Community structure of epibenthic megafauna in the Chukchi Sea

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ABSTRACT: Climate change and increased focus on resource development in Arctic Seas have fueled interest in the Chukchi Sea, yet few quantitative studies have been conducted on the larger, epifaunal component of seafloor communities, which serves important roles in sediment biogeochemical processes and provides a food source for fishes and marine mammals. Here we provide quantitative data on the present condition of benthic epifaunal abundance and biomass from the Chukchi shelf and examine the influence of environmental variables on epifaunal communities. We collected 45 beam trawl samples in the Russian and United States sectors of the Chukchi Sea in 2004, 2007 and 2008. Gross abundance estimates ranged from 229 to 70 879 ind. 1000 m^{-2}, and gross biomass estimates ranged from 1628 to 217 023 g wet wt 1000 m^{-2}. Overall, abundance and biomass were dominated by echinoderms (66 and 45 %, respectively) and crustaceans (17 and 31 %, respectively). The ophiuroid *Ophiura sarsi* and the snow crab *Chionoecetes opilio* overwhelmingly dominated abundance and biomass. The holothurian *Myriotrochus rinkii* also occurred in large numbers, and the urchin *Strongylocentrotus pallidus* was another major contributor to biomass. A total of 165 taxa (mostly species) were identified; the highest numbers were Mollusca (45) and Crustacea (33). Cluster analysis identified 6 distinct groups plus 6 unique stations with 54 to 88 % between-cluster dissimilarity, with separation based largely on substrate type and latitude. Water mass characteristics and indices of food availability appeared less influential in generating the observed composition, abundance and biomass patterns. Comparisons with previous studies suggested an increase in overall epibenthic biomass since 1976, including an increase in the biomass of *C. opilio*.

KEY WORDS: Benthos · Epifauna · Chukchi Sea · Arctic · Community structure · Benthic–pelagic coupling · Temporal change · *Chionoecetes opilio*

INTRODUCTION

The Chukchi Sea, fed by Pacific waters through the Bering Strait, is the only Pacific gateway to the western Arctic proper. The inflow of nutrient-rich waters supports a productive marine ecosystem on parts of the Chukchi shelf (Coachman et al. 1975). Various ecosystem components, including the macrofaunal benthos, are relatively well-studied in this region (e.g. Grebmeier et al. 2006a). However, despite the significant change in sea-ice cover and other climate-forcing variables, the increased focus on resource development in the Chukchi Sea (Stroeve et al. 2005, Federal Register 2007), and the important role rich epifaunal communities play in carbon cycling on other Arctic shelves (Ambrose et al. 2001, Piepenburg et al. 1995, 2001), the epifaunal component of the megafauna in the Chukchi Sea ecosystem is poorly understood, with the exception of mollusks (Feder et al. 1994a). Here we present a relatively extensive quantitative dataset on epibenthic community structure, including sites throughout the United States and Russian sectors of the Chukchi shelf.

A significant portion of the seasonally ice-covered continental shelf of the Chukchi Sea under Bering Shelf Anadyr water is characterized by tight benthic–pelagic coupling due to shallow depths (<150 m) and the advection of nutrient-rich waters from the northern

Bering Sea northward through the Bering Strait (Coach-man et al. 1975, Springer & McRoy 1993, Grebmeier et al. 2006a, Iken et al. in press). High primary productivity and rapid settlement of organic matter from the water column in these waters support high macrofaunal biomass, with peak values (25 to 60 g C m^{-2}) being among the highest on the world's shallow shelves (Grebmeier et al. 1988, 2006a, Highsmith & Coyle 1990, 1992, Sirenko & Gagaev 2007). Phytoplankton and macrofaunal biomass levels are particularly high in the south-central Chukchi Sea, exceeding that of any other region on the Bering and southern Chukchi shelf (Walsh et al. 1989, Grebmeier 1993, Springer et al. 1996, Feder et al. 2007). Under the Alaska Coastal Water (ACW) in the eastern Chukchi Sea, benthic macrofaunal biomass is generally much lower (<10 g C m^{-2}; Feder et al. 2007, Sirenko & Gagaev 2007), and benthic coupling to the water column tends to be weaker (Dunton et al. 2005, Iken et al. in press). Few data exist for epifaunal abundance and biomass in this region, but, where they have been determined, values are high compared to those on other Arctic shelves (up to 53 000 ind. km^{-2}; >2000 kg wet wt km^{-2} in the southeastern Chukchi Sea and Kotzebue Sound; Feder et al. 2005). These rich benthic communities serve as prey for a range of fishes, diving sea birds, and marine mammals (Feder & Jewett 1981, Oliver et al. 1983, Coyle et al. 1997, Lovvorn et al. 2003).

Much of our knowledge regarding the ecology of the Chukchi Sea benthos comes from extensive studies of smaller macrofauna (e.g. Grebmeier et al. 2006a and references therein), whereas data for epibenthic megafauna are scarce. However, many of these large-bodied epifaunal organisms contribute significantly to the overall benthic biomass on Arctic shelves, despite their patchy occurrence (Ambrose et al. 2001). Several groups are also highly mobile and play an important role in the redistribution and remineralization of the organic carbon reaching the seabed, in particular the often dominant echinoderms (Piepenburg & Schmid 1996a,b, Piepenburg et al. 1995, 1996, 1997, 2001, Starmans et al. 1999, Piepenburg 2000, Sejr et al. 2000, Ambrose et al. 2001). The few quantitative studies on the epifauna in the Chukchi Sea have concentrated on the southeast (southeastern shelf extending into Kotzebue Sound; Feder et al. 2005) and inshore area of the northeastern region (Ambrose et al. 2001, Feder unpubl. data), including assessment of snow crab *Chionoecetes opilio* (Paul et al. 1997) and epifaunal mollusk populations (Feder et al. 1994a). Qualitative epifaunal information is available from near Point Hope around the Project Chariot site (Sparks & Pereyra 1966) and from Point Barrow (MacGinitie 1955, 1959). Russian expeditions on the western Chukchi shelf have been conducted since the 20th

century, but publications remain difficult to access, and trawl sampling was only qualitative in nature (Ushakov 1952). These information gaps are hindering attempts to quantify large-scale and/or long-term trends in epibenthic community structure, biomass and carbon flux in the face of increased human impacts such as oil and gas development (Federal Register 2007), rapid climatic change (Stroeve et al. 2005), and potential future fishing efforts (NPFMC 2009).

While biological continuous time-series data from the Chukchi Sea are not yet available, several recent studies have documented decadal-scale changes in biomass of various benthic components farther south in the northern Bering Sea, and trends appear to differ between size classes of organisms. Biomass of ampeliscid amphipods (Moore et al. 2003, Coyle et al. 2007), as well as total macrofaunal biomass (Dunton et al. 2005, Grebmeier et al. 2006b), declined roughly 50 % from the 1980s to the early 2000s. In contrast, significant increases in epibenthic abundance and biomass were recorded for the benthic community in Norton Sound from 1976 to 2002 (Hamazaki et al. 2005) and the southeastern Chukchi Sea from 1976 to 1998 (Fair & Nelson 1999, Feder et al. 2005) and for ground fishes in the southeastern Bering Sea from 1960 to 2000 (Conners et al. 2002). In all cases, the changes have at least in part been attributed to North Pacific or Bering Sea regime shifts (e.g. Rodionov & Overland 2005) and/or long-term climate change, but predation pressure imposed through selective bottom-feeding by marine mammals is another possible cause (Coyle et al. 2007). The goal of the present study was to provide quantitative data for epibenthic megafaunal abundance, biomass, and community structure for a large area of the Chukchi shelf and to examine relationships to environmental variables. Specifically, our main objectives were to: (1) quantify gross abundance, biomass, and diversity of epibenthic fauna (>4 mm), (2) identify environmental variables that correlate with epifaunal abundance and biomass, and (3) discuss potential temporal changes of Chukchi Sea epifauna with suggestions for monitoring strategies.

MATERIALS AND METHODS

The present study is part of the ongoing Russian–American Long-Term Census of the Arctic (RUSALCA) program launched with an interdisciplinary cruise in 2004 aboard the Russian vessel 'Professor Khromov'. The goal of this census is to gather long-term physical, chemical and biological data on the northern Bering and Chukchi Sea ecosystems to document their present conditions and to predict future change in this

region. Additional sampling was conducted in 2009 and is also planned for 2012. Thus, the data presented here will enable us to compare future time-series data. In order to increase spatial coverage for this analysis, we also incorporated data collected with the same sampling methods at additional sites visited on 3 cruises in the United States sector of the Chukchi Sea (2007 to 2008) aboard the Japanese vessel 'Oshoro Maru' and the United States NOAA vessel 'Oscar Dyson' (Table 1).

Seventeen stations were sampled between 8 and 25 August 2004 at depths of from 39 to 54 m during RUSALCA (Fig. 1, Table 1, station designation 'R'). Six stations were sampled between 6 and 10 August 2007 at depths of from 25 to 50 m (stations 'OM') and 7 stations were sampled between 4 and 14 September 2007 at depths of from 31 to 60 m (stations 'OD'). An additional 15 stations were sampled between 7 and 13 July 2008 at depths of from 36 to 51 m (stations 'OM-08') with the same gear but analyzed at lower taxonomic resolution. The entire region sampled covered an area

from 65.12 to 72.32°N and from 163.71 to 175.99°W. In summary, we sampled 44 stations in the Chukchi Sea and Bering Strait, and 1 station in the northern Bering Sea during 4 expeditions from 2004 to 2008 (Fig. 1, Table 1).

Study area. The Chukchi Sea is a shallow shelf sea (~50 m average depth) that extends ~800 km northward from the Bering Strait to the shelf break at the 200 m isobath. Two canyons incise the shelf in the north, of which we sampled Herald Canyon in the northwestern Chukchi Sea (Fig. 1). Sediments are mostly muddy on the outer shelf and coarser, with sand and gravel, on the inner shelf and at locations with relatively high currents such as the Bering Strait (www.ngdc.noaa.gov/mgg/geology/size.html; Naidu 1988).

The mean flow over much of the shelf is northward due to the Pacific–Arctic pressure gradient (Winsor & Chapman 2004, Weingartner et al. 2005). The study area is influenced by 3 dominant water masses (Coachman 1987, Walsh et al. 2005, Weingartner et al. 2005). ACW in the east is characterized by low productivity and nutrient concentrations, warm surface temperatures, and low salinities (≤31.9). Anadyr water (AW) in the western Chukchi Sea is characterized by high primary productivity and nutrient concentrations and colder, more saline waters (≥32.5). Bering Shelf Water (BSW), which is relatively high in nutrients, particulate organic carbon concentrations, and primary productivity, is located between these 2 water masses, and has salinities between 31.9 and 32.5. AW and BSW mix, are often referred to as Bering Shelf Anadyr water (BSAW) (salinity >31.9; Feder et al. 2005, Grebmeier et al. 2006a), and are combined as such in our analysis below. Stn R27 (Fig. 1) had the strong freshwater signal of a coastal lagoon (Pickart 2006), and the location may, at times, be located under the Siberian Coastal Current (Weingartner et al. 1999). During the RUSALCA cruise, a mass of cold and salty northward flowing winter water (WW), apparently formed from a reservoir of winter water in the area southeast of Wrangel Island and from water advected through the Bering Strait, remained in part of Herald Canyon from the previous winter (Pickart et al. 2005, in press).

Trawl collections. A plumb staff beam trawl (after Gunderson & Ellis 1986) with a 2.26 m effective opening and a net mesh of 7 mm, with a 4 mm cod end liner, was used for epibenthic collections. Tow duration ranged from 1 to 6 min, area swept ranged from 107 to 1257 m^2 and towing speed was approximately 1.5 knots. Wire was deployed at a rate of 3.5 m m^{-1} of water depth; details can be found in Norcross et al. (in press). Tows at Stns R10, R11 and R15 were not quantitative because of unknown area covered, but were included for determination of relative composition and number of taxa.
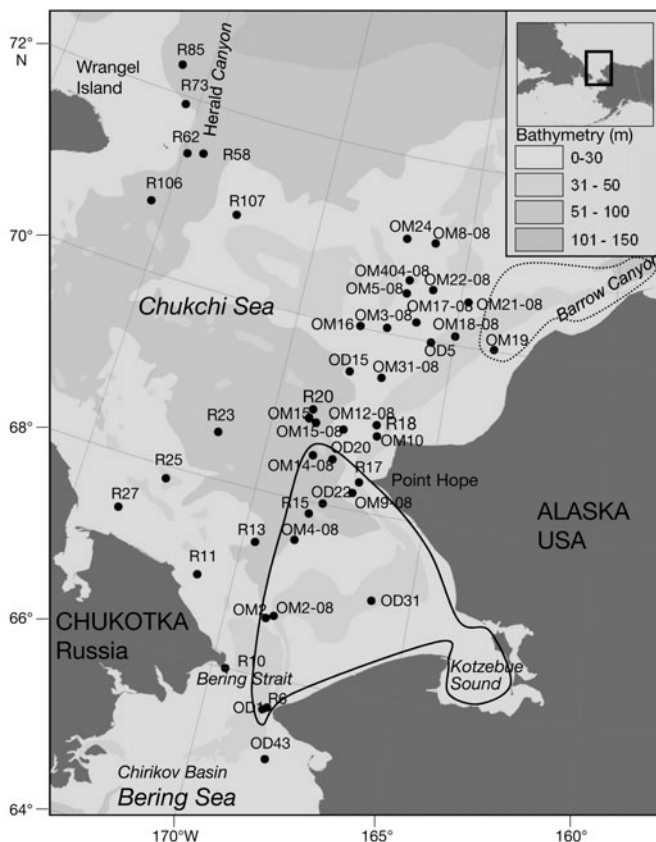

Fig. 1. Map of the study are with 45 sampling locations from 4 cruises marked. R: RUSALCA 2004; OM: Oshoru Maru 2007; OD: Oscar Dyson 2007; OM-08: Oshoru Maru 2008. Solid line shows the area studied by Feder et al. (2005); dotted line shows the area studied by Ambrose et al. (2001)

Table 1. Station table for RUSALCA 2004 (R), Oshoru Maru 2007 (OM) and 2008 (OM-08) and Oscar Dyson (OD) 2007 cruises. Stations are listed in the chronological sequence sampled. Taxonomic resolution during the Oshoru Maru 2008 cruise did not allow calculation of diversity indices. ACW: Alaska Coastal Water; BSAW: Bering Sea Anadyr Water; FW: freshwater; WW: winter water (descriptions see 'Materials and methods'); na: not applicable

Station	Date	Lat. °N	Long. °W	Mean depth (m)	Abundance (ind. 1000 m⁻²)	Biomass (g wet wt 1000 m⁻²)	No. of species	Pielou's evenness J'	Shannon's diversity $\log_2 H'$	Coarse substrate category	Grain size (mm)	Bottom temp. (°C)	Bottom salinity	Bottom oxygen (ml l⁻¹)	Water mass
R6	9 Aug 2004	65.68	–168.30	50	4676	68630	37	0.52	1.88	Hard	4.197	10.5	30.6	6.5	ACW
R10	11 Aug 2004	66.00	–169.62	49	na	na	32	0.36	1.26	Hard	3.451	3.0	32.6	7.0	BSAW
R11	11 Aug 2004	66.93	–170.99	43	na	na	28	0.48	1.61	Soft	0.036	1.7	33.2	6.2	BSAW
R13	11 Aug 2004	67.43	–169.64	51	9712	30478	22	0.57	1.77	Soft	0.017	2.5	32.9	5.1	BSAW
R15	12 Aug 2004	67.87	–168.32	59	na	na	26	0.71	2.30	Soft	0.027	2.8	32.6	5.6	BSAW
R17	12 Aug 2004	68.32	–167.07	38	1828	17027	46	0.77	2.93	Hard	0.177	7.0	31.0	6.6	ACW
R18	13 Aug 2004	68.98	–166.89	46	6133	60249	20	0.35	1.06	Hard	0.551	7.9	31.3	6.7	ACW
R20	13 Aug 2004	69.00	–168.86	54	16594	64475	22	0.25	0.77	Soft	0.012	3.7	32.3	7.2	BSAW
R23	14 Aug 2004	68.51	–171.46	56	11605	7821	17	0.78	2.20	Soft	0.009	2.2	32.9	5.3	BSAW
R25	15 Aug 2004	67.86	–172.57	49	10848	9693	20	0.82	2.45	Soft	0.012	1.7	33.0	5.2	BSAW
R27	15 Aug 2004	67.41	–173.64	34	2858	1628	21	0.69	2.11	Hard	0.041	–1.5	32.9	5.5	FW
R106	17 Aug 2004	70.76	–175.52	72	31270	51118	18	0.42	1.21	Soft	0.014	–1.8	33.5	5.8	WW
R73	20 Aug 2004	71.91	–175.45	71	44221	55839	35	0.32	1.12	Soft	0.008	–1.7	33.3	5.8	WW
R85	20 Aug 2004	72.32	–175.99	101	4580	17299	33	0.63	2.21	Soft	0.008	–1.4	33.7	4.9	WW
R58	21 Aug 2004	71.44	–174.36	60	4983	28458	17	0.58	1.64	Soft	0.015	1.9	32.6	6.5	BSAW
R62	21 Aug 2004	71.39	–174.87	77	2958	56898	33	0.35	1.22	Hard	0.597	–1.8	33.5	5.9	WW
R107	21 Aug 2004	70.89	–172.72	40	818	10070	20	0.75	2.25	Soft	0.028	2.0	32.4	8.3	BSAW
OM2	5 Aug 2007	66.64	–168.86	41	7681	71864	33	0.80	2.79	Hard	0.916	3.2	32.6	6.8	BSAW
OM10	6 Aug 2007	68.86	–166.82	40	4107	5884	19	0.72	2.12	Hard	0.551	7.1	31.9	6.9	ACW
OM15	7 Aug 2007	68.90	–168.92	50	8236	36526	16	0.35	0.98	Soft	0.015	2.7	32.4	7.3	BSAW
OM16	8 Aug 2007	70.02	–167.99	45	1914	39062	33	0.51	1.77	Hard	0.209	2.9	32.5	7.4	BSAW
OM19	8 Aug 2007	70.02	–163.71	26	2345	23114	34	0.50	1.78	Soft	0.021	1.7	31.9	7.8	ACW
OM24	9 Aug 2007	71.08	–167.08	43	70879	15656	28	0.65	2.15	Soft	0.027	9.8	31.9	6.5	ACW
OD1	3 Sep 2007	65.65	–168.41	52	591	48402	13	0.53	1.36	Hard	1.468	3.3	32.3	7.2	ACW
OD5	5 Sep 2007	69.99	–165.71	43	428	5320	15	0.72	1.94	Soft	0.033	4.8	31.9	7.1	ACW
OD15	7 Sep 2007	69.50	–168.02	51	413	4070	17	0.49	1.38	Hard	0.133	3.4	32.5	7.3	BSAW
OD20	8 Sep 2007	68.51	–167.98	55	1659	5573	19	0.76	2.24	Soft	0.034	3.1	32.5	6.8	BSAW
OD22	8 Sep 2007	68.01	–167.99	56	229	4077	15	0.63	1.71	Soft	0.035	3.7	32.9	5.5	BSAW
OD31	10 Sep 2007	67.06	–166.09	31	1387	9560	18	0.56	1.62	Soft	0.051	7.8	32.1	6.8	ACW
OD43	13 Sep 2007	65.12	–168.07	50	557	19587	25	0.75	2.42	Hard	0.128	6.4	31.4	6.9	ACW
OM2-08	6 Jul 2008	66.68	–168.66	36	7111	108419				Hard	0.120	1.1	32.4	8.7	BSAW
OM3-08	7 Jul 2008	70.06	–167.16	44	14842	30120				Hard	0.078	–1.1	32.5	8.5	BSAW
OM5-08	8 Jul 2008	70.48	–166.75	46	6855	20763				Soft	0.020	–1.4	32.7	8.0	BSAW
OM8-08	8 Jul 2008	71.09	–166.13	41	2230	14044				Soft	0.025	–1.7	33.0	6.6	BSAW
OM404-08	8 Jul 2008	70.63	–166.74	45	898	6900				Hard	0.938	–1.3	32.7	8.3	BSAW
OM17-08	9 Jul 2008	70.18	–166.28	43	5504	10312				Soft	0.032	–0.7	32.2	8.6	BSAW
OM18-08	9 Jul 2008	70.10	–164.99	38	9027	20694				Hard	0.035	–0.6	33.1	7.3	BSAW
OM21-08	9 Jul 2008	70.50	–164.75	42	12366	27102				Hard	0.035	–1.1	32.8	7.5	BSAW
OM22-08	9 Jul 2008	70.57	–165.94	41	2908	9238				Soft	0.017	–1.4	32.7	7.9	BSAW
OM31-08	10 Jul 2008	69.50	–167.02	44	1935	6614				Soft	0.014	1.5	32.2	8.1	BSAW
OM9-08	11 Jul 2008	68.19	–167.20	44	14241	217023				Hard	0.387	2.9	32.3	7.8	Bering Sea
OM12-08	11 Jul 2008	70.63	–167.84	47	7161	20005				Soft	0.026	2.8	32.4	8.0	BSAW
OM14-08	11 Jul 2008	68.51	–168.57	50	18619	209080				Soft	0.018	1.6	32.6	7.8	BSAW
OM15-08	11 Jul 2008	68.87	–168.69	51	11461	167457				Soft	0.012	2.2	32.5	7.8	BSAW
OM4-08	12 Jul 2008	67.55	–168.56	47	4435	70668				Soft	0.043	2.2	32.7	7.4	BSAW

Epibenthic invertebrates from trawl catches were washed on deck and sorted to the lowest possible taxonomic level, in most cases species level. Wet weight for each taxon was determined on deck using spring scales, and numbers of individuals were noted. For colonial organisms (sponges, colonial ascidians, bryozoans, hydrozoans), only wet weights were recorded. Voucher specimens from each taxon were preserved in 4% buffered formalin and later transferred to 50% isopropanol for long-term storage. Biomass and abundance were estimated from area swept (= net swath × distance towed) and normalized to 1000 m^{-2}. These commonly used estimates are considered semi-quantitative because of variable trawl performance across bottom types, net avoidance behavior of some taxa and difficulties in precisely weighting the gear to obtain ideal bottom contact; hence, we refer to these data as gross estimates (Eleftherious & MacIntyre 2005). However, alternative sampling gear (e.g. grabs and corers) sample much smaller areas and thus do not effectively sample the larger and/or rarer epifaunal taxa. Epifaunal assessments are ideally conducted using a combination of trawls and photographic surveys (Eleftherious & MacIntyre 2005), but photographic equipment was not available for use in the present study.

Taxonomic identifications were conducted by the authors and the taxonomists listed in Appendix 1. Upon publication, detailed taxonomic information will be made available through the Ocean Biogeographic Information System and the Global Biodiversity Information Facility.

Data analysis. All individuals were included in data analysis, whether identified to species or higher taxonomic units; colonial organisms were excluded in abundance-based analyses. Spatial patterns in abundance, biomass and number of taxa (see Figs. 2 to 5) were produced using ArcGIS v.9.1 (ESRI 2005), with bin sizes determined according to the Jenks' natural breaks classification scheme. This scheme selects breaks, relatively large jumps in the data values, in the ordered distribution of values that minimize the within-class sum of squared differences. Detailed community composition analysis was performed for the combined datasets of the 2004 and 2007 cruises, using multivariate statistics of the software package PRIMER v.6 (Clarke & Gorley 2006). Collections from the 2008 cruise were excluded from the community analysis due to low taxonomic resolution. The 2008 data were included in figures showing total abundance, biomass and relative faunal composition, as well as snow crab *Chionoecetes opilio* biomass, and in statistical tests on the relationship of total abundance and biomass to environmental variables (see Figs. 2 to 4). Bray-Curtis similarity was calculated for the fourth-root-transformed biomass matrix rather than

for the abundance matrix because abundance cannot be recorded for colonial taxa. In some cases, taxon groups were used for community analysis (e.g. *Argis lar* and *Neocrangon communis*; see Table 2) because they were not consistently separated on the species level during the initial trawl sorting. Non-metric multi-dimensional scaling (NMDS) was used to visualize the resulting patterns in similarity between stations. Species contributing most to the similarities of stations within and between clusters were identified using the Similarity of Percentages routine (SIMPER) in PRIMER. Diversity indices (Pielou's evenness, J'; Shannon's diversity, $\log_2 H'$) were calculated using the DIVERSE routine in PRIMER.

We compiled a set of environmental data for each station, including several variables related to water masses (bottom temperature, bottom salinity, oxygen concentration), sediment characteristics (substrate category, mean grain size), and indicators of food supply (integrated chlorophyll concentrations, macrofaunal biomass, sediment organic carbon content), as well as variables with (potentially) indirect relationships to community structure (latitude, water depth). All variables were chosen on the basis of their strong structuring effects on Arctic benthic communities (temperature: Mayer & Piepenburg 1996, Conlan et al. 2008; salinity: Feder et al. 1994a, Mayer & Piepenburg 1996, Deubel et al. 2003; oxygen: Deubel 2000, Conlan et al. 2008; grain size: Feder et al. 1994a; coarse substrate: Feder et al. 1994b, Mayer & Piepenburg 1996; primary production: MacDonald et al. in press; depth: Deubel 2000, Conlan et al. 2008, MacDonald et al. in press; latitude: Deubel 2000). Relationships between the bulk parameters abundance and biomass and several of the environmental variables were tested with Student's t-tests, ANOVA and Pearson correlations using SYSTAT software. Analysis of similarity (ANOSIM) was used to provide statistical tests of between-group similarity for stations grouped by substrate category and water mass, with global R = 1 indicating groups with completely distinct communities and global R = 0 indicating complete overlap in community composition between groups (Clarke & Warwick 2001). The entire normalized environmental matrix was correlated with the entire epifaunal species matrix based on biomass (excluding 2008 data) using the BIO-ENV procedure in PRIMER (Clarke & Gorley 2006).

Substrate category (hard/soft) was assigned based on visual inspection of trawls and grabs, with 'hard' assigned to stations with substantial amounts of gravel and/or cobble and often shell hash and 'soft' assigned to stations with mud and sand and no or little gravel and cobble. Mean sediment grain sizes (mm) were obtained from the Seafloor Sediment Grain Size Database NGDC Data Set G00127 (www.ngdc.noaa.gov/

mgg/geology/size.html) from locations near the sampling stations, because this information was not collected during all cruises reported here. These data were compiled from multiple contributors and collected during various expeditions over several decades (1950s to 2000s) using a variety of sampling tools; they should thus be considered with some caution. However, when these data were compared with grain size values determined on the basis of our RUSALCA 2004 samples (J. Grebmeier and L. Cooper, Univ. Maryland, unpubl. data), they matched reasonably well.

Bottom water temperature, salinity and oxygen concentrations (Table 1) were obtained from CTD casts performed concurrently at each sampling station by collaborating groups and were provided by Dr. R. Pickart (unpubl. data; Woods Hole Oceanographic Institution, RUSALCA cruise), the Oshoru Maru website (http://odyssey.fish.hokudai.ac.jp/IPY/) and Dr. L. Eisner (unpubl. data; NOAA Alaska Fisheries Science Center, Oscar Dyson cruise). Water masses were assigned based on bottom salinity values after Coachman (1987). Water column-integrated chlorophyll data were obtained from Lee et al. (2007; RUSALCA cruise), the Oshoru Maru website (http://odyssey.fish.hokudai.

ac.jp/IPY/) and Dr. L. Eisner (unpubl. data; NOAA Alaska Fisheries Science Center, Oscar Dyson cruise).

Macrofaunal biomass data for RUSALCA stations were provided by J. Grebmeier and L. Cooper (unpubl. data; University of Maryland). Additional macrofaunal biomass and sediment organic content data were taken from Grebmeier et al. (2006a), using the midpoint of the bins in their Figs. 4 and 5, respectively. To test a potential relationship between trawl-collected epibenthic megafauna and macrofaunal biomass determined from grab samples, we compiled a dataset of paired measurements for these 2 size classes using macrofaunal biomass from Grebmeier and Cooper (unpubl. data) and Grebmeier et al. (2006a) and epifaunal biomass from the present study, from the same locations. Additionally, a subset of epifaunal data from Feder et al. (2005) was paired with a subset of macrofaunal data from Feder et al. (2007), using only locations that were very close to each other. A total of 61 locations were considered. We also conducted a preliminary comparison of epifaunal biomass and community composition at 8 stations in the southeastern Chukchi Sea that were sampled in 1976 (Feder et al. 2005; their Fig. 1), as well as in the present study.
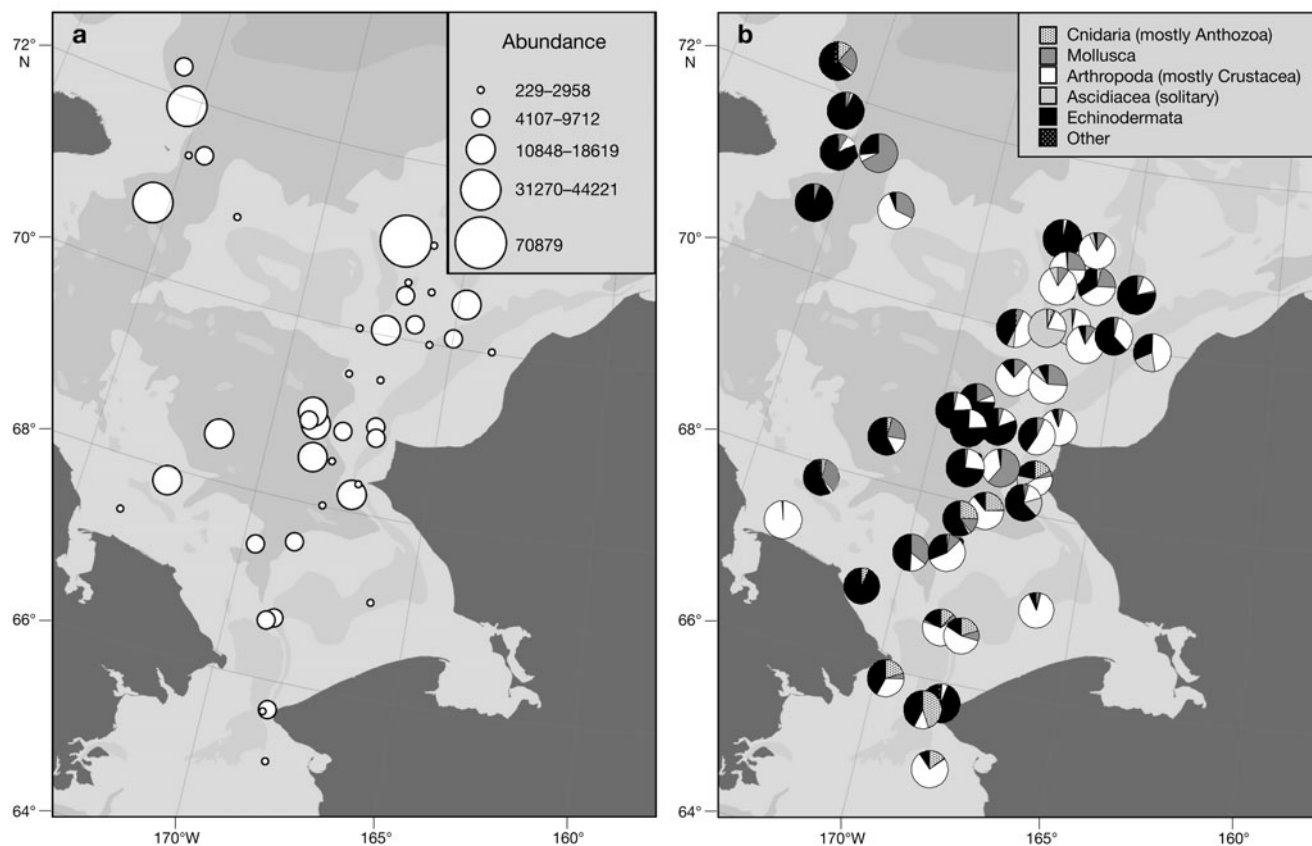

Fig. 2. Epifaunal abundance. (a) Absolute abundance (ind. 1000 m^{-2}). Bins delineated according to Jenks' natural breaks criteria (see 'Materials and methods'). (b) Relative composition

RESULTS

Distribution, abundance and biomass

Gross abundance ranged from 229 ind. 1000 m^{-2} at Stn OD22 to 70879 ind. 1000 m^{-2} at Stn OM24 (mean ± SD across all stations 8736 ± 12647 ind. 1000 m^{-2}) (Table 1, Fig. 2a). There was no discernable latitudinal or longitudinal trend in abundance, although stations with particularly high abundance were farthest north. Gross biomass estimates ranged from 1628 g wet wt m^{-2} at Stn R27 to 217023 g wet wt m^{-2} at Stn OM9-08 (mean ± SD across all stations 38863 ± 49418 g wet wt m^{-2}) (Fig. 3a). Biomass values were generally highest in the area from the Bering Strait to an area northwest of Point Hope and in Herald Canyon.

Abundance and biomass were dominated by echinoderms at many stations (67% of mean abundance and 45% of mean biomass across all stations). The group was particularly prevalent in the Herald Canyon area and the Bering Strait in both abundance and biomass, and also numerically at most stations between about 67 and 69°N (Fig. 2b). Echinoderm biomass was also dominant at many central stations (Fig. 3b). Crusta-

ceans contributed most to abundance and biomass at some of the southeastern and northeastern stations. The group made up 18% of the mean abundance and 31% of the mean biomass in the study area and, numerically, 90% of the crustaceans at Stn R27, where amphipods overwhelmingly dominated. Overall, mollusks contributed 8% to mean abundance and 9% to mean biomass in the study area. Stns R58 (Herald Canyon) and OD20 (central Chukchi) were numerically dominated by mollusks, mostly gastropods (68 and 61%, respectively), and, at Stns R15 and R25 (southwestern Chukchi), mollusks dominated biomass (42 and 36%, respectively, of station biomass). Ascidians comprised 5% of the overall mean abundance and 8% of the mean biomass in the study area. Stns OM17-08 and OM3-08 (northeastern Chukchi) were numerically dominated by solitary ascidians (49 and 72%, respectively), and, at Stn OM9-08 (near Pt. Hope), ascidians contributed most to biomass (51%; majority of the group 'other'). Cnidarians (mostly Actinaria) did not dominate abundance or biomass at any station, but made up about 3% of the mean abundance and 4% of the mean biomass in the study area, while sponges and bryozoans each contributed <1% to total biomass.
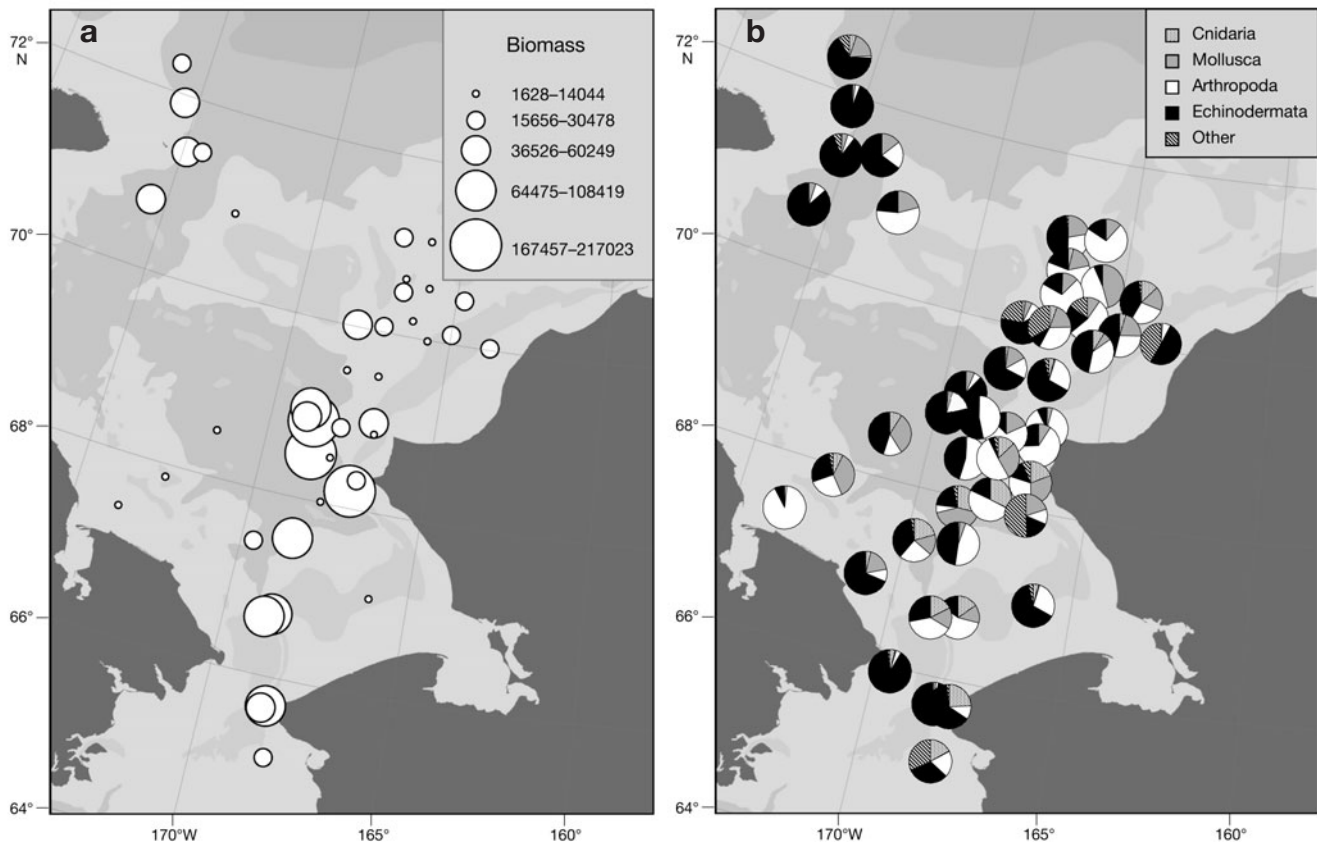

Fig. 3. Epifaunal biomass. (a) Absolute biomass (g wet wt 1000 m^{-2}). Bins delineated according to Jenks' natural breaks criteria (see 'Materials and methods'). (b) Relative composition

The vast majority (>70%) of all individuals collected in all trawls combined consisted of only 3 species: the brittle star *Ophiura sarsi* (60.0%), the sea cucumber *Myriotrochus rinkii* (8.6%) and the snow crab *Chionoecetes opilio* (4.8%). Similarly, only 3 species contributed >10% each to the total biomass in the sampling area: *O. sarsi* (16.9%), the sea urchin *Strongylocentrotus pallidus* (14.1%) and *C. opilio* (13.0%). The abundance of *C. opilio*, a commercially valuable species in the Bering Sea and northwestern Atlantic, ranged from 0 (at Stn OD1) to 4017 ind. 1000 m^{-2} at St OM14-08 (mean ± SD across all stations: 765 ± 1103). The contribution of *C. opilio* abundance to total abundance reached a maximum of 67% at Stn OM404-08. *C. opilio* biomass ranged from 0 at Stn OD1 to 111 552 g wet wt 1000 m^{-2} at Stn OM5 (mean ± SD across all stations 10 135 ± 22 052) and was highest in the south-central and southeastern Chukchi Sea (Fig. 4). The relative contribution of *C. opilio* biomass to total biomass reached a maximum of 69% at Stn OM404-08 (mean ± SD: 20 ± 18%).
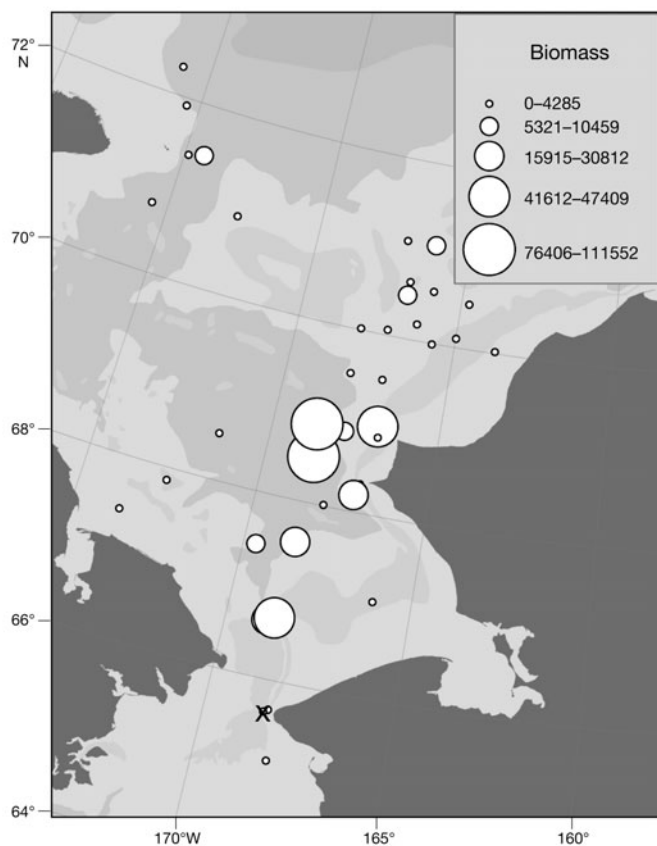

Fig. 4. *Chionoecetes opilio.* Biomass (g wet wt 1000 m^{-2}) of this commercially harvested species in the Bering Sea. Bins delineated according to Jenks' natural breaks criteria (see 'Materials and methods'). The cross marks the only sampling location (OD1 in the Bering Strait) where no snow crabs were caught

Taxon numbers and diversity

The total number of taxa was 165, 10 of which were taxonomically only identified to a family or higher level, while all others were considered individual species or putative species (see Appendix 1). Across the whole study area, mollusks had the highest number of taxa (45), followed by crustaceans (33), bryozoans (23), echinoderms (23), ascidians (14), cnidarians (13) and sponges (8). The numbers of taxa were highest in the Bering Strait and Herald Canyon areas, and at stations near the Alaskan coast (Fig. 5a). The maximum number of taxa was 47 at Stn R17 (Point Hope), and the lowest number was 13 at Stn OD22, about 35 km away. Gastropods contributed most to the total number of taxa at soft-bottom stations, whereas colonial taxa (Porifera, Bryozoa and Ascidia) contributed substantially to the total number of taxa at hard-bottom sites (Fig. 5b). Neither the Shannon diversity index (range from 0.77 at Stn R20 to 2.93 at Stn R17), nor Pielou's evenness (range from 0.25 at Stn R20 to 0.82 at Stn R25; Table 1) showed any discernable spatial trends.

Station similarity

Cluster analysis of fourth-root-transformed biomass data resulted in 6 significant station clusters and 6 unique stations not included in any of the significant clusters (p = 0.05, Similarity Profile test in PRIMER). Bray-Curtis similarity within clusters was from 53 to 71%, except for 1 cluster at only 34% similarity (Table 2, Fig. 6a). Dissimilarity between pairs of clusters ranged from 54 to 88% (Table 3). Mostly, clusters included stations in a connected geographic area (Fig. 6a). Ordination of stations in the NMDS (Fig. 6b) showed little overlap between stations from different clusters, with the exception of R11 and OD31. Three of the unique stations identified using fourth-root-transformations were part of multi-station clusters using square-root-transformations in the cluster analysis; OM19 grouped with OD31, OD22 grouped with the central & north (CN) cluster, and R62 grouped with the south/southeast (SSE) cluster (not shown). We found no significant difference using 'cruise' as a factor (ANOSIM, global R = 0.062, p = 0.208), indicating that station clusters were not the result of investigator- or method-related bias between the 3 cruises.

Four to 6 taxa, mostly within echinoderms, crustaceans and mollusks, contributed ~50% of the similarity within each of the 6 main station clusters (Table 2), while 15 or more species contributed 50% to the dissimilarity between clusters, of which the 3 dominant taxa are given for each cluster in Table 3. The 5 bio-

mass-dominant taxa per cluster were mostly echinoderms and crustaceans, but also included several actinarians and gastropods, all of which contributed ~60 to >90% to the total biomass in each cluster (Table 4). Most of the dominant species had a broad latitudinal distribution across the study area (Fig. 7). Exceptions included the sea star *Lethasterias nanimensis* and the anemone *Cribrinopsis* sp., which only occurred in the southern Chukchi Sea, and the sea stars *Ctenodiscus crispatus* and *Urasterias linkii*, which only occurred at the northern stations in Herald Canyon.

Environmental and biological linkages

The combination of environmental variables that best matched the biological matrix (excluding OM-08 stations) included 7 variables (water depth, latitude, substrate category, grain size, bottom temperature, oxygen and sediment organic content) with a moderately high correlation coefficient of 0.533 (BIO-ENV; Table 5). The combination of latitude and substrate yielded a correlation coefficient of 0.535, which increased very little with the addition of other variables.

When correlated to the variable 'substrate category', station groups 'soft' and 'hard' were significantly different with substantial separation (ANOSIM, global R = 0.42, p = 0.001). Station similarity based on water masses had a low global R = 0.21 (ANOSIM, p = 0.011), suggesting little separation. Pairwise tests indicated no difference in community structure between stations in the 2 main water masses in the region, ACW and BSAW (R = 0.05, p > 0.05). Differences were larger and significant between ACW and WW (R = 0.41, p = 0.019).

Overall, bulk abundance and biomass were not significantly different at hard- versus soft-bottom stations (p = 0.479 and p = 0.099, respectively, *t*-test), between different water masses (p = 0.663 and p = 0.263, respectively, ANOVA), or between different station clusters identified from cluster analysis (p = 0.285 and p = 0.497, respectively, ANOVA). When sessile (Porifera, Cnidaria, Bivalvia, Cirripedia, Ascidiacea, Brachiopoda, Bryozoa) and mobile fauna (other fauna) were analyzed separately, results were similar, except
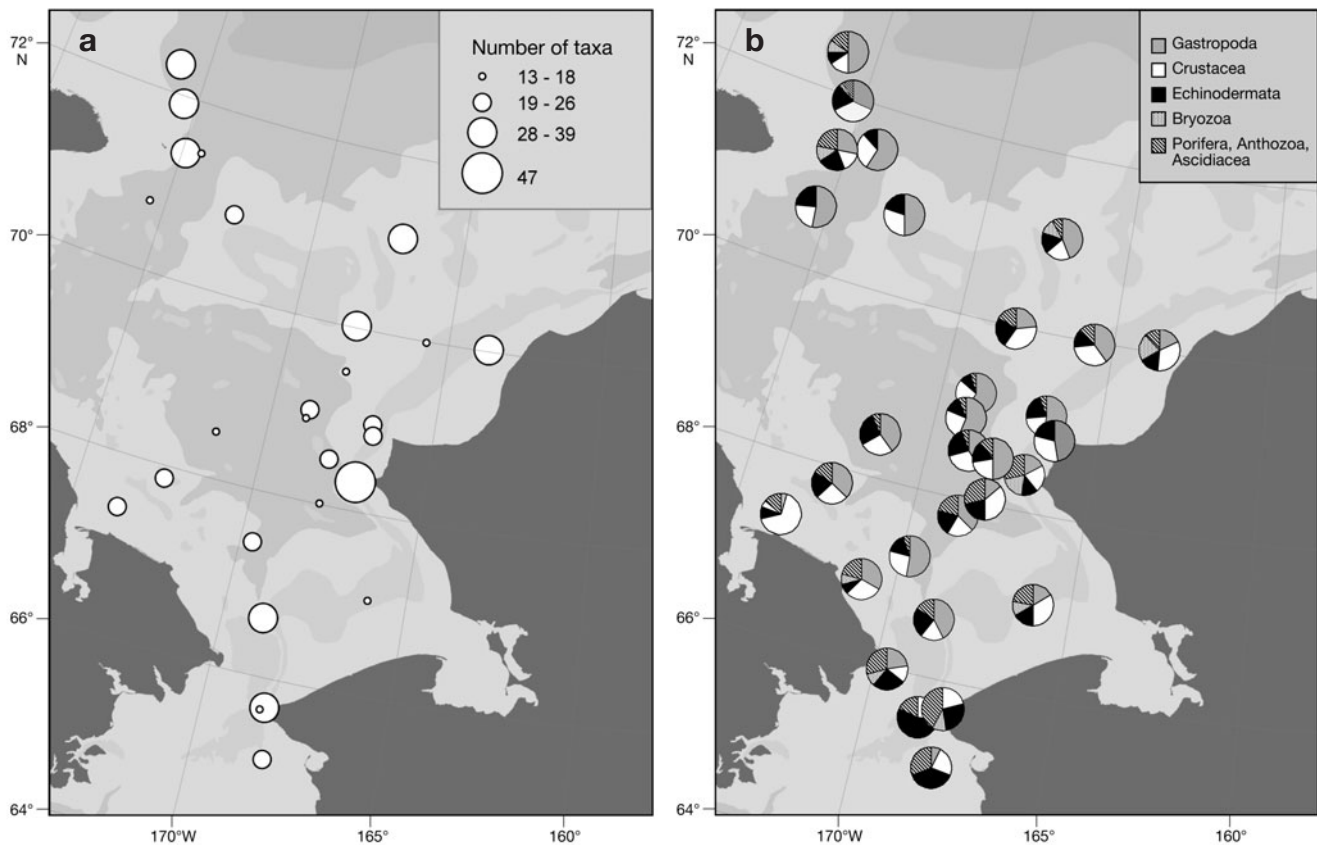

Fig. 5. Number of epifaunal taxa in the Chukchi Sea. (a) Absolute numbers of taxa. Bins delineated according to Jenks' natural breaks criteria (see 'Materials and methods'). (b) Relative taxonomic composition. Note: 2008 data were excluded

Table 2. Epifaunal species contributing approximately 50% of the similarity within each of the 6 main cluster groups identified from hierarchical clustering. Sim.: similarity; SD: standard deviation; Contrib.: contribution; Cum.: cumulative

	Av. biomass (g wet wt $100\ m^{-2}$)	Av. similarity (%)	SD of Sim.	Contrib. (%)	Cum. (%)
Group south/southeast (SSE), average similarity: 34%					
Strongylocentrotus pallidus	6.9	3.4	1.0	10.2	10.2
Leptasterias groenlandica	5.0	3.0	2.6	9.1	19.3
Chionoecetes opilio	4.7	2.8	1.4	8.2	27.5
Hyas coarctatus	5.1	2.6	1.4	7.8	35.3
Argis lar & *Neocrangon communis*	3.9	2.4	1.4	7.2	42.5
Gersemia sp. (cf. *rubiformis*)	4.7	2.3	1.0	6.9	49.5
Group southwest (SW), average similarity: 55%					
Myriotrochus rinkii	9.9	10.9		20.0	20.0
Henricia tumida	6.3	6.9		12.7	32.6
Chionoecetes opilio	7.1	5.4		9.8	42.5
Cribrinopsis/Epiactis sp.	6.6	4.7		8.6	51.0
Group south-central–west (SCW), average similarity: 58%					
Urticina sp.?	5.5	6.0	8.9	10.3	10.3
Chionoecetes opilio	5.2	5.8	7.1	9.9	20.3
Cryptonatica affinis	5.5	5.7	4.1	9.8	30.1
Lunatia pallida	4.5	4.9	59.3	8.5	38.5
Myriotrochus rinkii	4.4	4.4	3.5	7.6	46.1
Amphiodia craterodmeta	5.0	4.3	1.2	7.4	53.5
Group central & north (CN), average similarity: 53%					
Chionoecetes opilio	7.8	8.2	7.8	15.5	15.5
Pagurus rathbuni	6.3	6.3	5.5	11.9	27.4
Leptasterias polaris	5.2	5.6	3.9	10.6	38.0
Argis lar & *Neocrangon communis*	4.7	5.4	5.5	10.2	48.2
Buccinum elatior	4.5	4.7	5.9	9.0	57.1
Group Herald Canyon area (HC), average similarity: 63%					
Ctenodiscus crispatus	10.8	12.9		20.2	20.2
Chionoecetes opilio	8.2	9.9		15.6	35.9
Tachyrhynchus erosus	5.9	6.6		10.5	46.3
Pagurus rathbuni	4.3	5.4		8.5	54.8
Group central-east (CE), average similarity: 71%					
Gorgonocephalus caryi	6.1	9.5		13.4	13.4
Chionoecetes opilio	5.1	8.2		11.6	25.0
Neptunea ventricosa	4.1	6.9		9.7	34.7
Argis lar & *Neocrangon communis*	3.7	6.5		9.1	43.8
Pagurus rathbuni	3.7	5.5		7.7	51.5

that sessile biomass was significantly different between the clusters SSE and CN, CN and unique Stn OM19, and Herald Canyon and unique Stn OM19 (ANOVA p = 0.014). Epifaunal biomass was not significantly correlated with sediment grain size (Pearson correlation coefficient = 0.126, p = 0.426, Bartlett's chi-square = 0.634, n = 42), number of taxa (Pearson correlation coefficient = 0.367, p = 0.060, Barlett's chi-square

= 3.547, n = 27), sediment organic carbon content (Pearson correlation coefficient = 0.194, p = 0.130, Barlett's chi-square = 2.288, n = 42), integrated chlorophyll concentration (Pearson correlation coefficient = 0.138, p = 0.49, Bartlett's chi-square = 0.47, n = 27), bottom temperature (Pearson correlation coefficient = 0.021, p = 0.897, Bartlett's chi-square = 0.017, n = 42), bottom salinity (Pearson correlation coefficient = −0.027, p = 0.865, Bartlett's chi-square = 0.029, n = 42), or bottom oxygen concentration (Pearson correlation coefficient = 0.231, p = 0.141, Bartlett's chi-square = 2.164, n = 42). Analyzing sessile and mobile biomass separately yielded the same result (i.e. no significant correlations with the above-listed variables), except that sessile biomass alone was correlated with the number of taxa (Pearson correlation coefficient = 0.632, p < 0.001, Bartlett's chi-square = 14.013, n = 27).

The number of taxa was not significantly different between hard-bottom (mean ± SD: 27.4 ± 9.7) and soft-bottom stations (mean ± SD: 22.4 ± 6.7; p = 0.115, *t*-test, n = 30), clusters (p = 0.127, ANOVA, n = 30), or water masses (p = 0.546, ANOVA, n = 30). Shannon-Wiener's *H'* was virtually the same at hard-bottom (mean ± SD: 1.84 ± 0.60) and soft-bottom stations (mean ± SD: 1.78 ± 0.50), and did not differ significantly between water masses (p = 0.475, ANOVA) or clusters (p = 0.468, ANOVA). Similarly, Pielou's *J'* was not different between hard-bottom (mean ± SD: 0.56 ± 0.16) and soft-bottom stations (mean ± SD: 0.58 ± 0.17), clusters (p = 0.390, ANOVA), or water masses (p = 0.266, ANOVA). *J'* and *H'* were negatively correlated with total biomass (*J'*: Pearson correlation coefficient = −0.632, p < 0.001, Bartlett's chi-square = 12.476; *H*: Pearson correlation coefficient = −0.499, p < 0.008, Bartlett's chi-square = 7.018, n = 27 for both). Once mobile and sessile biomass were separated, however, there was no correlation of diversity indices *J'* and *H'* with sessile biomass. A Pearson correlation of epifaunal and macrofaunal biomass failed to show a significant correlation (Pearson coefficient = 0.073, p = 0.575, Bartlett's chi-square = 0.315, n = 61; Fig. 8).

Fig. 6. Station similarity. Color code is shared in all panels. (a) Station clusters obtained from hierarchical clustering of the epifaunal biomass matrix (fourth-root-transformed, Bray-Curtis similarity). Red lines connect stations that are not statistically unique (p = 0.05, SIMPROF). (b) NMDS of the epifaunal biomass matrix. (c) Spatial distribution of epifaunal clusters in the Chukchi Sea, with unique stations marked with black. Note: 2008 data were excluded (see 'Materials and methods').
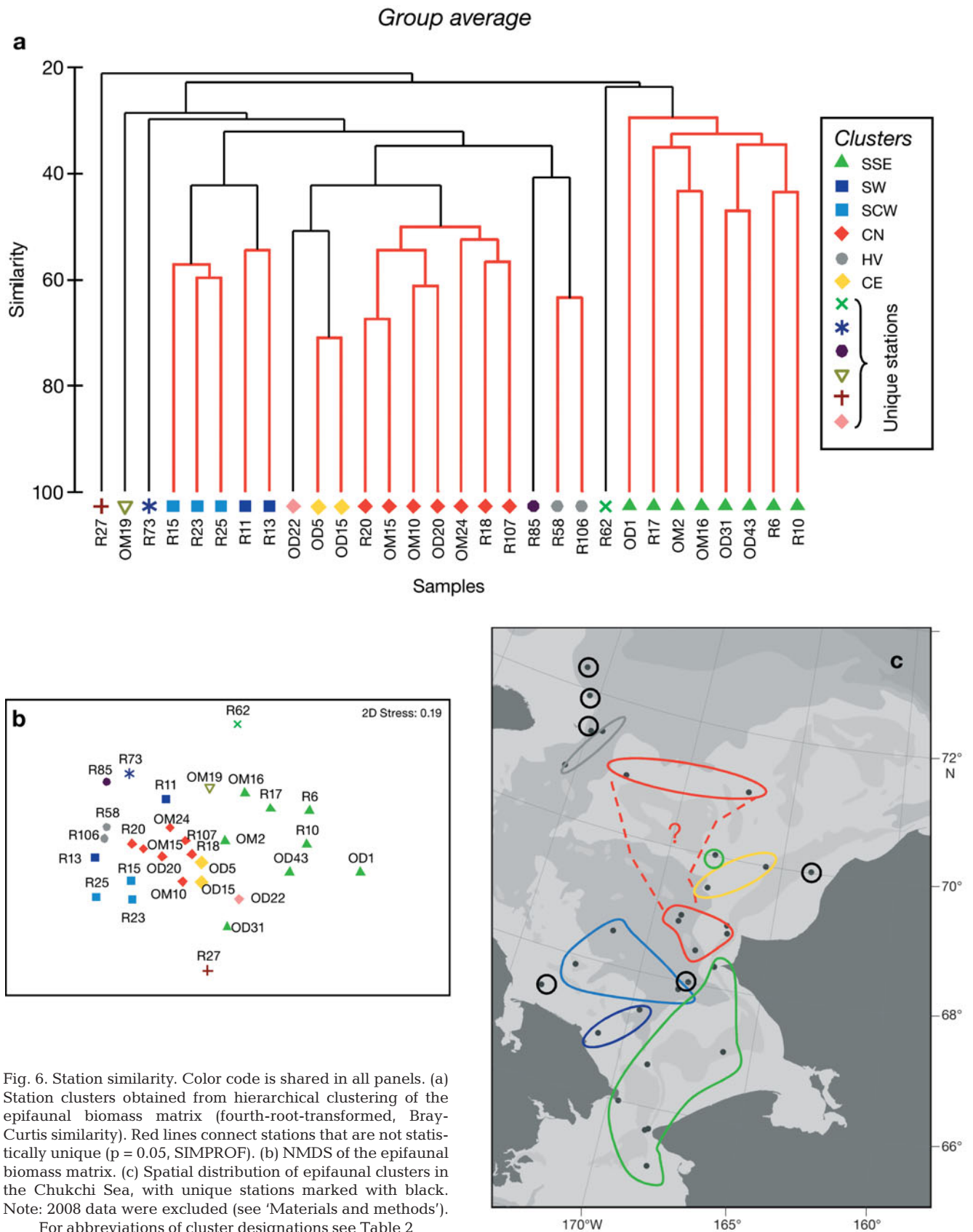For abbreviations of cluster designations see Table 2

Table 3. Top 3 epifaunal species contributing most to dissimilarity between each of the 6 main clusters identified from hierarchical clustering. for other abbreviations see Table 2

Species	Average biomass (g wet wt. 100 m^{-2})		Average dissimilarity	SD of dissimilarity	Contrib. (%)	Cum. (%)
Groups SSE & SW, average dissimilarity = 79%	**SSE**	**SW**				
Myriotrochus rinkii	0.0	9.9	5.0	5.0	6.3	6.3
Strongylocentrotus pallidus	6.9	0.0	3.4	1.4	4.3	10.6
Cryptonatica affinis	0.5	5.9	2.8	2.1	3.5	14.0
Groups SSE & SCW, average dissimilarity = 80%	**SSE**	**SCW**				
Strongylocentrotus pallidus	6.9	0.0	3.6	1.4	4.5	4.5
Cryptonatica affinis	0.5	5.5	2.7	2.6	3.3	7.9
Amphiodia craterodmeta	0.3	5.0	2.6	1.7	3.2	11.1
Groups SW & SCW, average dissimilarity = 88%	**SW**	**SCW**				
Myriotrochus rinkii	9.9	4.4	3.3	4.5	5.7	5.7
Cribrinopsis/Epiactis sp.	6.6	1.2	3.3	1.7	5.6	11.3
Urticina sp.?	0.0	5.5	3.2	6.1	5.6	16.9
Groups SSE & CN, average dissimilarity = 74%	**SSE**	**CN**				
Strongylocentrotus pallidus	6.9	0.0	3.6	1.4	4.9	4.9
Ophiura sarsi	0.5	6.0	3.1	1.0	4.2	9.0
Buccinum elatior	0.0	4.5	2.4	3.3	3.2	12.3
Groups SW & CN, average dissimilarity = 69%	**SW**	**CN**				
Myriotrochus rinkii	9.9	0.0	5.8	12.1	8.5	8.5
Cribrinopsis/Epiactis sp.	6.6	0.0	3.9	2.6	5.7	14.2
Henricia tumida	6.3	0.0	3.7	12.1	5.4	19.6
Groups SCW & CN, average dissimilarity = 65%	**SCW**	**CN**				
Urticina sp.?	5.5	0.0	3.5	5.7	5.3	5.3
Ophiura sarsi	2.4	6.0	3.4	1.1	5.1	10.4
Amphiodia craterodmeta	5.0	0.0	3.2	2.0	4.9	15.3
Groups SSE & HC, average dissimilarity = 83%	**SSE**	**HC**				
Ctenodiscus crispatus	0.0	10.8	5.7	4.6	6.9	6.9
Strongylocentrotus pallidus	6.9	0.0	3.6	1.4	4.3	11.2
Amphiodia craterodmeta	0.3	6.4	3.4	1.0	4.0	15.2
Groups SW & HC, average dissimilarity = 63%	**SW**	**HC**				
Ctenodiscus crispatus	0.0	10.8	6.3	21.7	10.1	10.1
Myriotrochus rinkii	9.9	0.8	5.4	8.1	8.5	18.6
Cribrinopsis/Epiactis sp.	6.6	0.0	3.9	2.4	6.2	24.8
Groups SCW & HC, average dissimilarity = 63%	**SCW**	**HC**				
Ctenodiscus crispatus	0.0	10.8	6.8	13.1	10.8	10.8
Amphiodia craterodmeta	5.0	6.4	4.1	2.3	6.4	17.2
Tachyrhynchus erosus	0.0	5.9	3.8	6.3	5.9	23.1
Groups CN & HC, average dissimilarity = 59%	**CN**	**HC**				
Ctenodiscus crispatus	0.0	10.8	6.8	10.4	11.6	11.6
Amphiodia craterodmeta	0.0	6.4	4.0	1.0	6.8	18.4
Ophiura sarsi	6.0	0.0	3.7	1.0	6.3	24.7
Groups SSE & CE, average dissimilarity = 72%	**SSE**	**CE**				
Strongylocentrotus pallidus	6.9	0.0	4.2	1.4	5.9	5.9
Leptasterias groenlandica	5.0	0.0	2.9	2.7	4.0	9.9
Leptasterias polaris	5.3	4.7	2.9	1.5	4.0	14.0
Groups SW & CE, average dissimilarity = 70%	**SW**	**CE**				
Myriotrochus rinkii	9.9	0.0	6.9	48.8	9.8	9.8
Cribrinopsis/Epiactis sp.	6.6	0.0	4.6	2.4	6.6	16.4
Gorgonocephalus caryi	0.0	6.1	4.3	4.4	6.1	22.5
Groups SCW & CE, average dissimilarity = 69%	**SCW**	**CE**				
Gorgonocephalus caryi	0.0	6.1	4.7	4.4	6.7	6.7
Urticina sp.?	5.5	0.0	4.2	6.2	6.0	12.8
Amphiodia craterodmeta	5.0	0.0	3.9	1.9	5.6	18.4
Groups CN & CE, average dissimilarity = 54%	**CN**	**CE**				
Gorgonocephalus caryi	0.0	6.1	4.7	4.3	8.7	8.7
Ophiura sarsi	6.0	0.9	4.1	1.0	7.6	16.3
Neptunea communis	3.3	0.0	2.4	2.2	4.5	20.8
Groups HC & CE, average dissimilarity = 67%	**HC**	**CE**				
Ctenodiscus crispatus	10.8	0.0	8.2	23.3	12.2	12.2
Amphiodia craterodmeta	6.4	0.0	4.8	0.9	7.1	19.3
Gorgonocephalus caryi	0.0	6.1	4.7	4.4	6.9	26.2

Table 4. The 5 dominant epibenthic taxa in each of the 6 main clusters identified from cluster analysis, their contribution to total cluster biomass and their mean biomass (± SD) at the cluster stations (see Fig. 6 for station clusters). na: not applicable

| Cluster	Dominant taxa by biomass	Percent of total cluster biomass	Mean biomass (g wet wt 1000 m^{-2})	SD
South/southeast (SSE)	*Strongylocentrotus pallidus*	24.6	8942	12013
	Leptasterias polaris	14.2	5172	7122
	Chionoecetes opilio	8.4	3071	6526
	Lethasterias nanimensis	5.1	1867	4420
	Hyas coarctatus	4.9	1778	2005
	Sum/mean total biomass	57.3	34455	26536
Southwest (SW)	*Myriotrochus rinkii*	40.7	9602	179
	Chionoecetes opilio	15.8	3735	4489
	Cribrinopsis sp.	14.1	3318	4240
	Cryptonatica affinis	8.3	1964	2387
	Henricia tumida	6.7	1578	45
	Sum/mean total biomass	85.7	23579	9757
South-central–west (SCW)	*Amphiodia craderodmeta*	14.5	1241	1093
	Cryptonatica affinis	13.8	1184	869
	Urticina sp.	12.5	1072	901
	Chionoecetes opilio	9.9	851	649
	Myriotrochus rinkii	5.7	493	469
	Sum/mean total biomass	56.4	8590	979
Central & north (CN)	*Chionoecetes opilio*	39.7	8870	16072
	Ophiura sarsi	25.1	5603	10951
	Pagurus rathbuni	13.0	2896	4204
	Leptasterias polaris	3.9	866	722
	Neptunea ventricosa	2.7	598	662
	Sum / mean total biomass	84.4	22326	21843
Herald Canyon (HC)	*Ctenodiscus crispatus*	34.5	13715	4345
	Amphiodia craderodmeta	34.1	13554	na
	Chionoecetes opilio	11.4	4553	1087
	Urasterias linki	9.8	3881	na
	Tachyrhynchus erosus	3.3	1317	793
	Sum/mean total biomass	93.0	39788	16023
Central–east (CE)	*Gorgonocephalus caryi*	34.1	1643	1445
	Leptasterias polaris	21.1	1013	1352
	Chionoecetes opilio	15.8	759	586
	Neptunea ventricosa	6.4	306	190
	Pagurus rathbuni	5.3	255	265
	Sum/mean total biomass	82.6	4810	1047
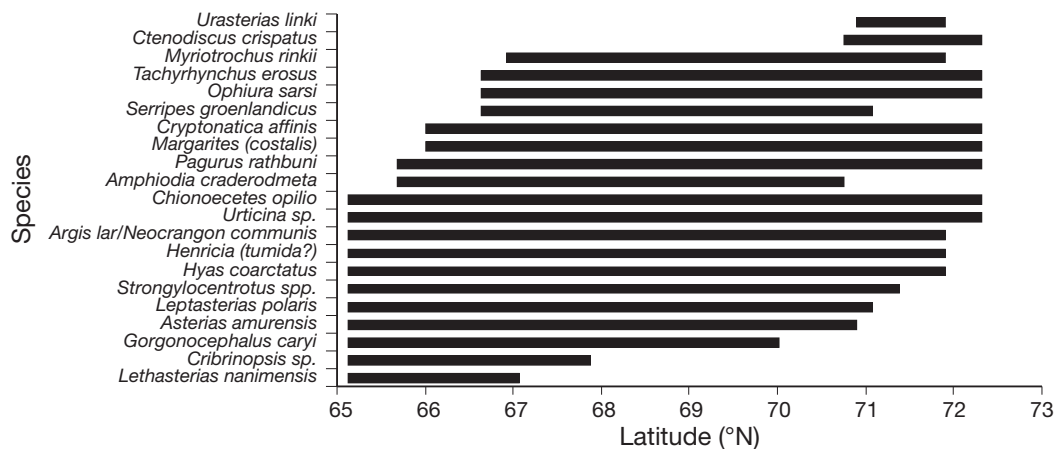
Fig. 7. Latitudinal ranges of dominant species found in the study area. Dominant taxa include the top 5 contributors to abundance and biomass in each of the cluster groups (see Table 2, Fig. 6), as well as any additional taxa that dominated at a single station and occurred at >3 stations

Table 5. Results of the BIO-ENV procedure providing the combinations of environmental variables best matching the community similarity matrix, based on biomass. Correlation coefficients are given in parentheses. In addition to the variables given below, macrofaunal biomass and integrated chlorophyll concentration were included in the analysis, but did not strongly influence biotic variables

Number of variables	Best variable combination	Second best variable combination
1	Latitude (0.379)	Substrate (0.363)
2	Latitude, substrate (0.503)	Latitude, salinity (0.442)
3	Latitude, substrate, salinity (0.535)	Water depth, latitude, substrate (0.510)
4	Latitude, substrate, salinity, organic content (0.531)	Water depth, latitude, substrate, salinity (0.526)
5	Latitude, substrate, grain size, temperature, organic content (0.542)	Latitude, substrate, grain size, salinity, organic content (0.541)
6	Water depth, latitude, substrate, grain size, salinity, oxygen (0.549)	Water depth, latitude, substrate, grain size, salinity, organic content (0.547)
7	Water depth, latitude, substrate, grain size, temperature, oxygen, organic content (0.553)	Water depth, latitude, substrate, grain size, salinity, oxygen, organic content (0.552)

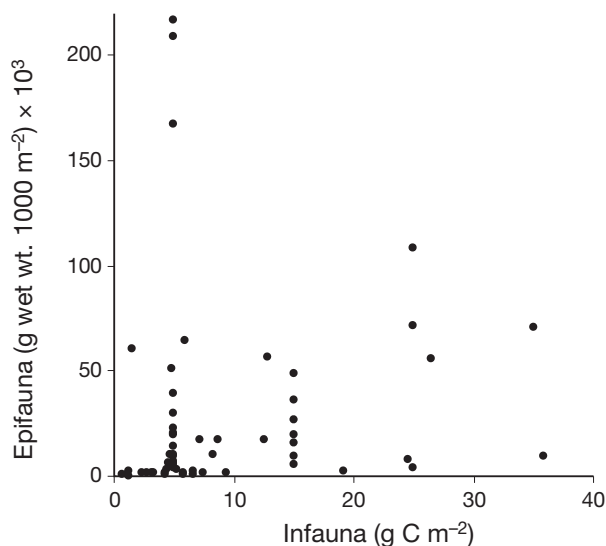Fig. 8. Relationship betwee macrofauna and epifauna, no significant correlation (Pearson coefficient = 0.073, p = 0.575, Bartlett's chi-square = 0.315, n = 61)

DISCUSSION

Community composition

Echinoderms and crustaceans dominated epifaunal abundance and biomass on the Chukchi shelf, while gastropods were the most species-rich taxon (Figs. 2b, 3b & 5b). The dominance of echinoderms is consistent with previous studies of both shelf and deep-sea regions of the Arctic (see references in Table 6 and MacDonald et al. in press). All echinoderm classes, except crinoids, were commonly encountered on the Chukchi shelf, with ophiuroids most prevalent in the northern areas and asteroids dominating in the southern Chukchi and the northern Bering Seas (Table 6). Certain sea stars, such as *Ctenodiscus crispatus*, only occurred at the northern stations, but did not significantly influence total biomass.

The single most abundant brittle star (and echinoderm) we encountered in the Chukchi Sea was *Ophiura sarsi* (see also Frost & Lowry 1983, Ambrose et al. 2001, Feder et al. 2005, Sirenko et al. unpubl. data), a wide-ranging boreal-Arctic species with circumpolar distribution (Anisimova 1989). *O. sarsi* is also common in the adjacent Beaufort Sea (Carey 1977, Loggerwell & Rand 2009) and in the Japanese Pacific (Fujita & Ohta 1989). On Eurasian Arctic shelves, the much smaller brittle star *Ophiocten sericeum* dominates (Starmans et al. 1999, Piepenburg 2000; see also Table 7), although *O. sarsi* is also common in Svalbard waters (Piepenburg et al. 1996). Like *O. sarsi*, *O. sericeum* is also described as a wide-ranging boreal-Arctic species (Anisimova 1989), but was rarely encountered in our Chukchi Sea samples.

The abundance of *Ophiura sarsi* was of the same order of magnitude as previously reported from an inshore region in the northeastern Chukchi Sea (Ambrose et al. 2001), but higher than in the southeastern Chukchi/Kotzebue Sound area (Feder et al. 2005) (Table 7). The cause for a north to south decrease in ophiuroid dominance is unclear. Worldwide, dense ophiuroid beds have been discovered in most marine habitats, including continental shelves, slopes and abyssal plains (Table 7), and are thought to favor areas where predation pressure is low (Aronson & Sues 1987). For example, *O. sarsi* is reported to exhibit avoidance behavior in the presence of mobile sea stars and buccinid snails (Fujita & Ohta 1989), although we found Buccinidae to be very abundant in both the

Table 6. Dominant epibenthic taxa by biomass in the northern Bering, Chukchi and Beaufort Seas. Note that *Strongylocentrotus droebachiensis* in Feder et al. (2005) is probably in fact *S. pallidus* (H. M. Feder pers. comm.). *Neptunea heros* in Feder et al. (2005) is referred to as *N. ventricosa* in the Russian and European literature and in the present study

Study area	Dominant taxa by biomass	Source
Chukchi Sea	*Ophiura sarsi, Chionoecetes opilio, Strongylocentrotus pallidus, Leptasterias polaris*[a]	Present study
Northeastern Chukchi Sea	Ophiuroids (*Ophiura. sarsi, O. maculata, Ophiopholis aculeata, Stegophiura nodosa*), *Echinarachnius parma*	Ambrose et al. 2001
Southern Chukchi Sea, Kotzebue Sound	*Asterias amurensis, Neptunea heros, Leptasterias polaris, Chionoecetes opilio, Strongylocentrotus droebachiensis, Lethasterias nanimensis*[a]	Feder et al. 2005
Norton Sound	Sea stars (*Asterias amurensis, Lethasterias nanimensis, Evasterias* spp.)[b]	Hamazaki et al. 2005
Northeastern Bering Sea (Chirikov Basin and Norton Sound)	*Asterias amurensis, Gorgonocephalus caryi, Lethasterias nanimensis*[a]	Jewett & Feder 1981
Southeastern Bering Sea	*Chionoecetes opilio, C. bairdi, Paralithodes camtschatika, Asterias amurensis, Styela rustica*[a]	Jewett & Feder 1981
Alaskan Beaufort Sea	*Ophiura sarsi, Chionoecetes opilio, Musculus niger*[a]	Loggerwell & Rand 2009

[a]Each >5% of all taxa; [b]Not specified if by biomass or abundance

Table 7. Ophiuroid abundance and biomass in the Arctic and comparative areas

Species	Density range (average all stations) (ind. m^{-2})	Biomass range (average all stations) (g AFDM)	Study area	Source (and method)
Ophiura sarsi	0–99.9	0–3.8	NE Chukchi Sea	Ambrose et al. 2001 (video plus dredge)
Ophiura sarsi	0–0.1 (reported as 0–108267 ind. km^{-2})		Kotzebue Sound, SE Chukchi Sea	Feder et al. 2005 (otter trawl)
Ophiura sarsi	0–68.1 (5.5)	0–3.7[a] (0.3[a]	Chukchi Sea	Present study (beam trawl)
Ophiura sarsi	353 (1 station only)	8.4[a]	North Pacific off Japan	Fujita & Ohta 1989 (still images plus trawls)
Ophiocten sericeum *Ophiura sarsi*	0.3–566 (158), 0.4–35 (5.6)	<0.1–1.5 (0.5) <0.1–3.8 (0.5)	Laptev Sea	Piepenburg & Schmid 1997 (still images plus dredge)
Ophiocten sericeum, Ophiacantha bidentata	32–524 2–49	0.3–5.0 0.1–1.9	Barents Sea	Piepenburg & Schmid 1996 (still images & trawl)
Ophiocten sericeum	(6)		NE Greenland (79–81.3° N)	Starmans et al. 1999 (video)
Ophiocten sericeum	(5.3)		NE Greenland (75° N)	Mayer & Piepenburg 1996 (still images)
Ophiacantha abyssicola	390–1200		Continental slope of Nova Scotia	Metaxas & Griffin 2004 (still images)

[a]Converted from g wet wt to ash-free dry mass (AFDM) using AFDM = 0.034 × 2 × wet wt (Rowe 1983, Brey et al. 1988)

southern and the northern Chukchi Sea (Feder et al. 1994a, 2005, present study). Further, sea stars in Norton Sound and the southeastern Chukchi Sea are not known to feed on ophiuroids (Feder & Jewett 1978). Flatfishes and *Chionoecetes opilio* in the southeastern Bering Sea, however, do utilize ophiuroids as a food source (Feder & Jewett 1980, 1981), and both taxa are less prevalent in the northern than in the southern

Chukchi Sea (Barber et al. 1997, Mecklenburg et al. 2007, present study), possibly contributing to the dominance of ophiuroids in the north.

Dense patches of the gelatinous apodid holothurian *Myriotrochus rinkii* occurred at some soft-bottom stations where *Ophiura sarsi* was uncommon or absent. *M. rinkii* is also common in other Arctic shelf areas such as the Laptev Sea and around Baffin Island (Cross

& Thomson 1987, Piepenburg & Schmid 1997). Biomass in this taxon was particularly high in areas with high nutrient and chlorophyll concentrations (Lee et al. 2007). Holothurians are known to form these dense assemblages to exploit fresh phytodetritus pulses on soft bottoms. Examples include *Amperima rosea* aggregations in the Porcupine Abyssal Plain in the North Atlantic (Billett et al. 2001, Iken et al. 2001), high densities of *Kolga hyalina* in a phytodetritus-rich, pockmark-like depression on the Chukchi Cap in the Arctic Ocean (MacDonald et al. in press), and high densities of *Cucumaria frondosa* at the bottom of pockmarks in the Bay of Fundy (Wildish et al. 2008). This type of opportunistic feeding behavior suggests that holothurians may play a significant role in remineralization of newly deposited organic material, and could characterize regions of tight benthic–pelagic coupling on Arctic shelves.

Crustaceans were the second most abundant and biomass-rich group in the Chukchi Sea, particularly at eastern stations (Figs. 2b, 3b & 4). This pattern contrasts with the trend suggested by Feder et al. (2005) of epifaunal crustacean dominance in the south and echinoderm dominance in the north. However, over a larger spatial scale that includes the Bering Sea, the trend may indeed hold true (Table 6) and has been attributed to the smaller populations of large crabs and demersal fishes in the north (Barber et al. 1997, Paul et al. 1997, Feder et al. 2005), which provide vacant niches for other taxa. Alternatively, physiological differences may allow long-lived, slow-growing taxa such as echinoderms to dominate in very cold and food-limited parts of polar waters (Dahm 1996, Bluhm et al. 1998), while distributions of other taxa, such as crabs, are constrained at the sub-zero temperatures typical of the northern Chukchi (Frederich et al. 2000, present study).

Despite physiological constraints, crabs did constitute the most biomass-rich epifaunal crustacean group in the Chukchi Sea, dominated mainly by *Chionoecetes opilio*, but also with high local densities of several species of hermit crabs and the lyre crab *Hyas coarctatus* in some areas (see also Feder et al. 2005). In contrast, crabs are typically uncommon on other Arctic shelves (Mayer & Piepenburg 1996, Piepenburg et al. 1996, Starmans et al. 1999). The conspicuous scarcity of crabs in Antarctic waters (Thatje & Arntz 2004) has been attributed to the narcotizing effect of high magnesium concentrations in the haemolymph of some organisms at low temperatures, including *Chionoecetes* spp. (Frederich et al. 2000). However, *C. opilio* is metabolically restricted to water temperatures <5°C and is commonly found at temperatures between 0 and 1°C. It also occurs at sub-zero temperatures, even though it exhibits negative growth below 1°C (Taylor & O'Keefe 1986, Foyle et al. 1989). The records of *C.*

opilio reported here, to our knowledge, represent an expansion of the northernmost range limit of the species in the Pacific Arctic into Herald Canyon (72.30° N; Fig. 4), where water temperatures were below zero, although *C. opilio* biomass was low at these sites. In the eastern Atlantic, a recently established *C. opilio* population now occurs as far north as 76° N in water temperatures from −0.7 to 3.4°C, with most crabs found in waters <2°C (Alvsvåg et al. 2009).

While echinoderms and crustaceans were the dominant contributors to biomass and abundance, gastropods were the most species-rich group at our sites (Fig. 5b), which supports findings from earlier studies (Frost & Lowry 1983, Feder et al. 2005). Dominant taxa by biomass included the families Buccinidae and Naticidae (moon snails). Often preying on bivalves and polychaetes (Morton & Jones 2003), these carnivores and opportunistic scavengers find abundant food in the Chukchi Sea (Sirenko & Gagaev 2007). *Solariella obscura* and *S. varicosa* (Trochidae), grazers feeding on algae and small detritus, were particularly abundant in the south-central Chukchi Sea. High water-column chlorophyll concentrations (Lee et al. 2007) coupled with abundant epifaunal grazers and high macrofaunal biomass (Grebmeier et al. 2006a, Sirenko & Gagaev 2007) suggest that the transfer of detritus from the sediment into the benthic food web may be particularly efficient in this region.

Possible temporal trends in Chukchi Sea epifauna

While speculations regarding temporal trends in Chukchi Sea epifaunal communities are tenuous, particularly due to the limited number of stations sampled repetitively and the inconsistencies in sampling gear types, we offer here a cautious discussion of observed patterns in an effort to help direct future work. Only one of our stations overlapped with a station sampled by Ambrose et al. (2001) with an ROV in 1998; at their Stn 4, the sand dollar *Echinarachnius parma* dominated with abundances of 124 ind. m^{-2}. In 1986, near the stations Ambrose et al. (2001) sampled, Feder et al. (1994b) found *E. parma* in a mean abundance of 276 ind. m^{-2} (their group IV). In 2007, the sand dollar was still dominant in this area, although abundance estimates (Stn OM19) were much lower (4 ind. m^{-2}), suggesting a potential decrease of this taxon in the area. Earlier reports mention a band of sand dollars under the frontal zone between BSW and ACW just north of the Bering Strait (Grebmeier et al. 1989), where we did not find the species.

Preliminary comparisons of biomass and community composition at 8 station pairs in the southeastern Chukchi Sea sampled in both the present study (2004

to 2008) and by other researchers in 1976 (Feder et al. 2005) indicated that 1976 biomass estimates ranged from 1 to 67 % of present-day estimates. *Chionoecetes opilio* had increased in relative total abundance at 6 stations, and in biomass at all 8 stations (Table 8). Absolute crab biomass was 1 to 2 orders of magnitude higher in the present study than in the 1976 study, and was dominated in terms of biomass at 5 of the 8 stations in the present study, compared to none in 1976. Sparks & Pereyra (1966) did not mention *C. opilio* as a dominant taxon in their 1959 trawl collections either, but listed the species as occurring, as did MacGinitie (1955) with reference to his collection of *C. opilio* at several stations in from 10 to 145 m depth off Barrow, Alaska. A trend toward increased biomass in the 2000s, in particular for *C. opilio*, agrees with Feder et al.'s (2005) comparison of their own data in 1976 to a fisheries survey in 1998 (Fair & Nelson 1999), in which

biomass had at least doubled for several dominant groups in this period of time and average *C. opilio* abundance had increased by an order of magnitude. On a pan-Arctic scale, *C. opilio* concentrations have shifted northward in the Bering Sea (Orensanz et al. 2004, http://access.afsc.noaa.gov/reem/ecoweb/html/ EcoContribution.cfm?ID=38), and, in the European Arctic, a self-sustained population now occurs in the Barents Sea (Alvsvåg et al. 2008), where the first *C. opilio* were documented in 1996 (Kuzmin et al. 1998). These shifts are not only potential ecological indicators of climate warming, but also have clear implications for the current sub-Arctic crab fishery, as well as for any future Arctic fisheries that may develop. Based on the temperature preferences of *C. opilio* (see above), further northward range extensions or changes in biomass centers might only occur if average temperatures increase in those areas.

Table 8. Comparison of dominant species, with a focus on *Chionoecetes opilio*, by biomass at 8 locations in the southern Chukchi Sea in Feder et al. (2005) and in the present study. Note that *Strongylocentrotus droebachiensis* in Feder et al. (2005) is probably in fact *S. pallidus* (H. M. Feder pers. comm.). *Neptunea heros* in Feder et al. (2005) is referred to as *N. ventricosa* in the Russian and European literature and in the present study. *N. ventricosa* in Feder et al. (2005) is referred to as *N. behringiana* in the European and Russian literature. Species among the 5 dominant taxa at a given station in both studies are given in **bold print**. Species are underlined if they were common at many of the compared stations in Feder et al. (2005), but never or rarely observed in the present study

| Station number | | Biomass (g wet wt 1000 m^{-2}) | | | | Dominant species by biomass | |
| | | Total | | *Chionoecetes opilio* | | | |
Present study	Feder et al.	Present study	Feder et al.	Present study	Feder et al.	Present study	Feder et al.
R6	A54	68630	6106	1564	36	***Strongylocentrotus pallidus,*** *Leptasterias groenlandicus*, *Stomphia* sp., *Gersemia* sp., ***Hyas coarctatus***	*S. droebachiensis*, *Psolus japonicus*, *H. coarctatus*, *Lethasterias nanimensis*, *Paralithodes platypus*
OM2	A36	71864	746	19103	90	***Chionoecetes opilio,*** *Leptasterias polaris*, *H. coarctatus*, *Urticina* sp.	<u>*Neptunea heros*</u>, *Evasterias echinosoma*, *C. opilio*, <u>*Gorgonocephalus caryi*</u>, *Pagurus trigonocheirus*
OD31	A33	9560	1312	993	64	***Asterias amurensis,*** *Neocrangon communis/Argis lar*, ***L. nanimensis***, *C. opilio*, *Styela rustica*	*A. amurensis*, *Styela macrenteron*, *L. polaris*, *Scyphozoa*, *L. nanimensis*, <u>*N. heros*</u>
OM4-08	A16	70668	6272	30811	208	***C. opilio,*** *Leptasterias* sp., ***L. polaris, Ophiura sarsi,*** small gastropods	*L. polaris*, *O. sarsi*, *C. opilio*, *Henricia* sp., *Pagurus trigonocheirus*
OD22	A05	4077	2742	1936	63	*C. opilio*, *Actinostola* sp., ***L. polaris***, *Gersemia* sp., unidentified anemone	*L. polaris*, *Stomphia* sp., <u>*G. caryi*</u>, <u>*N. heros*</u>, *H. coarctatus*
R17	A03	17027	4393	89	0	*Chlamys* sp., *Stomphia* sp., *P. agurus rathbuni*, ***Neptunea ventricosa, H. coarctatus***	*L. polaris*, <u>*N. heros*</u>, *N. ventricosa*, <u>*G. caryi*</u>, *H. coarctatus*
OD20	A01	5573	1688	1675	72	*C. opilio*, ***N. ventricosa***, *P. rathbuni*, *Actinostola* sp., *N. communis/A. lar*	<u>*G. caryi*</u>, *L. polaris*, <u>*N. heros*</u>, *N. ventricosa*, *P. trigonocheirus*
OM14-08	A56	209080	1097	111552	27	***C. opilio***, *O. sarsi*, ***Leptasterias* sp.,** medium-sized gastropods	*L. polaris*, <u>*G. caryi*</u>, *C. opilio*, *Stomphia coccinea*, *Leptasterias* sp.

It is unclear if the body size of *Chionoecetes opilio*, an important measure of reproductive status and market value in commercial crabs, also changed over the decades in the Chukchi Sea. Studies on size-at-maturity in females demonstrated a smaller size in colder waters at high latitudes and a larger size in warmer temperatures at low latitudes in the Bering and southern Chukchi Seas (Jewett 1981, Orensanz et al. 2007). Our non-quantitative observations and an ongoing study in the northern Bering Sea measured very few large (>35 to 40 mm carapace width) and mature females occurring north of St. Lawrence Island (Lovvorn 2008), similar to studies in the late 1970s and 1980s in the southeastern and northern Chukchi Sea (Jewett 1981, Frost & Lowry 1983). The largest male *C. opilio* caught in the northeastern Chukchi Sea in 1976 was 75 mm (Frost & Lowry 1983), and only a few males larger than that were caught in the early 1990s (Barber et al. 1997). However, *C. opilio* as large as 114 mm were recently caught in the Alaskan Beaufort Sea (H. Chenelot, University of Alaska Fairbanks, pers. obs.), and the species dominated at several stations, though at greater depths than in the Chukchi Sea (Loggerwell & Rand 2009). Carey (1977), in contrast, did not list *C. opilio* among the dominant species in his Beaufort Sea trawls conducted in the 1970s. To clarify temporal changes and distribution pathways, consistent use of gear types, identification of source areas for snow crab larvae, and environmental limitations for larvae and adults in the Bering, Chukchi and Beaufort Seas are clearly needed.

In terms of temporal changes in community structure, 1 to 3 of the 5 dominant species among the 8 comparable stations pairs were identical between 1976 and the 2000s, which suggests that communities were still similar overall (Table 8). Likewise, 17 yr before Feder et al.'s (2005) sampling, sea stars, brittle stars, decapods and tunicates dominated the southeastern Chukchi Sea epifauna (Sparks & Pereyra 1966). Some quantitative differences in dominance, however, were obvious. The basket star *Gorgonocephalus caryi* and the gastropod *Neptunea ventricosa* (called *N. heros* in Feder et al. 2005), which were among the 5 dominant species at half of the compared locations in Feder et al. (2005), were absent (*G. caryi*) or only present at 2 stations (*N. ventricosa*) among the 5 dominant species in the current study. The snail also had decreased in frequency of occurrence, biomass and abundance in 1998 relative to 1976, while the basket star had not changed frequency of occurrence or biomass, but increased in abundance (Feder et al. 2005). Perhaps the increase in snow crab biomass had sufficiently heightened the competition for food resources, either directly or through indirect food web links, to result in a reduced snail population.

Environmental drivers

Important factors influencing benthos may differ for biomass and taxonomic composition and will be discussed separately. Benthic biomass, in general, is largely controlled by the supply of food derived from surface waters and reaching the seafloor through pelagic–benthic coupling processes (Graf 1989, Grebmeier & Barry 1991). Similarly, spatial patterns in macrofaunal biomass in the Chukchi Sea have been linked to variations in pelagic primary production and carbon flux (vertical and advective) to the sea floor under different water masses, namely the ACW and BSAW (Grebmeier et al. 2006a, Lee et al. 2007). In the present study, however, epibenthic abundance and biomass did not differ between these water masses or water mass characteristics. Moreover, epifaunal biomass was not significantly correlated with macrofaunal biomass (Fig. 8), suggesting different processes may be driving observed patterns in these 2 size classes. Interestingly, the 2 indicators of food availability we considered (sediment organic carbon and integrated water column chlorophyll concentration) did not appear to explain differences in epifaunal biomass, whereas food availability variables did correspond well with macrofaunal biomass (Grebmeier et al. 2006a). The lack of correlation to epifaunal biomass might be related to the small number of data points or the use of binned sediment organic carbon data. However, we suspect this difference reflects weaker pelagic–benthic coupling for epibenthic megafauna than for macrofauna (Grebmeier et al. 2006a). Coupling could be weak due to: (1) the higher mobility of many biomass-rich epifaunal organisms obscuring relationships of biomass to food availability at any given location (although sessile epifauna alone were not correlated to these variables either) or (2) the predatory, scavenging, or opportunistic feeding types of many of the biomass-dominating species such as *Ophiura sarsi* (Warner 1982), *Chionoecetes opilio* (Feder & Jewett 1981, Squires & Dawe 2003) and sea stars (Jangoux & Lawrence 1982), again obscuring pelagic–benthic coupling at any given station. In contrast, several of the biomass-dominating macrofaunal benthic species such as ampeliscid amphipods, macrofaunal clams and various polychaetes (Grebmeier et al. 1989, Feder et al. 2007, Sirenko & Gagaev 2007) are sessile suspension or filter feeders, directly exploiting fresh organic carbon from the water column (Iken et al. in press).

While none of the environmental variables tested appeared to explain biomass patterns, epibenthic community structure was most strongly related to substrate type and latitude (Table 5). In comparison, sediment

type along with temperature and salinity structured small demersal fish communities in the Chukchi Sea, while water mass characteristics alone determined the structure and spatial distribution of fish larvae (Norcross et al. in press) and zooplankton communities (Hopcroft et al. in press). Investigations on the East Greenland shelf also suggest coarse substrate is more important for structuring epibenthic communities than the degree of pelagic–benthic coupling or water mass characteristics (Mayer & Piepenburg 1996). Such differences in community structure between hard or rocky areas and soft muddy areas are not surprising, given the differences in feeding modes suited to these 2 environments. The effects of such differences in the ecology of soft- and hard-substrate environments were obvious in the list of taxa that contributed most to the dissimilarity between the south/southeastern (hard bottom) and other station clusters in the present study. In particular, some sites in the SSE cluster were dominated by *Strongylocentrotus pallidus*, *Hyas coarctatus* and various sea stars (Fig. 6, Table 4). Some mobile species such as crabs are thought to succeed in coarse substrate areas because their structural complexity provides shelter for larvae and early juveniles (Tapella et al. 2009). Taxonomic richness was also highest in the south/southeastern station group due to the presence of various sessile taxa that require coarse substrate for attachment (e.g. bryozoans, sponges). Further, coarse substrate occurs in areas with relatively high current velocities, where moving water delivers food resources to these sessile suspensions feeders (Leichter & Witman 1997).

Patterns in taxonomic composition again contrast with macrofaunal studies on Arctic shelves that indicate greater importance of grain size, sediment C/N ratios and porosity (northern Chukchi Sea; Feder et al. 1994b), water depth, temperature and oxygen concentration (Beaufort shelf; Conlan et al. 2008), or surface primary production or surrogates thereof (Laptev Sea; Steffens et al. 2006 and Canada Basin; MacDonald et al. in press). Latitude, which was important in epifaunal community structure in the present study, is likely an indirect indicator of some of these same features (e.g. water masses, primary production), but also suggests the influence of additional factors such as historical zoogeography and seasonal ice cover. Thus, it remains unclear exactly which combination of variables is most important in governing epifaunal community patterns and to what degree.

Conclusions and outlook

The Chukchi Sea has undergone dramatic changes in the last decades in some environmental character-istics such as ice cover and volume of water transported through the Bering Strait (Stroeve et al. 2005, Woodgate et al. 2006), with anticipated biological consequences. Additional pressures are related to the increased interest in oil exploration in the area. One of the goals of the RUSALCA program and the newly formed Marine Expert Group on the 'Conservation of Arctic Fauna and Flora' (CAFF) under the Arctic Council is to document biological changes and develop monitoring strategies. Our results offer some indications as to which ecosystem components are most in need of monitoring. Several approaches were chosen in other regions, including monitoring of total benthic biomass, e.g. in the St. Lawrence Island polynya in the Bering Sea (Grebmeier et al. 2006b), distribution and/or biomass of either dominant taxa (Zhang & Tingwei 2003), commercially important taxa, particular 'indicator species' (Carignan & Villard 2002), or indices of diversity (Noss 1990). For Chukchi Sea epifauna, any measure of benthic biomass, regardless of the target organism(s), can only be a useful climate change indicator if consistent gear is used, ideally including a combination of trawls and photographic methods, which are benign and have high accuracy (Eleftherious & MacIntyre 2005). Furthermore, our study demonstrates that many dominant epifaunal species are widely distributed across the Chukchi Sea, so that monitoring presence/absence alone will not detect changes; rather, abundance and/or biomass estimates and/or size distributions are needed. Measuring specific aspects of community structure, such as proportions of taxa with different habitat needs (e.g. cold versus warm water) may be most informative. Although recent findings on *Chionocetes opilio* in the Chukchi Sea suggest that a snow crab fishery is not viable at this point (Feder et al. 2005, Lovvorn 2008, NPFMC 2009, present study), this species should be closely monitored in terms of abundance, biomass, size distribution and reproductive stages, given preliminary evidence of a changing distribution and the potential for future commercial interest. Monitoring changes in the distribution of species that have their northern or southern distribution limits in the Chukchi Sea (e.g. Fig. 7) might also foreshadow ecosystem change. If water temperature is the main factor limiting the distribution of Pacific species to the north, one might expect range expansion in Chukchi Sea species as warming continues (see Sirenko & Gagaev 2007 for recent possible range extensions in the Chukchi Sea) and a decrease in the abundance of cold-water Arctic species. Species composition and number of taxa along a south–north gradient is informative on the location (and potential change) of the biogeographic boundary of Pacific versus Arctic species.

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Appendix 1. List of epifaunal taxa found during 3 cruises to the Chukchi Sea (2004 to 2007). Taxon identifications were by the authors and by the following taxonomists: Ole Tendal (Zoological Museum Copenhagen, Denmark; Porifera), Daphne Fautin (University of Kansas, Lawrence, USA; Actinaria), Estefania Rodriguez (Ohio State University, Columbus, USA; Actinaria), Ken Coyle (University of Alaska Fairbanks, USA; Amphipoda), Igor Smirnov (Zoological Institute, St. Petersburg, Russia; Ophiuroidea), Christopher Mah (Smithsonian Institution, Washington, DC, USA; Asteroidea), Andrey Gebruk (PP Shirshov, Moscow, Russia; Holothuroidea), Piotr Kuklinski (Institute of Oceanology, Sopot, Poland; Bryozoa) and Linda Cole (Smithsonian Institution, Washington, DC, USA; Ascidiacea)

	R6	R10	R11	R13	R15	R17	R18	R20	R23	R25	R27	R58	R62	R73	R85	R106	R107	OM2	OM10	OM15	OM16	OM19	OM24	OD1	OD5	OD15	OD2	OD22	OD31	OD43
Ascidiacea																														
Ascidian, solitary sp. 1													x																	
Boltenia echinata						x							x	x										x	x					
Boltenia ovifera		x	x																					x	x					
Chelyosoma macleayanum						x							x										x							
Corella cf. *inflate*	x																													
Cystodytes sp.	x				x																									
Dendrodoa aggregate (?)					x																									
Didemnum albidum	x				x								x																	
Diplosoma cf. *listerianum*	x				x																									x
Halocynthia aurantium					x														x								x			
Molgula retortiformis																						x								
Styela rustica					x														x	x	x								x	
Synascidian, brown	x																													
Synoicum sp.																														x
Cnidaria																														
Actiniidae sp. 2		x																												
Actinostola sp.				x											x	x	x		x	x		x	x				x	x		
Actinostolidae														x	x															
Anemone sp. 1	x	x																										x		
Anemone sp. 2																												x		
Anemone sp. 3																													x	x
Cribrinopsis/Epiactis sp.	x	x	x	x	x													x											x	x
Gersemia sp. (cf. *rubiformis*)	x	x				x							x	x		x					x	x	x					x		x
Haliatiidae					x					x																				
Metridium facimen	x																													
Stomphia sp.	x	x	x			x	x	x			x						x													x
Urticina sp. 1			x		x						x																			
Urticina sp. ?					x				x	x	x			x		x													x	x
Hydrozoa	x	x	x			x	x			x			x		x		x					x	x							
Crustacea																														
Acanthostepheria behringiensis													x																	
Anonyx sp.			x	x	x			x	x	x	x	x		x	x					x	x	x						x		
Eusirus cuspidatus	x																				x									
Hippomedon sp.													x																	
Lembos arcticus													x		x															
Melita dentata																				x	x					x				x
Monoculodes sp.													x																	
Other amphipods	x	x			x	x							x		x															

Appendix 1 (continued)

	R6	R10	R11	R13	R15	R17	R18	R20	R23	R25	R27	R58	R62	R73	R85	R106	R107	OM2	OM10	OM15	OM16	OM19	OM24	OD1	OD5	OD15	OD2	OD22	OD31	OD43
Paramphithoe polyacantha																														x
Paroediceros spp.											x																			
Rhachotropis aculeata											x		x	x					x											
Stegocephalidae (incl. *S. inflatus*)		x											x	x					x											
Stenothoidae																														
Cirripedia		x														x						x								
Chionoecetes opilio	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x
Hyas coarctatus	x	x	x	x		x	x				x		x	x			x	x			x	x	x		x	x		x	x	x
Labidochirus splendescens					x											x	x	x		x	x	x			x	x			x	x
Paguridae sp. 1							x																							
Pagurus capillatus (?)						x		x										x										x		x
Pagurus rathbuni	x		x		x	x	x	x	x	x	x			x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	
Paralithodes platypus	x																							x						
Telmessus cheiragonus					x																									
Isopoda					x								x	x																
Argis lar & *Neocrangon communis*	x		x	x	x	x	x	x	x	x	x			x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Other shrimps excl. Pandalidae			x																			x								
Sabinea septemcarinata												x	x	x	x															
Saduria sp.										x																				
Sclerocrangon sp.	x		x		x						x									x	x									
Spirontocaris sp. (incl *S. arcuata*)			x		x						x			x						x	x				x					
Pycnogonida														x																
Echinodermata																														
Asterias amurensis/rathbuni	x	x			x	x											x												x	x
Crossaster papposum	x	x			x								x	x			x		x		x			x						x
Ctenodiscus crispatus													x		x	x														
Henricia tumida (?)	x		x	x	x	x			x		x		x	x		x		x			x			x						x
Leptasterias groenlandica	x	x			x	x					x						x	x	x	x	x	x					x	x	x	x
Leptasterias polaris		x		x	x	x	x	x								x	x	x	x		x	x	x	x	x	x	x	x		x
Lethasterias nanimensis		x																						x					x	x
Pteraster cf. *tesselatus*																		x		x										
Pteraster obscurus													x																	
Solaster cf. *dawsoni*												x		x																
Urasterias linki												x		x		x						x								
Myriotrochus rinkii			x	x	x				x	x				x		x														
Ocnus sp.	x												x							x										x
Psolus fabricii	x																													
Psolus phantapus																		x		x					x					x
Gorgonocephalus caryi	x	x																x		x				x	x			x		x
Amphiodia craterodmeta	x			x	x				x	x					x															
Ophiacantha sp.						x							x							x										
Ophiura sarsi					x			x		x			x	x	x			x	x	x				x	x		x	x		
Stegophiura nodosa						x			x				x																	
Strongylocentrotus pallidus	x	x											x					x		x			x							x
Strongylocentrotus sp.	x	x																												
Echinarachnius parma																				x								x		
Mollusca																														
Amicula vestita													x							x										
Leptochiton aff. *assimilis* & *Stenosemus albus*	x																													
Admete viridula			x		x	x		x			x		x	x	x	x		x												
Anomolosipho conulus																						x								
Boreoscala groenlandica		x																												
Boreotrophon clathratus					x															x	x									
Buccinum angulosum		x											x		x	x														
Buccinum elatior			x	x		x	x						x	x		x	x	x		x	x			x	x		x	x	x	x
Buccinum spp. (incl. *B. ciliatum, B. plectrum, B. polaris, B. polium obsoletum*)		x	x	x	x	x		x					x			x	x	x	x		x	x			x					
Colus spp.				x	x	x			x			x	x		x		x	x	x		x			x	x	x		x		
Cryptonatica affinis		x	x	x	x		x	x	x	x			x		x	x	x		x		x			x	x	x	x	x		
Gastropod sp. 1													x																	
Gastropod sp. 3													x	x																
Gastropod sp. 2													x	x																

Appendix 1 (continued)

	R6	R10	R11	R13	R15	R17	R18	R20	R23	R25	R27	R58	R62	R73	R85	R106	R107	OM2	OM10	OM15	OM16	OM19	OM24	OD1	OD5	OD15	OD2	OD22	OD31	OD43
Latisipho hypolispus								x									x						x				x			
Limpet sp. 1		x											x																	
Limpet sp. 2													x																	
Lunatia pallida				x			x	x	x		x			x	x	x	x	x											x	
Neptunea beringia					x													x												
Neptunea communis		x	x	x	x		x	x			x			x	x	x	x			x	x	x	x				x			x
Neptunea lirata					x														x	x		x						x	x	
Neptunea ventricosa			x		x	x	x				x		x		x						x		x	x	x	x				
Nodulotrophon coronatus																							x							
Nudibranchia			x	x								x	x									x	x						x	x
Oenopatina sp.							x	x	x		x			x	x			x												
Plicifusus kroyeri																							x							
Plicifusus sp.																										x				
Propebela nobilis																				x			x							
Pyrulofusus deformis																		x												
Silichna alba									x	x																				
Solariella costalis & *S. varicosa*		x		x	x	x	x	x	x	x	x	x	x	x	x			x	x	x	x	x	x				x			
Tachyrhynchus erosus			x			x	x				x			x	x	x	x	x		x			x			x	x	x		
Trichotropis bicarinata			x		x									x	x						x									
Trichotropis carinata			x	x	x			x						x	x															
Velutina sp.													x																	
Volutopsis sp.								x																						
Chlamys sp.					x																	x								
Pododesmus macrochisma																														
Serripes groenlandicus			x		x		x	x	x						x			x	x	x	x		x				x			
Octopus														x																
Echiura				x	x																									
Nemertini			x	x	x			x	x													x								
Priapulida				x																										
Sipunculida		x												x								x				x				
Porifera																														
Halichondria panicea	x	x																												
Halichondria sitiens	x												x																	
Haliclona aquaeductus													x																	
Hymeniacidon assimilis	x	x												x	x								x							
Porifera sp. 1					x																									
Porifera sp. 2			x																											
Porifera sp. 3					x																									
Suberites ficus															x															
Brachiopoda					x																									
Bryozoa																														
Alcyonidium gelatinosum	x	x	x		x									x								x	x							
Bowerbankia composita & *Patinella* sp.		x									x			x								x								
Bryozoa sp. 1					x																									
Bryozoa sp. 2														x																
Bryozoa sp. 3			x																											
Cauloramphus sp.																							x							
Cellepora sp.																							x							
Dendrobeania cf. *fruticosa*	x				x																									
Dendrobeania levinseni																							x							
Eucratea loricata		x			x																									x
Flustra nordenskjoldi	x				x								x										x							
Flustra serratula					x																									
Myriapora subgracilis & *M. coarctata*					x								x																	
Porella beringia																							x							x
Porella compressa & *Tegella* sp.	x												x										x							
Porella saccata													x																	
Rhamphostomella sp.													x																	
Sarsiflustra securifrons					x																									
Semibugula birulai																						x								