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Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. II. Benthic community structure

Jacqueline M. Grebmeier*, Howard M. Feder, C. Peter McRoy

Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska 99775-1080, USA

ABSTRACT: Benthic fauna abundance, biomass and diversity were investigated in the northern Bering and Chukchi Seas to determine factors influencing faunal distribution in this polar region. The hypothesis tested whether sediment grain size and water mass characteristics, such as organic carbon supply to the benthos and temperature, are regulating factors in benthic community structure. Benthic communities under the cold, highly productive (~250 to 300 g C m^{-2} yr^{-1}) Bering Shelf-Anadyr Water (BSAW) are dominated by a high biomass of amphipods (F. Ampeliscidae and F. Isaeidae) and bivalves (F. Nuculidae and F. Tellinidae). A diverse, low biomass fauna exists in benthic communities under the warmer, less productive (~50 g C m^{-2} yr^{-1}) Alaska Coastal Water (ACW), including amphipods (F. Isaeidae and F. Ampeliscidae), bivalves (F. Tellinidae and F. Thyasiridae), polychaetes (F. Maldanidae and Nephtyidae), and sand dollars (F. Echinarachniidae). Faunal diversities are lowest for stations under BSAW, characterized by high food supply and moderately homogeneous (well-sorted), sandy sediments. Highest diversities occur at stations in ACW, which is characterized by low food supply and a more heterogeneous (poorly-sorted) mixture of silt and clay, sand and gravel sediments. Faunal diversity also increased to the north in the Chukchi Sea, where food availability in the bottom water and surface sediments was greater and more heterogeneous, finer-grain sediments occur. The findings indicate that sediment heterogeneity, silt and clay fractions, and temperature are major regulating factors on benthic community structure, with each positively influencing faunal diversity. Lower diversity was correlated to an increase in fine sand fractions. Food supply, both in the bottom water and surface sediments, has a more variable influence on benthic community structure, although it has a direct positive influence on benthic biomass.

INTRODUCTION

Shallow marine benthic systems in polar regions can exhibit high faunal abundances and biomass in spite of low temperatures and seasonal, spring and summer, fluxes of particulate organic matter to the benthos (White 1977, Petersen & Curtis 1980, Grebmeier 1987). An important question in marine ecology concerns the mechanisms that regulate benthic community structure (Valiela 1984). In Arctic and Antarctic benthic fauna, slow growth and long life spans, along with variable food supplies and diverse substrate conditions, are factors known to influence benthic faunal abundance and biomass (White 1977, 1984, Clarke 1980, Petersen & Curtis 1980, Feder & Jewett 1981, Stoker 1981, Grebmeier 1987).

Past studies in shallow regions of the Bering and Chukchi Seas indicate that high benthic abundance and biomass values often correspond to areas of enhanced deposition of phytodetritus to the benthos, particularly in low temperature, high salinity water mass regimes (Haflinger 1981, Stoker 1981, Feder at al. 1985). A synoptic view of the location of major water masses during the summer, water column chlorophyll *a* concentrations, differences in annual primary production, and variance in benthic community structure and biomass in the northern Bering and Chukchi Seas indicates a strong coupling between water mass characteristics, food supply and benthic processes (Grebmeier 1987). In the present study, we examine the distribution, diversity and biomass of benthic stations combined by similarity analysis of faunal abundance in relation to hydrographic and sediment characteristics.

Hydrographic characteristics on the shallow shelf (<50 m) of the northern Bering and Chukchi Seas have

* Address for correspondence: Graduate Program in Ecology, University of Tennessee, Knoxville, Tennessee 37996–1610, USA

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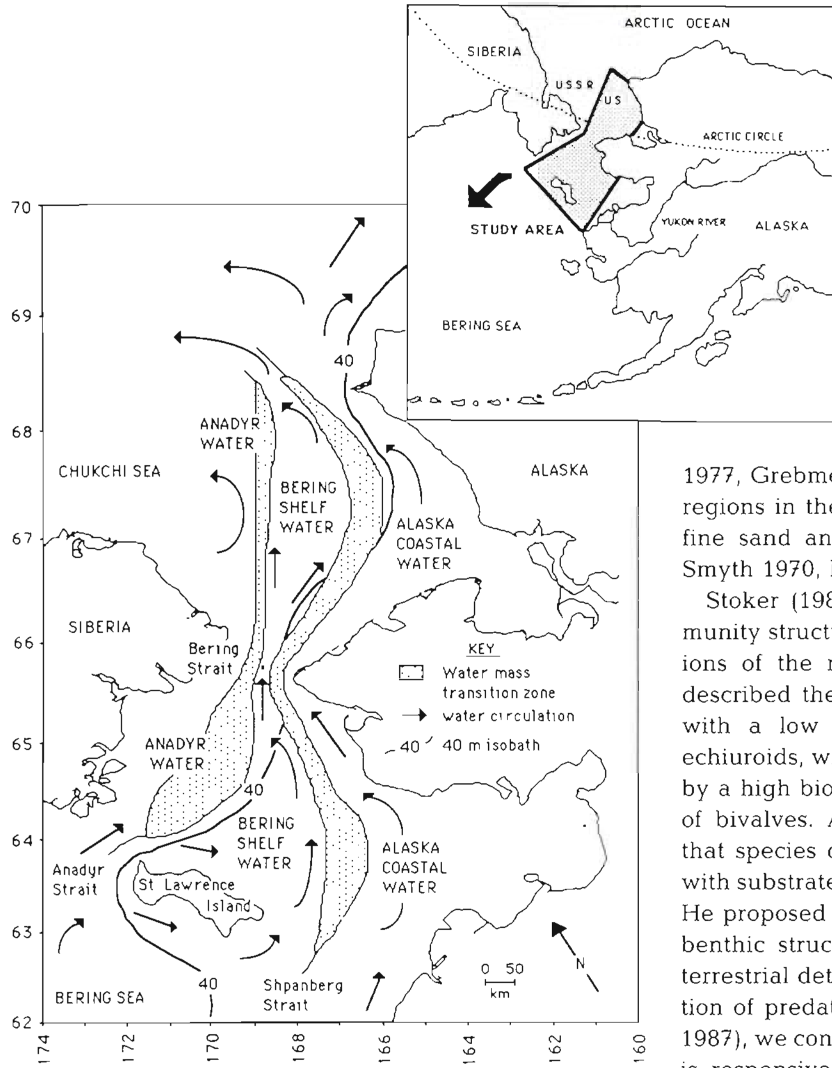

Fig. 1. Study area in the northern Bering and Chukchi Seas showing local water circulation, water masses, and bathymetry (modified from Coachman et al. 1975, Nelson et al. 1981, and Coachman 1987)

been described previously (Grebmeier 1987, Grebmeier et al. 1988; Fig. 1). This area contains 3 northward-flowing water masses: the Anadyr and Bering Shelf waters, forming a modified Bering Shelf-Anadyr Water (BSAW) to the west, characterized by low temperatures (-1 to $+2.0\,°C$) and relatively high salinity (>31.8 ‰), and Alaska Coastal Water (ACW) to the east, characterized by higher temperatures ($>+2\,°C$) and lower salinity (<31.8 ‰; Coachman et al. 1975, Coachman 1987). BSAW has an estimated annual primary production of 250 to 300 g C m^{-2} compared to an annual primary production of 50 g C m^{-2} in ACW (Sambrotto et al. 1984, Walsh et al. 1987, Springer 1988). The central regions of the northern Bering Sea are characterized by fine and very fine sand, with coarser grained sand, gravel and cobbles near the outer boundaries of the northern Bering Sea, also known as the Chirikov Basin, and in the Anadyr and Bering Straits (Creager & McManus 1967, McManus et al. 1977, Grebmeier 1987; Fig. 1). In comparison, offshore regions in the Chukchi Sea are characterized by very fine sand and silt and clay sediments (McManus & Smyth 1970, McManus et al. 1977, Grebmeier 1987).

Stoker (1981) reported differences in benthic community structure between the coastal and offshore regions of the northern Bering and Chukchi Seas. He described the benthos along the Alaska coast as one with a low biomass of polychaetes, bivalves, and echiuroids, while the offshore region was characterized by a high biomass of amphipods and different species of bivalves. Although Stoker qualitatively concluded that species distribution and biomass were correlated with substrate type, he had limited environmental data. He proposed 4 potential factors which could influence benthic structure and biomass: primary productivity, terrestrial detrital input, current regimes, and distribution of predators. In a related study (Grebmeier et al. 1987), we concluded that benthic biomass in this region is responsive to the quality and quantity of organic carbon reaching the benthos from the overlying water column in the northern Bering and Chukchi Seas. In this study we investigate the effect of food supply on faunal abundance and diversity and the role of other environmental variables on benthic community structure.

Food supply from high primary production has been proposed as a regulating factor in benthic community structure in shallow marine waters in the Antarctic (Clarke 1980). Dayton & Oliver (1977) found benthic abundance was highest on the east side of McMurdo Sound under eutrophic waters compared to low faunal abundance in the oligotrophic west side of the Sound. Stewart et al. (1985) suggested that the benthic faunal groupings they observed on the Canadian continental shelf and slope corresponded the best with major water mass and temperature regimes in the area, although no water column primary production or phytoplankton biomass were investigated.

Sediment grain size composition plays an important role in determining the structure of benthic communities (Gray 1981). For example, Fresi et al. (1983), in a study off the coast of Italy, demonstrated that zonation of benthic communities correlated most strongly with sediment structure, interpreted as a reflection of water motion gradients. Heterogeneous sediments have been implicated as influences of high benthic faunal diversities in the Gulf of St Lawrence, as well as water temperature and depth (Long & Lewis 1987). In another study in the Gulf of St Lawrence, Robert (1979) proposed that species richness increased with sand content, regardless of associated water depth. The percentage of very fine sand and the combined silt and clay fraction have been shown to differentiate biotic assemblages on the continental shelf off North Carolina (Weston 1988). This study also demonstrated the importance of sediment sorting in determining dominant fossorial (tube-building) species. We hypothesize that both sediment heterogeneity and water characteristics are regulating factors in community structure in the northern Bering and Chukchi Seas.

MATERIALS AND METHODS

Water column and benthic sampling occurred in the northern Bering and Chukchi Seas during the open-water season (Fig. 1). Four replicate 0.1 m^2 van Veen grabs (weighted with 32 kg lead) were taken at each station for sampling the benthos. Samples were washed on 1 mm sieve screens, preserved in 10 % hexamethyltetramine-buffered formalin, stored in plastic Whirl-pak^{TM} bags, and saved for laboratory analysis. Animals were identified to family level, counted, and weighed to determine abundance and wet weight biomass. Previous work in this region has shown that only 1 to 5 species occurred in each dominant family, with a majority of families containing only 1 or 2 species (Stoker 1981, Grebmeier 1987). Therefore, the familial level determinations were considered an adequate measure of faunal composition and the clustering program presented a valid methodology for analysis. Preserved wet weight biomass was converted to carbon biomass using the conversion values of Stoker (1978) following the method of Grebmeier (1987).

Highly motile epifaunal organisms (crabs, predatory gastropods and sea stars) were excluded from the analysis. Stations dominated by relatively sessile and sessile epifaunal organisms, such as sea anemones, barnacles, bryozoans, and sea urchins were included. Colonial organisms (sponges, sea anenomes, and ectoprocts) were given an abundance count of 1 for each colony observed. Fragments were given an abundance value of 1 and then weighed as a sum total of fragments for that taxon determination. The van Veen grab was unable to capture deep-dwelling bivalves, Myidae and Mactridae, a problem also recognized by previous workers (Stoker 1981, Feder et al. 1985).

Abundance data were used in a numerical clustering program to group stations according to faunal similarities (Stoker 1981, Feder et al. 1985). The program clusters stations on the basis of similarities in relative percent of faunal composition using the Czekanowski similarity coefficient (Stephenson et al. 1972). Log transformations of abundance data $[\ln(x + 1)]$ were used because the Czekanowski coefficient is sensitive to extremely large abundance values (Boesch 1973), which occurred in our data. A mean biomass was calculated for station groups by determining the mean of the stations combined by cluster analysis.

The Shannon-Weaver indices of diversity (H') and evenness (J) were determined for stations and station cluster groups, based on families, following the methodology of Long & Lewis (1987). Family diversity and evenness are used in comparisons of station groups within defined water types.

Sediment samples were collected with a Haps corer or MK3 box corer. Subsamples were taken with either 6 or 13 cm diameter plexiglas cores, 26 cm long, and frozen for later laboratory analysis. Based upon indications at a subset of stations in both BSAW and ACW that there was no change of sediment grain size with depth in the top 5 to 10 cm, only surface sediment values were used. Surface sediments (0 to 1 cm) were sectioned, dried, homogenized and sampled for sediment grain size analysis by dry sieving, using standard geological sieves (−1 and 1 to 4 phi sizes) and a Ro-tap machine (Folk 1980). Sediments were weighed after sieving and a modal sediment size and percent composition calculated.

A sediment sorting coefficient (Graphic Standard Deviation) was calculated and represents the degree of mixing of different sediment types (Gray 1981). Well-sorted sediments, indicative of homogeneous sediments, normally occur in high energy areas, while poorly-sorted sediments, indicative of heterogeneous sediments, normally occur in low energy areas. A ranking of sediment heterogeneity based on sorting coefficients was determined for all stations using the index presented in Fig. 2.

Correlations between station variables and sediment parameters were investigated using both parametric (Pearson product-moment r) and nonparametric (Spearman's rho) correlation tests. Parametric tests were utilized when a large enough sample size was available to assume a normal distribution. A microcomputer statistical package was utilized (BrainPower Inc. 1985) and test statistics were evaluated using standard tables (Rohlf & Sokal 1969, Conover 1980).

Bottom salinity, temperature, depth and chlorophyll *a* biomass data were obtained in conjunction with other investigators using a Niel Brown conductivity-temperature-depth (CTD) profiler and Nisken rosette (McRoy & Tripp 1986, 1987). The method for determining total organic carbon (TOC) and nitrogen (TON) for surface sediments and the subsequent data used in this study have been described elsewhere (Grebmeier 1987, Grebmeier et al. 1988). Station numbers are presented as the 2-digit cruise number followed by the 3-digit consecutive station number for that cruise.

	Index for Sediment Sorting Coefficient (ϕ)				
Sorting coefficient	<.35	.35	.50	.71	1.0 – 2.0
Class of sediments	very well sorted	well sorted	moderately well sorted	moderately sorted	poorly sorted
Sediment heterogeneity (rank of sorting coefficient)	1	2	3	4	5
	Homogeneous sediments ⟵				⟶ Heterogeneous sediments

Fig. 2. Index for sediment sorting coefficients (from Gray 1981), the corresponding class of sediment, and an associated gradient to rank sediment sorting in relation to sediment heterogeneity

RESULTS

Benthic stations were occupied over 3 field seasons from July to September in the years 1984 to 1986 using the RV 'Alpha Helix'. Temperature and salinity data confirm presence of a front dividing Bering Shelf-Anadyr Water (BSAW) from Alaska Coastal Water (ACW; Coachman 1987). The average location of the seasonal front was used to designate station locations relative to BSAW and ACW. Hydrographic data, along with benthic faunal abundance, biomass, diversity and evenness, were analysed for 49 stations (Fig. 3, Table 1). Surface sediments were collected at 33 of these stations and modal size class, grain size composition, sorting coefficients and sediment heterogeneity were subsequently determined (Table 2).

Sediment composition

The percent composition of various grain size classes in the surface sediments showed a separation of stations between the northern Bering and Chukchi Seas (Fig. 4). A majority of the Bering Sea stations were in the >70 % sand substrate class, while those in the Chukchi Sea are near the 50 % sand/silt and clay sediment class. Stations with highest coarse sand and gravel content typically are in ACW in both the northern Bering and Chukchi Seas.

There were significant correlations between surface sediment TOC and TON and percent silt and clay, percent fine sand, and sediment heterogeneity, based on sediment sorting (Table 3). Surface sediment TOC and TON are positively correlated with percent silt and clay, which was highest in the Chukchi Sea, and were negatively correlated with increasing percent fine sand, the major sediment type in the northern Bering Sea (Fig. 4). Sediment sorting and heterogeneity were positively correlated with TOC and TON (Table 3).

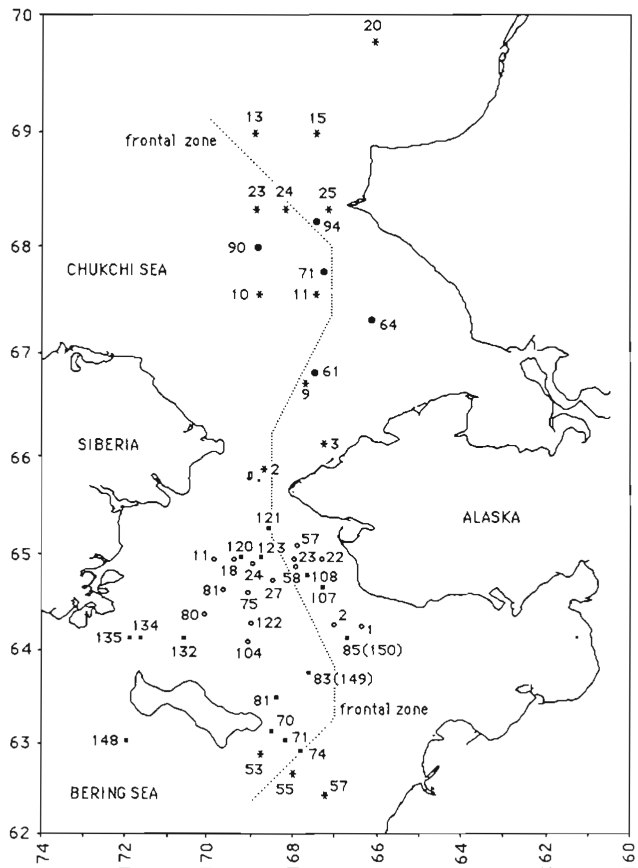

Fig. 3. Location of benthic sampling stations in the northern Bering and Chukchi Seas for Cruises 59 (■), 73 (○), 74 (*) and 85 (●). A frontal zone separates Bering Shelf-Anadyr Water in the west from Alaska Coastal Water in the east

Benthic community structure

A total of 60 faunal families comprised 95 % of the ranked abundance and biomass during the study (Table 4); many different families comprise the remain-

Table 1. Summary of station hydrographic and biological measurements for Cruises 59, 73, 74 and 85 in the northern Bering and Chukchi Seas. Benthic faunal diversity (H') and evenness (J) were calculated from the abundance data. Blanks: no data available

Station	Bottom temp. (°C)	Bottom salinity (‰)	Bottom sigma-t	Depth (m)	Benthic Abundance (ind. m^{-2})	Benthic Biomass (g C m^{-2})	H'	J
59070	−0.98	33.429	26.88	26	313	22.9	2.22	0.75
59071	−0.24	33.229	26.69	20	463	18.6	1.01	0.40
59074	0.00	33.237	26.68	19	140	2.6	2.42	0.87
59081	−0.68	33.412	26.85	25	900	13.7	2.02	0.74
59107	0.16	33.377	26.79	27	7770	2.0	0.61	0.20
59108	−0.16	33.183	26.65	36	315	3.0	1.69	0.61
59120	−0.21	32.750	26.30	47	7383	32.2	0.89	0.28
59121	0.82	32.635	26.15	50	2865	29.5	1.13	0.34
59123	0.07	33.030	26.51	49	5548	26.8	0.74	0.22
59132	0.90	32.309	25.89	31	188	20.9	1.16	0.59
59134	−0.72	32.677	26.26	51	1558	11.3	0.90	0.32
59135	0.80	32.517	26.06	43	1810	13.7	1.14	0.37
59148	−0.67	33.101	26.63	55	2293	13.3	2.59	0.76
59149	−0.46	33.368	26.81	31	3195	9.0	1.47	0.48
59150	−0.33	33.257	26.71	30	1190	10.4	2.64	0.76
73001	1.10	32.197	25.79	24	1418	7.4	2.91	0.78
73002	1.89	32.168	25.71	26	1190	8.5	2.86	0.75
73011	0.31	32.656	26.20	45	5845	19.7	0.99	0.29
73018	0.71	32.646	26.17	42	7628	21.3	0.98	0.28
73022	—	—	—	26	1535	1.8	0.99	0.32
73023	—	—	—	42	2510	22.3	3.04	0.77
73024	—	—	—	44	6398	25.9	1.44	0.42
73027	1.25	—	—	40	8605	12.8	1.75	0.49
73057	2.62	32.313	25.77	31	305	1.0	2.37	0.82
73058	0.88	32.432	25.99	28	5785	2.9	0.81	0.23
73075	1.12	32.779	26.25	43	8908	24.5	1.25	0.34
73080	1.47	32.774	26.23	40	1668	17.7	2.15	0.63
73081	1.42	32.840	26.28	42	3245	17.4	1.82	0.57
73104	1.88	32.522	26.00	34	14365	20.1	1.35	0.39
73122	2.13	32.777	26.18	40	5555	14.0	1.24	0.37
74002	2.56	32.428	25.87	49	1080	11.6	3.16	0.84
74003	8.58	28.207	21.87	22	2765	3.2	1.80	0.51
74009	4.79	32.149	25.44	32	2623	4.6	2.45	0.70
74010	3.01	32.719	26.06	48	9188	59.0	2.00	0.56
74011	3.27	32.591	25.94	46	2548	15.1	2.25	0.73
74013	2.70	32.850	26.19	51	488	1.3	2.19	0.73
74015	3.62	32.378	25.74	46	890	1.7	2.20	0.75
74020	4.71	32.064	24.38	42	545	9.9	2.23	0.77
74023	2.64	32.692	26.07	53	2068	20.1	2.16	0.64
74024	2.85	32.421	25.84	49	2178	7.9	2.43	0.69
74025	8.51	30.847	23.94	37	193	3.9	2.49	0.88
74053	−0.23	32.199	25.86	38	7923	16.7	1.75	0.52
74055	1.47	31.883	25.51	30	4423	4.5	2.59	0.69
74057	7.29	31.488	24.62	25	2370	8.3	2.73	0.79
85061	5.80	32.300	25.44	28	2433	7.4	2.76	0.80
85064	3.73	32.254	25.63	35	785	1.7	2.86	0.90
85071	2.03	32.517	25.98	54	2048	8.5	2.68	0.78
85090	2.97	32.741	26.08	54	12115	32.4	2.49	0.69
85094	4.71	32.135	25.44	45	687	19.2	3.14	0.86

ing 5 %. The cluster analysis delineated 11 station groups (Figs. 5 and 6). Six of the 49 stations did not combine with other stations and were deleted from further analysis. The majority of the multiple station groups clustered at the 43 to 76 % level.

Groups I, III, IV and XI all occur under BSAW and have abundance values ranging from 1684 to 6940 ind. m^{-2} and biomass values ranging from 11.3 to 24.2 g C m^{-2} (Table 5). Groups I (northern Bering Sea) and III (Chukchi Sea) are comprised of stations primarily located in the central basins of BSAW and have the highest abundance (5365 to 6940 ind. m^{-2}) and biomass (22.2 to 24.2 g C m^{-2})

Table 2. Summary of station sediment measurements for Cruises 59, 73, 74, and 85. SC: sorting coefficient; SH: sediment heterogeneity; TOC: total organic carbon; TON: total organic nitrogen

Station	Percent: Silt and clay (≥ 5 phi)	Very fine sand (4 phi)	Fine sand (3 phi)	Medium sand (2 phi)	Coarse sand (1 phi)	Gravel (≤ 0 phi)	Modal size class (phi)	SC (phi)	SH (rank)	TOC (mg g^{-1})	TON (mg g^{-1})
59081	19.4	51.7	28.6	0.0	0.3	0.0	4.0	0.6	3	3.52	0.46
59108	0.0	0.0	10.0	74.5	11.9	0.0	2.0	0.5	2	0.93	0.10
59123	13.8	28.2	53.0	4.1	0.9	0.0	3.0	0.8	4	3.43	0.47
59149	49.1	29.2	21.4	0.0	0.3	0.0	4.5	0.7	3	9.13	1.26
59150	27.1	28.5	41.5	2.5	0.5	0.0	4.0	0.8	3	4.35	0.54
73001	64.9	19.9	7.6	6.3	1.0	0.3	≥ 5.0	0.7	3	9.13	1.10
73002	32.6	4.5	19.1	32.1	11.7	0.0	3.0	1.5	5	5.48	0.69
73011	0.1	46.0	44.3	3.3	0.5	0.0	4.0	0.6	3	3.00	0.46
73018	7.7	39.3	50.3	2.1	0.6	0.0	3.0	0.6	3	3.52	0.56
73022	1.0	0.8	10.3	65.0	23.0	0.0	3.0	0.6	3	1.09	0.08
73023	9.5	4.9	46.0	34.4	5.2	0.0	3.0	0.8	4	3.88	0.54
73024	10.0	12.5	66.1	10.2	1.0	0.3	3.0	0.7	3	3.95	0.55
73027	7.3	6.7	67.4	16.6	2.0	0.0	3.0	0.5	2	4.48	0.70
73057	2.2	1.2	65.4	30.4	0.8	0.0	3.0	0.5	2	1.59	0.20
73058	0.5	0.3	13.9	84.7	0.6	0.0	2.0	0.3	1	1.09	0.11
73075	4.0	28.5	57.0	8.0	2.5	0.0	3.0	0.6	3	2.16	0.33
73081	9.8	48.4	37.3	3.6	1.0	0.0	4.0	0.7	3	3.73	0.54
73104	2.0	32.5	62.9	2.5	0.1	0.0	3.0	0.5	2	2.04	0.29
73122	7.4	43.5	45.7	3.1	0.4	0.0	4.0	0.6	3	4.27	0.65
74002	11.3	8.4	26.7	33.3	19.1	1.9	2.0	1.3	5	5.38	0.53
74009	42.9	49.0	7.3	0.5	0.2	0.0	4.0	0.5	2	4.36	0.54
74010	35.0	50.0	10.2	3.9	0.9	0.0	4.0	0.6	3	12.10	1.98
74011	65.5	11.5	11.8	10.9	0.3	0.0	≥ 5.0	0.9	4	7.16	0.89
74013	56.9	12.5	10.5	19.1	1.0	0.0	≥ 5.0	1.2	5	15.01	2.13
74015	37.0	56.3	6.1	0.5	0.0	0.0	4.0	0.5	2	5.34	0.69
74020	28.4	24.3	32.9	8.5	1.5	4.4	4.0	1.0	4	14.09	2.07
74023	45.7	25.5	17.3	10.9	0.6	0.0	4.0	1.0	4	19.35	2.78
74024	39.7	25.8	18.7	15.2	0.6	0.0	4.0	1.1	5	15.41	2.33
85061	63.8	30.1	4.9	1.2	0.0	0.0	≥ 5.0	0.4	2	7.21	1.01
85064	49.2	30.8	12.4	7.4	0.2	0.0	4.0	0.8	4	9.96	1.38
85071	50.7	21.4	19.2	8.4	0.4	0.0	≥ 5.0	0.9	4	13.44	1.95
85090	57.5	18.2	10.2	13.5	0.7	0.0	≥ 5.0	1.0	4	13.62	2.16
85094	9.6	10.0	25.0	22.9	21.5	11.1	2.0	1.7	5	6.40	0.93

in the study. Amphipods (Ampeliscidae and Isaeidae) and bivalves (Tellinidae, Nuculidae and Astartidae) dominate the abundance and biomass at these station groups (Table 6). Groups IV and XI are located in the boundary region of the Chirikov Basin in the northern Bering Sea under BSAW. These groups have intermediate abundance (1684 to 2048 ind. m^{-2}) and biomass (11.3 to 12.5 g C m^{-2}) values. These stations are dominated by amphipods (Ampeliscidae), bivalves (Nuculidae and Tellinidae), polychaetes (Nephtyidae), ophiuroids (Ophiuridae and Ophiactidae), and sea urchins (Strongylocentrotidae).

Groups V, VII, VIII, IX and X occur in ACW (Table 5) and show a wide range of abundance (641 to 4193 ind. m^{-2}) and biomass (2.0 to 15.4 g C m^{-2}). A majority of station groups have low biomass (2.0 to 5.3 g C m^{-2}). The exception is Group VIII (biomass = 15.4 g C m^{-2}) which is composed of 4 stations that occur in the frontal zone between BSAW and ACW (Fig. 6). The dominant fauna in Groups V, VII, VIII, IX and X are amphipods (Isaeidae, Oediceratidae, Ampeliscidae and Phoxocephalidae), bivalves (Tellinidae, Cardiidae and Thyasiridae), polychaetes (Maldanidae, Sternaspidae and Nephtyidae), echiuroids (Echiuridae), sipunculids (Golfingiidae), ophiuroids (Ophiuridae), sand dollars (Echinarachniidae) and tunicates (Molgulidae and Styelidae; Table 6).

Two Groups (II, VI) are composed of stations located in both BSAW and ACW. Abundance values are in the medium range observed for the area (1595 to 2529 ind. m^{-2}) as are the biomass values (8.3 to 8.6 g C m^{-2}; Table 5). Amphipods (Isaeidae, Ampeliscidae and Phoxocephalidae), bivalves (Tellinidae and Nuculidae), polychaetes (Oweniidae and Nephtyidae), echiuroids (Echiuridae), ophiuroids (Ophiuridae) and sand dollars (Echinarachniidae)

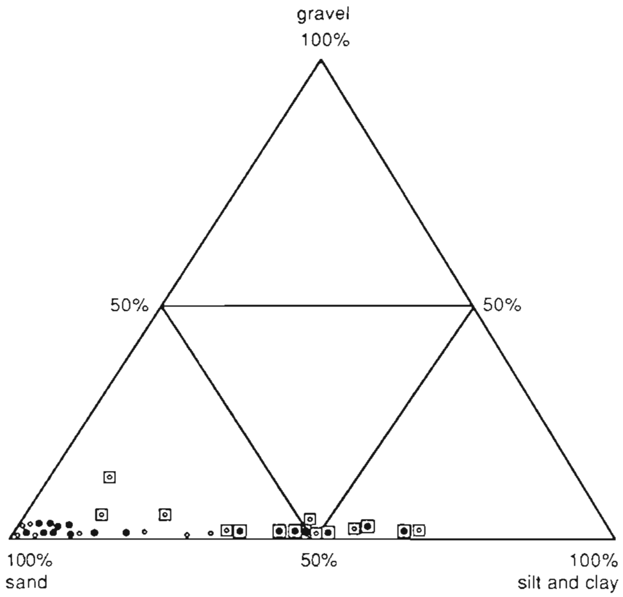

Fig. 4. Ternary diagram for surface sediment grain size class composition. (•) Stations located in Bering Shelf-Anadyr Water; (○) stations in Alaska Coastal Water; Boxed: stations located in the Chukchi Sea; unboxed: those in the Bering Sea

were dominant fauna at these 2 station groups (Table 6).

Feeding groups

Selective detritus- and suspension-feeding fauna (primarily amphipods and bivalves) dominate the faunal abundance at a majority of station groups in the region (Table 7). Deposit-feeding polychaetes and/or bivalves are also dominant fauna in station groups where silt and clay content ranged from 16 to 52% (excluding Group X; Tables 5 and 7).

Diversity

Diversity (H') and evenness (J) are positively correlated with each other ($r = 0.900$, $p < 0.01$, $n = 49$). Thus, while the following discussion outlines the environmental variables correlated to diversity (H') only, the results are the same for evenness (Table 8). Sediment sorting, and consequently sediment heterogeneity, is better correlated than any other variable to faunal diversity at all stations. Stations located in high percent silt and clay sediments are positively correlated to diversity, while stations in high percent fine sand are negatively correlated with diversity. Surface sediment TOC and TON are positively correlated to diversity. The 2 water column variables that correlate to benthic faunal diversity are bottom temperature (positively) and bottom chlorophyll *a* (negatively).

BSAW and ACW stations clearly show a positive relation between diversity and sediment sorting, an indicator of sediment heterogeneity (Fig. 7). Diversity is more highly correlated with sediment sorting at stations in BSAW than with stations in ACW, although both are significant ($p < 0.05$). Benthic faunal diversity is more variable in well-sorted, homogeneous sediments in ACW than in BSAW. In more poorly-sorted, heterogeneous sediments, diversity data for both water types had a better fit to the regression line (Fig. 7). In addition, stations located in the Chukchi Sea have the highest diversity indices, and while heterogeneous sediments characterize BSAW, a wide variety of sediment composition occur in ACW.

The Shannon-Weaver indices (H' and J) are lowest for BSAW station groups (H'=1.06 to 2.65, J = 0.33 to 0.66) and highest for ACW station groups (H'=1.75 to 3.57, J = 0.50 to 0.84; Table 5). This trend can be

Table 3. Pearson product-moment correlation statistics between sediment total organic carbon and total organic nitrogen and sediment composition, sorting and heterogeneity at all benthic stations (n = 33). r: correlation coefficient; p: level of significance; ns: no significance

Surface sediment composition	Sediment parameter: Total organic carbon (mg g^{-1})		Total organic nitrogen (mg g^{-1})	
	r	p	r	p
% Silt and clay	0.772	<0.01	0.673	<0.01
% Very fine sand	0.096	ns	0.107	ns
% Fine sand	−0.485	<0.01	−0.403	$0.01 < p < 0.05$
% Medium sand	−0.336	ns	−0.320	ns
% Coarse sand	−0.261	ns	−0.270	ns
% Gravel	0.107	ns	0.121	ns
Sediment sorting	0.394	$0.01 < p < 0.05$	0.468	<0.01
Sediment heterogeneity	0.445	$0.01 < p < 0.05$	0.524	<0.01

Table 4. Dominant faunal families in 95 % of ranked abundance and biomass for stations in the northern Bering and Chukchi Seas

Foraminifera	Mollusca
Cnidaria	Bivalvia
Anthozoa	Astartidae
Rhynchocoela	Cardiidae
Annelida	Montacutidae
Polychaeta	Myidae
Ampharetidae	Nuculidae
Capitellidae	Nuculanidae
Cirratulidae	Tellinidae
Flabelligeridae	Thyasiridae
Goniadidae	Veneridae
Lumbrineridae	Gastropoda
Maldanidae	Cylichnidae
Magelonidae	Muricidae
Nephtyidae	Trochidae
Ophelidae	Turridae
Orbiniidae	Polyplacophora
Oweniidae	Ectoprocta
Pectinariidae	Alyconidiidae
Phyllodocidae	Ectoprocta sp.
Polynoidae	Echinodermata
Sabellidae	Echinoidea
Sigalionidae	Echinarachniidae
Spionidae	Strongylocentrotidae
Sternaspidae	Holothuroidea
Syllidae	Synaptidae
Terebellidae	Ophiuroidea
Arthropoda	Amphiuridae
Crustacea	Ophiactidae
Balanidae	Ophiuridae
Amphipoda	Priapulida
Ampeliscidae	Sipunculida
Corophiidae	Golfingiidae
Gammaridae	Echiurida
Haustoriidae	Echiuridae
Isaeidae	Chordata
Lysianassidae	Ascidiacea
Oediceratidae	Molgulidae
Phoxocephalidae	Pyuridae
Pleustidae	Styelidae
Cumacea	
Diastylidae	
Lampropidae	
Leuconidae	
Isopoda	
Anthuridae	

seen more clearly by separating the diversity indices into 3 categories: low, medium and high (Table 9). Within the low diversity category ($H' = 0.5-1.4$), 31 % of all stations are located in BSAW compared to only 6 % in ACW. As the diversity level increases in the medium category ($H' = 1.5–2.4$), the percentage of stations occurring in BSAW decreases (20 %) and increases (14 %) in ACW. Finally, within the high diversity category ($H' = 2.5–3.4$) only 6 % of all benthic stations are located in BSAW compared to 22 % in ACW.

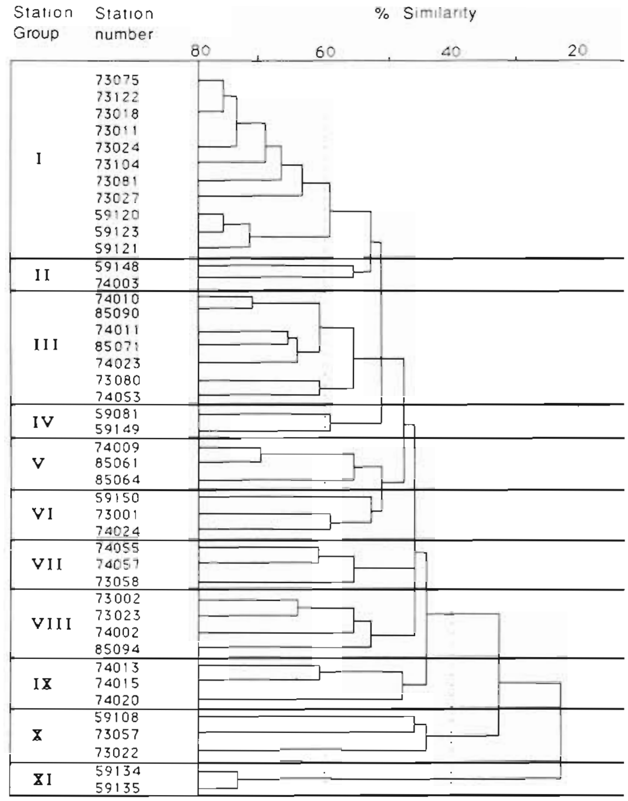

Fig. 5. Dendrogram showing station groups formed by cluster analysis of abundance data based on station-to-station faunal similarities

DISCUSSION

Benthic community diversity in soft sediment habitats can be regulated by many processes, including structural heterogeneity, food availability, predation and/or disturbance, environmental stability, competition and hydrodynamics that can influence larval recruitment (Gray 1981, Valiela 1984, Butman 1987, Palmer 1988).

Based on the results of this study, we conclude that sediment heterogeneity, together with food supply and temperature, are major regulating factors in benthic community structure (Fig. 8). Predation/disturbance has a less definable role. Competition and environmental stability are less likely to affect diversity in this region because of the dynamic nature of the environment (Stoker 1981). Our cluster group distribution indicates that faunal composition is also strongly correlated to environmental variables.

Sediment heterogeneity

Structural heterogeneity in sedimentary habitats can be described by grain size and sorting coefficients, with

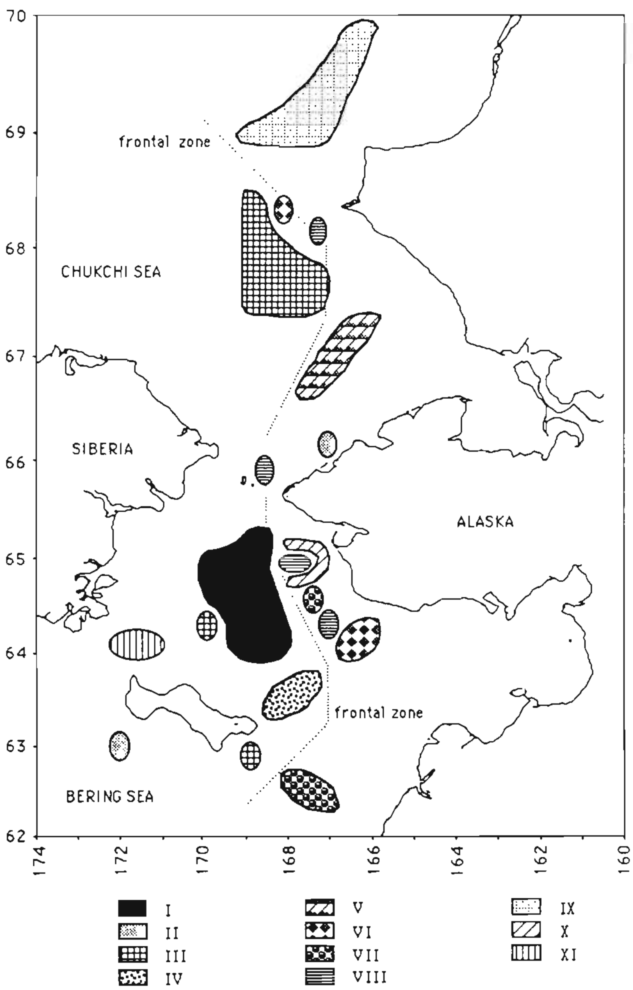

Fig. 6. Distribution of faunal communities based on cluster group analysis (see Table 6 for list of dominant fauna)

more structural heterogeneity hypothesized to provide increased niche space and higher diversity (Gray 1981). In addition, grain size and sediment sorting are characteristics of specific hydrographic regimes, with coarse sediments indicative of high current and wave action compared to silt and clay sediments that indicate reduced currents (Gray 1981, Weston 1988). Sediment structure can describe the local environment and influence the biological pressures (i.e. habitat selection for settlement, food resource type and availability) that benthic fauna experience in a sedimentary habitat (Sanders et al.. 1962, Butman 1987, Riddle 1988).

In our study, benthic faunal diversity is highly correlated ($p < 0.01$) with 5 sediment parameters: sediment sorting and heterogeneity, percent silt and clay, TOC and TON, with diversity correlated with percent fine sand at a lower significance level ($0.01 < p < 0.05$). TOC and TON are positively correlated with percent silt and clay and sediment heterogeneity, and negatively with percent fine sand. This is consistent with our hypothesis that benthic diversity should be higher in the Chukchi Sea (higher silt and clay content, more heterogeneous sediments) than the northern Bering Sea (higher sand content, more homogeneous sediments; Figs. 7 and 8).

An example of the relation between changes in sediment heterogeneity and faunal diversity can be demonstrated for faunal groups in BSAW. Station Group I, in the central Chirikov Basin, characterized by moderately homogeneous, sandy sediments, has a low diversity of 1.38 (Table 5). By comparison, stations located in increasingly heterogeneous sediments should show higher diversities. This can be demonstrated in Station Group III in the southern Chukchi Sea, characterized by more heterogeneous, very fine

Table 5. Mean benthic abundance, biomass, diversity (H'), evenness (J), sediment heterogeneity (SH), and sediment composition for benthic station groups located in Bering Shelf-Anadyr Water (BSAW) and Alaska Coastal Water (ACW)

Group	Water type	Mean abundance (ind. m^{-2})	Mean biomass (g C m^{-2})	H'	J	SH (rank)	Sediment composition (%) Silt and clay	Very fine sand	Fine sand	Med. sand	Coarse sand	Gravel
I	BSAW	6940	22.2	1.38	0.34	3	6.9	31.7	53.8	5.9	1.0	0.0
II	Both	2529	8.3	2.51	0.67	–	–	–	–	–	–	–
III	BSAW	5365	24.2	2.65	0.66	4	50.9	25.3	13.7	9.5	0.6	0.0
IV	BSAW	2048	11.3	1.73	0.55	3	34.3	40.5	25.0	0.0	0.3	0.0
V	ACW	1947	4.6	2.86	0.75	3	52.0	36.6	8.2	3.0	0.1	0.0
VI	Both	1595	8.6	3.14	0.79	4	43.9	24.7	22.6	8.0	0.7	0.1
VII	ACW	4193	5.3	2.25	0.56	1	0.5	0.3	13.9	84.7	0.6	0.0
VIII	ACW	1367	15.4	3.57	0.84	5	15.8	7.0	29.2	30.7	14.4	3.3
IX	ACW	641	4.3	2.68	0.78	4	40.8	31.0	16.5	9.4	0.8	1.5
X	ACW	718	2.0	1.75	0.50	2	1.1	0.7	28.6	56.7	11.9	0.0
XI	BSAW	1684	12.5	1.06	0.33	–	–	–	–	–	–	–

Table 6. Dominant benthic fauna by percent abundance and biomass occurring in station Groups I to XI in Bering Shelf-Anadyr Water (BSAW) and Alaska Coastal Water (ACW). Mean abundance and biomass values for station groups are listed in Table 5

Station Group	Water type	Dominant family by % abundance	% abundance	Dominant family by % biomass	% biomass
I	BSAW	Ampeliscidae	70	Ampeliscidae	36
		Isaeidae	11	Tellinidae	23
		Phoxocephalidae	4	Astartidae	15
II	Both	Oweniidae	34	Tellinidae	65
		Isaeidae	10	Ophiuridae	6
		Ampeliscidae	9	Sternaspidae	4
III	BSAW	Ampeliscidae	21	Tellinidae	32
		Isaeidae	16	Nuculidae	25
		Nuculidae	13	Ampeliscidae	9
IV	BSAW	Nuculidae	54	Tellinidae	36
		Tellinidae	13	Nuculidae	22
		Ampeliscidae	11	Ampeliscidae	9
V	ACW	Tellinidae	13	Styelidae	48
		Thyasiridae	10	Cardiidae	12
		Styelidae	10	Sternaspidae	12
VI	Both	Echiuridae	12	Nephtyidae	23
		Nuculidae	12	Echinarachniidae	18
		Phoxocephalidae	7	Nuculidae	14
VII	ACW	Isaeidae	46	Echinarachniidae	48
		Oediceratidae	8	Cardiidae	17
		Echiuridae	8	Nephtyidae	7
VIII	ACW	Ampeliscidae	9	Molgulidae	52
		Phoxocephalidae	7	Nephtyidae	10
		Isaeidae	7	Ampharetidae	9
IX	ACW	Maldanidae	15	Golfingiidae	25
		Ophiuridae	15	Nephtyidae	20
		Ampeliscidae	13	Maldanidae	16
X	ACW	Isaeidae	56	Tellinidae	31
		Echinarachniidae	17	Nephtyidae	20
		Nuculidae	5	Veneridae	10
XI	BSAW	Ophiuridae	76	Strongylocentrotidae	34
		Ophiactidae	10	Nephtyidae	15
		Strongylocentrotidae	4	Alyconacea Neptheidae	11

sand/silt and clay sediments, with a higher diversity of 2.65. In addition, although the most common fauna, which are selective detritus/suspension feeders, are similar for both station groups, there is a noticeable change in percent faunal dominance by abundance between the groups. Ampeliscid amphipods dominate 70 % of the abundance in Station Group I, dropping to only 21 % of the abundance in Station Group III (Table 7). Bivalves compose less than 5 % of the abundance in Group I, yet make up 13 % of the abundance in Group III.

In another comparison, station groups in ACW, such as Groups V and X, which are dominated by selective detritus/suspension feeders, show lower diversities in more homogeneous, medium sand sediments (X, $H'=1.75$), compared to higher diversities in more heterogeneous, silt and clay sediments (V, $H'=2.86$; Table 5). No station groups in ACW have similar fauna with which to compare faunal composition changes as with Station Groups I and III in BSAW Nevertheless, the combined data for both BSAW and ACW support the conclusion that sediment grain size composition has a direct influence on faunal diversity (Fig. 7). However, faunal diversity within homogeneous sediments in both ACW and BSAW is not uniformly similar, indicating that additional factors influence benthic community structure.

Food supply

Sediment structure can be considered an indicator of food availability, which is influenced by hydrographic

Table 7. Dominant fauna and percent abundance occurring in feeding categories for station groups in the northern Bering and Chukchi Seas. Dominant fauna are those families that compose ≥ 5 % of the total station abundance. Feeding modes are based on descriptions by Stoker (1978), Fauchald & Jumars (1979), Barnes (1980), and Feder at al. (1985)

Station Group	Selective detritus	(%)	Deposit	(%)	Suspension	(%)	Selective detritus/ suspension	(%)
I	Isaeidae	11					Ampeliscidae	70
II	Leuconidae	5	Orbiniidae	6	Alcyoniididae	8	Oweniidae	34
	Isaeidae	10					Ampeliscidae	9
III	Isaeidae	6					Ampeliscidae	21
	Nuculidae[a]	13						
	Phoxocephalidae	9						
	Haustoriidae	7						
	Leuconidae	6						
IV	Nuculidae[a]	54					Tellinidae	13
	Isaeidae	5					Ampeliscidae	11
V	Phoxocephalidae	10			Thyasiridae	10	Tellinidae	14
	Oediceratidae	10			Styelidae	10		
	Nuculidae[a]	10						
	Leuconidae	6						
VI	Echiuridae	12	Capitellidae	6			Amphiuridae	6
	Nuculidae[a]	12	Sternaspidae	6			Echinarachniidae	5
	Phoxocephalidae	7	Maldanidae	5				
	Cirratulidae	6						
VII	Isaeidae	46						
	Oediceratidae	8						
	Echiuridae	8						
	Ampharetidae	6						
	Phoxocephalidae	5						
VIII	Phoxocephalidae	7	Orbiniidae	5			Ampeliscidae	9
	Isaeidae	7					Corophidae	5
	Leuconidae	5						
IX	Nuculidae[a]	11	Maldanidae	15			Ophiuridae[b]	15
	Leuconidae	10	Capitellidae	5			Ampeliscidae	13
X	Isaeidae	56					Echinarachniidae	17
	Nuculidae[a]	5						
XI							Ophiuridae[b]	76
							Ophiactidae	10

[a] Also a deposit-feeder
[b] Also a carnivore

regimes, and these factors combine to influence animal feeding strategies (Sanders et al. 1962). It has been hypothesized that faunal diversities will be low at low food resource conditions due to limiting resources (Valiela 1984). The positive correlations of sediment TOC and silt and clay content (which are also correlated to each other) with diversity indicates that low food supply is related to low faunal diversity and that as surface sediment TOC and silt and clay content increases in the Chukchi Sea, so does faunal diversity. However, it has also been hypothesized (Valiela 1984) that faunal diversity will be low at high resource conditions, when a few animals would dominate a community. In this study, bottom water chlorophyll *a* is negatively correlated to benthic diversity, indicating that higher food availability in the bottom water of BSAW may have a negative influence on diversity.

As a result, this high resource availability negatively affecting diversity may be acting in concert with homogeneous sediment composition in the central Chirikov Basin in Station Group I, where selective detritus/suspension-feeding ampeliscid amphipods dominate both in abundance and biomass (as described above). Blackburn (1987) proposed that in the northern Bering Sea under BSAW, the microbial component of carbon degradation is displaced by direct macrofaunal feeding by high amphipod populations, resulting in low organic carbon accumulation in spite of

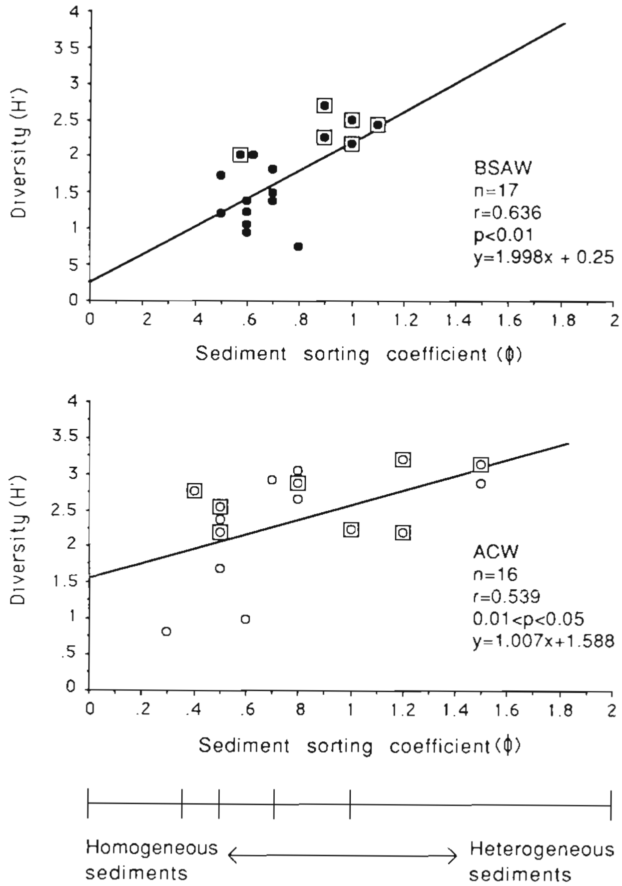

Fig. 7. Relation between benthic faunal diversity and sediment sorting (as an indicator of sediment heterogeneity) for stations in Bering Shelf-Anadyr Water (upper graph) and Alaska Coastal Water (lower graph). Boxed: stations located in the Chukchi Sea; unboxed: those in the Bering Sea

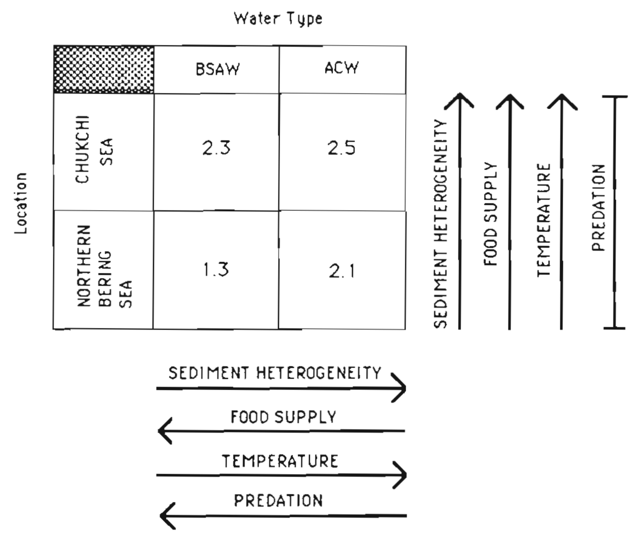

Fig. 8. Average benthic diversity for stations located in the northern Bering and Chukchi Seas in each water type. Arrows indicate our study results for factors influencing diversity; solid predation line indicates an estimated constant value

high organic carbon supply to the benthos. By contrast, Station Group III in the Chukchi Sea, also in a region thought to have a high particulate organic carbon flux to the benthos (Grebmeier 1987), but where organic carbon accumulates and more heterogeneous sediments occur, has higher diversity of selective detritus/suspension-feeding fauna. In addition, sediments with medium to high silt and clay content in the Bering and Chukchi Seas have an increased number of deposit-feeding animals (Table 7), suggesting both food supply

Table 8. Pearson product-moment correlation matrix between environmental variables and benthic faunal diversity (H') and evenness (J) for all stations. r: correlation coefficient; p: level of significance

Environmental variable	Number of stations	Diversity (H')		Evenness (J)	
		r	p	r	p
Sediment sorting	33	0.540	<0.01	0.462	<0.01
Sediment heterogeneity	33	0.461	<0.01	0.390	<0.01
Percent silt and clay	33	0.521	<0.01	0.543	<0.01
Sediment TOC	38	0.491	<0.01	0.451	<0.01
Bottom water temp.	46	0.440	<0.01	0.415	<0.01
Sediment TON	38	0.416	<0.01	0.385	$0.01<p<0.05$
Percent fine sand	33	−0.383	$0.01<p<0.05$	−0.417	$0.01<p<0.05$
Bottom water chl *a*	47	−0.305	$0.01<p<0.05$	−0.297	$0.01<p<0.05$
Percent gravel	33	0.318	ns	0.289	ns
Integrated chl *a*	34	−0.290	ns	−0.309	ns
Bottom water sigma t	45	−0.267	ns	−0.238	ns
Modal sediment grain size	33	0.225	ns	0.293	ns
Bottom water salinity	45	−0.207	ns	−0.156	ns
Percent coarse sand	33	0.184	ns	0.109	ns
Percent very fine sand	33	−0.164	ns	−0.109	ns
Percent medium sand	33	−0.119	ns	−0.130	ns
Depth	49	−0.008	ns	−0.082	ns

Table 9. Categories for Shannon-Weaver information index for diversity (H') and the percentage of all benthic stations (n = 49) in each water type

Shannon-Weaver information index H'	Diversity	Percentage of all stations in each water type	
		Bering Shelf-Anadyr Water	Alaska Coastal Water
0.5–1.4	Low	31	6
1.5–2.4	Medium	20	14
2.5–3.4	High	9	22

and sediment structure influence the higher diversities observed.

Since food is relatively unlimited in BSAW during the summer, sediment heterogeneity must be the major factor affecting benthic diversity in offshore waters of the Chukchi Sea (Fig. 8). Food supply, nevertheless, influences benthic biomass (Grebmeier 1987, Grebmeier et al. 1988). We compared biomass for the dominant station groups under BSAW and observed similar values, 22.2 g C m^{-2} for Group I (northern Bering Sea) and 24.2 g C m^{-2} for Group III (southern Chukchi Sea; Table 5). However, a more detailed analysis of individual stations in these groups shows a northerly maximum in benthic biomass in the Chukchi Sea (Group III, Station 74010, biomass = 59.0 g C m^{-2}, H' = 2.00), which is almost twice the value for the highest biomass station in Group I (Station 59120, biomass = 32.2 g C m^{-2}, H' = 0.89; Table 1). Surface sediment TOC is positively correlated to percent silt and clay and sediment heterogeneity, both of which increase in the Chukchi Sea sediments, which then influences both community structure and benthic biomass.

By comparison, food supply is limited in ACW but variability in benthic diversity occurs. Benthic faunal diversities are highest in the Chukchi Sea, where sediment TOC is highest, although sediment heterogeneity is variable (Fig. 7). In addition, faunal diversity is most variable in homogeneous sediments in ACW. Based upon our data from this subarctic system, we propose that in food-limited systems, especially in homogeneous sediments, food supply will be increasingly important in regulating faunal diversity.

Environmental stability

Environmental stability is defined by constant environmental variables, such as temperature, salinity and oxygen. Although relatively constant temperature, salinity, oxygen and primary production can occur within each water type seasonally during the summer, this shallow system is disturbed by frequent storms and variable transport conditions which influence hydrographic and biological conditions throughout the open-water period (Walsh et al. 1987). The front which develops during the ice-free period fluctuates seasonally, emphasizing the dynamic nature of this region.

Faunal diversities are lowest at stations in BSAW and highest at stations in ACW, indicating a relation between water type characteristics and benthic diversity (Table 9). Of all the water column variables we measured, summer bottom water temperature showed the highest positive correlation with faunal diversity. Bottom water temperatures are higher seasonally in ACW (>+2 °C), where faunal diversity is highest, compared to BSAW (−1 to +2 °C), where faunal diversity is lowest (Figs. 7 and 8; Coachman 1987). In addition, summer bottom water temperatures in the Chukchi Sea are warmer (2 to 9 °C) for both BSAW and ACW, corresponding to increased benthic diversity, than average bottom water temperatures in the northern Bering Sea (−1 to +3 °C) where diversity is lower (Figs. 7 and 8; Coachman 1987).

Predation

Predation crops the prey population, often lowering competiton among species that would otherwise exclude each other, and thus allow more species to occupy the same region (Valiela 1984). However, in some soft bottom communities where predation is less effective, such as estuaries and lagoons, evidence suggests that reduced epifaunal predation allows increased benthic diversity (Peterson 1979). Predators can also act as disturbance agents on soft-bottom communities and influence community structure (Gray 1981). Thus, predators can reduce faunal abundance both by direct consumption and through mortality caused by activities that disturb benthic communities (Kneib 1985, Palmer 1988).

Marine mammals are important predators on sediment-dwelling benthic fauna on the Bering/Chukchi shelf and appear to both positively and negatively influence diversity. Approximately 15 000 gray whales *Eschrichtius robustus*, which feed primarily on amphipods, and 200 000 Pacific walrus *Odobenus rosmarus*, which feed primarily on bivalves, migrate seasonally through the area (Fay et al. 1984, Nerini 1984). Both gray whales and walruses disturb the sediments during feeding activities, creating temporal and spatial patches which would theoretically increase benthic diversity and possibly enhance secondary productivity through sediment reworking (Oliver at al. 1983a, b, Valiela 1984, Oliver & Slattery 1985). During feeding, gray whales increase erosion of fine-grained sediments, as well as open up space for recolonization, and thus influence successional processes (Oliver & Slattery 1985, Nelson & Johnson 1987). Their feeding activity has been proposed to be one reason for the variability in benthic faunal distribution measured in the region (Stoker 1981).

Ampeliscid amphipod communities, which dominate high biomass regions in this study, are characterized by low to medium faunal diversity. The major feeding areas for gray whales and walruses are in the high benthic biomass areas of the Chirikov Basin and Chukchi Sea (Fay et al. 1977, 1984, Nelson & Johnson 1987). Thus, the predation hypothesis of increased diversity in regions of high predation is not consistent with patterns we observed in the Chirikov Basin. Although patch formation occurs, the faster currents in the region transport finer sediments northward to the Chukchi Sea (Nelson & Johnson 1987), thus reducing sediment heterogeneity. However, it is possible in the southern Chukchi Sea, where diversity is higher, that marine mammal feeding activities increase the structural heterogeneity of the environment and that the reduced currents in the region allow a more heterogeneous sediment regime to occur, thus influencing diversity. Overall, the seasonal occurrence of large populations of benthic-feeding marine mammals in these waters necessitates the presence of a productive and reliable invertebrate food source.

Epifaunal predation is estimated to be an order of magnitude lower than marine mammal predation in the study area (Grebmeier 1987). Furthermore, fish predation on benthic animals is believed reduced due to extremely low temperatures (Neiman 1963, Jewett & Feder 1980), and this probably reduces its influence on benthic community structure in the area (Jewett & Feder 1981).

Benthic community stability

Faunal groupings characterized by Stoker (1978) correspond in general location and composition to those station cluster groupings found in this study (Fig. 6). In a more detailed study, Grebmeier (1987) found no major change in faunal structure between these faunal groups and those determined by Stoker over 10 yr earlier. In addition, faunal biomass for similar faunal groups was not significantly different between the 2 studies. These comparisons indicate a stable system is present in this region. In both studies, highest benthic biomass occurred in BSAW and lowest benthic biomass occurred in ACW, indicating that high water column primary production in the spring and summer produces a persistent food supply which influences benthic biomass in the region. Both studies support the conclusion that the northern Bering and Chukchi Seas are detritus-based systems, influenced by variability in sediment composition, water column productivity and current regimes.

CONCLUSIONS

Sediment sorting, indicative of sediment heterogeneity, percent silt, clay and fine sand composition, and temperature, influence benthic community structure in the northern Bering and Chukchi Seas. Food availability and predation are more variable regulating factors in community structure, although food supply has a direct positive influence on biomass. Benthic faunal structure and biomass have not changed significantly in the area over a 10 yr period, indicating that a seasonally persistent quantity and quality of phytodetrital food supply has a positive impact on population stability in this polar system.

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