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The shallow benthic food web structure in the high Arctic does not follow seasonal changes in the surrounding environment

Monika Kędra [a,b,*], Karol Kuliński [a], Wojciech Walkusz [a,c], Joanna Legeżyńska [a]

[a] Institute of Oceanology, Polish Academy of Sciences, Powstańców Warszawy 55, 81-712 Sopot, Poland
[b] Chesapeake Biological Laboratory Center for Environmental Science, University of Maryland, P.O. Box 38, Solomons, 20688 MD, USA
[c] Department of Fisheries and Oceans, 501 University Crescent, Winnipeg, R3T 2N6, MB, Canada

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ABSTRACT

Seasonality, quality and quantity of food resources strongly affect fitness and survival of polar fauna. Most research conducted in polar areas has been carried out during the summer, rarely including aspects of seasonality; therefore, there are gaps in our knowledge of the structure of food webs in the Arctic, particularly information is lacking on the possible shifts in winter feeding strategies of organisms. This study is the first to compare potential shifts in benthic food-web structure between winter and summer in a shallow-water Arctic fjord (Kongsfjorden, Svalbard). Winter data were collected in March when conditions are representative of winter and when Arctic shallow benthic fauna is likely to be most affected by absence of fresh food supply as opposed to summer (August). Samples of particulate suspended organic matter (POM), settled organic matter, surface sediment and benthic organisms were taken and analyzed for stable isotopes signatures ($\delta^{13}C$ and $\delta^{15}N$). Four relative trophic levels (TL) were distinguished in both winter and summer, and no differences in the structure of benthic food web were found between seasons. Our study shows that the shallow sublittoral benthos depends on primary production, fresh and reworked settled organic matter and, to a certain degree, on terrestrial input. We also demonstrate that shallow water polar benthic fauna is characterized by a high level of omnivory and feeds at multiple trophic levels showing strong resilience to changing seasonal conditions.

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1. Introduction

Knowledge of seasonal changes in species assemblages, diversity and food-web structure is especially important for understanding polar ecosystems. Arctic aquatic ecosystems are characterized by seasonal or permanent ice cover, variable light availability and nearshore salinities, and seasonally variable levels of organic carbon input (Grebmeier and Barry, 1991). At high latitudes, strong seasonality and food availability are closely linked and greatly affect fitness and survival of fauna (Clark, 1998). In many Arctic shelf systems, benthic biomass is high due to tight benthic–pelagic coupling (Ambrose and Renaud, 1995). Overall, abundance and distribution of benthic organisms are shaped by the downward flux of organic material from the overlying water column (Piepenburg et al., 1997; Piepenburg, 2005). Seasonal phytodetritus pulses are known to be responsible for seasonal variability in benthic ecological processes and carbon cycling (Grebmeier and McRoy, 1989). On shallow Arctic shelves benthic food webs play an important role in overall system production, turnover rates and remineralization of organic matter (Renaud et al., 2008; Iken et al., 2010). Although our knowledge of benthic food web structures in the Arctic has greatly improved recently (Hobson et al., 2002; Iken et al., 2005; Bergmann et al., 2009; Iken et al., 2010; Renaud et al., 2011; Feder et al., 2011), trophic responses of benthic organisms to seasonal variability, particularly to winter conditions, remain largely unknown (Piepenburg, 2005; Echeverria and Paiva, 2006).

Food-web structure, apart from describing trophic connections also reflects biodiversity, species interactions and ecosystem structure (Dunne et al., 2002). Trophic structure together with food chain length and food sources may depict the relative stability of the ecosystem. Winter in polar regions, when no primary production occurs, changes the trophic relations between species. Furthermore, the temperature increase in the Arctic is accelerating with global warming, leading to possible changes in the seasonality of primary production and trophic interactions (Grebmeier et al., 2006; Grebmeier, 2012). Consequently, knowledge of variability in the trophic relations of marine organisms in the Arctic between winter and summer is becoming especially important.

* Corresponding author. Present address: Chesapeake Biological Laboratory Center for Environmental Science, University of Maryland, P.O. Box 38, Solomons, 20688 MD, USA.
E-mail address: kedra@umces.edu (M. Kędra).

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Establishing trophic relationships within communities in polar marine ecosystems is difficult, particularly during the winter period, when sampling becomes very challenging. Most food-web studies conducted in polar areas have so far been carried out during summer (Piepenburg, 2005; Echeverria and Paiva, 2006; Feder et al., 2011), and rarely included aspects of seasonality (Renaud et al., 2011). Scarce winter studies in the Arctic mainly dealt with the pelagic domain (Søreide et al., 2008; Berge et al., 2009) or sympagic fauna (Werner and Auel, 2005). However, none of the above-mentioned studies focused on benthic food-web structure during the winter.

This study uses stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes ratios in the tissue of consumers that can generally be related to their food source, and reflect a longer term diet of weeks to months rather than a recent snapshot of material consumed prior to collection. It has been shown that naturally occurring stable isotopes of nitrogen and carbon show a stepwise enrichment with heavier isotopes between prey and consumer tissue. On average, in marine benthic ecosystems, consumers are enriched relative to their food by about 3–4‰ in $\delta^{15}N$ and by <1‰ in $\delta^{13}C$ (Hobson and Welch, 1992). The large enrichment factor in $\delta^{15}N$ makes it useful for delineating trophic levels whereas the small to negligible enrichment in $\delta^{13}C$ distinguishes food sources with distinctly different carbon signatures.

The aim of this study was to examine benthic food-web structure in the shallow sublittoral of a high Arctic fjord. Also, the study assessed if, and how, the food web changes with respect to winter and summer conditions, by collecting samples in March (after a long period of adverse winter conditions) and August (when diverse food sources are accessible).

2. Material and methods

2.1. Study area

Kongsfjorden is an open fjord situated on the north-western coast of Svalbard (12° E 79° N; Fig. 1). The fjord is divided into two parts by a chain of islands (Lovénøyane): a well separated inner basin of 50–60 m average depth with Kongsbreen, an active tidal glacier at the head (glacial bay), and an outer basin with average depths of 200–300 m widely open to the Fram Strait. The fjord hydrology is influenced by relatively warm Atlantic Water carried by the West Spitsbergen Current. Strong seasonality in the advection of Atlantic water and glacial input occurs (Walkusz et al., 2009). The hydrological conditions at shallow depths may vary seasonally, and are strongly influenced by ice melting and fresh water input (Jørgensen and Gulliksen, 2001). During the winter (March 2009) sea-water temperatures, at the top 35 m, ranged from −1.5 °C to −1.9 °C, and sea ice formed. In summer (August 2008) temperatures varied from 3.4 °C to 5.3 °C at the surface and from 3.5 °C to 3.9 °C at 35 m depth (Kędra et al., 2011). Kongsfjorden was extensively investigated, and the biological results of these studies are summarized in Hop et al. (2002) with the physical conditions described by Svendsen et al. (2002).

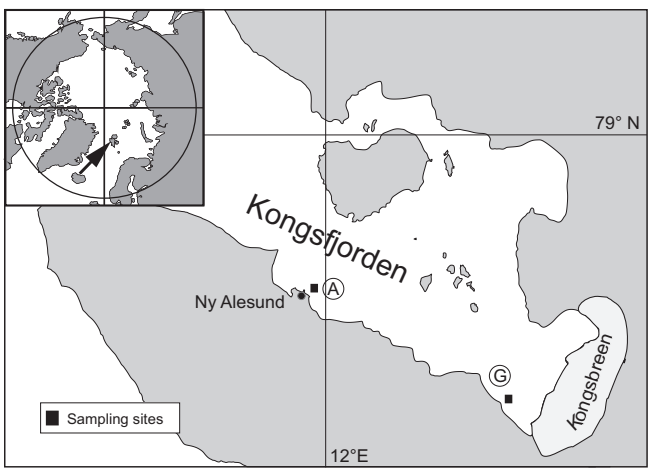

Fig. 1. Sampling locations in Kongsfjorden.

2.2. Sampling

Sampling was carried out at two shallow locations (15 m): one in the inner basin, close to the glacier – Kongsbreen (hereafter G station) and one in the outer basin, in the vicinity of the Ny-Ålesund settlement (hereafter A station) (Fig. 1, Table 1). Samples were collected during summer, in August 2008 and during the following winter, in March 2009. Winter sampling was performed when the fjord was frozen, with an average ice thickness of 47 cm. Although daylight was already present, there were no signs of the spring bloom of primary production (Kędra et al., 2011).

Prior to sampling, a CTD probe (Mini CTD, Sensordata SD204) was deployed through the opening in the ice. Samples of suspended particulate organic matter (POM), were obtained by filtering a volume of 0.2–2 l of sea surface water (large plankton was removed) on pre-combusted Whatman GF/F glass fibre filters. Benthic organisms were taken with a Petit Ponar grab (0.045 m^2 sampling area), operated by hand directly from the ice in winter and from a Zodiac boat in summer. Additional benthic material was collected during the summer from R/V Oceania (0.1 m^2 Van Veen grab and bottom dredge). Samples of settled organic matter and surface sediment were taken in both seasons. Scavenging amphipods were collected by setting traps with unavailable bait to prevent them from feeding. Whenever possible, organisms were collected in replicates; however, sometimes only one sample was obtained. In many cases, several or more individuals per species were combined to provide samples large enough for stable isotopes analysis due to small size of specimens captured. Thirteen species were collected in both seasons but some species were found in one season only and in many cases no replicate samples were available preventing the assessment of variability. The overall number of samples and replicates collected was limited by logistical restrictions, especially during the winter. Live animals were kept in filtered sea water at temperature and salinity corresponding to the ambient environmental situation for several hours to purge although no longer than 12 h after sampling. Organisms were then cleaned of their epibionts and debris, identified to the lowest possible taxonomic level, rinsed with distilled water and frozen at −80 °C until the time of analyses.

2.2.1. Isotopic analysis

In the laboratory samples were freeze-dried and acidified with fumes of concentrated HCl for 24 h to remove carbonates. Then they were dried again and homogenized. Since Arctic shelf benthos has been found to be very low in lipids across multiple major taxa

Table 1
Basic information on sampling locations in the present study.

Date	Station	Location	Depth (m)	Sediment type
1.08.2008	G	78° 52′ N	15	Mud
21.03.2009		12° 23′ E		
1.08.2008	A	78° 55′ N	15	Muddy sand
27.03.2009		11° 55′ E		

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(Graeve et al., 1997; Iken et al., 2010), lipids were not extracted from the samples in order to avoid the negative impact of this process on nitrogen isotopes. Stable isotopes analyses ($\delta^{13}C$ and $\delta^{15}N$) were done on an Elemental Analyzer Flash EA 1112 Series combined with an Isotopic Ratio Mass Spectrometer IRMS Delta V Advantage (Thermo Electron Corp., Germany). Isotopic ratios $\delta^{13}C$ and $\delta^{15}N$ were calculated using the laboratory working pure reference gases; CO_2 and N_2 calibrated against IAEA standards: CO-8 and USGS40 for $\delta^{13}C$ and N-1 and USGS40 for $\delta^{15}N$. Results of $\delta^{13}C$ and $\delta^{15}N$ are given in the conventional delta notation, i.e., versus PDB for $\delta^{13}C$ and versus air for $\delta^{15}N$ as parts per thousand (‰) according to the following equation:

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

where: X is ^{13}C or ^{15}N of the sample and R is a corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. All standards and some 3% of the total number of environmental samples were measured in replicate. The standard deviation for replicate samples ($n = 7$) was less than 0.15‰ and 0.20‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Particulate organic matter (POM) that can be used as a food web baseline consists of phytoplankton, bacteria and other particulate matter and is a strongly heterogeneous source with large spatial and temporal variations in its isotopic signature (Cabana and Rasmussen, 1996; Iken et al., 2010). Instead, in order to avoid heterogeneous source, taxa classified as primary consumers can be used as a food web baseline (Cabana and Rasmussen, 1996; Vander Zanden and Fetzer, 2007; Iken et al., 2010). A bivalve – *Serripes groenlandicus* – was selected to serve as a baseline organism in our study due to its wide distribution in both seasons and known suspension feeding behavior (Khim, 2001, 2002).

The trophic levels (TL) of consumers were determined for each season using the equation (primary consumer ratios were used as baseline):

$$\text{TL} = \left(\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{primary consumer}}\right)/3.4 + 2$$

In our study a $\delta^{15}N$ enrichment factor of 3.4‰ per TL was used since it was identified as the average trophic nitrogen fractionation for aquatic consumers (Vander Zanden and Rasmussen, 2001; Post, 2002; Iken et al., 2010).

Non-parametric Kruskal–Wallis (Dunn's post hoc test) was used to check for significant differences in isotopic signature between different feeding groups and seasons, as normality in data distribution could not be achieved.

3. Results

A total of 51 invertebrate taxa were analyzed for $\delta^{13}C$ and $\delta^{15}N$ signatures across both seasons. In winter 24 species were sampled for stable isotopes analyses while in summer 33 species were collected which covers about 40% of species diversity found in the studied area (Kędra et al., 2011; Table 2). The sediment $\delta^{15}N$ values at A (Ny-Ålesund) station were higher during winter (0.7 ± 1.41‰) than during summer (0.56‰). A similar situation was observed at the station G close to the Kongsbreen (−0.12 ± 0.58‰ in winter and −0.74‰ in summer). The sediment $\delta^{13}C$ values were similar for both stations (A: −24.09 ± 1.29‰ in winter and −24.00‰ in summer; G: in winter −22.70 ± 1.61‰ and in summer −23.31‰; Table 2). POM $\delta^{15}N$ values were higher at station G than at station A. In both cases winter values surpassed summer ones (G winter: 6.24 ± 0.04‰, summer: 0.5 ± 0.06‰; A winter: 2.43 ± 0.16‰, summer: −1.81 ± 0.58‰; Table 2). The POM $\delta^{13}C$ values were lower in summer (A: −30.5 ± 0.09‰; G: −29.48 ± 1.06‰) than in winter (A: −26.19 ± 1.55‰; G: −26.28 ± 0.72‰; Table 2).

Benthic fauna displayed a wide range of $\delta^{15}N$ signatures in both seasons (Table 2). In winter it ranged from 0.61‰ for the bivalve *Macoma calcarea* to 10.86‰, for the amphipod *Onisimus caricus* and 12.02‰, for the gastropod *Buccinum* sp. In summer, $\delta^{15}N$ values ranged from 0.65‰, for the cumacean *Eudorella emarginata* to 11.58‰ and 11.17‰, for the polychaetes *Maldane sarsi* and *Agalophamus malmgreni*, respectively. In both seasons four trophic levels (TL) were recognized, though only few species were classified at TL4 (gastropod *Buccinum* sp. in winter; amphipod *Anonyx nugax* and polychaete *M. sarsi* in summer; Fig. 2). The range of $\delta^{13}C$ values across the food web was wider in winter than in summer (Table 2) and it spanned from −22.12‰, for the bivalve *M. calcarea* to −16.78‰, for the polychaete *Nephtys ciliata*. Summer values ranged from −22.46‰, for the bivalve *Ciliatocardium ciliatum* to −18.63‰, for the polychaete *M. sarsi*.

Most of the deposit- and suspension feeding taxa occupied the second trophic level (TL) while carnivorous taxa occupied the third and fourth TL in both seasons (Fig. 2, Table 2). The $\delta^{15}N$ signatures of carnivores differed significantly from the values noted in the two other groups (Kruskal–Wallis test; $H(5, N = 125) = 62.86$, $p = 0.00$), but no differences were found between seasons for each group (Dunn's test; Fig. 3). Carnivores had the highest $\delta^{15}N$ values in winter and summer (10.26 ± 0.97‰ and 9.11 ± 1.57‰, respectively), followed by deposit feeders (7.85 ± 1.91‰ and 6.9 ± 2.69‰) and suspension feeders (4.69 ± 2.1‰ and 6.22 ± 1.57‰; Fig. 3). Some taxa (polychaetes: *Pholoe minuta*, *Maldane sarsi*, *Scoloplos armiger*/*Leitoscoloplos mammosus* and cirratulids, amphipod *Anonyx nugax* and bivalve *Macoma calcarea*) changed their $\delta^{15}N$ signature and TL between seasons (Table 2). There were no significant differences between the $\delta^{13}C$ signatures of particular trophic guilds except for the suspension feeders in summer versus deposit feeders in winter (Kruskal–Wallis test; $H(5, N = 125) = 16.62$; $p = 0.005$, Fig. 4). Deposit feeders had enriched $\delta^{13}C$ values in winter and summer (mean: −20.18 ± 1.24‰ and −20.47 ± 1.32‰, respectively), followed by carnivores (−20.75 ± 1.38‰ and −21.02 ± 1.35‰) and suspension feeders (−21.23 ± 1.48‰ and −22.07 ± 0.94‰; Fig. 4). No correlation was found between $\delta^{15}N$ and $\delta^{13}C$ for both seasons (Fig. 5).

4. Discussion

Despite the pronounced seasonality in the Arctic, we found little difference in benthic food-web structure between winter and summer which implies relative stability. In high Arctic fjords, seasonality is most evident in sea ice presence and light availability with a resulting periodicity of primary production and food accessibility (Dayton et al., 1994). Seasonal ice cover, lack of sunlight, low temperatures, changing salinity and limited organic carbon input make winter survival in shallow areas challenging for benthic fauna. Despite this, the abundance and biomass of shallow benthic fauna in Kongsfjorden were similar in both seasons with species numbers only slightly lower in winter than during the summer (Kędra et al., 2011).

4.1. Food sources

As phytoplankton and ice algae were not present during the winter in Kongsfjorden, no primary production was available to support the winter food web of benthic fauna (Kędra et al., 2011). Higher POM $\delta^{15}N$ values were noted in winter than in summer which may be attributed to the heterogeneous composition of POM with heterotrophic flagellates, ciliates, bacteria and faecal pellets in POM (Iken et al., 2001; Hirche et al., 2006). The difference may result from the fact that marine heterotrophs have higher nitrogen isotopic signatures than phytoplankton which only settles to the bottom in summer (Schulz and Zabel, 2006). Relatively high POM

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Table 2
Mean stable isotopes values (‰) and feeding types of sampled invertebrates and fish: s – suspension feeding, d – deposit feeding, c – carnivory; nr – number of replicates; TL – trophic level. * – not all representatives belong to the indicated feeding type.

Species/Taxon	Winter							Summer					
		nr	δ^{15} N	±SD	δ^{13} C	±SD	**TL SER**	nr	δ^{15} N	±SD	δ^{13} C	±SD	**TL SER**
POM Ny-Ålesund		2	2.43	0.16	−26.19	1.55		2	−1.81	0.58	−30.5	0.09	
POM Kongsbreen		2	6.24	0.04	−26.28	0.72		3	0.5	0.06	−29.48	1.06	
Sediment Ny-Ålesund		6	0.70	1.41	−24.09	1.29		1	0.56		−24.00		
Sediment Kongsbreen		6	−0.12	0.58	−22.70	1.61		1	−0.74		−23.31		
Settled Organic Matter		1	7.64		−24.34								
Macroalgae		2	2.82	0.13	−28.28	4.27	**1.5**						
Meiofauna													
Harpacticoida	s*							1	4.34		−19.12		**1.9**
Nematoda	c*							2	9.06	1.56	−21.34	1.12	**3.3**
Actinaria													
Cerianthus lloydi	d	1	7.33		−21.70		**2.8**						
Bryozoa													
Alcyonidium disciforme	s	1	3.67		−21.76		**1.8**						
Priapulida													
Priapulus caudatus	d	2	9.81	0.08	−19.02	0.42	**3.7**						
Nemertea													
Nemertea sp.1	c	3	8.76	0.13	−19.39	0.47	**3.3**						
Echinodermata													
Ophiura sarsi	c	1	9.04		−22.02		**3.3**						
Amphipoda													
Themisto libellula	c							1	7.58		−22.48		**2.8**
Ampelisca eschrichtii	s							1	6.79		−22.08		1
Monoculodes borealis	d							1	6.73		−19.45		**2.6**
Paroediceros lynceus	d							8	8.93	0.80	−20.39	0.68	**3.2**
Anonyx nugax	c	10	10.51	0.83	−21.58	0.70	**3.8**	2	11.10	0.52	−22.26	0.59	**4.0**
Anonyx sarsi	c	6	10.37	0.61	−20.62	0.35	**3.7**	1	9.65		−20.31		**3.9**
Onisimus caricus	c	10	10.86	0.56	−21.98	0.22	**3.9**	1	10.86		−22.14		**3.8**
Onisimus edwardsii	c	2	9.27	0.33	−20.94	0.14	**3.4**	2	8.84	1.83	−21.10	1.85	**3.2**
Orchomenella minuta	c	1	8.70		−19.46		**3.2**						
Caprella septentrionalis	d							1	5.45		−22.32		**2.2**
Halirages fulvocincta	d							1	5.52		−22.41		**2.2**
Haploops tubicola	s							2	6.57	0.42	−22.32	0.62	**2.4**
Melita formosa	d							3	5.94	0.73	−19.88	2.49	**2.3**
Melita quadrispinosa	d							1	5.45		−20.80		**2.2**
Pleustes panopla	d							1	6.00		−21.97		**2.4**
Unciola leucopis	d							1	6.65		−20.87		**2.5**
Cumacea													
Diastylis goodsiri	s							1	4.97		−21.36		**2.0**
Eudorella emarginata	d							1	0.65		−20.78		**0.8**
Decapoda													
Eualus gaimardi	c							2	8.36	0.02	−19.61	0.25	**3.0**
Pagurus pubescens	c							1	6.70		−19.97		**2.6**
Bivalvia													
Astarte montagui	s	1	6.76		−21.64		**2.7**						
Hiatella arctica	s	1	5.76		−21.25		**2.4**						
Yoldia hyperborea	s	1	6.45		−17.93		**2.6**						
Ciliatocardium ciliatum	s	1	5.07		−21.92		**2.2**	1	5.06		−22.46		**2.1**
Macoma calcarea	d	1	0.61		−22.12		**0.9**	1	4.94		−21.95		**2.0**
Axinopsida orbiculata	d	1	6.11		−20.46		**2.5**						
Serripes groenlandicus	s	1	4.52		−22.02		**2.0**	1	4.80		−22.33		**2.0**
Gastropoda													
Gastropoda sp.1								1	8.31		−22.33		**3.0**
Buccinuum sp.	c	2	12.02	0.24	−18.1	0.36	**4.2**						
Polychaeta													
Agalophamus malmgreni	c	2	9.04	0.26	−19.43	0.66	**3.3**	1	11.17		−19.69		**3.9**
Harmothoe cf. *vridis*	c							1	7.22		−19.93		**2.7**
Lumbrineris mixochaeta	c	2	9.78	0.64	−20.06	0.10	**3.5**	2	9.95	0.01	−20.77	1.69	**3.5**
Nephtys ciliata	c	1	10.84		−16.78		**3.9**						
Pholoe assimilis	c	2	9.45	0.68	−19.15	0.60	**3.5**	1	7.46		−20.74		**2.8**
Phyllodoce groenlandica	c							1	8.50		−19.14		**3.1**
Maldane sarsi	d	1	10.9		−18.79		**3.9**	1	11.58		−18.63		**4.0**
Terebellides stroemi	d	2	8.17	0.59	−19.20	0.10	**3.1**						
Apistobranchus tullbergi	d	3	7.43	0.44	−20.34	0.20	**2.9**						
Cirratulidae	d	3	7.58	0.39	−20.48	1.00	**2.9**	2	3.85	4.32	−21.43	1.14	**1.7**
Cossura longocirrata	d	1	6.62		−20.98		**2.6**						
Eteone sp.	d	2	9.37	1.01	−20.60	0.36	**3.4**						
Lysippe labiata	d	2	7.72	0.08	−19.35	0.19	**2.9**						
Pectinaria (Cistenides) hyperborea	d	1	5.97		−20.06		**2.4**						
Scoloplos armiger/ *Leitoscoloplos mammosus*	d	2	6.28	0.83	−20.36	2.01	**2.5**	1	9.39		−18.95		**3.4**

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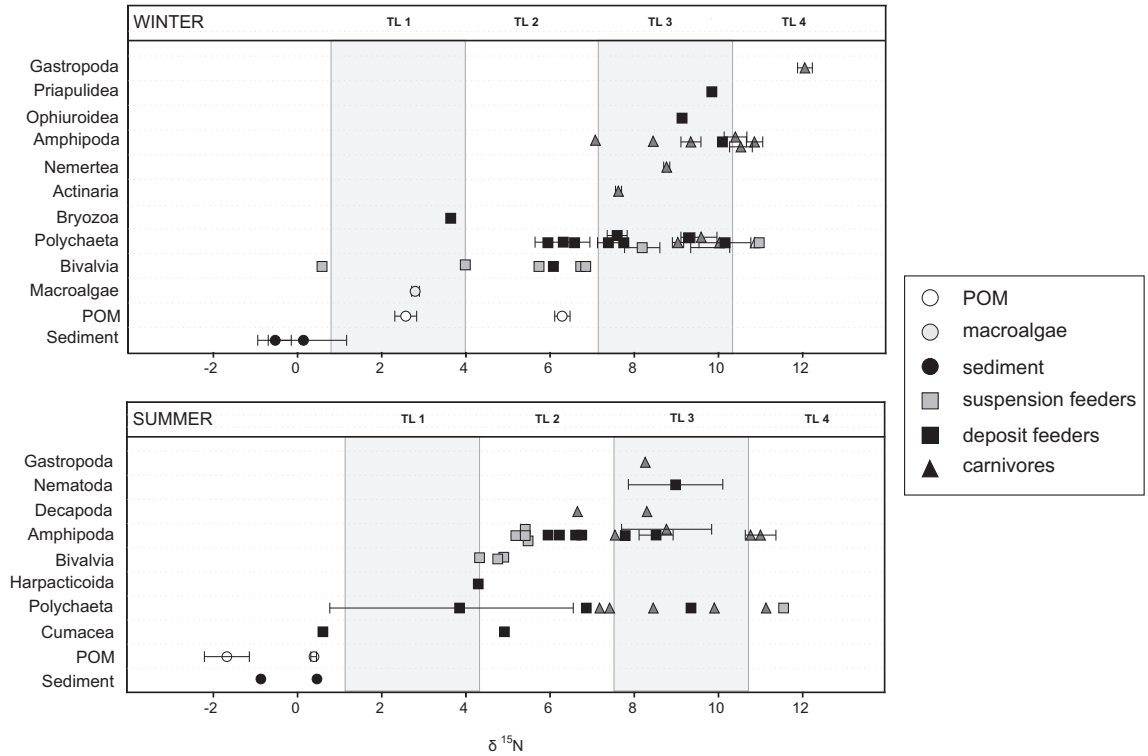

Fig. 2. Mean $\delta^{15}N$ signatures of sediment, POM and taxonomic groups collected in Kongsfjorden. Trophic levels identified are relative to the $\delta^{15}N$ signature of *Serripes groenlandicus*.

$\delta^{15}N$ signatures were noted at the G station, which can be attributed to higher rates of heterotrophic organisms and low diatom contributions in the glacial bay (Piwosz et al., 2009). Values of $\delta^{15}N$ for POM obtained in this study were generally lower than values reported from other Arctic locations, including the deeper parts of Kongsfjorden (Renaud et al., 2011) which may be related to the constant freshwater and terrestrial load observed in shallow Kongsfjorden areas. Depleted $\delta^{15}N$ POM signals were reported from the southeastern Chukchi Sea and reflected mixing of terrestrial/freshwater sources from the Yukon River and marine-derived ^{15}N enriched materials (Iken et al., 2010). Low $\delta^{15}N$ values were also found in the Antarctic (Wada et al., 1987) and Mediterranean (Darnaude et al., 2004; Carlier et al., 2007a,b), in lagoons and close to river water discharge where terrestrial input was obviously significant.

Very few suspension feeders feeding on the fresh POM were reported in this study. In high latitudes, the input of food to the benthic food web is pulsed and spatially variable (Clarke, 1988). As a result, many benthic invertebrates exhibit a high degree of omnivory, relying on multiple primary food sources including phytoplankton, settling sea ice algae, in situ production of benthic diatoms, detritus and advected organic material, as well terrestrial

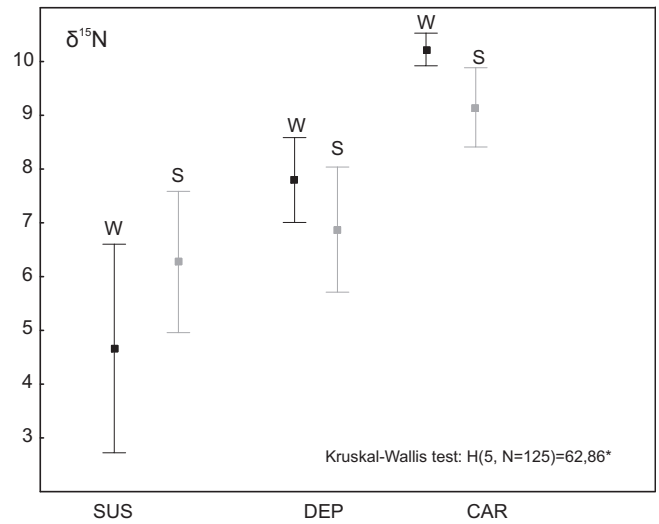

Fig. 3. Mean ± 0.95 confidence intervals of $\delta^{15}N$ signatures for different feeding guilds: SUS – suspension feeders, DEP – deposit feeders, CAR– carnivores, W – winter, S – summer.

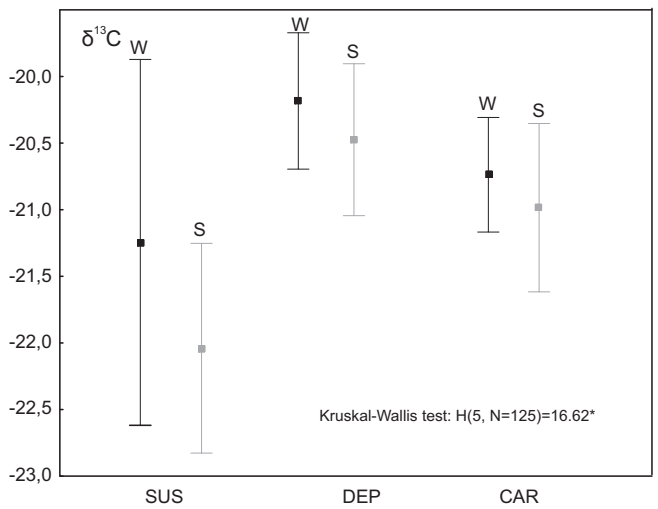

Fig. 4. Mean ± 0.95 confidence intervals of $\delta^{13}C$ signatures for different feeding guilds: SUS – suspension feeders, DEP – deposit feeders, CAR– carnivores, W – winter, S – summer.

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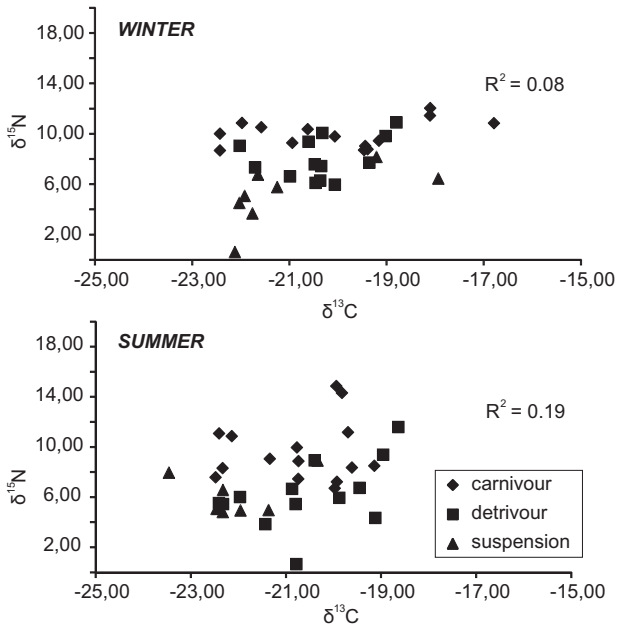

Fig. 5. $\delta^{13}C$ versus $\delta^{15}N$ for taxa collected in Kongsfjorden in winter and summer. Each point represents one taxon, and a mean is represented where multiple replicates were analyzed.

input (Dayton, 1990; Arntz et al., 1994; Norkko et al., 2007). Fresh and reworked settled organic matter, microphytobenthos and organic matter of terrestrial origin are probably the main carbon sources contributing to the benthic food web structure in the present study. In shallow fjord areas terrestrial input may be an important source of carbon, especially during spring/summer when river runoff is the strongest. Constant freshwater and terrestrial load to the shallow sublittoral in Kongsfjorden coming via small rivers, melting snow and ice from the land and meltwaters from the glacier may cause the lower $\delta^{13}C$ POM values observed during summer in Kongsfjorden. Low C/N ratio in surface sediments noted at A station in summer (4.8, Kędra et al., 2011) suggest deposition of high quality, fresh marine phytodetritus, while high winter value of this ratio (>10, Kędra et al., 2011) may indicate presence of either low quality, older, and more refractory detrital material or terrestrial deposits or both (Grebmeier et al., 1988). High C/N ratio observed at G station in summer (11.5, Kędra et al., 2011) probably results from massive sedimentation due to glacial runoff. Therefore, apart from the marine primary production, terrestrial carbon contributing to the shallow areas of fjord seems to have some importance for this shallow benthic food web.

Due to the high cellulose content most marine species have limited ability to digest and assimilate terrestrial organic matter (Schell, 1983). However, some marine organisms may consume considerable amounts of terrestrial organic material and an increase in food web chain length was observed in areas influenced by freshwater and increased terrestrial input (e.g. Mackenzie River; Dunton et al., 1989, 2006). Iken et al. (2010) and Feder et al. (2011) found that at least some terrestrial material was used by benthic consumers in the southeastern Chukchi Sea. In our study, deposit feeding polychaetes (*Scoloplos armiger*/*Leitoscoloplos mammosus*) were depleted in ^{13}C in winter, suggesting some use of terrestrial material deposited in the sediment. Deposit feeding cirratulids on the other hand were depleted in ^{13}C in summer. Since primary deposit feeding cirratulid species can also facultatively suspension feed (Rouse and Pleijel, 2001), this may suggest that they use some fresh production in the summer. The predatory polychaete, *Pholoe assimilis*, showed a similar trend. These results are confirmed with low $\delta^{15}N$ signatures, which may also become lower with the use of terrestrial material or fresh phytodetritus. Renaud et al. (2011) reported little seasonal (spring–summer–autumn) difference in the food-web structure of soft-sediment benthos within Kongsfjorden and on the shelf outside the fjord. However, both locations investigated by Renaud et al. (2011) were deeper than 200 m, too far from the shore to expect any organic input from the vegetated terrestrial habitats, where in situ primary production is probably the major source of organic matter to bottom sediments. Limited information on the POM isotopic signature in that study prevents further comparisons.

4.2. Food web structure

Most marine benthic animals feed on any available food and due to the high level of omnivory they do not appear to be restricted to fixed positions in the food web (Isaacs, 1973). Physical environmental conditions and primary production strongly affect trophic relationships and food web structure, especially in coastal and shallow communities (Barry and Dayton, 1991). One of the most important characteristics of the Arctic environment is its extreme seasonality with highly compressed primary production seasons resulting in supplies of food of variable quality and isotopic signatures throughout the year (Søreide et al., 2008; Tamelander et al., 2008, 2009). Our study identified four trophic levels (TL) in the benthic realm (4.2 TL in winter and 4.0 TL in summer; only benthic animals, without fish, mammals and birds). This is similar to other Arctic locations (e.g. Hobson et al., 1995, 2002; Iken et al., 2005, 2010; Feder et al., 2011) and to the results obtained by Renaud et al. (2011) for the deeper parts of Kongsfjorden (4.4 TL, including fish but without mammals and birds). It shows that Arctic marine food chains have similar length to the ones from lower latitudes (Vander Zanden and Fetzer, 2007). In our study, neither food web length nor structure differed noticeably between seasons and most consumers' stable isotopes ratios (especially $\delta^{13}C$) did not vary significantly between seasons. Similar lack of seasonal changes (spring–summer–autumn) in benthic food webs was observed by Renaud et al. (2011) in deep areas of Kongsfjorden and outer shelf; however, no observations were made for the winter. The strong seasonal stability can be related to the early (May–June) and late (September) phytoplankton blooms near the mouth of Kongsfjorden leading to multiple pulses of fresh organic material production during the year and therefore no shortage of food throughout the most of the year (Renaud et al., 2011). Further, it may suggest the dominance of mixed diets of consumers and high adjustability of the shallow benthic communities to different food sources. Marine food webs are often characterized by trophic continua rather than distinct trophic steps (Post and Takimoto, 2007; Iken et al., 2010) due to high degree of omnivory displayed by dominating trophic guilds.

Shallow areas are relatively rich in detritus and the remains of benthic animals resulting from variety of disturbance including wave action, changes in salinity and temperature and ice scouring throughout the whole year (Slattery and Oliver, 1986; Barnes, 1999; Smale and Barnes, 2008). Detritus can influence trophic conditions, and increase food-web stability and persistence (Moore et al., 2004). The ability to utilize deposited material by deposit feeders and resuspended material by suspension feeders makes the survival during long periods without fresh phytoplankton supply in polar areas possible (Gili et al., 2001; Mincks et al., 2005, 2008). The survival of benthic deposit and suspension feeders during the winter results in a food source available to predators and scavengers, resulting in little change in overall food web structure through the year.

Benthic species cover the full spectrum of trophic levels due to their diverse feeding strategies and at least some consumers are

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able to change their diet temporally, which may lead to seasonal variability in food-web structure and thus changes in diet choice would result in shorter food chain length (Kondoh and Ninomiya, 2009). However, in our study the food chain length did not change (4.2 in winter and 4.0 in summer) and only few species changed their trophic level between seasons. Moreover, according to the assumption of 3.4 difference between TL, only cirriatulids (difference between winter and summer of $\delta^{15}N = 3.73$) changed the TL between the seasons. Also, in the case of benthic organisms changes of $\delta^{15}N$, smaller than 3‰, may result from e.g. local nitrogen dynamics rather than indicate changes in trophic level (Nordström et al., 2010).

Suspension feeding organisms receive particles directly from sedimentation processes from the water column or, more often in shallow waters, through resuspension. Most benthic suspension feeders were placed at TL 1 and 2 and their $\delta^{13}C$ signature indicated utilization of phytoplankton as a food source. It is likely that this is due to their direct connection to the settling phytodetritus. Trophic fractioning may range between 2‰ and 5‰ for any single trophic transfer and, therefore, the use of 3.4‰ may be a valid estimation only when averaged over multiple trophic pathways (Adams and Sterner, 2000; Post, 2002). It may also be an explanation for the low enrichment of some consumers (Bergmann et al., 2009).

Most of the low TL species maintained their status in the food web through the seasons, with the exception of *Macoma calcarea*, which increased its TL from 0.9 in winter to 2.0 in summer. Its low TL and low $\delta^{13}C$ values may suggest that it utilizes fresh phytoplankton during the summer or feeds on fresh phytodetritus while in winter it may suffer from a food shortage. It is known that the representatives of the genus *Macoma*, although mainly deposit-feeders, can utilize suspension feeding in response to the availability of suspended organic matter relative to that of sedimentary organic matter (Rassmussen, 1973; Levinton, 1991). Another deposit feeder, the cumacean *Eudorella emarginata*, had a surprisingly low $\delta^{15}N$ with TL 0.8. Representatives of this genus are believed to be deposit feeders that consume benthic diatoms and benthic organic matter (Błażewicz-Paszkowycz and Ligowski, 2002). Cumaceans are often reported to have unexpectedly low $\delta^{15}N$ values (Iken et al., 2005; Bergmann et al., 2009) suggesting use of very fresh, and thus isotopically light, phytoplankton and/or deposited material of POM. Another explanation was provided by Søreide and Nygård (2012) who showed that in case of species with high exoskeleton/soft tissue ratios there is a risk for underestimating the trophic levels when stable nitrogen isotope analysis is performed on whole individuals.

Deposit feeders occupied mainly the second and third TL with higher $\delta^{15}N$ signatures and higher $\delta^{13}C$ as they generally utilize reworked benthic organic matter in the sediment which is enriched in $\delta^{15}N$ (Lopez and Levinton, 1987). The role of detritus in the structure and function of food webs is of high importance, since most of the primary production in high latitudes is returned to the ecosystem as detritus and incorporated through deposit feeders (Hairston and Hairston, 1993; Polis and Strong, 1996), thus increasing system stability and persistence (Moore et al., 2004). Similarly to our results, Norkko et al. (2007), in the Antarctic, observed that detritus may provide higher trophic levels with a more constant food supply, and thus dampen seasonality. Deposit feeding or omnivore fauna capable of flexible food utilization is favored in high latitudes where food sources may be temporally and spatially constrained and unpredictable.

Deposit feeders may have a widely spread selectivity for certain particles. Species with lighter isotopic signature such as actinians, some polychaetes and bivalves are likely to be selective deposit feeders that feed on freshly deposited phytoplankton particles on the sediment surface. These recently settled particles would not have been reworked in the sediment by biological processes and consequently are lighter isotopically. The actinian, *Cerianthus lloydi*, is generally considered to predominantly feed on small pelagic prey (Eleftheriou and Basford, 1983). However, some authors indicate that it may also capture and phagocitize fine deposited particles and bacteria as well as plant remains. Chintiroglou and Koukouras (1992) suggest that there may be a seasonal change in the relative importance of these two feeding methods.

Cirratulids are opportunistic, unselective surface-feeding detrivorous polychaetes that decreased their TL level from 2.9 in winter to 1.7 in summer. Their lower carbon signature presumably relates to their preference towards fresh phytoplankton when available. In contrast, most species that occupied the third TL were nonselective surface and subsurface deposit feeders. The polychaete, *Maldane sarsi*, had relatively high nitrogen and carbon signatures and occupied 3.9 TL in winter and 4.0 in summer. Their $\delta^{13}C$ signature remained similar though the seasons (−18.79 in winter vs. −18.63 in summer) indicating that they feed on a similar type of highly reworked detritus. Most maldanids are head-down, conveyor-belt deposit feeders, and transport particles from various feeding depths to the sediment surface through their gut (Fauchald and Jumars, 1979). They also transport freshly deposited surface particles to a feeding cavity at depth, where they 'hoe' surface sediments using their posterior end (Levin et al., 1997; Dufour et al., 2008). Subsurface deposit feeding *Scoloplos armiger*/*Leitoscoloplos mammosus* increased its TL from 2.5 in winter to 3.4 in summer, along with carbon isotopic signature, which suggest the use of reworked organic matter during summer. *Scoloplos armiger* burrows in the upper 10–15 cm of the sediment and crawls through the top layer, but does not roam on the sediment surface. It shows a distinct and identifiable food preference for organic detritus (Hartmann-Schröder, 1996), however, it probably relies mainly on organic matter already reworked by unselective surface deposit-feeders. Material available to subsurface feeders is enriched in carbon as a result of the bioturbation resulting from their feeding activities which also brings surface carbon to lower sediment depths (Clough et al., 1997). Similar seasonal patterns are found in other Arctic locations with selective surface deposit-feeding species occupying lower TL than non-selective subsurface feeders (Iken et al., 2005).

Carnivores occupied the third and fourth TL with some exceptions at the upper range of the second TL. Bergmann et al. (2009) reported a wide range of predators and scavengers with $\delta^{15}N$ values that suggested a broad trophic niche due to opportunistic dietary habits. All scavenger amphipods occupied TL 3 up to 4. Predator polychaetes kept their predatory behavior in both seasons. However, *Pholoe assimilis*, a mobile predatory polychaete (Fauchald and Jumars, 1979), decreased its TL from 3.5 in winter to 2.8 in summer, which may either suggest a change in diet towards omnivory or feeding on isotopically lighter prey.

5. Conclusions

This study distinguished four trophic levels in summer and winter and stable isotopes analyses applied to winter/summer data point to strong resilience of benthic fauna to changing seasonal conditions. By using stable isotope analyses to winter/summer benthic food webs we provide an insight into understanding and interpreting overwintering strategies of different polar taxa. The shallow-water benthos depends mainly on reworked organic material and, according to our study, is most likely supported to a limited extent by terrestrial input. We believe that, although climate change is occurring in polar regions, it may not have immediate and strong negative effect on shallow benthic communities due to the complex feeding habits of benthic species and their ability to withstand significant disturbance.

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