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Benthic food-web structure under differing water mass properties in the southern Chukchi Sea

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ABSTRACT

We used carbon and nitrogen stable isotope ratios as markers of food source connections and trophic position to evaluate whether benthic food-web structure varied among water masses with different productivity regimes in the southern Chukchi Sea. Benthic communities and suspended particulate organic matter (POM) were sampled at nine stations located in four water masses during the 2004 Russian-American Long-term Census of the Arctic (RUSALCA) cruise. POM δ^{13}C values were depleted in the relatively unproductive Alaska Coastal Water (ACW, −24.2‰) and at the Russian Coast (RC, −24.5) compared to the enriched signatures of highly productive Anadyr Water (AW, −21.1‰) and the intermediate value (−23.6‰) of Bering Shelf Water (BSW). Corresponding differences in POM C/N reflected higher nutritive content of AW (6.19) compared to ACW (8.45). Carbon isotopic values of sediments were also most depleted in the nearshore waters of the ACW (−24.8‰) and RC (−23.4‰), versus BSW (−22.8‰) and AW (−22.1‰). In addition, the low δ^{15}N values and high C/N ratios associated with sediments under the ACW (2.9‰ and 10.0, respectively) compared to the other three water masses (range 4.5–4.9‰ and 6.8–7.5, respectively) are likely explained by a terrestrial signal associated with the higher freshwater input into the ACW. Consequently, the δ^{13}C value of POM in the ACW is likely driven by a large fraction of refractory material of terrestrial origin, and POM may not always be a reliable baseline for trophic level calculations in the ACW. Excluding POM, δ^{15}N isotope spread among the same 42 taxa of invertebrates and fishes was 8.5‰ in ACW and 7.5‰ in AW, compared to 12.0‰ and 9.6‰ with the inclusion of δ^{15}N POM values. Almost without exception, consumers in the ACW had higher δ^{15}N values than their AW counterparts (average difference 2.5‰). However, food webs in ACW and AW (as well as in the BSW and RC) did not differ substantially in length (four trophic levels) when based on primary consumers as the baseline. The relatively high proportion of consumers within the first trophic level in AW suggests that there is a more direct coupling of benthic consumers to the very high pelagic primary production in these waters, which is also reflected in the high benthic infaunal biomass at low trophic levels (TL2) reported in the literature for this area. We conclude that differences in regional water column productivity in the southern Chukchi Sea may be manifested primarily in the quantitative representation of various trophic levels and less in qualitative characteristics such as food-web length or relative distribution of trophic levels.

1. Introduction

Many Arctic shelf systems are characterized by high benthic biomass (Grebmeier et al., 1995; Carmack and Wassmann, 2006). This is particularly true for the Chukchi Sea shelf, where macroinfaunal biomass can accumulate up to 50–100 g C m^{-2} (Grebmeier et al., 1988, 2006; Feder et al., 2007). In Arctic shelf regions where these benthic communities are particularly rich, they provide important feeding grounds for bottom-feeding marine mammals such as gray whales and walrus, and for diving ducks (Oliver et al., 1983; Highsmith et al., 2006; Lovvorn et al., 2003). This high biomass is the consequence of tight pelagic–benthic coupling, specifically because of a lack of significant grazing of the primary production in the water column, resulting in large amounts of organic material settling onto the seafloor (Andersen, 1988; Grebmeier and Barry, 1991; Carroll and Carroll, 2003; Campbell et al., 2009). As a result, benthic food webs on shallow Arctic shelves play a larger role in overall system production, turnover rates and remineralization than at lower latitudes (Petersen and Curtis, 1980; Grebmeier and Barry, 1991; Ambrose and Renaud, 1995; Ambrose et al., 2001; Renaud et al., 2008). The strength of this pelagic–benthic coupling varies with a

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number of factors, including the magnitude of primary production in sea ice and water column, timing of the seasonal sea ice cover, and the structure and trophic dynamics of the zooplankton community in relation to phytoplankton development (Wassmann et al., 1996; Turner, 2002; Renaud et al., 2007).

The Chukchi Sea shelf is characterized by high productivity, rich benthic communities and tight benthic–pelagic coupling when compared on a pan-Arctic scale (Dunton et al., 1989; Sakshaug, 2003; Carmack and Wassmann, 2006; Grebmeier et al., 2006). On a regional scale within the Chukchi shelf, however, benthic biomass varies substantially by one to two orders of magnitude (Dunton et al., 2005; Grebmeier et al., 2006; Sirenko and Gagaev, 2007). For example, macro benthic biomass in the south-eastern Chukchi Sea is about $6\,\mathrm{g\,C\,m^{-2}}$ compared to about $23\,\mathrm{g\,C\,m^{-2}}$ in the south-central Chukchi Sea (Grebmeier et al., 1988), and can be up to $60\,\mathrm{g\,C\,m^{-2}}$ in the south-western Chukchi Sea (Grebmeier, 1993). Key water masses driving productivity patterns on the Chukchi Sea shelf are the nutrient-rich Anadyr Water (AW) entering the Chukchi Sea through Bering Strait on the western side, the nutrient-poor and freshwater-influenced Alaska Coastal Water (ACW) on the eastern side, and the intermediate Bering Shelf Water (BSW); BSW and AW start mixing on the southern Chukchi shelf (Coachman, 1987). Shelf primary production is high under AW influence (up to $470\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, Walsh et al., 1989; Springer et al., 1996; Sakshaug, 2003; Hill and Cota, 2005) based on the nutrients that are being upwelled onto the Bering shelf in the Gulf of Anadyr and advected northward ($\sim 20\,\mu\mathrm{M\ NO_3}$; Walsh et al., 1989; Hansell et al., 1993; Codispoti et al., 2005). By comparison, nutrient input (sometimes $<1\,\mu\mathrm{M\ NO_3}$, Hansell et al., 1989; Lee et al., 2007) and primary production is much lower under the ACW (up to $60\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, Walsh et al., 1989). Based on persistent and consistent sampling efforts over the last three decades, infaunal biomass patterns in the Chukchi Sea and their relationship to primary production, sedimentation patterns and water mass properties are reasonably well known (reviewed in Grebmeier et al., 2006). In contrast, regional patterns of epibenthic megafauna communities (Ambrose et al., 2001; Feder et al., 2005, Bluhm and Iken, unpubl. data) and of benthic food-web structure are only beginning to emerge.

Despite the importance of benthic systems to top predators in the Chukchi Sea (Lowry et al., 1981), little is known of whether and how patterns in water mass properties and productivity translate into characteristics of benthic food-web structure. Food webs are highly relevant multi-species networks, because they not only describe trophic connections in an ecosystem but also reflect biodiversity, species interactions and ecosystem structure (Dunne et al., 2002). Food-web length in aquatic systems, as one variable of food webs, influences ecosystem functioning and diversity, food-web stability, contaminant accumulation, etc. (Pimm and Lawton, 1977; Cabana and Rasmussen, 1994; Sterner et al., 1997; Worm et al., 2002; Hoekstra et al., 2003; Duffy et al., 2005). Typically, energy transfer efficiency between trophic levels in benthic systems is about 10–15% (Lindemann, 1942; Pimm, 1982; Brown and Gillooly, 2003), and most aquatic food webs consist of no more than four to five trophic levels (Sterner et al., 1997; Pauly et al., 1998). The classical productivity hypothesis suggests that the available energy in a system, and the inefficiency with which it is transferred between trophic levels, limits food-web length (Hutchinson, 1959; Persson et al., 1992; Kaunzinger and Morin, 1998, and others), although that theory has been controversially discussed for aquatic systems (e.g., Briand and Cohen, 1987). Other food-web theories invoke ecosystem size (Schoener, 1989; Post et al., 2000) and local ecosystem stability (Jenkins et al., 1992) as determinants of food-web length and, by extension, of community and ecosystem structure. Food-web length can be determined using nitrogen stable isotopes as a continuous integrative measure of trophic position of species (Cabana and Rasmussen, 1994; Post, 2002).

The purpose of this study was to examine regional benthic food-web structure in the southern Chukchi Sea and to assess if and how it differs between the water masses in the region, which have different primary productivity patterns. Benthic macrofauna biomass differs vastly between these water masses and it has been suggested that these biomass differences are driven by absolute differences in primary production and the carbon flux to the benthos (Dunton et al., 2005; Grebmeier et al., 2006). Here we hypothesize that also food-web length differs among these water masses, ultimately contributing to those differences in benthic community structure. If food-web structure differs among the contrasting water masses of the Chukchi Sea, it may be an ideal long-term, system-level indicator of energy flow and carbon cycling in different water masses and their potential changes over time.

2. Materials and methods

2.1. Study area

Samples for food-web analysis were collected from 10–16 August 2004 onboard the Russian vessel "Professor Khromov" in the southern Chukchi Sea within the framework of the RUSALCA (Russian-American Long-term Census of the Arctic) program. Sampling stations were aligned between the Alaskan and the Russian Coasts (Fig. 1, Table 1) at water depths between 39 and 54 m. Bottom substratum was generally composed of fine sediments except for stations 6 and 10, where gravel, cobbles and shell hash were embedded within the soft substrate, and station 27, which was characterized by small gravel (Table 1). Stations were assigned to water masses based on salinity data obtained from CTD casts (see representative examples for stations 6, 10, 20 and 27 in Fig. 1, Table 1): ACW is characterized by bottom salinities of $<31.8‰$; BSW has bottom salinities between 31.8‰ and 32.5‰, and AW is characterized by saline ($>32.5‰$) bottom waters (Coachman, 1987). Although bottom water at station 27 reflected the properties of AW, this area receives runoff from a coastal lagoon and is sometimes influenced by the Siberian Coastal Current (Weingartner et al., 1999). With no data available upstream the Siberian coast to confirm the influence of the Siberian Coastal Current at the time of sampling, this station is here designated as Russian Coastal (RC) station.

2.2. Sample collection and preparation

Particulate organic matter (POM) from the chlorophyll maximum layer (Lee et al., 2007) was sampled at each station as one reference of the primary food source (= isotopic endmember; see Section 2.3 for a second approach to calculate isotopic baseline reference based on nitrogen isotope values of primary consumers). POM was filtered from water collected using Niskin bottles attached to a CTD rosette. Three replicate water samples per station were taken from different Niskin bottles from the same CTD cast. Between 100 and 400 ml, depending on POM concentration, were filtered onto a pre-combusted, 25 mm diameter GF/F filter. Visible swimmers on the filters were removed. Sediment was collected to about 1 cm depth of the surface of an undisturbed van Veen grab sample ($0.01\,\mathrm{m^2}$) into a sterile plastic bag for analysis of sediment stable isotopes in replicates of three per station.

Benthic macro-infauna was collected from van Veen grabs after surface sediment samples were taken. Sediments were sieved over 1 mm mesh and 3–5 individuals of representative infaunal

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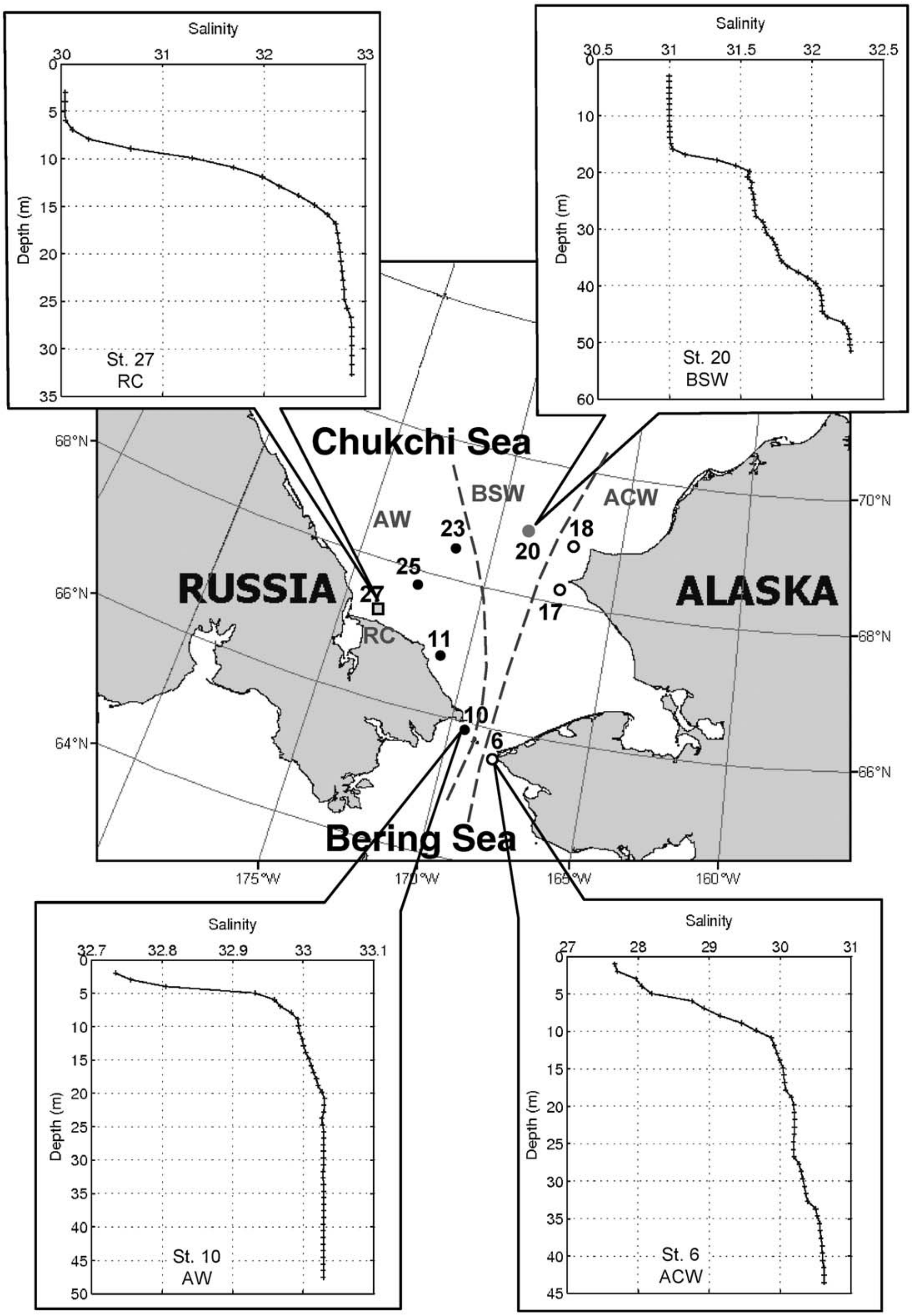

Fig. 1. Map of study area; sampling stations grouped by water masses as explained in text. Open circles: Alaska Coastal Water (ACW), gray circle: Bering Shelf Water (BSW), black circles: Anadyr Water (AW), gray box: Russian Coast (RC) station. Salinity profiles obtained from CTD casts are given for stations 6, 10 and 20 as examples for water mass characteristics of ACW, AW and BSW, respectively, and also for the Russian Coast station 27. Note the different scales for the salinity plots at the different stations.

taxa were selected. Epibenthic invertebrates and fishes were collected with a beam trawl (7 mm net mesh, 4 mm codend mesh). Fauna was sorted to species or higher taxon level and 3–5 replicate individuals per taxon sampled for stable isotope analysis. Occasionally, epibenthic samples were complemented from an otter trawl. In general, the most abundant community representatives were collected at each station.

Replicate individuals of benthic taxa were sub-sampled for muscle tissue, or pieces of body wall where muscle tissue could not be distinguished. Whole organisms were collected when sub-sampling did not yield sufficient mass. All samples were kept frozen at −20 °C until drying at 60 °C for 24 h.

Prior to stable isotope analysis, samples that contained carbonate were treated with 1 N HCl until bubbling ceased. HCl

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Table 1
Station location, hydrographic and substratum characteristics and water mass attribution during RUSALCA 2004.

Station	Date 2004	Latitude (°N)	Longitude (°W)	Depth (m)	Salinity[a](‰)	Temperature[a](°C)	Substratum	Sediment C:N (±sd)[b]	POM C/N (±sd)[b]	Water mass
6	10-Aug	65° 40.372	168° 17.750	48	30.62	10.5	Cobble, shell hash, mud	nd	8.69 ± 1.29	ACW
10	11-Aug	66° 00.222	169° 36.340	53	33.03	2.3	Cobble, shell hash, mud	nd	7.28 ± 0.25	AW
11	12-Aug	66° 55.690	170° 59.610	40	33.17	1.8	Sand, mud	5.53 ± 0.66	5.87 ± 0.28	AW
17	13-Aug	68° 18.240	167° 02.760	40	nd	nd	Gravel, sand, mud	8.56 ± 1.93	8.21 ± 0.23	ACW
18	14-Aug	68° 56.997	166° 54.737	48	31.30	7.9	Mud	11.38 ± 1.29	nd	ACW
20	14-Aug	69° 00.145	168° 52.366	54	32.27	3.7	Mud	8.76 ± 0.32	6.78 ± 0.32	BSW
23	15-Aug	68° 31.367	171° 27.650	53	32.91	2.2	Mud	8.36 ± 0.45	6.10 ± 0.20	AW
25	16-Aug	67° 52.222	172° 33.033	49	33.05	1.8	Mud	8.38 ± 0.18	5.50 ± 0.08	AW
27	16-Aug	67° 24.463	173° 36.281	39	32.87	−1.5	Gravel	7.53 ± 1.17	5.88 ± 0.36	RC

nd—not determined. For salinity and temperature, no CTD cast was taken at this station. Water mass assignment is based on its intermediary position along the main water flow between stations 6 and 18, both of which are ACW. For sediment C/N, no sediment could be sampled using grabs because of course sediment type.
Water masses: ACW—Alaska Coastal Water, AW—Anadyr Water, BSW—Bering Shelf Water, RC—Russian Coast

[a] Bottom salinity and temperature, taken approximately 3 m above bottom.
[b] sd = standard deviation, $N = 3$.

was subsequently removed and samples were again dried at 60 °C. POM filters were fumed at saturated HCl vapors for 48 h and dried before analysis. Samples were not extracted for lipids because Arctic shelf benthos has been found to be very low in lipids across multiple major taxa (Graeve et al., 1997). In addition, in another study we compared isotope ratios before and after lipid extraction in individuals of several plankton and benthic taxa collected in 2005 in the Beaufort Sea/Canada Basin, and found that lipids were not confounding carbon isotope values in benthic organisms (Fig. 2). While lipid extraction in plankton organisms increased the $\delta^{13}C$ value by about 1.5–2‰, the difference in benthic taxa was on average only about 0.4‰, and in some cases values were even slightly depleted after lipid extraction. Hence, samples were not lipid-extracted to avoid the effect that lipid extraction can have on nitrogen isotopes and thus bias trophic level estimates (Mintenbeck et al., 2008).

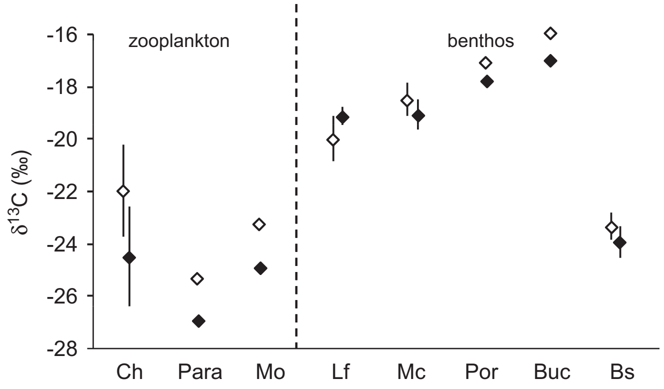

Fig. 2. $\delta^{13}C$ ratio of plankton and benthos organisms before lipid extraction (closed symbols) and after lipid extraction (open symbols) to demonstrate effects of lipid extraction. Organisms were collected in the Beaufort Sea/Canada Basin in summer 2005. Subsamples of the same individuals were analyzed ($N = 1$–3). Ch: *Calanus hyperboreus*, Copepoda, Para: *Paraeuchaeta* sp., Copepoda, Mo: *Mertensia ovata*, Ctenophora, Lf: cf *Liocyma fluctuosum*, Bivalvia, Mc: *Minuspio cirrifera*, Polychaeta, Por: Porifera, Buc: *Buccinum* sp., Gastropoda, Bs: *Boreogadus saida*, Pisces.

2.3. Stable isotope analysis

Samples were measured at the Alaska Stable Isotope Facility at the University of Alaska Fairbanks on a Thermo Finnigan Delta Isotope Ratio Mass-Spectrometer with PDB and atmospheric N_2 as standards for carbon and nitrogen, respectively. Analytical instrument error was 0.1‰ for ^{13}C and 0.2‰ for ^{15}N. Sample isotopic ratios are expressed in the conventional δ notation as parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N of the sample and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Isotopic values of POM and surface sediments, respectively, were analyzed for significant differences among water masses using analysis of variance (ANOVA, $\alpha = 0.05$) after appropriate log-transformation of $\delta^{13}C$ values to comply with requirements of homoscedacity and normal distribution (no transformation was needed for $\delta^{15}N$ values). Differences among groups were evaluated by the Tukey post-hoc test. In addition, isotope signatures of POM and surface sediments were compared for each water mass (t-tests, $\alpha = 0.05$).

Isotope measurements automatically also provided overall C and N content of samples. The C/N ratio is commonly used as an indicator of food quality with lower values indicating higher food quality (Gnaiger and Bitterlich, 1984; Dorgelo and Leonards, 2001). C/N ratios of water column POM and surface sediment POM (see Table 1) were compared among water masses using ANOVA ($\alpha = 0.05$, log-transformation for POM C/N values) and the Tukey post-hoc test.

It has to be noted that POM as the food-web baseline is a heterogeneous source comprising phytoplankton, bacteria, other particulate matter, etc. with large spatial and temporal variations in its isotopic signature. This is especially due to differences in biogeochemical processes (e.g., ammonium and nitrate availability) and fast turnover times during phytoplankton growth cycles (e.g., Altabet and McCarthy, 1985; Paerl and Fogel, 1994; Cabana and Rasmussen, 1996). High $\delta^{15}N$ variability can complicate cross-system comparisons of food-web structure; correction models for the isotopic baseline variability are based on mean $\delta^{15}N$ values of all taxa classified as primary consumers (Cabana and Rasmussen, 1996; Vander Zanden and Fetzer, 2007). Here, we used this method as a second approach to estimating food-web baselines in addition to using POM isotope values to compare water mass food-web structure, specifically those under AW and ACW influence. Primary consumers were identified based on their published feeding behavior and included taxa common in the

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study area: selected bryozoans (*Alcyonidium gelatinosum anderssoni*, *Eucratea loricata*, *Flustra* spp., *Bowerbankia composita*; Winston, 1977; Riisgård and Manriquez, 1997), bivalves (*Liocyma fluctuosum*; McMahon et al., 2006), *Macoma calcarea*, which can be either a deposit or suspension feeder, Reid and Reid, 1969; Holte et al., 1996; Rossi et al., 2004) and ampeliscid amphipods (*Ampelisca macrocephala*, *Byblis gaimardi*; Coyle and Highsmith, 1994). Instead, the use of a single, specialized primary consumer could be advantageous to avoid variation due to the high variability in feeding modes of benthic primary deposit feeders (Dunton et al., 1989). Bryozoans could be ideal based on their size-selective feeding mode (Winston, 1977). No bryozoan species occured in all water masses but we compared results for AW and ACW when using the δ^{15}N signature of just *A. gelatinosum anderssoni* versus the combination of the above-mentioned primary conumers and the results were not different (within 0.04–0.08 TL).

Trophic levels of consumers were determined for each water mass using the equations:

$$\mathrm{TL}_{(\mathrm{POM})} = (\delta^{15}\mathrm{N}_{\mathrm{consumer}} - \delta^{15}\mathrm{N}_{\mathrm{POM}})/3.4 + 1$$

and

$$\mathrm{TL}_{(\mathrm{PC})} = (\delta^{15}\mathrm{N}_{\mathrm{consumer}} - \delta^{15}\mathrm{N}_{\mathrm{primary\ consumer}})/3.4 + 2$$

where 3.4 is the assumed enrichment in δ^{15}N between successive trophic levels (TL), which has been identified as an average trophic nitrogen fractionation for aquatic consumers (Vander Zanden, Rasmussen, 2001; Post, 2002). $\mathrm{TL}_{(\mathrm{POM})}$ refers to trophic levels with POM as the food-web baseline and $\mathrm{TL}_{(\mathrm{PC})}$ with the mean δ^{15}N of primary consumers used as baseline reference.

3. Results

POM δ^{13}C values were significantly enriched in AW compared to all other water masses (ANOVA, $p<0.001$), while there were no significant differences among the other water masses. POM δ^{15}N values also were significantly different among water masses, with ACW values being significantly lower than all other water masses (ANOVA, $p\leq 0.001$). Most enriched POM δ^{15}N values occurred at RC, which were also significantly higher than AW ($p=0.017$) but not different from BSW.

Surface sediment isotope values were significantly depleted in both carbon and nitrogen in ACW compared to all other water masses ($p\leq 0.001$), except compared to δ^{15}N sediment values at RC, which were not statistically different from ACW ($p=0.073$). Surface sediments were significantly depleted in δ^{13}C compared to the respective water mass POM values in ACW and AW (*t*-tests, $p\leq 0.01$) but significantly enriched in BSW and RC (*t*-tests, $p\leq 0.01$). Surface sediments were significantly depleted in ^{15}N compared to POM values in all water masses (*t*-tests, $p\leq 0.05$).

C/N ratios of water column POM (ANOVA, $p\leq 0.001$) and surface sediment organic matter (ANOVA, $p=0.034$) differed significantly among water masses. C/N ratios of ACW POM were significantly higher than POM C/N ratios in other water masses ($p<0.01$), with the higher C/N values indicative of lower food quality and more refractory material. For sediment C/N ratios, ACW was significantly higher only compared to AW ($p=0.024$) and there was no difference among the other water masses.

The distributions of δ^{13}C (Fig. 3A) and δ^{15}N (Fig. 3B) were compared for some (32 out of 42 representing a variety of taxa and feeding types) of the same taxa occurring in ACW and in AW. Sampling effort in these water masses was similar and occurred at several stations within each of the water massses (see Fig. 1, Table 1) and we consider the selection of organisms a good representation of the benthic communities present. ACW and AW are the two hydrographically most distinct water masses entering the southern Chukchi Sea from the Bering Sea (Table 1, Coachman, 1987). Overall, mean δ^{13}C values of all species and including POM ranged over 7.5‰ in ACW compared to only 5.1‰ covered by the same species in AW (Fig. 3A). Some of this difference (1‰) in the isotopic spread between the two water masses was driven by the much-depleted δ^{13}C POM values in ACW compared to AW (also see Table 2). A similar pattern was seen for δ^{15}N (Fig. 3B), where mean values of all species and POM ranged over 12.0‰ in ACW compared to 9.6‰ in AW. More so than with the range in δ^{13}C values this difference (1.5‰) was again driven in part by depleted POM δ^{15}N values in ACW compared to AW. In addition, in all cases but one (*M. calcarea*), ACW individuals were more enriched in δ^{15}N than in AW. The general relative isotopic arrangement, however, was similar between water masses with suspension-feeding bryozoans, ascidians and sponges having more depleted ^{13}C and ^{15}N values than omnivorous or scavenging/predatory asteroids, anemones, polychaetes, decapods, neogastropods and fishes.

Food-web length differed among water masses when POM was used as the baseline food source (Fig. 4). ACW and BSW had longer food webs than AW and RC, both comprising five trophic levels, although for BSW this was driven by a single high-trophic level organism, *Crossaster papposus*. AW and RC only comprised four trophic levels. In contrast, food-web length was similar among water masses when primary consumers were used as baseline (Fig. 4), with food webs in all water masses comprising four trophic levels, except for a few taxa at the very low fifth trophic level in AW and RC and the single *Crossaster papposus* record in BSW mentioned above. Hence, the largest difference in food-web length using POM versus primary consumers as baselines was observed for ACW, where food-web length was shorter by about 0.5 trophic levels when using primary consumers as baseline. The longer, POM-based food web in ACW coincided with the large gap between δ^{15}N values for POM and consumers described above (Fig. 3B).

Food-web structure did not only vary in total length when different baseline references were used, but also in the distribution of taxa within the different trophic levels (Figs. 4 and 5, Table 2). Again the most dramatic differences occurred within the ACW system, where the community was characterized by about equal proportions of third, fourth and fifth trophic level consumers with POM as baseline, but had only about 15% second trophic level consumers and a lack of fifth trophic level consumers when primary consumers were used for trophic level calculations. Fewer changes occurred in trophic level composition in other water masses, and changes in RC and BSW have to be considered in light of a much smaller sample size of the communities, where a change in trophic level calculations of few taxa can significantly impact our overall perception of food web structure (Fig. 5).

4. Discussion

Marked regional differences in food-web structure and lengths were observed in relation to POM as the primary food source, where food webs in ACW were longer than in AW. These differences were less pronounced when food-web length was based on the trophic position of primary consumers, resulting in food webs of about equal length in ACW and AW. Hence, differences in food-web length were mainly driven by regional differences in the POM source. Benthic consumers in ACW were more enriched in δ^{15}N than the same consumers in AW, which is likely linked to differences in water mass nutrient regimes and

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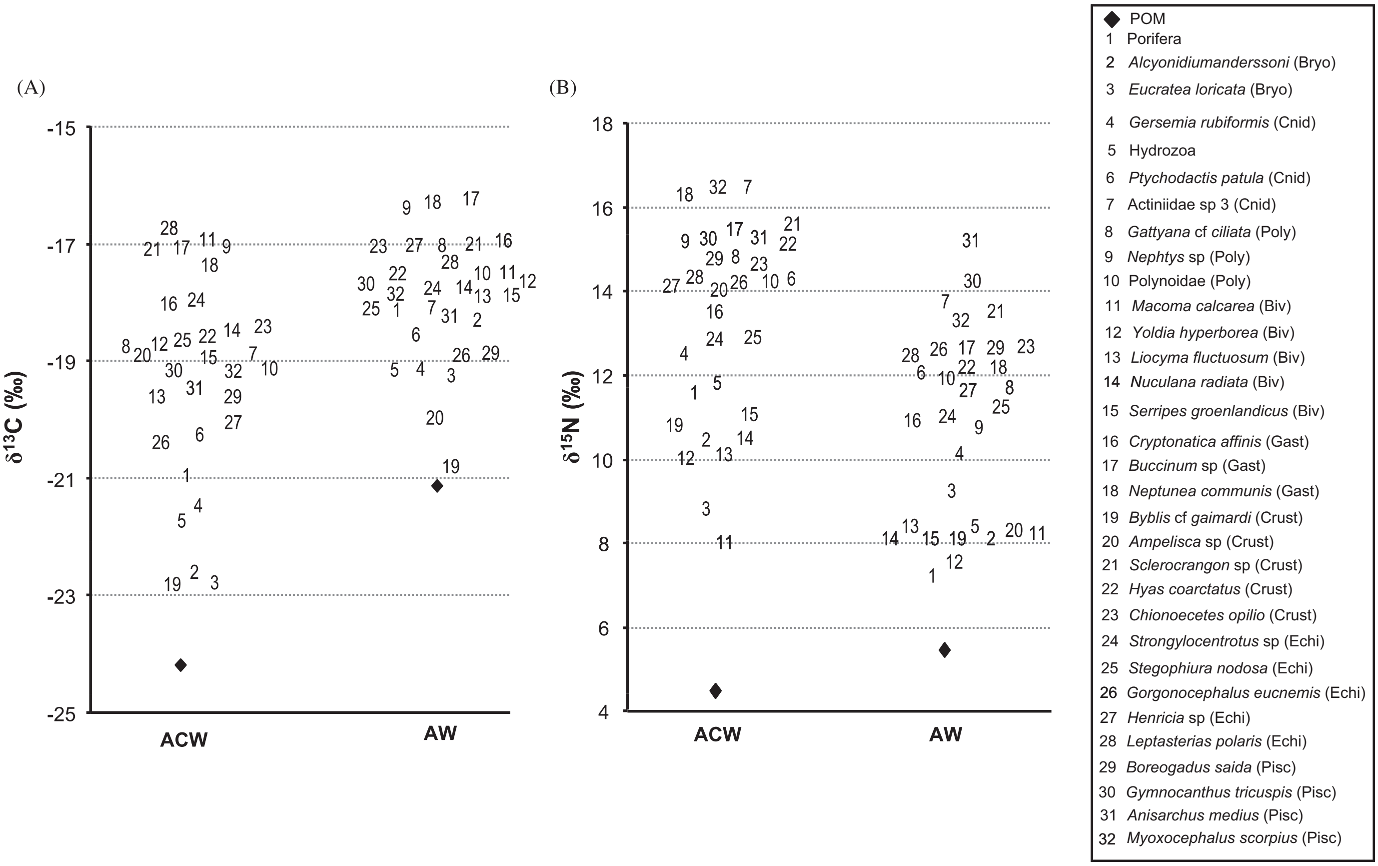

Fig. 3. $\delta^{13}C$ (3A) and $\delta^{15}N$ (3B) comparison of a selection of the same organisms between ACW and AW (for complete list see Table 2). POM is depicted as a black triangle. Numbers represent organisms given in the legend. Higher taxonomic identifications are given in parentheses: Bryo—Bryozoa, Cnid—Cnidaria, Biv—Bivalvia, Gast—Gastropoda, Crust—Crustacea, Echino—Echinodermata, Poly—Polychaeta, Pisc—Pisces. Water masses are: ACW—Alaska Coastal Water, AW—Anadyr Water.

water mass productivity as found elsewhere (Hansson et al., 1997; Needoba et al., 2006).

4.1. *Organic matter sources*

POM sources in the ACW were considerably depleted in ^{13}C and ^{15}N compared to those in AW, raising the question of how accurately POM represents the base of the food web. As one possibility, the influence of freshwater and terrestrial materials in the southern Chukchi Sea may, at least in part, explain the depleted $\delta^{13}C$ POM signals and the significantly lower sediment $\delta^{15}N$ values in the ACW, and, consequently, the differences in food-web length between the western and eastern sides of the study region (if based on the POM signal). Terrestrially derived carbon is isotopically lighter than marine-derived material (Naidu et al., 2000; Kendall et al., 2001). A strong fluvial signal stems from the Yukon River as a result of approximately 8×10^{12} g carbon that the river delivers annually into the Bering Sea system (Striegl et al., 2007). This carbon source is composed of 30% organic carbon (DOC and POC) from plant debris with a $\delta^{13}C$ of −26.4‰ and 70% inorganic carbon (DIC) with a $\delta^{13}C$ of −7‰ to −8‰ (Striegl et al., 2007). In contrast, marine-derived carbon is more enriched with a DIC $\delta^{13}C$ of 0‰ (Kroopnick, 1985; Boutton, 1991) and Arctic marine POC is typically between −22‰ and −24‰ (Hobson and Welch, 1992; Iken et al., 2005; Lovvorn et al., 2005; Søreide et al., 2006; Tamelander et al., 2006a). The freshwater carbon from the Yukon River is entrained in the ACW and carried northwards along the Alaska coast into the eastern Chukchi Sea (Mathis et al., 2005). We suggest that the depleted ^{13}C and ^{15}N isotopic signals of POM measured in the ACW reflect the mix of terrestrial, lighter with marine-derived, more enriched materials, similar to regional patterns recently documented for the Beaufort Sea with the marine-influenced Amundsen Gulf and the terrestrially influenced Mackenzie shelf (Morata et al., 2008).

Most marine organisms seem to have only limited ability to digest and assimilate plant material of terrestrial origin because of the high cellulose content (Schell, 1983); however, some marine consumers in the Beaufort Sea incorporated significant amounts of material of terrestrial origin (Parsons et al., 1988; Dunton et al., 2006). Dunton et al. (1989, 2006) detected an increase in food-web length along a gradient from the Bering and Chukchi Seas to the eastern Alaskan Beaufort Sea, coincident with the increasing influence of westward flowing freshwater and terrestrial inputs derived from the Mackenzie River. It is unknown how much of the terrestrially derived organic carbon in the eastern Chukchi Sea (ACW) is incorporated directly by marine consumers or how much of the DIC is taken up during primary production, although considerable removal of terrestrial organic carbon through microbial remineralization and photochemical transformation into labile matter on the ocean shelves have been suggested (Miller and Zepp, 1995; Moran and Zepp, 1997; Cauwet, 2002; Hernes and Benner, 2003). Likely, different organisms selectively assimilate various proportions of this isotopically depleted carbon source, thus spreading overall carbon values of consumers over a larger range in the freshwater-influenced ACW (~6‰ $\delta^{13}C$) than in the marine-dominated AW (4.6‰ $\delta^{13}C$, Fig. 3A). The depleted $\delta^{13}C$ of some primary consumers (suspension feeders) like the

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Table 2
Benthic taxa stable isotope values (δ^{15}N and δ^{13}C) with standard deviation (±sd), number of replicates (N) and trophic level (TL) based on primary consumers for baseline calculations (see text for details).

Species/taxon	**ACW**						**AW**						**BSW**						**RC**					
	δ^{15}N	**±sd**	**δ^{13}C**	**±sd**	**N**	**TL**	**δ^{15}N**	**±sd**	**δ^{13}C**	**±sd**	**N**	**TL**	**δ^{15}N**	**±sd**	**δ^{13}C**	**±sd**	**N**	**TL**	**δ^{15}N**	**±sd**	**δ^{13}C**	**±sd**	**N**	**TL**
POM	4.56	0.54	−24.20	0.23	7		5.51	0.45	−21.12	0.96	12		5.63	0.47	−23.59	0.32	3		6.31	0.53	−24.51	0.25	6	
Sediment	2.93	0.45	−24.82	0.52	6		4.68	1.15	−22.09	0.28	9		4.87	0.22	−22.78	0.10	3		4.50	0.42	−23.45	0.54	3	
PORIFERA	11.46	0.71	−20.98	0.50	10	**2.4**	7.12	0.59	−18.24	0.92	12	**1.1**												
CNIDARIA																								
Hydrozoa	11.42	0.34	−20.71	0.45	6	**2.4**	8.36	0.30	−18.27	0.80	9	**1.5**												
Actinaria																								
Actiniidae sp. 3	16.57	1.17	−18.75	0.76	7	**3.9**	13.82	0.36	−17.95	0.85	2	**3.6**	13.95	0.88	−18.81	0.62	3	**3.4**						
Actiniidae sp. 1							13.31	0.54	−17.95	0.90	6	**3.5**							13.59	1.07	−19.13	0.12	2	**3.4**
Ptychodactis patula	14.45	0.45	−20.13	0.23	3	**3.3**	12.13		−18.41		1	**3.1**												
Urticina sp. 1							12.83	0.62	−17.87	0.33	3	**3.3**												
Gersemia rubiformis	12.64	1.02	−21.33	0.55	6	**2.8**	10.21	0.63	−19.01	0.39	3	**2.6**												
Cribrinopsis sp.							14.85	0.17	−18.74	0.50	3	**3.9**												
NEMERTEA							12.59	0.572	−17.75	1.09	12													
ECHIURA							10.98	0.46	−17.75	2.13	4													
SIPUNCULA																								
Golfingia sp.							12.84		−18.66		1	**3.3**												
PRIAPULA																								
Priapulus caudatus							13.92	1.63	−16.85	1.32	3	**3.6**												
POLYCHAETA																								
Brada sp.1							11.62	1.25	−17.52	0.42	4	**3.0**												
Brada sp. 2							10.24	0.86	−18.87	0.69	6	**2.6**												
Chaetozone setosa							7.55	0.19	−19.45	0.72	4	**1.8**							9.65	0.09	−19.23	0.68	3	**2.2**
Gattyana ciliata	14.95		−18.61		1	**3.4**	11.87		−16.89		1	**3.0**												
Leitoscoloplos pugettensis																			13.75	0.12	−18.52	0.34	3	**3.4**
Lumbrineridae							11.12	1.00	−17.81	0.13	2	**2.8**												
Nephtys ciliata							12.98		−16.21		1	**3.4**	13.78	0.21	−17.92	0.40	3	**3.3**	13.12	0.93	−17.83	0.57	3	**3.2**
Nepthtys sp.	15.15		−17.07		1	**3.5**	10.85	1.10	−16.41	0.24	3	**2.7**												
Neremyra aphroditoides							10.54	0.21	−17.90	1.25	2	**2.7**							12.25	0.40	−18.62	0.28	3	**3.0**
Nicomache sp.	13.78	0.36	−18.27	0.58	3	**3.1**																		
Notomastus latericeus							10.73	0.53	−18.69	0.55	5	**2.7**												
Ophelina acuminata							11.38	0.01	−18.79	0.79	2	**2.9**							14.92		−19.40		1	**3.8**
Cistenides hyperborea							10.77	0.28	−18.25	0.07	3	**2.7**												
Pholoe sp.																			13.38	0.56	−18.78	0.39	3	**3.3**
Anaitides groenlandica							11.52	1.09	−17.86	0.56	5	**2.9**							13.71	0.19	−18.95	0.16	3	**3.4**
Polynoidae	14.19	0.67	−19.08	0.68	5	**3.2**	11.95	1.42	−17.75	0.68	9	**3.1**	12.55		−18.72		1	**3.0**						
Praxillella sp.	13.78	1.01	−18.64	0.47	3	**3.1**																		
Proclea emmi													11.13		−18.12		1	**2.6**						
Scalibregma inflatum							11.04	0.91	−18.27	0.70	6	**2.8**												
Lumbrineris fragilis	12.98		−19.80		1	**2.8**																		
Sternaspis scutata							12.09	0.50	−17.69	0.35	2	**3.1**							12.51	1.20	−17.27	0.80	2	**3.1**
Terebellides stroemi							9.03		−19.50		1	**2.2**							12.70		−16.51		1	**3.1**
Typosyllis armillaris	15.08	1.57	−19.86	0.41	3	**3.5**																		
MOLLUSCA																								
Gastropoda																								
Admete viridula							14.67	2.69	−16.51	0.90	6	**3.9**							14.35	1.03	−16.92	0.16	2	**3.6**
Buccinum angulosum							10.82	0.30	−17.92	0.12	3	**2.7**												
							12.85	0.96	−16.86	0.83	3	**3.3**	15.22	0.38	−16.78	0.37	3	**3.8**						

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Table 2 (*continued*)

Species/taxon	**ACW**						**AW**						**BSW**						**RC**					
	$\delta^{15}N$	**±sd**	**$\delta^{13}C$**	**±sd**	**N**	**TL**	**$\delta^{15}N$**	**±sd**	**$\delta^{13}C$**	**±sd**	**N**	**TL**	**$\delta^{15}N$**	**±sd**	**$\delta^{13}C$**	**±sd**	**N**	**TL**	**$\delta^{15}N$**	**±sd**	**$\delta^{13}C$**	**±sd**	**N**	**TL**
Buccinum scalariforme																								
Buccinum sp.	15.58	0.39	−16.94	0.27	3	**3.6**	12.71	0.53	−16.07	0.26	3	**3.3**												
Colus sp.													15.64	0.13	−16.04	0.16	3	**3.9**						
Cylichna alba							12.86	1.34	−16.87	0.55	5	**3.3**							15.14		−18.65		1	**3.8**
Euspira pallida							10.11	0.70	−17.72	0.20	6	**2.5**	12.20	0.21	−17.98	0.33	3	**2.9**						
Cryptonatica affinis	13.59		−17.90		1	**3.0**	10.99	0.58	−16.79	0.68	9	**2.8**	12.89	0.47	−17.23	0.08	3	**3.1**						
Neptunea communis	16.41	0.45	−17.25	0.31	3	**3.9**	12.28	0.38	−16.14	0.50	3	**3.2**	15.26	0.62	−16.37	0.86	3	**3.8**						
Neptunea ventricosa	15.01	0.38	−17.26	0.48	6	**3.4**	11.61	0.87	−16.33	0.69	3	**3.0**	15.28	0.83	−16.10	1.02	3	**3.8**						
Solariella sp.	12.86	0.21	−18.75	0.04	3	**2.8**	10.34	0.55	−18.07	0.31	6	**2.6**	12.22	0.25	−18.63	0.40	3	**2.9**	11.07	0.22	−18.55	0.10	2	**2.6**
Trichotropis bicarinata	10.80	0.14	−19.69	0.07	3	**2.2**																		
Trichotropis coronata													9.84	0.51	−18.43	0.12	3	**2.2**						
Tachyrhynchus erosus	10.58		−19.20		1	**2.1**							9.85	0.59	−18.84	0.19	3	**2.2**						
Bivalvia																								
Astarte borealis	12.29		−18.39		1	**2.6**																		
Clinocardium ciliatum	11.07		−19.32		1	**2.3**	8.78	0.38	−17.53	0.06	3	**2.1**	10.26	0.72	−18.55	0.15	3	**2.3**						
Liocyma fluctuosum	10.17		−19.50		1	**2.0**	8.45	0.26	−17.75	0.15	6	**2.0**	9.21	0.38	−18.99	0.09	3	**2.0**						
Macoma calcarea	8.10		−16.83		1	**1.4**	8.17	0.66	−17.32	0.22	9	**2.0**							9.50	0.38	−17.99	0.22	3	**2.2**
Ennucula tenuis							7.97	0.83	−17.75	0.40	9	**1.9**							9.36	0.63	−18.90	0.22	3	**2.1**
Nuculana radiata	10.58	0.33	−18.37	0.36	3	**2.1**	8.07	0.48	−17.59	0.31	9	**1.9**							9.70	0.50	−18.30	0.06	2	**2.2**
Pecten sp.	12.52	0.11	−18.53	0.29	3	**2.7**																		
Serripes groenlandicus	11.19		−18.82		1	**2.3**	8.07	1.05	−17.74	0.31	6	**1.9**	10.15	0.59	−18.33	0.58	3	**2.3**	8.86		−18.74		1	**2.0**
Yoldia hyperborea	10.10		−18.59		1	**2.0**	7.59	0.44	−17.50	0.23	9	**1.8**	9.36		−17.94		1	**2.0**	9.09	0.09	−18.41	0.34	3	**2.0**
CRUSTACEA																								
Amphipoda																								
Ampelisca sp.	13.99	0.41	−18.92	0.39	3	**3.1**	8.10	0.58	−20.00	0.35	6	**1.9**												
Stenothoidae							8.85	0.40	−19.09	0.53	3	**2.2**												
Anonyx nugax							13.00	1.54	−17.87	0.93	9	**3.4**	15.20	0.13	−19.08	0.72	3	**3.8**	15.98	0.24	−20.01	0.32	3	**4.1**
Byblis cf *gaimardi*	10.93	0.97	−22.69	0.67	3	**2.2**	8.08	0.48	−20.68	0.42	6	**1.9**												
Paroediceros sp.																			14.19	0.28	−18.16	0.34	3	**3.5**
Acanthostepheia behringiensis																			16.40	0.32	−18.76	0.20	3	**4.2**
Hippomedon sp.																			9.91	0.69	−20.72	0.53	3	**2.3**
Amphipod sp. 1							7.77	0.23	−21.48	0.74	3	**1.8**												
Amphipod sp. 2							7.02	0.86	−19.33	0.62	3	**1.6**												
Amphipod sp. 3							10.63	1.43	−19.23	0.23	3	**2.7**												
Amphipod sp. 4																			14.91	1.49	−19.53	0.81	3	**3.8**
Amphipod sp. 5							8.17	0.30	−20.44	0.34	3	**2.0**												
Amphipod sp. 6							10.22	0.97	−20.05	0.37	3	**2.6**	10.64	1.15	−19.76	1.18	3	**2.4**						
Decapoda																								
Argis lar	14.63	0.70	−17.15	0.34	6	**3.3**	14.48	1.00	−16.42	0.72	5	**3.8**	14.42	0.70	−16.66	0.81	3	**3.5**	16.27	0.49	−16.73	0.66	3	**4.2**
Chionoecetes opilio	14.75	0.62	−18.30	0.46	9	**3.4**	12.74	0.93	−16.92	0.65	12	**3.3**	14.59	0.24	−17.47	0.39	3	**3.6**	14.56		−17.37		1	**3.7**
Crangon sp.	14.97	0.56	−17.35	0.23	3	**3.4**	13.41	0.54	−17.93	0.85	3	**3.5**												
Paguridae	13.20	1.06	−18.58	0.89	9	**2.9**	12.46	0.61	−16.83	0.65	6	**3.2**	13.26	0.52	−17.54	0.52	3	**3.2**	13.03		−18.00		1	**3.2**
Hyas coarctatus	15.22	0.82	−18.48	0.32	8	**3.5**	12.26	1.36	−17.37	0.49	6	**3.2**							14.70	0.74	−17.57	0.14	3	**3.7**
Sclerocrangon sp.	15.73	0.68	−16.98	1.07	6	**3.7**	13.61	0.17	−16.86	0.56	2	**3.6**							15.94	0.74	−17.17	0.19	2	**4.1**
Benthopelagic shrimp	14.83	0.49	−19.02	0.27	9	**3.4**	13.12	1.09	−17.87	1.01	8	**3.4**	13.49	0.88	−18.42	0.29	3	**3.3**	15.31	0.88	−17.88	1.01	3	**3.9**
Spirontocaris sp.	14.87	0.40	−18.38	0.47	3	**3.4**																		

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Telmessus cheiragonus	15.50	0.54	−18.84	0.42	3	**3.6**																		
Other crustaceans																								
Balanoidea							8.08	0.50	−19.15	0.46	3	**1.9**												
Saduria sp.							12.06	1.01	−17.98	1.74	3	**3.1**												
ECHINODERMATA																								
Asteroidea																								
Asterias amurensis	15.41	1.02	−17.74	1.50	8	**3.6**	10.42	0.37	−19.65	0.28	3	**2.6**												
Crossaster papposus	15.45	1.24	−19.28	1.44	6	**3.6**							18.44		−15.32		1	**4.7**						
Leptasterias groenlandica	15.00	1.43	−19.48	1.15	9	**3.4**	12.19	0.27	−18.17	0.32	3	**3.1**							13.73	0.33	−17.45	0.92	3	**3.4**
Henricia sp.	14.20	0.60	−19.91	0.51	3	**3.2**	11.75	0.54	−16.90	0.47	6	**3.0**							13.21		−18.30		1	**3.3**
Leptasterias polaris	14.30	1.60	−16.73	1.30	9	**3.2**	12.59	0.08	−17.50	0.75	3	**3.3**	15.03	0.45	−15.68	1.06	3	**3.7**						
Ophiuroidea																								
Gorgonocephalus eucnemis	14.31	0.74	−20.27	0.90	5	**3.2**	12.71	0.17	−18.76	0.78	3	**3.3**												
Amphiodia craterodmeta							11.68	0.39	−17.77	0.65	3	**3.0**												
Stegophiura nodosa	12.90	1.07	−18.53	0.42	3	**2.8**	11.34	0.54	−17.96	0.47	3	**2.9**												
Ophiura sarsi							11.80	0.17	−17.71	0.12	3	**3.0**	13.83	0.27	−17.89	0.25	3	**3.4**						
Holothuroidea																								
Myriotrochus rinkii							11.84	0.78	−18.35	0.49	9	**3.0**												
Psolus sp.	9.49	0.76	−22.00	0.17	3	**1.8**																		
Echiuridea																								
Strongylocentrotus sp.	12.89	1.12	−17.84	0.78	6	**2.8**	11.09	0.49	−17.61	1.25	3	**2.8**												
BRYOZOA																								
Alcyonidium gelatinosum anderssoni	10.53	0.36	−22.48	0.81	6	**2.1**	8.10	0.46	−18.17	0.19	5	**1.9**												
Bowerbankia composita							8.08	0.29	−17.96	0.64	3	**1.9**							8.39		−18.60		1	**1.8**
Flustra nordenskjoldi	9.26	1.00	−22.69	0.19	7	**1.8**																		
Flustra serrulata	9.86	0.46	−22.41	0.55	3	**1.9**																		
Eucratea loricata	8.72	0.72	−22.78	0.09	2	**1.6**	9.27	0.39	−19.11	1.60	3	**2.3**												
Dendrobeania cf *fructicosa*	10.08	0.75	−21.29	0.37	3	**2.0**																		
BRACHIOPODA	12.97	0.34	−20.86	0.81	3	**2.8**																		
TUNICATA																								
Boltenia ovifera							8.74	0.73	−18.91	0.28	4	**2.1**												
Diplosoma cf. *listerianum*	9.93	0.27	−23.09	0.87	6	**2.0**																		
Didemnum albidum	9.89	0.34	−22.33	0.73	3	**1.9**																		
Ascidea sp. 1	10.03	0.61	−20.64	1.50	3	**2.0**													8.60		−18.96		1	**1.9**
cf *Chelyosoma macleayanum*	12.17	0.09	−19.27	0.31	3	**2.6**																		
PISCES																								
Anisarchus medius	15.13	0.79	−19.46	0.37	3	**3.5**	15.11	0.57	−18.24	0.44	5	**4.0**	14.75	0.56	−18.76	0.36	3	**3.6**						
Artediellus scaber	16.24	0.69	−18.88	0.04	3	**3.8**													15.80	0.37	−17.94	0.26	3	**4.0**
Boreogadus saida	14.92	0.62	−19.49	0.10	3	**3.4**	12.73	0.55	−18.71	0.22	4	**3.3**												
Eleginus gracilis	15.21	1.75	−20.79	1.82	6	**3.5**																		
Enophrys diceraus	16.55	0.14	−18.10	0.22	3	**3.9**																		
Gymnocanthus tricuspis	15.31	0.75	−19.03	0.85	9	**3.5**	14.30	1.33	−17.54	0.46	9	**3.8**	15.45	0.32	−19.36	0.31	2	**3.8**	15.19	0.28	−18.34	0.16	3	**3.8**
Hippoglossoides robustus	15.16	0.82	−19.72	0.78	3	**3.5**	13.31	0.79	−18.79	1.13	6	**3.5**	14.26	0.64	−19.46	0.88	3	**3.5**						
Limanda aspera	15.77		−18.48		1	**3.7**																		
Lumpenus fabricii	15.72	0.60	−18.85	1.07	9	**3.7**	13.28	0.67	−18.26	1.13	4	**3.5**	16.20		−17.89		1	**4.1**	14.76	0.27	−18.16	0.17	3	**3.7**
Nautichthys pribilovius	15.65	0.07	−20.25	1.28	3	**3.6**																		

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Table 2 (continued)

Species/taxon	ACW						AW						BSW						RC					
	$\delta^{15}N$	±sd	$\delta^{13}C$	±sd	N	TL	$\delta^{15}N$	±sd	$\delta^{13}C$	±sd	N	TL	$\delta^{15}N$	±sd	$\delta^{13}C$	±sd	N	TL	$\delta^{15}N$	±sd	$\delta^{13}C$	±sd	N	TL
Myoxocephalus polyacanthocephalus	15.52		−18.13		1	**3.6**																		
Myoxocephalus scorpius	16.54	0.42	−19.06	0.33	9	**3.9**	13.39	1.56	−17.71	0.50	6	**3.5**							12.04	0.36	−18.72	0.25	3	**2.9**
Stichaeus punctatus	16.22	0.67	−19.39	1.33	6	**3.8**																		
Theragra chalcogramma	14.33	0.86	−19.52	0.55	3	**3.2**																		
Triglops pingelii	16.29	0.65	−18.97	0.50	5	**3.8**													14.15	1.23	−18.94	0.18	2	**3.5**
Ulcina olriki																			14.40	0.70	−18.29	0.56	2	**3.6**

amphipod *Byblis* sp., the soft coral *Gersemia rubiformis* and the bryozoan *A. gelatinosum anderssoni* in the ACW compared to the more enriched values of the same taxa in the AW suggest that at least some portion of this terrestrial material may be incrporated by benthic consumers. Terrestrial influence also probably explains the depleted $\delta^{13}C$ POM value at the Russian Coast station (27, Fig. 1), which is under the influence of a coastal lagoon outflow and which was isotopically more similar to ACW conditions in the east than to the geographically closer AW stations in the west.

Another factor that could influence the $\delta^{13}C$ value of POM is the presence of other unacknowledged endmembers, particularly ice algae. While ice algae contribute only a small to moderate fraction of total annual primary production on shallow continental shelves with seasonal ice cover (Horner, 1985; Gosselin et al., 1997; Hegseth, 1998; Gradinger, 2009), they can contribute significantly to benthic food webs (e.g., Tamelander et al., 2006a). Ice algae could not be sampled in our study, but are often enriched in isotope ratios compared to open water POM by 2–10‰ (Hobson and Welch, 1992; Hobson et al., 1995; Gradinger and Bluhm, 2005; Lovvorn et al., 2005; Søreide et al., 2006; Tamelander et al., 2006a), depending on ice-physical conditions influencing CO_2 permeability and ice algal growth (Korb et al., 1998; Kennedy et al., 2002; Thomas and Papadimitriou, 2003; Iken et al., 2005). Estimates of isotopic turnover times in polar organisms are scarce, but half-life times of around 20 days for both isotopes in spring were measured in Arctic amphipods (Kaufman et al., 2008). Arctic bivalves showed measurable increases in $\delta^{13}C$ from an ice algal diet after 4 weeks (McMahon et al., 2006). An ice algal bloom in April before the onset of the phytoplankton bloom in May (Alexander and Niebauer, 1981; Wang et al., 2005) can sink to the bottom fast. Up to 100% of ice-derived material on the Chukchi shelf can reach the bottom within approximately 6 weeks (Cooper et al., 2005). In addition, significant ice algal accumulations on the seafloor have been observed in early June on the northern Chukchi shelf (Ambrose et al., 2001). If ice-derived production is available to the benthos by June, it is conceivable that an ice algal isotopic signature could be traceable in benthic consumer tissues by the time of our sampling in August. The overall heavier carbon isotope signatures of AW benthic organisms compared to ACW could be caused by a more pronounced ice algal influence in the diet of benthic consumers in the AW. While our present data do not allow us to evaluate ice algal significance, their importance in southern Chukchi Sea benthic food webs is a central aspect remaining to be elucidated more fully in future studies.

Benthic consumers were isotopically enriched in ACW relative to AW, a finding we attribute to the nature and processing of particles generated during primary production and sedimentation. Rather than feeding selectively on fresh phytodetritus, some macrobenthic invertebrates rely on more refractory material deposited in surface sediments (Webb, 1993; van de Bund et al., 2001; Hansen and Josefson, 2004; Moore et al., 2004). The utilization of this deposited material has been used to explain how polar benthos can sustain significant biomass for long periods without fresh phytoplankton deposition (Mincks et al., 2005). Suspended material is deposited to the seafloor in multiple forms, e.g., as dead phytoplankton cells, feces of pelagic grazers or marine snow, which has implications for the isotopic composition of the settling material (Mintenbeck et al., 2007). Settling phytoplankton increases in $\delta^{15}N$ during sinking because of selective (microbial) degradation of chemical compounds, a process that will be enhanced in slower-sinking small particles (Levinton, 1972; Altabet and McCarthy, 1985; Hansen and Josefson, 2004). Zooplankton fecal pellets, which can have relatively fast sinking rates depending on their size, are usually

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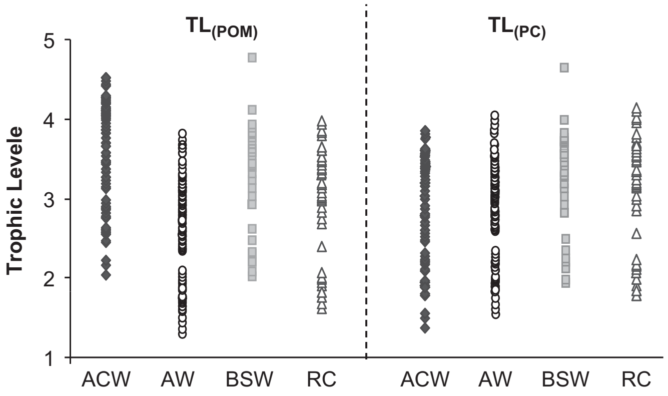

Fig. 4. Trophic level structure at different water masses with δ^{15}N POM (TL_{POM}) as baseline (POM defined as TL1) and with a mean δ^{15}N value for primary consumers (TL_{PC}) as baseline (defined as TL2).

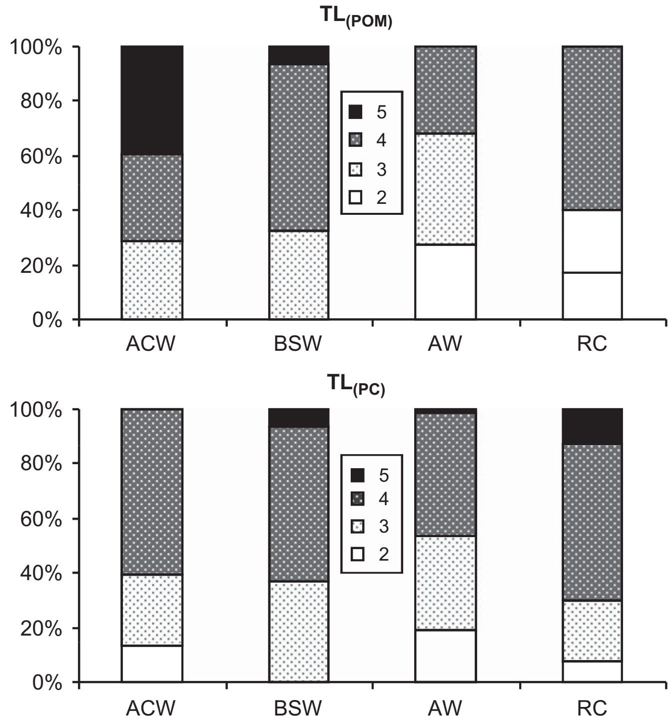

Fig. 5. Relative contribution of taxa to trophic levels (2–5) at different water masses with δ^{15}N POM (upper panel) or mean δ^{15}N of primary consumers (lower panel) used as trophic baseline.

enriched in δ^{15}N over phytoplankton because of the preferential loss of the lighter isotope during excretion (Checkley and Entzeroth, 1985). Occasionally, however, copepod fecal pellets are isotopically depleted compared to the food source, which may be related to the organisms' metabolic activity depending on seasonal feeding activity, reproduction and growth as well as the degree of isotope fractionation of lipid versus non-lipid compounds during digestion (Breteler et al., 2002; Tamelander et al., 2006b). Assimilation of isotopically enriched material can explain the often considerable isotopic enrichment of benthic organisms compared to water column POM (McConnaughey and McRoy, 1979; Hobson et al., 1995; Iken et al., 2001, 2005). Phytoplankton communities in AW are dominated by large phytoplankton (94%>20 μm) while ACW phytoplankton is dominated by smaller plankton fractions (Lee et al., 2007). Large cells have faster sinking rates, depositing labile phytodetritus material quickly to the seafloor in AW. Sinking rates of the smaller ACW phytoplankton may be slowed even more by stable stratification of the water column from the freshwater influence in the eastern Chukchi Sea (Woodgate et al., 2006). Freshwater stratification is a major determinant of particle residence time in the water column (Olli et al., 2002). Copepod communities were characterized by high abundance of small species in the ACW and lower abundance of large species in the AW, resulting in overall higher copepod (and other zooplankton taxa) biomass in the AW (Hopcroft and Kosobokova, this issue). This high copepod biomass in AW is likely to result in higher fecal pellet production in AW than in the ACW, and fecal pellets in AW are likely larger than in ACW, thus having faster sinking rates. Thus, zooplankton fecal pellets represent another efficient vector of depositing suspended material effectively to the seafloor in the western Chukchi Sea. This would provide a more isotopically enriched detrital food source to benthic consumers in ACW than in AW, which would explain the enriched nitrogen isotopic signatures in ACW benthic consumers (Fig. 3B).

Interestingly, surface sediments in this study were not enriched but rather depleted in both isotopes compared to POM in both ACW and AW, with surface sediments in AW being more enriched than those in ACW. While the isotopic depletion of sediments compared to POM is unusual, it could represent the deposition of more terringenous materials in the ACW, which are well-defined by their depleted ^{13}C and ^{15}N isotopic signatures (Naidu et al., 2000; Kendall et al., 2001; Morata et al., 2008). This relatively refractory organic carbon is likely associated with Yukon River water that is entrained within the ACW. Grebmeier et al. (2006) also noted depleted sediment ^{13}C values (<-23‰) along the Alaskan Chukchi coast that originated near the mouth of the Yukon and which extended northward into the western Beaufort Sea. Since we analyzed bulk surface sediment, and because refractory organic carbon would not be easily assimilated by particle-size-selective benthic deposit feeders (Levinton, 1979; Iken et al., 2001; Mintenbeck et al., 2007; Mincks et al., 2008), the carbon and nitrogen isotopic values of these animals are unlikely to reflect the isotopic enrichment of bulk sinking POM. It is likely that deposit feeders would prefer a more labile food source, as characterized by the lower sediment C/N ratios representing higher N content as measured in the AW.

The above considerations suggest that POM is likely an accurate representation of the food source for benthic organisms in AW but possibly not in ACW. We suggest that this finding emphasizes the importance of measuring the POM food sources in isotope food-web studies as it can obviously provide important information about the variability, and potential factors causing it, in the primary food source. For the purpose of identifying food-web length, however, and for the comparison of other food-web structure characteristics among different systems, it may be more accurate to rely on primary consumers as the second trophic level baseline (Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999; Post, 2002; Vander Zanden and Fetzer, 2007).

4.2. Food-web structure

Benthic food-web length did not differ noticeably among the different water masses in the southern Chukchi Sea when primary consumers as the second trophic level were used as baseline. According to food-web theory, the classical productivity or energy hypothesis predicts longer food webs in more productive systems because more energy can be transferred between trophic levels, ultimately sustaining longer food webs (Hutchinson, 1959; Persson et al., 1992; Kaunzinger and Morin, 1998). The controversial findings regarding the productivity hypothesis in other systems (e.g., Briand and Cohen, 1987) gave rise to new

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theories that include the degree of stablility of food webs (Sterner et al., 1997) or levels of system complexity combining resource availability with dynamic properties such as predator–prey interactions (Post, 2002; Trussell et al., 2006). We lack the data to test these hypotheses thoroughly for the food webs under different water mass influence in the southern Chukchi Sea. But food-web length as well as overall benthic community composition (Sirenko and Gagaev, 2007, Bluhm and Iken, unpubl. data) in the ACW and AW masses was relatively similar while productivity is higher in the western than the eastern Chukchi Sea (Lee et al., 2007). Hence, our study did not support the productivity hypothesis as the food web in the AW was not longer than those in the other water masses.

Most of these food-web theories were developed for terrestrial and lake system, which are characterized by mostly distinct trophic levels and are relatively defined systems; but it is questionable how well these theories may apply to marine systems (Link, 2002). High degrees of omnivory and of connectivity are among the major characteristics typical for benthic marine systems. Benthic systems are dominated by suspension and deposit feeders, and food webs are characterized by continua rather than distinct trophic steps (Cousins, 1987; France et al., 1998; Shurin et al., 2006; Post and Takimoto, 2007). Hence, in addition to food-web length, quantifying the distribution of taxa within the trophic continuum may also be appropriate to discern differences in food-web structure. Considering only ACW and AW, where we are confident that the communities were representatively sampled, proportional distribution of taxa among trophic levels was very similar in these two benthic communities, except for slightly more primary consumers in the second trophic level in AW. These primary consumers are mainly sponges, bryozoans and filter-feeding bivalves that feed on a lower trophic level in AW (TL2) than in ACW, where they mostly occupy the third trophic level.

When food-web length and relative proportions of trophic levels are similar, it is ultimately the amount of energy passed through the food webs that controls the proportional biomass or abundance of key taxa at each trophic level, i.e. how the trophic levels are quantitatively represented in the communities. Overall, benthic infaunal communities were about one order of magnitude higher in abundance and biomass at AW compared to ACW (Sirenko and Gagaev, 2007). Dominant macrobenthic species in AW were suspension and surface-deposit feeding clams like *M. calcarea* ($>$70% of total biomass), *Yoldia hyperborea* and *Ennucula tenuis* (Sirenko and Gagaev, 2007), all of which are primary consumers (TL2). In contrast, infaunal communities in ACW were dominated by polychaetes like *Nepthys ciliata* (Sirenko and Gagaev, 2007), which occupy TL4. Dominance of subsurface-deposit feeding polychaetes was also found in other benthic community studies in the ACW region, although also some surface-deposit feeding polychaetes and amphipods were locally abundant (Feder et al., 2007). Epifaunal communities in ACW were dominated by predatory/scavenging crabs (*Chionoecetes opilio* TL4, Paguridae TL3) and surface-deposit feeding urchins (*Strongylocentrotus* sp. TL3), comprising about 60% of epifaunal biomass (Bluhm and Iken, unpubl. data). Similarly, key epifauna in AW also contributed mainly to higher trophic levels, e.g., the predatory/scavenging sea star *Leptasterias* sp. (TL4), and surface-deposit feeding holothurians (*Myriotrochus rinckii* TL4) and ophiuroids (*Amphiodia craterodmeta*, TL3), comprising about 55% of epifaunal biomass (Bluhm and Iken, unpubl. data). Thus, relative epifaunal biomass distribution to trophic levels was relatively similar in ACW and AW, with main contributions to higher trophic levels in both systems. The relatively high epifaunal biomass of opportunistic higher trophic levels in the ACW is, in addition to local production, also sustained by a large inflow of laterally advected material from the northern Bering Strait (Feder et al., 2005). In addition, high feeding plasticity in members of detritus-based food webs assists in maintaining higher trophic levels in low productivity systems (Stenroth et al., 2008).

Hence, even though overall food-web length and the relative proportions of trophic levels were similar between benthic communities in the AW and ACW water masses, AW communities were quantitatively dominated by infaunal primary consumers capitalizing on the abundance of fresh, labile material. In contrast, ACW benthic infaunal biomass was dominated by higher trophic levels able to exploit more refractory particle sources and dependent on predation and scavenging.

5. Conclusions

Benthic food webs in the southern Chukchi Sea differed in their primary food source (POM) with respect to the POM's quality and isotopic signature reflecting terrestrial influence in ACW. However, the greater spread in carbon isotopic signatures in ACW compared to AW likely reflects a food web that probably has contributions from multiple carbon sources in the ACW, notably from freshwater input. Secondly, about one quarter of the consumers in AW is within one trophic level (3.4‰ δ^{15}N) of the POM signature while none of the consumers in the ACW are within a trophic level of the respective POM signature for that region (Fig. 5). This difference suggests that there is a more direct coupling of benthic consumers to the very high pelagic primary production associated with the AW. Once normalized to primary consumer baselines, food webs were similar in length and relative distribution of trophic levels. Food webs with four trophic levels including invertebrates and fishes are similar to what has been established in other benthic Arctic systems (Hobson and Welch, 1992; Hobson et al., 1995; Hoekstra et al., 2003; Iken et al., 2005; Lovvorn et al., 2005; Tamelander et al., 2006a), although the inclusion of marine birds and mammals often adds one more trophic level (Hobson and Welch, 1992; Hobson et al., 1995). Our findings also coincide with generalized predictions of food-web length in marine systems as being limited to four levels, although marine mammals can add 2/3 of a trophic level (Vander Zanden and Fetzer, 2007).

While overall food-web length (based on primary consumers) did not differ in Chukchi Sea regional food webs, we suggest that they differ in how benthic biomass (Sirenko and Gagaev, 2007, Bluhm and Iken, unpubl. data) contributes towards these trophic levels. The low trophic level of the biomass dominants (Sirenko and Gagaev, 2007) in the western Chukchi Sea would suggest that the high benthic infaunal biomass there may be mainly driven by the high primary production and effective conversion of this labile material into biomass. This study shows how important it is to evaluate not only food-web length or trophic level distribution but that the quantitative distribution of communities within trophic levels may be necessary to decipher small-scale regional differences in benthic food webs. This is likely to be particularly true for detritus-based systems, which are not prone to exhibit distinct trophic levels or react in clear trophic cascades because of the overall large overlap and plasticity in feeding types (Moore et al., 2004; Sweeting et al., 2005; Post and Takimoto, 2007).

Based on the recently observed increased freshening and heating of Bering Strait inflow (Woodgate et al., 2006), a decrease in nutrient inflow to the western Chukchi Sea (AW) could reduce food availability for benthic communities. The subsequent change in AW benthic food-web structure may result in a system more similar to ACW food webs because of a decrease of fresh, labile food. Organisms that currently rely on fresh phytodetritus such as

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filter-feeding and surface-deposit feeding bivalves in the AW may successively be replaced by those that are more reliant on refractory material or by omnivorous feeders. Obviously, such scenarios of changing benthic food webs can also be expected to have severe consequences for top trophic level benthic feeders such as gray whales, walrus and diving ducks (e.g., Moore et al., 2003) as well as for humans depending on these food webs (Krupnik and Jolly, 2002).

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