 1988. Estimating carbon flux to pelagic grazers in the ice-edge zone of the eastern Bering Sea. Marine Biology 98, 299–306.

Coyle, K.O., Highsmith, R.C., 1994. Benthic amphipod community in the northern Bering Sea: analysis of potential structuring mechanisms. Marine Ecology Progress Series 107, 233–244.

Coyle, K.O., Pinchuk, A.I., 2002. Climate-related differences in zooplankton density and growth on the inner shelf of the southeastern Bering Sea. Progress in Oceanography 55, 177–194.

Coyle, K. O., Bluhm, B., Konar, B., Blanchard, A., Highsmith, R. C., 2007. Amphipod prey of gray whales in the northern Bering Sea: comparison of biomass and distribution between the 1980s and 2002–2003. Deep-Sea Research II, doi:10.1016/j.dsr2.2007.08.026.

Cressie, N., Hawkins, D.M., 1980. Robust estimation of the variogram, I. Mathematical Geology 12 (2), 115–125.

Dahle, S., Denisenko, S.G., Denisenko, N.V., Cochrane, S.J., 1998. Benthic fauna in the Pechora Sea. Sarsia 83, 183–210.

Dement'ev, A.A., 1991. Year-to-year oscillations of air temperature in the Greenland and Norwegian Seas. Problemy Arktiki i Antarktiki 65, 6–13 (in Russian).

Denisenko, S.G., 2001. Long-term changes of zoobenthos biomass in the Barents Sea. Proceedings of the Zoological Institute, Russian Academy of Sciences 289, 59–66.

Denisenko, S.G., Denisenko, N.V., Dahle, S., Cochrane, S.J., 2005. The zoobenthos of the Pechora Sea revisited: a comparative study. Reports on Polar and Marine Research 501, 55–73.

Dickson, R.R., Meincke, J., Malmberg, S.A., Lee, A.J., 1988. The "Great Salinity Anomoly" in the northern North Atlanic, 1968–1982. Progress in Oceanography 20, 103–151.

Dunstan, P.K., Johnson, C.R., 2003. Competition coefficients in a marine epibenthic assemblage depend on spatial structure. Oikos 100 (1), 79–88.

Ebbesmeyer, C.C., Cayan, D.R., McClain, D.R., Nichols, F.H., Peterson, D.H., Redmond, K.T., 1990. 1976 step in Pacific climate: forty environmental changes between 1968–1975 and 1977–1984. In: Betancourt, J.L., Tharp, V.L. (Eds.), Proceedings of the Seventh Annual Pacific Climate (PACLIM) Workshop, April, California Department of Water Resources, Interagency Ecological Study Program Technical Report 26, pp. 115–126.

Eckman, J.E., 1996. Closing the larval loop: linking larval ecology to the population dynamics of marine benthic

invertebrates. Journal of Experimental Marine Biology and Ecology 200 (1–2), 207–237.

Feder, H.M., Paul, A.J., Paul, J.M., 1979. The pinkneck clam *Spisula polynyma* in the eastern Bering Sea: growth, mortality, recruitment and size at maturity. In: Proceeding of the 29th Alaska Science Conference, Sea Grant Report 79-6, pp. 717–738.

Feder, H.M., Naidu, A.S., Jewett, S.C., Hameedi, J.M., Johnson, W.R., Whitledge, T.E., 1994a. The northeastern Chuckchi Sea: benthos–environmental interactions. Marine Ecology Progress Series 111, 171–190.

Feder, H.M., Foster, N.R., Jewett, S.C., Weingartner, T.J., Baxter, R., 1994b. Mollusks in the Northeastern Chukchi Sea. Arctic 47, 145–163.

Galbraith, H., Jones, R., Park, R., Clough, J., Herrod-Julius, S., Harrington, B., Page, G., 2002. Global Climate Change and Sea Level Rise: Potential Losses of Intertidal Habitat for Shorebirds. Waterbirds 25 (2), 173–183.

Graham, M.H., Dayton, P.K., Erlandson, J.M., 2002. Ice ages and ecological transitions on temperate coasts. Trends in Ecology and Evolution 18, 33–40.

Grebmeier, J.M., 1993. Studies of pelagic–benthic coupling extended onto the Soviet Continental Shelf in the northern Bering and Chukchi Seas. Continental Shelf Research 13, 653–668.

Grebmeier, J.M., McRoy, C.P., Feder, H.M., 1988. Pelagic–benthic coupling on the shelf of the Northern Bering and Chukchi Seas. 1. Food supply source and benthic biomass. Marine Ecology Progress Series 48, 57–67.

Greshanovich, D.E., 1964. Donyye otlozheniya tsentrl'nykh i vostochnykh oblastey Beringova morya (Benthic sediments of the central and eastern Bering Sea). In: Moiseev, P.A. (Ed.), Soviet Fisheries Investigations in the Northeastern Pacific. Proceedings TINRO, vol. 52, Pishchevaya Promyshlennost' Press, Moscow, pp. 31–81.

Haflinger, K., 1978. A numerical analysis of the distribution of the benthic infauna of the southeastern Bering Sea shelf. Masters Thesis, University of Alaska Fairbanks, 136pp, unpublished.

Haflinger, K., 1981. A survey of benthic infaunal communities of the southeastern Bering Sea shelf. In: Hood, D.W., Calder, J.A. (Eds.), The Eastern Bering Sea Oceanography and Resources. Office of Marine Pollution Assessment, NOAA, University of Washington Press, Seattle, pp. 1091–1103.

Hassol, S.J., 2004. Impacts of a Warming Arctic: Arctic Climate Impact Assessment. Cambridge University Press, Cambridge UK, 139pp.

Highsmith, R.C., Coyle, K.O., 1990. High productivity of northern Bering Sea benthic amphipods. Nature 344, 862–864.

Highsmith, R.C., Coyle, K.O., 1991. Amphipod life histories: community structure, impact of temperature on decoupled growth and maturation rates, productivity and *P:B* ratios. American Zoologist 31, 861–873.

Highsmith, R.C., Coyle, K.O., 1992. Productivity of arctic amphipods relative to gray whale energy requirements. Marine Ecology Progress Series 83, 141–150.

Hunt Jr., G.L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R.D., Napp, J.M., Bond, N.A., 2002. The eastern Bering Sea: evidence for change and a new hypothesis linking ecosystem control and climate. Deep-Sea Research II 49 (26), 5821–5853.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54, 187–211.

Iken, K., Brey, T., Wand, U., Voigt, J., Junghans, P., 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. Progress in Oceanography 50 (1–4), 383–405.

IPCC, 1998. The Regional Impacts of Climate Change: An Assessment of Vulnerability. Cambridge University Press, Cambridge, UK.

IPCC, 2001. Climate Change 2001: The Scientific Basis. In: Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Xiaosu, D. (Eds.), Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge, UK, 944pp.

Kachel, N.B., Hunt, G.L., Salo, S.A., Schumacher, J.D., Stabeno, P.J., Whitledge, T.E., 2002. Characteristics and variability of the inner front of the southeastern Bering Sea. Deep-Sea Research II 49 (25), 5889–5909.

Kern, J.W., Coyle, K.O., 2000. Global block kriging to estimate biomass from acoustic surveys for zooplankton in the western Aleutian Islands. Canadian Journal of Fisheries Aquatic Science 57, 2112–2121.

Kinder, T.H., Schumacher, J.D., 1981. Hydrographic structure over the continental shelf of the southeastern Bering Sea. In: Hood, D.W., Calder, J.A. (Eds.), The Eastern Bering Sea Oceanography and Resources. Office of Marine Pollution Assessment, NOAA, University of Washington Press, Seattle, pp. 31–52.

Livingston, P.A., Low, L.L., Marasco, R.J., 1999. Eastern Bering Sea trends. In: Sherman, K., Tang, Q. (Eds.), Large Marine Ecosystems of the Pacific Rim: Assessment, Sustainability and Management. Blackwell Science Inc., Malden, MA, USA, pp. 140–162.

Moiseev, P.A., 1964. Nekotorye itogi issledovaniy Beringovomorskoy nauchno-promyslovoy expeditsii (Some results of the Bering Sea scientific and fisheries expedition). In: Moiseev, P.A. (Ed.), Soviet Fisheries Investigations in the Northeastern Pacific. Proceedings of TINRO, vol. 52, Pishchevaya Promyshlennost' Press, Moscow, pp. 7–29.

McDonald, J., Feder, H.M., Hoberg, M., 1981. Bivalve mollusks of the Southeastern Bering Sea. In: Hood, D.W., Calder, J.A. (Eds.), The Eastern Bering Sea Oceanography and Resources. Office of Marine Pollution Assessment, NOAA, University of Washington Press, Seattle, pp. 1155–1204.

Napp, J.M., Hunt Jr., G.L., 2001. Anomalous conditions in the south-eastern Bering Sea 1997: linkages among climate, weather, ocean and biology. Fisheries Oceanography 10 (1), 61–68.

Neyman, A.A., 1963. Kolichestvennoe raspredelenie bentosa na shel'fe i verkhnikh gorizontakh sklona vostochnoy chasti Beringoga moray (Quantitative distribution of benthos on the shelf and upper slope of the eastern Bering Sea). In: Moiseev, P.A. (Ed.), Soviet Fisheries Investigations in the Northeastern Pacific. 5. Proceedings of TINRO, vol. 50, Pishchevaya Promyshlennost' Press, Moscow, pp. 145–20.

Niebauer, H.J., Alexander, V.A., Henrichs, S.M., 1990. Physical and biological oceanographic interactions in the spring bloom at the Bering Sea marginal ice zone. Journal of Geophysical Research 95, 22229–22242.

Niebauer, H.J., Alexander, V.A., Henrichs, S.M., 1995. A time-series study of the spring bloom at the Bering Sea ice edge. I. Physical processes, chlorophyll, and nutrient chemistry. Continental Shelf Research 15, 1859–1877.

Nirini, M.K., Oliver, J.S., 1983. Gray whales and the structure of the Bering Sea benthos. Oecologia 59, 224–225.

Overland, J.E., Stabeno, P.J., 2004. Is the climate of the Bering Sea warming and affecting the ecosystem? EOS, Transactions, American Geophysical Union 85 (33), 309–316.

Overland, J.E., Bond, N.A., Adams, J.M., 2001. North Pacific atmospheric and SST anomalies in 1997: links to ENSO. Fisheries Oceanography 10 (1), 69–80.

Osterkamp, T.E., 1994. Evidence for warming and thawing of discontinuous permafrost in Alaska. EOS, Transactions, American Geophysical Union 75, 85.

Parkinson, C.L., 1991. Interannual variability of the spatial distribution of sea ice in the North Polar Region. Journal Geophysical Research 96, 4791–4801.

Pearson, R.G., Dawson, T.P., 2003. Research review: predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12 (5), 361–371.

Pettibone, M., 1963. Marine polychaetes of the New England region. Smithonian Institution, Washington, DC, 356pp.

Rabouille, C., Witbaard, R., Duineveld, G.C.A., 2001. Annual and interannual variability of sedimentary recycling studied with a non-steady-state model: application to the North Atlantic Ocean (BENGAL site). Progress in Oceanography 50 (1–4), 147–170.

Rho, T., Whitledge, T.E., Goering, J.J., 2005. Interannual variations of nutrients and primary production over the southeastern Bering Sea shelf during the spring of 1997, 1998 and 1999. Oceanology 45, 376–390.

Sainte-Marie, B., 1991. A review of the reproductive bionomics of aquatic gammaridean amphipods: variation of life history traits with latitude, depth, salinity and superfamily. Hydrobiologia 223, 189–227.

Sambrotto, R.N., Niebauer, H.J., Goering, J.J., Iverson, R.L., 1986. Relationships among vertical mixing, nitrate uptake, and phytoplankton growth during the spring bloom in the southeast Bering Sea middle shelf. Continental Shelf Research 5 (1–2), 161–198.

Semenov, V.N., 1964. Kolichestvennoe raspredelenie bentoca na shel'fe yugo-vostochnoy chasti Beringova morya (Quantitative distribution of benthos on the southeastern Bering Sea shelf). In: Moiseev, P.A. (Ed.), Soviet Fisheries Investigations in the Northeastern Pacific. Proceedings of TINRO, vol. 52, Pishchevaya Promyshlennost' Press, Moscow, pp. 177–184.

Smith, R.C., Ainley, D., Baker, K., Domak, E., Emslie, S., Frasier, B., Kennett, J., Leventer, A., Mosely-Thompson, E., Stammerjohn, S., Vernet, M., 1999. Marine Ecosystem sensitivity to climate change. Bioscience 49, 393–404.

Smith, S.L., Vidal, J., 1986. Variations in the distribution, abundance, and development of copepods in the southeastern Bering Sea in 1980 and 1981. Continental Shelf Research 5 (1–2), 215–239.

Stabeno, P.J., Bond, N.A., Kachel, N.B., Salo, S.A., Schumacher, J.D., 2001. On the temporal variability of the physical environment over the south-eastern Bering Sea. Fisheries Oceanography 10 (1), 81–98.

Stockwell, D.A., Whitledge, T.E., Zeeman, S.I., Coyle, K.O., Napp, J.M., Brodeur, R.D., Pinchuk, A.I., Hunt Jr., G.L., 2001. Anomalous conditions in the south-eastern Bering Sea, 1997: nutrients, phytoplankton and zooplankton. Fisheries Oceanography 10 (1), 99–116.

Suyker, A.E., Verma, S.B., Burba, G.G., 2003. Interannual variability in net CO_2 exchange of a native tall grass prairie. Global Change Biology 9 (2), 255–265.

Thomson, D.H., Martin, L.R., 1986. Feeding ecology of gray whales (*Eschrichtius robustus*) in the Chirikov Basin, summer 1982. NOAA, US Department of Commerce, OCSEAP Final Report 43, pp. 377–460.

Vidal, J., Smith, S.L., 1986. Biomass, growth, and development of populations of herbivorous zooplankton in the southeastern Bering Sea during spring. Deep-Sea Research 33 (4), 523–556.

Wadhams, P., 2000. Further evidence of ice thinning in the Arctic Ocean. Geophysical Research Letters 27 (24), 3973–3975.

Walsh, J.J., McRoy, C.P., 1986. Ecosystem analysis in the southeastern Bering Sea. Continental Shelf Research 5 (1–2), 259–288.

Weller, G., Lange, M., 1999. Impacts of global climate change in the Arctic regions. An initial assessment. International Arctic Science Committee (IASC), Oslo, Norway, 30pp.

Whitledge, T.E., Reeburgh, W.S., Walsh, J.J., 1986. Seasonal inorganic nitrogen distribution and dynamics in the southeastern Bering Sea. Continental Shelf Research 5, 109–132.

Williamson, C.E., Grad, G., DeLange, H.J., Gilroy, S., Karapelou, D.M., 2002. Temperature-dependent ultraviolet responses in zooplankton: implications of climate change. Limnology Oceanography 47 (6), 1844–1848.

Wyllie-Echeverria, T., Wooster, W.S., 1998. Year-to-year variations in Bering Sea ice cover and some consequences for fish distributions. Fisheries Oceanography 7 (2), 159–170.

Zenkevich, L.A., 1927. Quantitative estimation of the bottom fauna of the Pechora region of the Barents and White Seas. Proceedings of the Floating Marine Science Institute 2 (4), 3–64.

Zheng, J., Kruse, G., 2000. Recruitment patterns of Alaskan crab in relation to decadal shifts in climate and physical oceanography. ICES Journal of Marine Science 57, 438–451.