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PRIMARY RESEARCH PAPER

When season does not matter: summer and winter trophic ecology of Arctic amphipods

Joanna Legeżyńska · Monika Kędra · Wojciech Walkusz

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Abstract Polar marine ecosystems' functioning is known to be strongly affected by the seasonality of water column production. However, a response of benthic organisms may range from close coupling to total decoupling from seasonal variability of environmental processes, depending on a feeding strategy. In this study, we used a multi-method approach (gut content, lipid and stable isotope analyses) to examine trophic ecology and major food sources of a large set of Arctic sub-littoral amphipods, and to evaluate whether their feeding strategies undergo seasonal changes. The wide range of δ^{15}N values (5.45-12.43‰) indicates that amphipods form a trophic continuum from primary herbivores to carnivores/scavengers. Three main feeding modes, namely scavenging/predatory, deposit-feeding/predatory and phytodetrivory, were distinguished based on the multivariate analysis of whole fatty acid profiles. Total lipid content was low in all species and included primarily short-term energy reserves of triacylglycerols. In general, amphipods feeding habits appeared to be independent of the seasonal phytodetritial pulses. Low reliance on lipid reserves and lack of major changes in the trophic strategies over time suggest that these crustaceans feed continuously, taking advantage of a variety of food sources that are available year-round in shallow polar waters.

Keywords Amphipoda · Arctic · Trophic ecology · Seasonality · Fatty acids · Stable isotopes

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J. Legeżyńska (✉) · M. Kędra · W. Walkusz
Institute of Oceanology, Polish Academy of Sciences, Powstańców Warszawy 55, 81-712 Sopot, Poland
e-mail: zosia@iopan.gda.pl

W. Walkusz
Department of Fisheries and Oceans, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

Introduction

Understanding the dietary habits of benthic invertebrates is pivotal to studies of food webs and energy flows in marine ecosystems, but basic information on the feeding ecology of most taxa are lacking. Benthic amphipods are important both numerically and functionally in Arctic ecosystems and can create extremely productive communities locally (Highsmith & Coyle, 1990). Despite a vast literature on benthic amphipod communities (e.g., Just, 1970, 1980; Węsławski, 1990; Tzvetkova, 1995; Bryazgin, 1997; Brandt, 1997; Stransky & Svavarsson, 2010), surprisingly little detailed information exists on the ecofunctional role of these crustaceans in Arctic food webs. Amphipods are an important link between primary and secondary production and higher trophic levels such as fish, birds and mammals (Bradstreet & Cross, 1982; Oliver & Slattery, 1985; Grebmeier & Harrison, 1992; Lønne & Gabrielsen, 1992). As consumers, benthic amphipods

are known to have versatile feeding repertoires (Schram, 1986), and many species display habitat, ontogenetic or seasonal changes in feeding preferences, which further contributes to the complexity of trophic strategies (Auel et al., 2002; Richoux et al., 2005; Legeżyńska, 2008). Indeed, most species can exhibit feeding opportunism. Versatility and the transitory nature of dominant feeding modes in amphipods can complicate the understanding of their ecofunctional roles (MacNeil et al., 1997).

The actual feeding behaviour of most Arctic amphipods species remains poorly understood. Several studies have focused on the diet of sympagic amphipods, which are the main macrofaunal taxa found on the under-side of sea ice (Bradstreet & Cross, 1982; Scott et al., 1999; Poltermann, 2001; Tamelander et al., 2006; Werner, 2006). Arctic lysianassoids are another group that has been relatively well studied in terms of its trophic status. They are efficient scavengers in both deep-sea (Premke et al., 2006) and shallow sub-littoral waters (Oliver & Slattery, 1985; Sainte-Marie, 1986; Legeżyńska et al., 2000). Whereas some species appear to be obligate necrophages, the majority, and particularly shallow-water taxa, have complex feeding habits (Sainte-Marie, 1986; Legeżyńska, 2008). Additionally, seasonal changes in feeding modes in response to environmental conditions have been identified in several species (Carey & Boudrias, 1987; Werner et al., 2004).

Traditionally, amphipod feeding preferences have been assessed using in situ and laboratory observations (Busdosh et al., 1982; Klages & Gutt, 1990; Dauby et al., 2001), feeding experiments (Sainte-Marie, 1987), gut-content analysis (Sainte-Marie, 1986; Carey & Boudrias, 1987; Dauby et al., 2001; Poltermann, 2001; Legeżyńska, 2008) and studies of the functional morphology of feeding appendages (Sainte-Marie, 1984; Sainte-Marie & Lamarche, 1985; Steele & Steele, 1993; Arndt et al., 2005). Knowledge of amphipod feeding ecology has recently expanded thanks to the use of biomarkers such as lipids and fatty acids (FAs) (Graeve et al., 1997, 2001; Scott et al., 1999, 2001) and stable isotopes (Nyssen et al., 2002). The utility of these methods lies in the fact that, in contrast to gut content examination, which provides insight into short-term preferences, they provide dietary information integrated over periods of weeks to months.

The total lipid content, composition and relative proportions of the stored lipids in the organisms studied mirror their adaptive feeding strategies related to patterns of food availability (Percy, 1979; Hagen & Auel, 2001). FAs, which are major constituents of most lipids, are particularly useful trophic markers. They are primarily synthesized at low trophic levels, with certain FAs being characteristic of specific groups of microorganisms. These marker FAs can be deposited largely unaltered in consumer tissues thus providing evidence of feeding preferences and major food sources (Stübing & Hagen, 2003). While they are generally reliable in assessing the diets of primary consumers, at higher trophic levels they become relatively ubiquitous, and are thus less useful to evaluate dietary connections in higher consumers (Iverson, 2009). Moreover, considerable overlap in the FA composition of major groups of producers can sometimes hamper the interpretation of results (Iverson, 2009). Some FAs can also be synthesized by animals (Scott et al., 2002; Budge et al., 2007; Drazen et al., 2009; Iverson, 2009). Oleic acid, 18:1(n-9), an end product of FA biosynthesis, has been used as a general indicator of carnivorous feeding (e.g., Graeve et al., 1997; Nelson et al., 2001; Nyssen et al., 2005).

Stable isotope ratios in the proteins of consumers predictably reflect those in their diets. The nitrogen ratio (δ^{15}N) has been used to evaluate the relative trophic position of organisms in food web structures because there is a stepwise enrichment of δ^{15}N by 3–4‰ between subsequent trophic levels. On the other hand, the ratio of carbon isotopes (δ^{13}C) changes little as carbon moves through the food web (0.5–1‰ per trophic step), and it is widely used to determine different carbon sources (e.g., Hobson & Welch, 1992; Iken et al., 2001, 2010; Søreide et al., 2006b; Mincks et al., 2008; Bergmann et al., 2009). Inference from stable isotopes values, however, is not straightforward since they are influenced by many factors such as food source, species, tissue type and composition, different physiological pathways, nutritional or hydric stress (Vanderklift & Ponsard, 2003). Furthermore, isotopic enrichment and the actual period across which diet is integrated also depend on the turnover rate of the sampled tissue (Bodin et al., 2007; Kaufman et al., 2008). One of the assumptions made in interpreting trophic connections in food webs is that the consumers' isotopic values are in equilibrium with their diets,

however, few estimates are available for turnover times of isotopes signatures in marine organisms (Schmidt et al., 2003; Bodin et al., 2007; Kaufman et al., 2008). Despite these problems, stable isotope analysis has been applied successfully for determining food web structures in the Arctic (e.g., Hobson & Welch, 1992; Hobson et al., 1995, 2002; Iken et al., 2001, 2010; Søreide et al., 2006b; Tamelander et al., 2006; Bergmann et al., 2009; Feder et al., 2011).

Neither lipid nor stable isotope analyses can precisely describe complex trophic interactions when used alone. Therefore, combined approaches are recommended to attain better accuracy and higher trophic resolution in amphipod studies (MacNeil et al., 1997; Dauby et al., 2001; Graeve et al., 2001; Nyssen et al., 2005).

The main aim of the current study was to investigate the feeding ecology of benthic amphipods commonly noted in Svalbard fjords (Węsławski, 1990). We provide unique information on the feeding strategies of a large species set that includes taxa characteristic of different habitats and depth zones. To obtain the highest possible accuracy when evaluating species feeding modes, lipid and stable isotope signatures were compared with the results of gut content examinations. Further, information is provided on the winter feeding of several shallow-water Amphipoda species; this is crucial for the understanding of their overwintering strategies. To the best of the authors' knowledge, this study is the first to employ combined methods (stable isotope, lipid and gut content analyses) to describe for winter and summer seasons the feeding strategies of the most important benthic amphipod species occurring in the Arctic.

Materials and methods

Sampling

Amphipods were collected in four glacial fjords of Spitsbergen, namely Hornsund, Kongsfjorden, Magdalenefjorden, and Smereenburgfjorden (76°N–80°N; Fig. 1). Scavenging lysianassoid amphipods (genera *Anonyx* and *Onisimus*) were collected in baited traps in winter (March 2009) and summer (July/August 2008 and 2009) in Kongsfjorden. Traps with unavailable bait were deployed at two stations located in the Kongsbreen glacial bay and close to Ny-Ålesund at depths of 5 and 15 m. Other taxa were collected during summer cruises of the r/v *Oceania* to Spitsbergen fjords in 2008 and 2009 (Table 1). During the cruises, a variety of gears, including Van Veen grabs, epibenthic sledges, and small rectangular dredges, were deployed to collect samples at depths between 2 and 280 m in Hornsund, Kongsfjorden, Magdalenefjorden and Smeerenburgfjorden. Immediately after sampling, the amphipods were sorted by species and measured. Specimens for gut content analysis were immediately preserved in a 4% formaldehyde solution. Individuals for lipid and isotope analyses were kept in filtered seawater for several hours to allow gut clearance and then deep frozen and stored at −80°C until processing. Additional samples were collected in both seasons in Kongsfjorden to assess the isotopic composition (δ^{13}C and δ^{15}N) of potential food sources. Samples of suspended particulate organic matter (POM), representing the pelagic production used by suspension feeders, 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. Zooplankton species (*Calanus finmarchicus* and *C. glacialis*, 15–40 individuals per sample) were collected with a zooplankton net (WP2 net; 180 μm mesh) from depths of 35 m to the surface. Surface sediment samples were obtained using a Petit Ponar grab (0.045 m^2 sampling area). Detritus and macroalgal fragments were sorted from grab and dredge samples.

Gut content examination

Gut content analysis was performed on 16 amphipod species, 12 of which were collected in summer and four in winter. The digestive tracts of formaldehyde-fixed specimens were excised and gut fullness was estimated (0–100%). Food items inside the guts were examined microscopically (Nikon SMZ 1500, Nikon TE 300), identified as precisely as possible, measured and classified into several broad categories of phytoplankton, macroalgae, Crustacea, Polychaeta, unidentifiable animal tissue, Foraminifera, Nematoda and others (Nemertea, Oligochaeta, Sipuncula, Halacarida and Mollusca). The frequency of occurrence of each food item was calculated for each species. The proportion of each food item in individual guts was determined visually using a counting chamber. Afterwards, the relative volumetric contributions of each dietary category to the diet of a given species were

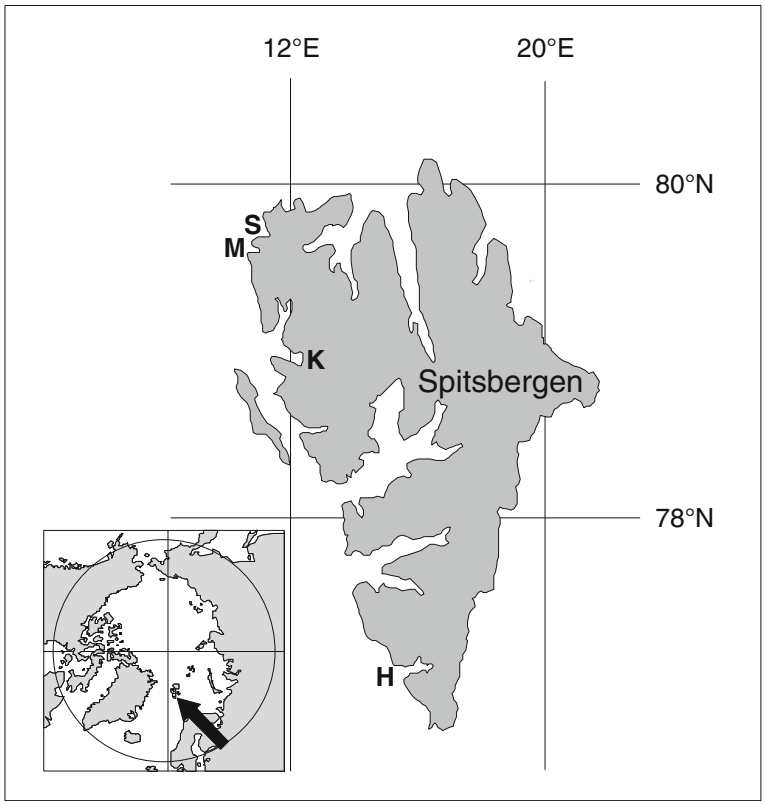

Fig. 1 Map of the sampling area; *H* Hornsund, *K* Kongsfjorden, *M* Magdalenefjorden, *S* Smeerenburgfjorden

expressed using the adopted points method, which takes into account gut fullness (Dauby et al., 2001). Additionally, in most species, the mouthparts of single specimens were dissected for morphological comparisons.

Lipid analysis

Lipid analysis was performed on 18 species, but lipid class composition was determined only for 12 species collected in Kongsfjorden. Individuals of the same species/size-class were pooled as single samples according to size. Total lipids were extracted from samples of known wet/dry weight with chloroform:methanol (2:1 v/v) according to Folch et al. (1957). After filtration and water phase removal with 0.88% KCl, the extracts were dried under nitrogen and weighed to obtain the total lipid mass. The samples were then divided and treated separately for total lipid and FA analyses. The lipid class composition of total lipid was determined by quantitative thin-layer chromatography (HPLC-ELSD). The remaining extract was spiked with a known amount of the FA 21:0 as an internal standard and methylated in methanol containing 1% sulphuric acid with toluene at 50°C overnight. The reaction products were cleaned with $KHCO_3$, the organic phase was transferred using hexane:ether and purified on silica columns. FA composition was analysed with gas chromatography (GC-FID). All percentages of FAs are presented in this text as weight %. Reference material and blind sample measurements were performed for every 6–8 samples.

Isotope analysis

Values of $\delta^{13}C$ and $\delta^{15}N$ signatures were determined in 19 amphipod species, 2 *Calanus* species, 9 samples of POM, 14 samples of sediment, 8 samples of macroalgae and one of detritus. Individual amphipods and *Calanus* spp. of the same species/size-class were pooled as single samples according to size.

Lipids were not removed. Some authors suggest extracting lipids from samples prior to stable isotope analysis (e.g., Hobson & Welch, 1992; Hobson et al., 1995, 2002; Tamelander et al., 2006) because lipids are depleted in ^{13}C relative to other major tissue

Table 1 Species list, habitat preferences and methods applied in the current study

Taxon\season	Ge	L N_s (N_i)	Lc N_s (N_i)	FA N_s (N_i)	SI N_s (N_i)	Site	*D* (m)	Habitat	Abbrev.	Fam.
Winter										
Anonyx nugax	14	10 (39)	4 (39)	4 (39)	10 (28)	K	5–15	m, s	AN	LY
Anonyx sarsi	14	7 (38)	3 (38)	3 (38)	6 (38)	K	5	m, s, g, a	AS	LY
Arrhis phyllonyx					1 (1)	K	15	m, s	AP	OD
Onisimus caricus	18	3 (31)	3 (31)	3 (31)	10 (27)	K	5–15	m, s	OC	LY
Onisimus edwardsii	5	2 (20)	2 (20)	2 (20)	2 (20)	K	5	m, s, st, g, a	OE	LY
Orchomenella minuta					1 (14)	K	5	m, s, g	OM	LY
Paroediceros lynceus		1 (3)		1 (3)		K	5	m, s, st, g, a	PL	OD
Pontoporeia femorata		1 (2)	1 (2)	1 (2)		K	25	m, s, g	PF	PO
Summer										
Ampelisca eschrichtii	9	2 (4)	1 (2)	2 (4)	1 (2)	H, K, S	77–280	m	AE	AM
Anonyx nugax		2 (8)	1 (8)	2 (8)	2 (3)	K	15	m, s	AN	LY
Anonyx sarsi		1 (14)		1 (14)	1 (1)	H	10	m, s, g, a	AS	LY
Arrhis phyllonyx	11	1 (5)		1 (5)	1 (3)	H	64–240	m	AP	OD
Caprella septentrionalis	5	1 (4)		1 (4)	1 (5)	H	10	m, s, st, g, a	CS	CP
Gammarus setosus	5				3 (4)	H	2	m, s, st, g, a	GS	GA
Halirages fulvocincta					1 (5)	K	15	m, s, st, a	HF	CA
Haploops tubicola	10	1 (7)	1 (7)	1 (7)	2 (10)	H, K	100–280	m, st	HT	AM
Lepidepecreum umbo	5	2 (3)	1 (1)	2 (3)		H, K	100–240	m, s, st, g	LU	LY
Melita formosa	6	1 (13)	1 (13)	1 (13)	3 (13)	H, K	60–77	m	MF	ME
Melita quadrispinosa	6				1 (5)	H, K	79–270	m, s, st	MQ	ME
Monoculodes borealis					1 (13)	K	20	m, s, st	MB	OD
Onisimus caricus		1 (1)	1 (1)	1 (1)	1 (7)	K	15	m, s	OC	LY
Onisimus edwardsii		2 (33)	1 (10)	2 (33)	3 (25)	H, K	7–10	m, s, st, g, a	OE	LY
Paroediceros lynceus	11	2 (18)		2 (18)	8 (34)	H, K, M	7–80	m, s, st, g, a	PL	OD
Pleustes panoplus					1 (3)	K	15	m, s, st, g, a	PP	PE
Pontoporeia femorata		1 (3)		1 (3)		M	15	m, s, g	PF	PO
Rhachotropis aculeata		1 (2)		1 (2)	2 (2)	S	180	m, s, st	RA	EU
Stegocephalus inflatus	8	2 (3)	1 (1)	2 (3)	1 (1)	H, K	180–260	m, s	SI	ST
Unciola leucopis	6	2 (3)	1 (1)	2 (3)	1 (1)	H, K	120–260	m, s	UL	UN
Weyprechtia pinguis	5	1 (7)		1 (7)		K, M	10	m, s, st, g, a	WP	CA

Ge gut examination, *L* lipid content, *Lc* lipid classes, *FA* fatty acids, *SI* stable isotopes; N_s number of samples, N_i number of individuals. Site: *K* Kongsfjorden, *H* Hornsund, *M* Magdalenefjorden, *S* Smeerenburgfjorden; *D* depth (m); Habitat: *m* mud, *s* sand, *st* stones, *g* gravel, *a* algae; *Abbrev.* species abbreviations, *Fam.* family abbreviations; *AM* Ampeliscidae, *CA* Calliopiidae, *CP* Caprellidae, *EU* Eusiridae, *GA* Gammaridae, *LY* (Superfamily) Lysianassoidea, *ME* Melitidae, *OD* Oedicerotidae, *PE* Pleustidae, *PO* Pontoporeiidae, *ST* Stegocephalidae, *UN* Unciolidae

constituents and the fact that δ^{13}C values are strongly influenced by variations in body lipid content complicates interpretation of dietary sources of carbon. However, previous investigations documented that lipids can cause some error mostly in lipid-rich pelagic organisms (Søreide et al., 2006a), while in Arctic benthic invertebrates, which are generally low in lipids (Graeve et al., 1997), δ^{13}C values tend to be very similar in untreated and defatted samples (Iken et al., 2010). In addition, it is known that lipid extraction can affect δ^{15}N too, thus lipid-extracted samples are not suitable for trophic level estimates (Mintenbeck et al., 2008). In the amphipods studied herein lipid concentration rarely surpassed 10% in summer specimens and was lower than 20% in winter ones (Table 2). Therefore, following other authors studying benthic

Table 2 Lipid content (total lipid) as % of dry weight of the species studied

Taxon	Winter	Summer
Ampelisca eschrichtii		10.3 ± 1.3
Anonyx nugax (5–7 mm)	19.4 ± 4.5	
Anonyx nugax (7–10 mm)	11.2	
Anonyx nugax (15–20 mm)		7.4 ± 2.3
Anonyx nugax (20–27 mm)	19.1 ± 4.6	
Anonyx nugax (28–33 mm)	13.9 ± 5.7	
Anonyx sarsi (8–10 mm)	11.2 ± 1.4	
Anonyx sarsi (10–15 mm)		7.2
Anonyx sarsi (17–20 mm)	11.9 ± 3.8	
Anonyx sarsi (20–25 mm)	5.1 ± 0.2	
Arrhis phyllonyx		5.3
Caprella septentrionalis		6.2
Haploops tubicola		11
Lepidepecreum umbo		13.8 ± 2.8
Melita formosa		9.6
Onisimus caricus (4–6 mm)	11.4	
Onisimus caricus (15 mm)		5.1
Onisimus caricus (17–22 mm)	8.9 ± 2.7	
Onisimus edwardsii (6–8 mm)	11.5 ± 0.1	8.4 ± 0.4
Paroediceros lynceus	6.1	7.1 ± 0.4
Pontoporeia femorata	14.8	16.8
Rhachotropis aculeata		6.2
Stegocephalus inflatus		7.6 ± 0.3
Unciola leucopis		10.2 ± 3.4
Weyprechtia pinguis		13.5

food webs (e.g., Nyssen et al., 2002; Bergmann et al., 2009; Iken et al., 2010; Feder et al., 2011) we decided to use untreated samples.

In the laboratory, samples were freeze-dried and acidified in concentrated HCl fumes for 24 h to remove inorganic carbon. Afterwards samples were dried and homogenized again. Samples prepared as such were weighed into tin capsules (to the nearest 0.000001 g). Stable isotope analysis (δ^{13}C and δ^{15}N) was performed in an Elemental Analyzer Flash EA 1112 Series combined with a Delta V Advantage Isotopic Ratio Mass Spectrometer (Thermo Electron Corp., Germany). Isotopic ratios of δ^{13}C and δ^{15}N were calculated using pure laboratory reference gases CO_2 and N_2 calibrated against IAEA standards CO-8 and USGS40 for δ^{13}C and N-1 and USGS40 for δ^{15}N. The results of δ^{13}C and δ^{15}N analyses are presented in conventional delta notation, i.e. versus PDB for δ^{13}C and versus atmospheric air for δ^{15}N. The standard deviation for replicate samples ($n = 7$) was less than 0.15 and 0.20‰ for δ^{13}C and δ^{15}N, respectively.

POM δ^{15}N values are usually used as the baseline for determining trophic levels in marine food web studies. POM, however, is a heterogeneous source comprising phytoplankton, bacteria and other particulate matter with large spatial and temporal variation in isotopic signature (Iken et al., 2010). Since highly variably POM δ^{15}N can complicate cross-system comparisons, mean δ^{15}N values of primary consumers (PC) are proposed as the baseline reference for food web studies (Cabana & Rasmussen, 1996; Iken et al., 2010). In the present study, mean δ^{15}N values of the suspension-feeder, *Serripes groenlandicus*, collected in Kongsfjorden were used. This relatively large mollusc with a long life span integrates the temporal variability of primary producers and represents the long-term average baseline of the δ^{15}N signature.

Sample isotopic ratios are expressed in conventional δ notation as parts per thousand (‰) according to the following equation:

$$\delta X = \left[\left(R_{\text{sample}}/R_{\text{standard}}\right) - 1\right] \times 1,000$$

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

The trophic levels of the amphipods were determined using the equation:

$$TL_i = \left(\delta^{15}N_i - \delta^{15}N_{PC}\right)/3.4 + 2$$

where 3.4 is the assumed enrichment in $\delta^{15}N$ between successive trophic levels (TL) (Iken et al., 2010), TL_i is the trophic level of species i, $\delta^{15}N_i$ is the species $\delta^{15}N$ and $\delta^{15}N_{PC}$ is the $\delta^{15}N$ of primary consumer, *Serripes groenlandicus*, used as a baseline reference.

Statistical analyses

The whole FA profiles of pooled species/size-class samples were used in statistical analyses. Multivariate statistics (hierarchical clustering, multidimensional scaling and analysis of similarities—ANOSIM) were applied to Bray–Curtis similarities of untransformed data using PRIMER software (v. 6) (Clarke & Warwick, 2001). The SIMPER procedure was used to investigate similarities of groups obtained from cluster and MDS analyses. Since the normality of data distributions and the homogeneity of variance could not be assessed, non-parametric Kruskal–Wallis ANOVA was used on the arcsine-transformed data to compare the relative contribution of selected FA trophic markers in groups distinguished by multivariate analysis. Post hoc testing was performed with Dunn's test to investigate statistical differences between specific groups.

Results

Gut content analysis

In total, the guts of 138 Amphipoda specimens were examined. Four lysianassoid species were collected in winter, and 51 specimens were examined. The mean values of gut fullness ranged from 50% in *Anonyx nugax* to 93% in *Onisimus caricus*. Carrion predominated in their diet (49–100% of total food volume), followed by Polychaeta and Crustacea remains (15–25% and 4–7%, respectively) (Fig. 2). *Anonyx sarsi* had the most diverse diet with considerable shares of Mollusca, Nemertea and Oligochaeta (20% combined). Among the species collected in summer, *Unciola leucopis* exhibited the poorest nutritional status with only 15% of guts filled, while the highest mean values of gut fullness (above 80%) were noted in *Haploops tubicola*, *Melita quadrispinosa* and *Ampelisca eschrichtii*. Phytoplankton-derived items prevailed in the guts of most species, with diatoms as the most substantial contributors (up to 88% in *Weyprechtia pinguis*). Other planktonic elements (mainly Dinophyceae, Tintinnina and protist cysts) were important in the diets of *H. tubicola, Gammarus setosus* and *M. quadrispinosa* comprising over 50% of the total food volume in their guts. While animal food was not important to most species, four had highly carnivorous diets. In *Arrhis phyllonyx* nematodes, crustaceans (Cirripedia cypris) and foraminiferans were found in high quantities, and the diet was supplemented with polychaetes, Halacaroidea and sipunculans. Another oedicerotid, *Paroediceros lynceus,* had a different diet that consisted mainly of harpacticoids and polychaetes with nematodes being less important. The majority of guts from *Stegocephalus inflatus* contained little of any material with a mean gut fullness of 33%. The gut contents in this species were dominated by loose, greyish undetermined animal tissue pulp mixed with sponge spicules and mineral grains, and golden-brown ferritine crystals were abundant in the guts of three specimens. Unidentifiable soft tissue comprised 41% and amphipods remains 59% of the food ingested by *Lepidepecreum umbo*.

Lipid analysis

Total lipid and lipid classes

The 18 species analysed generally had moderate lipid contents. In winter, *A. nugax* had the highest lipid content (up to 19.4% of dry weight; DW), followed by *Pontoporeia femorata* (14.8% DW). The winter lipid content of *O. caricus*, *O. edwardsii* and *A. sarsi* did not exceed 12.0% DW and in *P. lynceus* it was only 6.1% DW. In summer, the lipid content in most species was less than 10.0% DW. The lowest values were observed in *O. caricus* (5.1% DW) and *A. phyllonyx* (5.3% DW), while *P. femorata* and *L. umbo* contained the

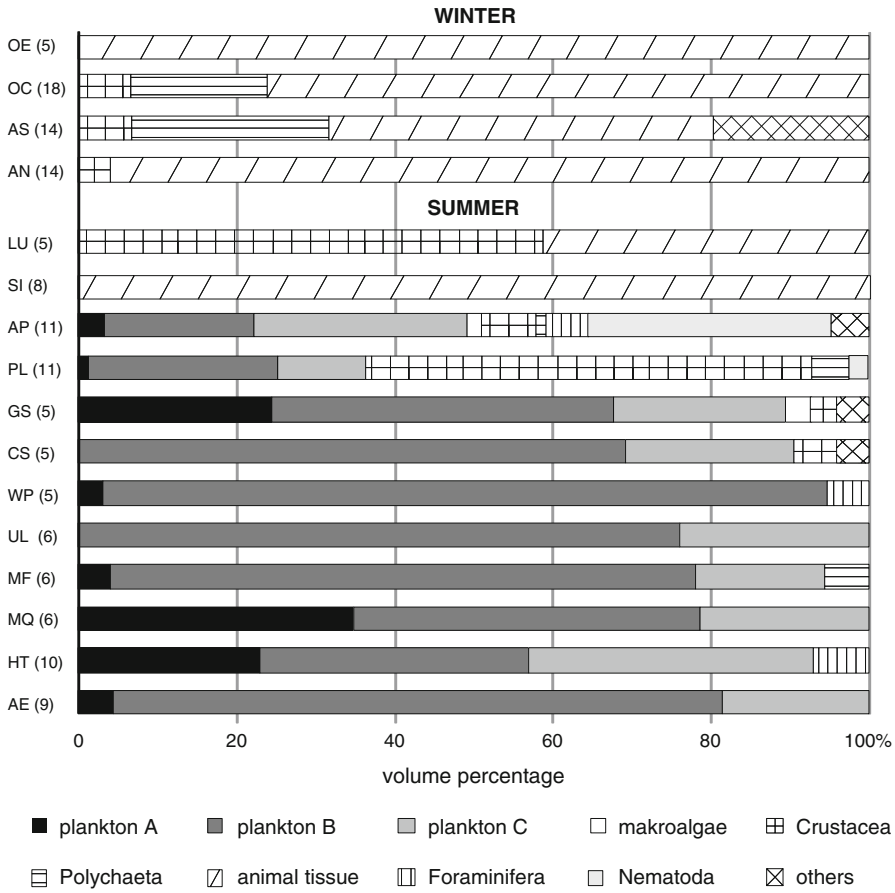

Fig. 2 Mean volume percentage of different food items in the guts of studied species. *plankton A* Dinophyceae, Tintinnina; *plankton B* Bacillariophyceae; *plankton C* protist cysts. Species abbreviations as in Table 1, number of individuals in *parentheses*

greatest quantity of total lipid (13.8–16.8% DW) (Table 2).

Data on the lipid class composition of 12 species collected in Kongsfjorden are presented in Table 3. Triacylglycerols (TAGs) comprised the major lipid class in all amphipods (51.1–92.9% of total lipid). Phospholipids were generally low except in summer individuals of *O. caricus* (48.3%), *S. inflatus* and *P. lynceus* (about 24.0%). Free FAs and cholesterol were detected in all amphipods and contributed 1.5–11.7% and 1.1–13.5% of total lipids, respectively. Proportions of wax ester, cholesterol ester, mono- and diacylglycerols and galactoerebrocide were always $<5\%$ of the total lipids.

Fatty acid profiles

Overall, 43 FAs were detected, but only 13 were present in all 18 amphipod species. The FA composition of all species was dominated by 16:0, 16:1(n-7), 18:1(n-7), 18:1(n-9), 20:5(n-3) and 22:6(n-3) (Tables 4, 5). The species were separated into four groups at 75% similarity levels based on the multivariate analysis of the Bray–Curtis similarities of complete FAs profiles (Fig. 3). Phytodetrivorous species (group A) were characterized by elevated levels of 16:1(n-7), 20:5(n-3) and 16:0 with a mean contribution to total FA content of 21, 18 and 13.5%, respectively. Group B consisted of deposit-feeding/predatory species rich in 20:5(n-3), 16:0 and 22:6(n-3) FAs, which contributed the most to the statistical similarity among these species (52% together). Oleic acid 18:1(n-9) was the most important FA in the carnivores of both groups C and D; however, far higher amounts of this FA were found in group C (up to 42.9% in summer specimens of *O. edwardsii* and up to 62% in *L. umbo*), than in group D (mean 30.8%). Group C had substantially lower percentages of 22:6(n-3) than group D, but this was compensated by higher percentages of 16:1(n-7), of which there was less in group D. The significant differences in the overall FA compositions between these groups

Table 3 Lipid class composition (% of total lipid) of amphipod species collected in Kongsfjorden

Species\season	WE	CE	C	FFA	MAG	DAG	TAG	GC	PL
Winter									
Anonyx nugax (5–7 mm)	1.0	2.1	3.0	3.0	2.4	3.9	78.7	0.6	5.4
Anonyx nugax (7–10 mm)	0.9	1.1	1.1	1.6	0.9	0.6	92.8		1.1
Anonyx nugax (20–27 mm)	1.0	2.1	3.4	2.4	1.4	2.6	80.9	0.5	5.6
Anonyx sarsi (8–10 mm)	0.6	0.7	4.9	4.5	4.0	7.4	67.1	0.8	10.1
Anonyx sarsi (17–20 mm)	0.5	0.6	3.8	3.8	2.5	3.8	73.2	1.1	10.7
Anonyx sarsi (20–25 mm)	1.6	1.5	2.8	4.7	2.0	1.1	74.3	0.9	11.2
Onisimus caricus (4–6 mm)	1.8	2.6	3.3	3.0	1.8	2.3	79.8	1.3	4.2
*Onisimus caricus** (17–22 mm)	1.1 ± 0.1	0.8 ± 0.1	3.7 ± 1.7	5.5 ± 3.1		0.7 ± 0.5	76.1 ± 11.9	1.6 ± 0.7	10.5 ± 5.8
*Onisimus edwardsii**	1.1 ± 0.1	0.5 ± 0.6	1.3 ± 0.1	1.7 ± 0.3	1.1 ± 0.1	0.4 ± 0.6	92.9 ± 0.2		1.0 ± 0.1
Pontoporeia femorata	1.0		2.0	8.7	1.6	1.4	76.9	1.1	7.4
Summer									
Ampelisca eschrichtii	1.5	1.3	4.5	5.8		2.1	67.1	0.9	16.7
Anonyx nugax	1.4	1.4	3.0	8.3	1.8	3.0	72.8	0.6	7.8
Haploops tubicola	1.4	1.1	5.4	2.8	1.2	2.6	70.0	0.8	14.8
Lepidepecreum umbo	1.4	1.4	1.9	1.5		1.2	88.5	0.9	1.5
Melita formosa	1.7	1.7	2.0	9.8	2.2	1.2	79.3	1.0	1.2
Onisimus caricus	4.3	3.0	13.5	7.9	3.1		17.7	2.2	48.3
Onisimus edwardsi	1.1	1.0	1.4	1.5	1.0	1.0	90.7		2.3
Paroediceros lynceus	1.1	0.8	6.8	11.7	1.9		51.1	2.3	24.3
Stegocephalus inflatus	1.4		5.8	4.9		3.5	59.1	0.9	24.4
Unciola leucopis	1.7	1.6	2.4	1.9	1.6	1.0	86.5	0.9	2.4

WE wax ester, *CE* cholesterol ester, *C* cholesterol, *FFA* free fatty acids, *MAG* monoacylglycerol, *DAG* diacylglycerol, *TAG* triacylglycerol, *GC* galactoerebrocide, *PL* phospholipids

* Mean ± SD of two samples

Table 4 Fatty acid composition (mean ± SD) as percentage of total lipid extracted from species of groups A and B

Group	A								B				
Species (N_s)	AE (2)	HT (1)	WP (1)	CS (1)	UL (2)	PF (1)	PF w (1)	MF (1)	AP (1)	RA (1)	PL (2)	PL w (1)	SI (2)
14:0	3.8 ± 0.1	3.6	3.5	5.5	3.7 ± 0.7	3.9	2.6	3.5	2.0	1.4	1.7 ± 0.1	1.1.	1.9 ± 0.3
15:0	0.3 ± 0.0	0.3	0.2	0.4	0.4 ± 0.0	0.6	1.7	0.8	1.1	0.6	0.3 ± 0.0	0.5	0.7 ± 0.1
16:0	10.0 ± 0.1	10.7	15.3	15.1	13.2 ± 0.4	16.3	16.5	29.6	11.8	13.5	14.3 ± 1.1	13.0	13.3 ± 0.8
17:0	1.3 ± 1.1	1.9	0.3	1.3	1.1 ± 0.5	1.0	1.0	1.5	1.5	1.0	0.9 ± 0.0	1.2	0.6 ± 0.0
18:0	1.1 ± 0.2	1.5	1.0	1.7	1.2 ± 0.1	1.0	1.4	2.7	1.3	1.2	1.8 ± 0.4	1.9	1.2 ± 0.1
24:0	0.3 ± 0.1	0.3	0.1	0.1	0.2 ± 0.0	0.3	0.4	0.5	1.3	0.6	0.3 ± 0.1	0.4	0.7 ± 0.1
ΣSFA	16.9 ± 1.4	18.7	20.4	24.9	20.5 ± 0.4	23.2	23.6	39.7	19.5	18.7	19.6 ± 1.7	18.7	19.6 ± 1.5
16:1(n-7)	21.3 ± 1.2	16.7	30.0	10.3	18.4 ± 3.2	28.6	23.6	23.7	11.9	5.4	8.1 ± 4.5	4.4	2.8 ± 0.5
16:1(n-5)	0.5 ± 0.1	0.7	0.2	0.5	0.7 ± 0.1	0.5	0.3	0.3	0.8	1.0	0.6 ± 0.1	1.4	2.9 ± 1.5
17:1	0.1 ± 0.0	0.1	0.1	0.1	0.2 ± 0.0	0.5	4.5	0.8	0.9	0.3	0.2 ± 0.0	0.3	0.4 ± 0.1
18:1(n-9)	7.6 ± 0.9	8.8	11.9	13.1	11.7 ± 3.3	10.7	16.1	10.3	8.0	9.9	12.9 ± 0.5	13.7	11.9 ± 2.1
18:1(n-7)	4.7 ± 0.3	4.9	5.3	4.1	3.7 ± 0.0	3.1	3.8	6.1	7.1	6.0	7.4 ± 0.8	8.6	5.5 ± 1.0
20:1(n-11)	0.1 ± 0.1	0.1		0.2	0.3 ± 0.1		0.1	0.2	0.5	1.3	1.2 ± 0.5	1.6	1.3 ± 0.7
20:1(n-9)	0.9 ± 0.2	0.8	0.4	1.5	0.6 ± 0.1	0.2	0.4	0.7	0.9	1.4	1.3 ± 0.7	1.2	1.6 ± 0.7
20:1(n-7)	1.1 ± 0.2	1.0	0.7	0.9	0.7 ± 0.0	0.4	0.6	0.9	1.1	1.7	2.0 ± 0.0	2.2	2.4 ± 0.6
22:1(n-11)	0.3 ± 0.1	0.4			0.2 ± 0.2			0.1	0.6	0.9	0.4 ± 0.4	0.3	0.2 ± 0.0
ΣMUFA	37.5 ± 2.8	34.2	49.0	31.8	37.0 ± 0.0	44.9	50.2	43.6	33.0	29.0	34.9 ± 5.5	34.9	29.9 ± 0.5
16:2(n-7)		1.2	1.3	0.9	1.1 ± 0.4	1.1	1.2	0.7		0.2	0.3 ± 0.5	0.2	0.1 ± 0.0
16:3(n-4)	2.0 ± 0.5	1.9	0.7	0.9	1.5 ± 0.6	1.2	1.6	0.6	0.5	0.3	0.5 ± 0.3	0.2	0.5 ± 0.3
16:4(n-1)	3.1 ± 1.4	3.1	0.8	1.4	2.3 ± 0.9	1.6	0.4	0.5	0.5	0.7	1.0 ± 0.1	0.5	2.3 ± 1.0
18:2(n-6)	1.1 ± 0.02	1.4	1.0	2.7	1.1 ± 0.2	1.0	0.5	0.6	1.7	1.3	1.5 ± 0.4	2.9	0.7 ± 0.0
18:3(n-3)	0.5 ± 0.3	0.5	0.5	1.4	0.6 ± 0.5	0.3	0.2	0.3	0.2	0.3	0.4 ± 0.1	0.5	0.1 ± 0.0
18:4(n-3)	5.7 ± 2.5	6.8	4.7	5.0	4.2 ± 1.0	6.0	2.2	2.4	2.3	2.0	1.7 ± 1.1	0.6	0.1 ± 0.0
20:4(n-6)	1.3 ± 0.3	1.2	1.1	2.9	1.4 ± 0.0	3.1	1.8	3.2	9.9	3.2	2.9 ± 1.4	4.5	3.0 ± 0.9
20:4(n-3)	1.2 ± 0.4	1.8	0.5	0.8	0.5 ± 0.0	0.3	0.4	0.5	0.4	0.6	0.6 ± 0.1	0.6	0.3 ± 0.0
20:5(n-3)	21.4 ± 0.0	18.9	15.9	18.6	20.3 ± 1.7	11.4	12.9	18.3	17.8	21.6	22.0 ± 3.0	18.8	17.2 ± 3.0
22:4(n-6)		0.1	0.1	0.1				0.1	0.4	0.3	0.2 ± 0.1	0.3	2.0 ± 0.6
22:5(n-3)	0.5 ± 0.1	0.4	0.4	0.5	0.5 ± 0.1	0.4	0.7	0.7	2.2	1.2	1.2 ± 0.2	1.3	5.3 ± 0.8
22:6(n-3)	6.6 ± 0.6	7.3	2.3	5.3	7.5 ± 1.5	4.2	3.0	7.3	10.1	19.0	11.5 ± 0.6	13.3	17.2 ± 2.5
ΣPUFA	45.5 ± 1.5	47.1	30.6	43.3	42.5 ± 0.4	31.9	26.1	36.6	47.5	52.3	45.5 ± 3.8	46.4	50.5 ± 1.9

Components present at <1.5% included in ∑SFA, ∑MUFA and ∑PUFA: 14:1(n-5), 16:0 Pristanic, 16:1(n-9), 17:0 Phytanic, 18:3(n-6), 18:5(n-3), 20:0, 20:2(n-6), 20:3(n-3), 20:3(n-6), 21:5, 22:0, 22:1(n-7), 22:1(n-9), 22:5(n-6), 24:0 and 24:1(n-9)

w Winter specimens, N_s number of samples in parentheses

were confirmed by one-way ANOSIM permutation tests (global $R = 0.928$, pair-wise comparisons $0.731 \leq R \leq 1$, $P < 0.001$ in all cases). SIMPER analysis revealed high within-group similarities and indicated that 18:1(n-9), 16:1(n-7), 20:5(n-3) and 22:6(n-3) were the FAs that contributed most to group separation (Fig. 3; Table 6). Significant inter-group differences were noted in the mean levels of FA trophic markers (Kruskal–Wallis ANOVA and subsequent Dunn's post hoc tests) (Table 7).

Isotopes analysis

The δ^{15}N and δ^{13}C values of amphipods collected in summer (18 species) and winter (6 species) are presented in Table 8 and Fig. 4. In summer, the range

Table 5 Fatty acid composition (± sd) as percentage of total lipid extracted from species of groups C and D

Group	C			D											
Species (N_s) Size (mm)	LU (2) 7	OE (2) 6–7	OE w (2) 8	AN (2) 15–20	AN w (1) 5–7	AN w (1) 7–10	AN w (1) 20-27	AN w (1) 28-33	AS (1) 10-15	AS w (1) 8–10	AS w (1) 17-20	AS w (1) 20-25	OC (1)	OC w (1) 4–6	OC w (2) 17–22
14:0	1.1 ± 0.2	1.4 ± 0.2	1.2 ± 0.1	1.5 ± 0.8	1.5	1.7	2.0	1.6	1.3	1.5	1.5	1.1	0.6	1.6	1.7 ± 0.2
15:0	0.1 ± 0.0	0.2 ± 0.2	0.2 ± 0.0	0.5 ± 0.2	0.2	0.6	0.3	0.4	0.3	0.3	0.3	0.4	0.2	0.3	0.3 ± 0.1
16:0	17.0 ± 0.4	17.9 ± 0.8	18.6 ± 0.8	17.6 ± 2.6	20.4	18.1	17.5	15.4	15.8	18.9	17.0	16.3	18.5	15.3	17.5 ± 0.2
17:0	0.1 ± 0.1	0.3 ± 0.0	0.4 ± 0.2	0.5 ± 0.1	0.4	0.5	0.4	0.5	0.5	0.4	0.4	0.7	0.4	0.5	0.6 ± 0.0
18:0	1.9 ± 0.1	2.5 ± 0.6	4.5 ± 0.6	3.0 ± 2.2	8.8	4.7	5.1	1.8	2.2	4.3	4.2	2.3	2.6	2.8	4.9 ± 0.3
24:0	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.2	0.1	0.1	0.1 ± 0.0
ΣSFA	20.5 ± 1.3	22.4 ± 1.5	25.3 ± 0.3	23.4 ± 3.7	31.7	26.0	25.8	20.2	20.4	25.8	24.0	21.4	22.9	21.2	25.4 ± 0.3
16:1(n-7)	13.8 ± 1.5	12.4 ± 1.5	7.1 ± 0.2	4.5 ± 1.5	2.4	3.6	5.2	5.3	8.2	5.7	6.1	3.6	2.6	4.8	4.3 ± 0.0
16:1(n-5)		0.2 ± 0.0	0.5 ± 0.0	0.4 ± 0.1	0.2	0.4	0.4	0.5	0.4	0.6	0.6	1.0	0.1	0.5	0.3 ± 0.1
17:1	0.1 ± 0.0	0.2 ± 0.0	0.4 ± 0.0	0.7 ± 0.6	0.3	1.2	0.3	0.3	0.3	0.4	0.3	0.4	0.3	0.5	0.7 ± 0.0
18:1(n-9)	55.1 ± 9.8	41.9 ± 1.4	32.6 ± 0.0	23.7 ± 1.5	36.4	32.9	32.4	27.6	32.8	33.7	30.4	22.1	31.6	28.9	37.8 ± 3.2
18:1(n-7)	0.5 ± 0.3	2.3 ± 0.2	4.3 ± 0.5	4.5 ± 0.7	3.2	3.5	3.5	3.4	4.4	4.6	5.3	6.8	3.4	3.3	2.8 ± 0.1
20:1(n-11)		0.1 ± 0.1	0.7 ± 0.2	1.4 ± 1.5	0.6	0.7	1.4	1.5	0.7	0.8	0.9	0.9	0.4	1.5	1.0 ± 0.1
20:1(n-9)	2.0 ± 2.5	0.8 ± 0.1	1.4 ± 0.3	3.9 ± 2.9	2.2	2.9	4.7	5.4	1.4	1.4	1.9	2.4	0.7	4.6	2.8 ± 0.3
20:1(n-7)	0.2 ± 0.3	0.3 ± 0.0	1.1 ± 0.0	0.9 ± 0.5	0.7	0.9	1.1	1.1	1.5	1.5	1.4	1.3	0.1	1.1	0.3 ± 0.0
22:1(n-11)		0.3 ± 0.1	0.2 ± 0.1	1.5 ± 1.4	0.7	1.3	2.1	2.7	0.3	0.2	0.4	0.6	0.3	2.4	1.1 ± 0.1
ΣMUFA	72.2 ± 7.7	59.0 ± 0.2	49.5 ± 1.3	42.4 ± 8.1	47.7	48.3	52.3	49.4	50.6	49.8	48.3	40.0	40.2	48.8	51.8 ± 3.4
16:2(n-7)		0.2 ± 0.1	0.1 ± 0.0	0.1 ± 0.0			0.1	0.1	0.1		0.1			0.1	0.1 ± 0.0
16:3(n-4)		0.2 ± 0.1	0.1 ± 0.0	0.1 ± 0.0		0.3	0.1	0.1	0.1	0.1	0.1	0.3		0.1	0.1 ± 0.0
16:4(n-1)		0.2 ± 0.1	0.1 ± 0.2	0.4 ± 0.2	0.2	0.3	0.3	0.2	0.3	0.5	0.3	0.1	0.1	0.4	
18:2(n-6)	1.0 ± 1.4	1.9 ± 0.8	5.3 ± 0.5	7.5 ± 8.4	8.7	7.2	3.9	1.2	2.7	5.3	4.1	3.3	8.3	3.4	4.2 ± 0.2
18:3(n-3)	0.8 ± 1.2	0.3 ± 0.0	0.7 ± 0.1	1.0 ± 0.5	0.9	1.0	0.7	0.5	0.9	0.8	0.8	0.6	0.9	0.8	0.7 ± 0.1
18:4(n-3)	0.1 ± 0.1	0.7 ± 0.4	0.5 ± 0.1	0.9 ± 0.7	0.2	0.7	0.6	0.6	0.9	0.4	0.7	0.2	0.1	1.0	0.6 ± 0.2
20:4(n-6)	0.1 ± 0.1	1.7 ± 0.2	2.4 ± 0.4	1.9 ± 0.8	0.9	1.3	0.9	1.9	2.0	2.1	2.9	6.5	3.1	1.5	1.3 ± 0.2
20:4(n-3)		0.2 ± 0.0	0.3 ± 0.0	0.3 ± 0.2	0.1	0.2	0.3	0.3	0.4	0.2	0.4	0.3	0.2	0.4	0.2 ± 0.0
20:5(n-3)	2.0 ± 0.9	7.9 ± 1.0	7.3 ± 0.8	9.7 ± 2.5	3.8	6.0	6.3	9.5	12.2	7.2	8.7	10.3	11.8	9.3	7.0 ± 1.2
22:4(n-6)		0.1 ± 0.0	0.3 ± 0.1	0.1 ± 0.1	0.1	0.1	0.1	0.3	0.1	0.3	0.2	0.4	0.1	0.1	
22:5(n-3)		0.2 ± 0.0	0.7 ± 0.1	0.6 ± 0.0	0.4	0.4	0.6	0.7	0.8	0.7	0.6	0.9	0.2	0.7	0.3 ± 0.0
22:6(n-3)	2.3 ± 1.8	4.4 ± 0.6	5.8 ± 0.4	10.7 ± 1.6	4.2	7.0	7.3	14.3	7.4	5.4	7.3	14.1	11.7	11.2	7.8 ± 1.7

Table 5 continued

Group	C			D										
Species (N_s)	LU (2)	OE (2)	OE w (2)	AN (2)	AN w (1)	AN w (1)	AN w (1)	AS (1)	AS w (1)	AS w (1)	AS w (1)	OC (1)	OC w (1)	OC w (2)
Size (mm)	7	6–7	8	15–20	5–7	7–10	20-27	10-15	8–10	17-20	20-25		4–6	17–22
ΣPUFA	7.3 ± 6.5	18.5 ± 1.4	25.2 ± 0.9	34.2 ± 4.4	20.6	25.7	21.9	30.4	29.0	24.4	27.8	38.6	36.9	30.0	22.8 ± 3.8

Components present at <1.5% included in ∑SFA, ∑MUFA and ∑PUFA: 14:1(n-5), 16:0 Pristanic, 16:1(n-9), 17:0 Phytanic, 18:3(n-6), 18:5(n-3), 20:0, 20:2(n-6), 20:3(n-3), 20:3(n-6), 21:5, 22:0, 22:1(n-7), 22:1(n-9), 22:5(n-6), 24:0 and 24:1(n-9)

w Winter specimens, N_s number of samples in parentheses

of δ^{15}N values was considerable from 5.45‰ for *M. quadrispinosa* and *Caprella septentrionalis* to 12.43‰ for *S. inflatus*, while δ^{13}C values ranged from −19.45‰ for *Monoculodes borealis* to −22.41‰ for *Halirages fulvocincta*. The average carbon and nitrogen isotope ratios in species collected in winter (five lysianassoids and one oedicerotid) ranged from −19.46‰ (δ^{13}C) and 8.70‰ (δ^{15}N) for *Orchomella minuta* to −21.97‰ (δ^{13}C) and 10.86‰ (δ^{15}N) for *O. caricus*. The trophic levels of the amphipods were determined using the δ^{15}N values of the primary consumer, the mollusc *S. groenlandicus* (4.52‰ in winter and 4.80‰ in summer). In summer, amphipods encompassed over three trophic levels with primary and secondary consumers clearly separated by differences in δ^{15}N signatures. Species collected in winter occupied the third trophic level, and no evidence of seasonal variability in stable isotope values of these species was noted.

Discussion

Food sources

The results of the combined approach revealed that the amphipods studied consume a wide range of food items from microorganisms to vertebrate carcasses, and that they occupy several trophic levels in the fjord food web. However, the narrow range of δ^{13}C detected suggests that all these species are likely supported by the same basal food source. Gut content analysis and FA signatures both suggest the important role of pelagic primary producers, particularly diatoms, in fuelling benthic amphipods. However, substantial enrichment in δ^{13}C between POM and amphipods (∼5–11‰) implies that phytoplankton-derived organic matter undergoes extensive reprocessing prior to uptake by amphipods. Polar benthic detritivores are often considerably δ^{13}C-enriched relative to POM, which is probably because the organic matter available on the bottom is recycled by bacterial and meiofaunal intermediates, and this raises carbon isotopic ratios considerably (Hobson et al., 1995; Nyssen et al., 2002; Lovvorn et al., 2005; Mincks et al., 2008). In the current study, the evidence from FA analysis suggests the bacterial input to the amphipod diet is not large, although elevated amounts of bacterial FAs [odd-numbered FAs + 18:1(n-7) (Stevens et al., 2004)] were noted in some detritus-feeding amphipods, such

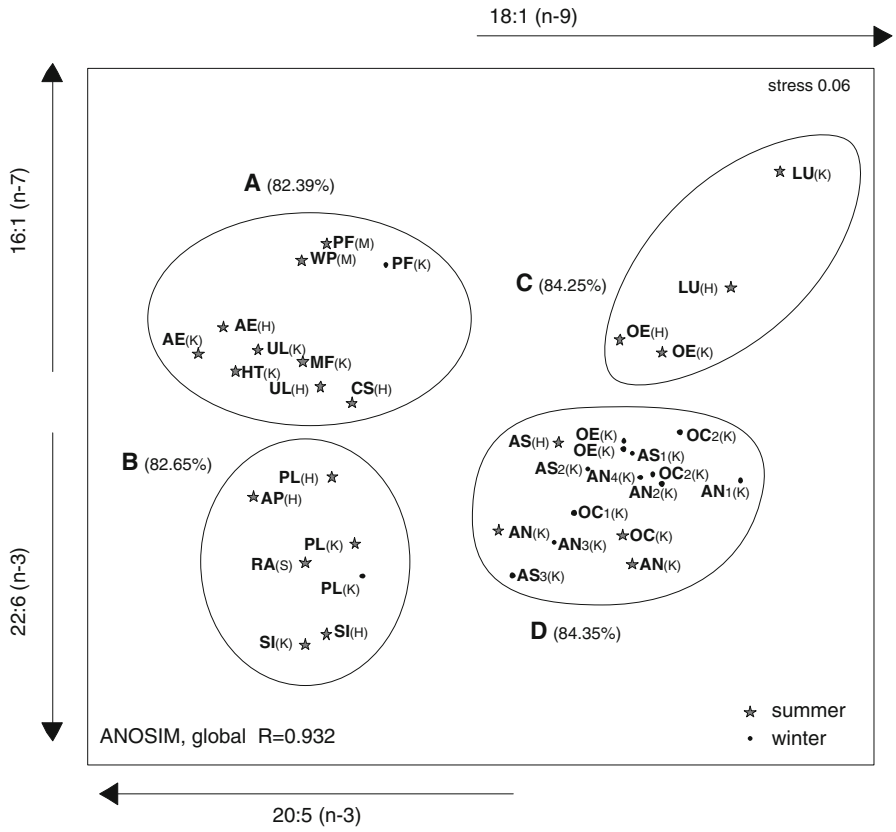

Fig. 3 nMDS plot of the amphipod species according to their winter and summer fatty acid composition. Species abbreviations as in Table 1, lysianassoids' size classes AN1: 5–7 mm, AN2: 7–10 mm, AN3: 20–27 mm, AN4: 28–38 mm; AS1: 8–10 mm, AS2: 17–20 mm, AS3: 20–25 mm; sampling site in *parentheses*: *H* Hornsund, *K* Kongsfjorden, *M* Magdalenefjorden, *S* Smeerenburgfjorden. Denotation of groups obtained with hierarchical cluster analysis; *A* herbivores, *B* deposit-feeding/predators, *C*, *D* opportunistic predators/scavengers; results of SIMPER within-group analysis of similarity (%) in *parentheses*

Table 6 Results of ANOSIM and SIMPER analyses

R—ANOSIM pair wise tests of the groups based on fatty acid profiles ($P < 0.005$), average inter-groups dissimilarity (%) and the most discriminant fatty acids

Group	*R*	Average dissmilarity (%)	Most discriminant fatty acids
A:B	0.838	29.27	16:1(n-7)/22:6(n-3)/20:5(n-3)
A:C	1	45.48	18:1(n-9)/20:5(n-3)/16:1(n-7)
A:D	0.997	41.15	18:1(n-9)/16:1(n-7)/20:5(n-3)
B:C	1	50.60	18:1(n-9)/20:5(n-3)/22:6(n-3)
B:D	0.969	35.20	18:1(n-9)/20:5(n-3)/22:6(n-3)
C:D	0.743	28.20	18:1(n-9)/16:1(n-7)/22:6(n-3)

as *P. femorata* (11.0%) and oedicerotids (up to 10.6%). One explanation for the high δ^{13}C values could be that these organisms are feeding on phytodetritus with a considerable admixture of ice algae, which are richer in δ^{13}C than phytoplankton (McMahon et al., 2006; Søreide et al., 2006b). At high latitudes, bloom material, and in particular ice algae, that sinks rapidly after the ice melts, can persist buried in the sediments for a number of months (Josefson et al., 2002; Mincks et al., 2005). The accumulation of phytodetritus in sediments can create a 'food bank' that is available for reasonable periods of time and provides benthic fauna with continuous supplies of high quality food that attenuates the effects of the strong seasonality of primary production (Mincks et al., 2005, 2008; McMahon et al., 2006; Norkko et al., 2007). In Svalbard fjords the general pool of detritus can be supplemented considerably by macrophyte-derived material. While the palatability of living macrophytes for amphipod mesograzers is efficiently reduced by their limited nutritional value and deterrent chemical or morphological defences (Duggins & Eckman, 1997; Huang et al., 2006; Wessels et al., 2006), a significant fraction of kelp standing-stock degrades into particulate or dissolved

Table 7 Comparison of the fatty acid trophic markers (FATMs)

	FATM	K–W ANOVA	Post hoc Dunn's test
Bacteria	Odd-number FA + 18:1(n-7)	25.1	A > C; B > C, D
Carnivory	18:1(n-9)/18:7(n-7)	29.8	A, B < C; A, B < D
Calanus spp.	20:1(n-9) + 22:1(n-11)	19.8	A < D
Diatoms 1	16:1(n-7)/16:0	25.2	A > B, D
Diatoms 2	16:1(n-7) + C16 PUFA + 20:5(n-3)	31.1	A, B > D
Flagellates	C18 PUFA + 22:6(n-3)	15.0	C < B, D

Results of Kruskal–Wallis ANOVA (KW-H (3, 38), $P \leq 0.001$) and significant inter-group differences, post hoc Dunn's tests ($P \leq 0.001$)

Table 8 Stable isotopes values (‰) and trophic levels measured during the study

Category	Winter					Summer				
	δ^{13}C	±SD	δ^{15}N	±SD	TL	δ^{13}C	±SD	δ^{15}N	±SD	TL
POM	−26.23	0.99	3.06	4.17		−29.89	0.93	0.24	2.81	
Macroalgae	−28.28	4.27	2.82	0.13		−18.24	5.30	3.86	2.98	
Sediment	−23.66	1.5	0.29	1.1		−23.66	0.9	−0.09	0.5	
Detritus	−24.34		7.64							
Zooplankton										
Calanus glacialis	−24.12	0.80	8.08	0.47	3.0	−24.52	0.67	7.75	0.69	2.9
Calanus finmarchicus	−23.49		8.54		3.2					
Amphipoda										
Melita quadrispinosa						−20.80		5.45		2.2
Caprella septentrionalis						−22.32		5.45		2.2
Halirages fulvocinctus						−22.41		5.52		2.2
Gammarus setosus						−20.82	0.04	5.84	0.18	2.3
Melita formosa						−19.88	2.49	5.94	0.73	2.3
Pleustes panopla						−21.97		6.00		2.4
Haploops tubicola						−22.32	0.62	6.57	0.42	2.5
Unciola leucopis						−20.87		6.65		2.5
Monoculodes borealis						−19.45		6.73		2.6
Ampelisca eschrichtii						−22.08		6.79		2.6
Onisimus edwardsi	−20.94	0.14	9.27	0.33	3.4	−21.10	1.85	8.84	1.83	3.2
Paroediceros lynceus						−20.39	0.68	8.93	0.80	3.2
Anonyx sarsi	−20.62	0.35	10.37	0.60	3.7	−20.31		9.65		3.4
Rhachotropis aculeata						−21.24	0.22	10.23	0.87	3.6
Arrhis phyllonyx	−20.32		10.07		3.6	−20.85		10.44		3.7
Onisimus caricus	−21.97	0.55	10.86	0.55	3.9	−22.14		10.86		3.8
Orchomenella minuta	−19.46		8.70		3.2					
Anonyx nugax	−21.58	0.70	10.51	0.83	3.8	−22.26	0.59	11.10	0.52	3.9
Stegocephalus inflatus						−19.47		12.43		4.2

fractions and can then be utilized by grazers and deposit- and suspension-feeders (Duggins & Eckman, 1997; Hop et al., 2002; Quijón et al., 2008). However, assessing the real importance of macrophyte detritus based on FA or isotopic signatures of consumers can be problematic because of overlap in the FA composition

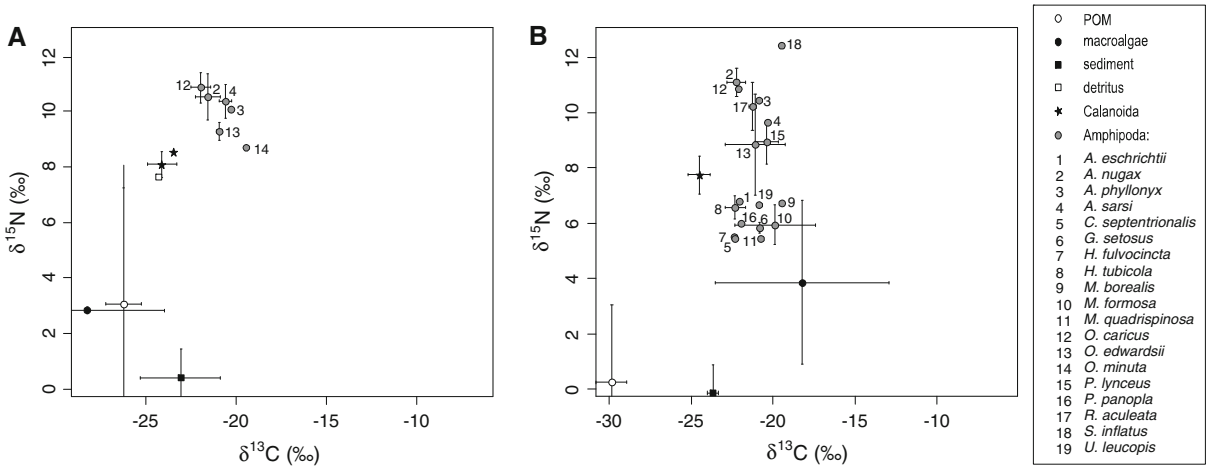

Fig. 4 Winter (**A**) and summer (**B**) carbon and nitrogen isotopic ratios of the species studied

of major groups of producers (Graeve et al., 2002) and the wide range of carbon isotopic ratios observed in macroalgae (Wiencke & Fisher, 1990).

Amphipods seem to exploit mostly benthic sources of animal food such as carrion, worms, crustaceans and meiofauna. It is evident from gut content examination and the negligible amounts of calanoid markers 20:1 (n-9) and 22:1(n-11) that planktonic organisms are not frequently consumed. Few of the specific animal tracers discovered thus far (Budge et al., 2007; Iverson, 2009; Drazen et al., 2009) were not detected in the current study material, and oleic acid, 18:1(n-9), which is a general indicator of carnivorous feeding (Graeve et al., 1997; Nelson et al., 2001; Nyssen et al., 2005), is not specific to any particular kind of organism. Therefore, gut examination and stable isotope analysis appear to be essential in evaluating feeding preferences and the trophic position of obligate or opportunistic carnivorous species.

Feeding ecology

The multi-method approach provides a highly consistent picture of the feeding preferences of different species. The consistency of the results of gut content analysis (representing recent feeding) with information derived from lipid and isotopic signatures (integrated over long time periods) demonstrates that general amphipod trophic strategies remain unchanged over time. Nyssen et al. (2002) reported similar findings for amphipods from the Weddell Sea.

One of the fundamental characteristics of the Arctic marine environment is its extreme seasonality. Benthic fauna is generally dependent upon seasonal phytodetritus pulses with pelago-benthic coupling, which is regarded as a crucial process in the regulation of benthic communities (Piepenburg, 2005). Therefore, it is plausible that seasonal changes in food supplies would affect the feeding strategies of benthic amphipods and, consequently, their lipid and isotopic signatures. The rate of incorporation of the diet-derived lipids and stable isotopes into consumer tissues can vary widely among species and tissues and remain poorly validated for most taxa. However, it is known that FAs composition and stable isotopes signatures of cold water amphipods change markedly within weeks following a shift in diet (Richoux et al., 2005; Kaufman et al., 2008). Thus, if the species studied display seasonal dietary shifts they should be distinct in the specimens collected in March (after long period of adverse winter conditions) and July/August (when abundant food sources are accessible). Nevertheless, no evidence of seasonal dietary shifts in amphipods was noted in the present study. Specimens of the same species collected in different seasons did not differ considerably in FA composition or trophic position based on δ^{15}N signatures.

Even if organic carbon at the bottom is derived primarily from the overlying water column, the polar benthos appears to experience reduced seasonality in food availability relative to pelagic organisms (Mincks et al., 2008). While it is known that benthic organisms can efficiently assimilate phytodetritus settling on the bottom in the course of days or weeks (McMahon et al., 2006; Quijón et al., 2008 and references therein), there

is growing evidence of substantial inertia in pelago-benthic coupling in polar seas. Mincks et al. (2005, 2008) observed that seasonal variability in the phytodetritus supply is only reflected slightly in the isotopic signatures of Antarctic benthic fauna. Similar observations have recently been made in Kongsfjorden (Arctic) (Renaud et al., 2011; Kędra et al., submitted). The amphipods studied utilize multiple food sources at different trophic levels. Moreover, the most important components of their diet, such as detritus, carrion and tiny benthic organisms appear to be available year-round in shallow polar waters (Slattery & Oliver, 1986; Smale et al., 2007; Kędra et al., 2011). Therefore, only relatively small variations in feeding mode that result in the lack of seasonal change in stable isotope signatures occur in most species.

The results of lipid analyses lend additional credence to the hypothesis that the Svalbard fjords provide benthic amphipods with sufficient food supplies throughout the year. Polar crustaceans such as herbivorous copepods that are confronted with strong seasonality of food supplies store large reserves of energy-rich lipids (wax esters) during periods of high food availability to cover energetic costs of offspring production and overwintering (Hagen & Auel, 2001). High lipid levels have also been noted in amphipods relying on temporary food sources, such as sympagic *Onisimus* spp. (35.4–38.6% of DW) (Scott et al., 1999) and deep-sea lysianassoids (23.0–43.0% of DW) (Bühring & Christiansen, 2001). In contrast, the amphipods from the current study did not exhibit high lipid accumulation. More opportunistic and flexible feeding strategies along with consistent food supply allow them to overwinter employing a 'business as usual' strategy that does not rely on lipid reserves (Torres et al., 1994).

Lipid content and composition in marine organisms can vary markedly throughout the year and reflect both nutritional and reproductive cycles (Percy, 1979). The sampling for this study covered only two seasons with few replications; therefore, neither seasonal nor ontogenetic differences can be tested statistically. Nevertheless, it is noteworthy that winter (March) lipid contents in *Anonyx* and *Onisimus* were consistently higher than those in summer (August). Similarly, Percy (1979) reported February–March lipid levels of *Onisimus affinis* to be higher than late summer values. This Arctic lysianassoid does not build up significant lipid reserves and has a fairly uniform lipid level throughout the year except for increases of up to 30% DW during the reproductive period (May–July). Once reproduction finishes, the lipid content immediately decreases to its former level, which is generally maintained during winter. Nygård et al. (2010) reported relatively stable lipid content and no build-up of energy stores prior to winter season in *Onisimus litoralis* collected in Adventfjorden (Svalbard). This species being omnivorous scavenger may cover metabolic costs by continuous feeding in addition to the proteins consumption. The closely related species examined in the present study have probably similarly low lipid variations during the year and similar overwintering strategy.

Conversely to low lipid levels, TAG values reported here are generally higher than those published for amphipods collected in the Antarctic (Graeve et al., 2001; Nelson et al., 2001), the deep north-east Atlantic (Bühring & Christiansen, 2001) and the Barents Sea (Graeve et al., 1997). TAGs are used as short-term energy reserves, and they are the major type of stored lipids in amphipods (Percy, 1979; Clarke et al., 1985; Nelson et al., 2001). High levels of TAG are interpreted as an adaptation for periods of food scarcity (Graeve et al., 2001). However, assuming that shallow polar waters create favourable feeding conditions for opportunistic scavengers and deposit feeders, high TAG levels most probably reflect recent feeding activity (Nelson et al., 2001).

Feeding strategies

The current results suggest highly diverse feeding strategies among Arctic amphipods. Dauby et al. (2001) interpreted high trophic diversity of the amphipods in the Weddell Sea as a function of species diversity related to the long evolutionary history of the Antarctic, abundance of accessible micro-habitats and variability of food sources. Species inventory is far from complete in either of the polar regions (Piepenburg, 2005 and references therein), but Arctic amphipod fauna is generally considered to be impoverished compared to that in the Antarctic both locally and overall (Knox & Lowry, 1977; Jażdżewski et al., 1995). Still, with more than 270 species, amphipods are the most species-rich group of macrofauna recorded in Svalbard waters (Palerud et al., 2004). It is likely that with the observed number of species more strategies will be recognized as knowledge of species

ecology grows. In general, high trophic diversity appears to be a general feature of amphipod communities and one of the most important factors responsible for the dispersal success of these crustaceans.

Multivariate analysis based on whole FA profiles clearly separated lysianassoids from other species due to the considerably higher levels of 18:1(n-9) oleic acid (Fig. 3). Similar separation within Antarctic species was observed by Nyssen et al. (2005), who underscored a striking similarity of the 18:1(n-9) dominant FA composition in species of this Superfamily. Indeed, elevated levels of oleic acid seem to be a characteristic feature of carrion-feeding lysianassoids (Bühring & Christiansen, 2001; Graeve et al., 2001; Nyssen et al., 2005; this study), but others, for example, the ice-associated detritivores *Onisimus nanseni* and *O. glacialis* (Arndt et al., 2005), contain moderate amounts of this FA (Scott et al., 1999).

Considerable differences of 18:1(n-9) levels split the lysianassoids into two groups. In *A. nugax*, *A. sarsi*, *O. caricus* and winter specimens of *O. edwardsii* (group D) oleic acid varied between 22 and 38% which is consistent with their carnivorous diet and resembles values reported for other scavenging amphipods (Nyssen et al., 2005). *Anonyx* and *Onisimus* are among the most common necrophages in Arctic waters, and are attracted to baited traps year-round (Legeżyńska et al., 2000; Nygård et al., 2009). In addition to a clear preference for carrion, they also consume other food sources in summer (Sainte-Marie & Lamarche, 1985; Sainte-Marie, 1986; Legeżyńska, 2008), but little remains known about trophic strategies outside this season. The current results suggest that lysianassoids have a highly carnivorous diet throughout the year. Winter data confirm earlier observations of scavenging and predatory behaviour in *A. sarsi* with polychaetes and crustaceans being the primary prey (Oliver & Slattery, 1985; Sainte-Marie, 1986; Ingolfsson & Agnarsson, 1999; Legeżyńska, 2008). The shallow-water Svalbard population of *A. nugax* exhibits ontogenetic dietary changes, but generally relies on carrion that comprises up to 90% of the food ingested in winter and summer (Legeżyńska, 2008; this study). Predation on zooplankton has been proposed as a major feeding strategy of *A. nugax* based on the high levels of calanoid FA biomarkers [$\sum$20:1(n-9) + 22:1 (n-11) = 32.9%] displayed by specimens caught at 250 m in the Barents Sea (Graeve et al., 1997). Low amounts of calanoid biomarkers (from 2.9 to 8.1% of total FAs, depending on size and season) in specimens collected in the Spitsbergen fjords indicate much lower consumption of Calanoida. The mass mortality of planktonic organisms (mainly Calanoida) has been observed during summer in the Spitsbergen fjords (Węsławski & Legeżyńska, 1998; Zajączkowski & Legeżyńska, 2001). Zooplankton die in summer from osmotic shock in areas with strong salinity gradients created by glacial run-off, and they are a major food source for *O. caricus* that inhabits glacial bays (Zajączkowski & Legeżyńska, 2001; Legeżyńska, 2008). In winter, when melting stops and fewer dead zooplankton settle to the bottom, *O. caricus* consumes mostly carrion and complements its diet with polychaetes and crustaceans. Unfortunately, that *O. caricus* feed on calanoids in summer could not be proven by the results of FA analysis. However, only a single specimen was examined and since this individual was characterized by a low lipid content and quite an unusual lipid signature dominated by phospholipids, its FA profile that was poor in 20:1(n-9) and 22:1(n-11) might not be typical of the population. Nevertheless, *A. nugax* and winter specimens of *O. caricus* displayed the highest levels of calanoid biomarkers among the amphipods analysed, which, combined with their δ^{13}C signatures, suggest at least partial dependence on planktonic food depleted in δ^{13}C. As is consistent with their carnivorous diet, *Anonyx* and *Onisimus* species are characterized by high δ^{15}N values in both winter and summer. As predators and scavengers, lysianassoids typically occupy a high trophic position in local food webs (Hobson et al., 2002; Iken et al., 2010; Kędra et al., submitted). Trophic levels derived from δ^{15}N mirror different feeding preferences of these lysianassoids. Small, opportunistic scavengers such as *O. minuta* and *O. edwardsii* consistently occupy lower trophic positions as opposed to large, highly mobile predators and scavengers such as *A. nugax* and *O. caricus* (Legeżyńska, 2008).

The amounts of 18:1(n-9) noted in *Lepidepecreum umbo* and summer specimens of *O. edwardsi* (group C) were surprisingly high and similar to those observed in highly specialized Antarctic and deep-sea lysianassoid necrophages (Bühring & Christiansen, 2001; Graeve et al., 2001; Nyssen et al., 2005). Neither *L. umbo* nor *O. edwardsii* seem to be particularly specialized scavengers. *O. edwardsii* has been noted frequently in baited traps (Legeżyńska et al., 2000), but its summer diet is highly versatile with large carrion as a

minor food source (Legeżyńska, 2008). Moreover, in both seasons this species is characterized by lower $\delta^{15}N$ values compared to larger species such as *A. nugax*, *A. sarsi* and *O. caricus*, thus is presumed to feed more omnivorously. Virtually nothing is known about the life mode of *L. umbo*. The mandible structure and the results of gut content and FA analyses clearly identify *L. umbo* as a carnivorous species, but the current results do not indicate whether the species feeds on live animals or dead material. Similarly to its congeners, *L. umbo* has never been reported in baited traps (Lowry & Stoddart, 2002; authors' observations) so scavenging cannot be presumed to be its primary feeding strategy. Additionally, its relatively small size (up to 12 mm) and weak gnathopods indicate that this species is not likely to be a highly adapted predator. The gut content suggests opportunistic scavenging or grazing on soft-bodied sessile organisms and micropredation on tiny amphipods. In consideration of the above, the 18:1(n-9) and 18:1(n-9)/18:1(n-7) ratio should be used cautiously as trophic indexes in evaluating the degree of carnivory in scavenging amphipods. The suitability of the 18:1(n-9)/18:1(n-7) ratio as a trophic marker has been questioned, because it might be correlated with total lipid content (Stübing & Hagen, 2003). However, this is not the case with *O. edwardsii* or *L. umbo*, the lipid content of which is within ranges observed for other lysianassoids. It has been also proposed that higher amounts of oleic acid found in some lysianassoids might originate partially from de novo synthesis in response to short periods of satiety followed by long periods of starvation (Nyssen et al., 2005). However, the opportunistic *O. edwardsii* would unlikely face starvation in its habitat (Legeżyńska, 2008); therefore, the accumulation of 18:1(n-9) may simply reflect more voracious feeding on highly degraded carrion-derived organic matter in summer (Graeve et al., 2001). Further detailed studies are required to explain the reasons for extremely high amounts of 18:1(n-9) FA in some lysianssoid species.

Another group designated by multivariate analysis (group B) consists of species representing different life styles and feeding modes: two oedicerotids (*A. phyllonyx* and *P. lynceus)*, the stegocephalid *S. inflatus* and the eusirid *Rhachotropis aculeata*, which are generally characterized by elevated levels of PUFA (up to 52.3% in *R. aculeata*). Enequist (1949) described oedicerotids as detritus-feeders that ingest accumulations of organic detritus in the mud–water interface, but they do not consume living multicellular organisms. This opinion was later well established in the literature (e.g., Chevrier et al., 1991; Buhl-Mortensen, 1996); however, detailed studies on mandible morphology and gut content analyses provide evidence that many species of the family prey on meiofauna (Beare & Moore, 1998; Yu et al., 2003). Similar to the oedicerotids studied by Dauby et al. (2001) in the Weddell Sea, *A. phyllonyx* and *P. lynceus*, can be classified as deposit-feeders/predators. Gut content revealed that they feed primarily on phytoplankton-derived detritus and different fractions of meiofauna. This finding is consistent with their FA signatures, which are rich in diatom and flagellate markers. High amounts of FAs suggested as bacterial markers [odd-number FAs + 18:1(n-7) (Stevens et al., 2004)] might reflect direct feeding on bacteria taken with phytodetritus and/or the consumption of small, bacteriovorus organisms. Additionally, considerable amounts of arachidonic acid, 20:4(n-6), were found in *A. phyllonyx* (9.9%). It has been suggested that high levels of 20:4(n-6) in amphipods come from macroalga ingestion (Graeve et al., 2001; Nyssen et al., 2005). This FA, however, is also important in many foraminiferan species (Gooday et al., 2002; Suhr et al., 2003); thus, elevated levels of it in macrobenthic taxa might also be attributed to feeding on Foraminifera (Würzberg et al., 2011). Considering the results of gut content analysis and the fact that macroalgal vegetation is not found in the muddy habitats populated by *A. phyllonyx*, it is more probable that high levels of 20:4(n-6) originates from foraminiferans. The mouthpart morphology of this species indicates it is well adapted to exploit this kind of food. *A. phyllonyx* has robust mandibles with strongly reduced incisors and powerful molars capable of grinding hard structures such as foraminifera tests. In contrast, the mandibles of *P. lynceus* with roughly toothed incisors and laciniae mobilis and non-triturative molars are designed for predation on soft-bodied organisms (Watling, 1993). In Svalbard fjords, *P. lynceus* tends to form dense aggregations on shallow vegetated bottoms (authors' observations). It is possible that this distribution is linked to the mass occurrence of its preferred prey, harpacticoid copepods, in phytal communities (Huys et al., 1996; authors' observations). Oedicerotids, including *A. phyllonyx*, feed as they burrow through superficial layers of loose sediments (Enequist, 1949). *P. lynceus*,

which is a stronger swimmer (Sainte-Marie & Brunel, 1985) with well-developed eyes and large gnathopods, can also feed as an epibenthic predator. Despite their mixed diets, the nitrogen signatures of oedicerotids are similar to those noted in highly carnivorous lysianassoids. Enriched nitrogen signatures in *A. phyllonyx* likely result from feeding on nematodes, which are an important component of its diet according to the current study. Nematodes display a wide range of δ^{15}N signatures, with the highest in predatory species (Moens et al., 2005). Unidentified nematodes collected in the Kongsfjorden sublittoral had relatively high nitrogen signature of 9.06‰, which placed them at the third trophic level in the local food web (Kędra et al., submitted). Similarly, high δ^{15}N values were reported in nematodes from the deep north-east Atlantic (Iken et al., 2001). Compared with *A. phyllonyx*, *P. lynceus* occupies a lower trophic position, which can be explained by the prevalence of harpacticoids in its diet. Harpacticoida operate at low trophic level ingesting small autotrophic and heterotrophic organisms, organic matter, detritus and bacteria associated with detritus (Huys et al., 1996), and this feeding mode is reflected in their low δ^{15}N signature. The isotopic analysis of the shallow-water food web in Kongsfjorden showed that the δ^{15}N value of Harpacticoida (4.34‰) was well below that of nematodes (Kędra et al., submitted). The other explanation for the high nitrogen isotope ratios in *A. phyllonyx* and *P. lynceus* could be from their feeding on detritus. Detrital lumps containing dead phytoplankton cells, faecal pellets of pelagic grazers, marine snow, animal remains and bacteria and fungi are isotopically enriched; thus, the assimilation of such reworked material could upgrade the δ^{15}N signature of deposit feeders (Iken et al., 2001, 2010 and references therein).

Despite being of similar FA composition, *Stegocephalus inflatus* occupies quite a different ecological niche than the two oedicerotids described above. According to Enequist's observations (1949), this species spends long periods standing or walking extremely slowly on substrate surfaces without any tendency to burrow, but it is also a 'rapid swimmer'. The current results of gut content analysis suggest they graze on sessile benthic invertebrates, which concurs with previously published information on the feeding strategies of Stegocephalidae (Moore & Rainbow, 1984; Moore et al., 1994). In general, they are described as micro-predators that feed on cnidarians; however, at least one genus (*Andaniotes*) is adapted to scavenging (Berge & Vader, 2001). Since cnidarians are iron-rich, amphipod consumers developed detoxification mechanisms by producing ferritin crystals in the ventral caeca. While the presence of such crystals in gut contents is an attribute of many stegocephalid species, their production is not universal within the family and can depend on local feeding opportunities. Since *S. inflatus* exhibits variability in the occurrence of ferritin crystals, it is inferred that the species does not rely exclusively on cnidarians (Moore & Rainbow, 1984; Moore et al., 1994). The current results concur with these observations since not all specimens analysed contained ferritin crystals and none of them contained cnidarian nematocysts. Nevertheless, the FA signature of *S. inflatus* provides further evidence of feeding on cnidarians as reflected in the elevated levels of 22:5(n-3) and 20:1(n-7) FAs. There are few marine animals that contain appreciable levels of these FAs. However, high amounts of 22:5(n-3) were found in different groups of polar Cnidaria, such as scyphomedusae (Nelson et al., 2000) and Actinaria (Graeve et al., 1997), and elevated levels of 20:1(n-7) were noted in the sea anemone *Anthosactis janmayeni* from north-east Greenland (Graeve et al., 1997). Feeding on sponges is evident from the presence of sponge spicules in some individuals. Although *S. inflatus* is rather opportunistic when it comes to prey selection, its choices are perhaps limited to soft-bodied sessile invertebrates. Its mandibles, which are characterized by roughly toothed incisors and reduced molars, can successfully snip off the soft tissues of sedentary organisms (Watling, 1993), but they cannot cope with hard items such as bryozoans with mineralized skeletons. It is also unlikely that *S. inflatus* can catch mobile prey because of its weak gnathopods. Feeding on a limited selection of organisms might be why the FA composition is generally similar between specimens from Svalbard (this study) and north-east Greenland (Graeve et al., 1997). The highest δ^{15}N values of all amphipod taxa were noted in *S. inflatus*. The same was reported from the Canadian Arctic (Hobson & Welch, 1992). This could have been caused by feeding on sponges and cnidarians, since their nitrogen-stable isotope ratios can be surprisingly high (Hobson & Welch, 1992; Iken et al., 2001; Hobson et al., 2002; Nyssen et al., 2005; Mincks et al., 2008; Bergmann et al., 2009).

The life style and trophic specialization of *Rhachotropis aculeata* (Eusiridae) obviously differ from other species in group B. It is a large (up to 45 mm), far-ranging species with strong swimming abilities (Sainte-Marie & Brunel, 1985). Eusirids are epibenthic and pelagic carnivores well adapted for this life style thanks to their large, multi-faceted eyes, complex antennual calceoli and powerfully developed gnathopods and maxillipedes (Bousfield & Hendrycks, 1995). Published information on the *Rhachotropis* diet suggests pelagic crustaceans are its preferred prey (Enequist, 1949; Dauby et al., 2001; Fanelli et al., 2009). Unfortunately, because this species was scarce in the study material, no individual from the Svalbard fjords was dissected. High levels of phytoplankton-derived FAs indicate strong links to pelagic production. However, it is evident from the high δ^{15}N signature that these FAs were not assimilated directly, but through the consumption of zooplankton or benthic invertebrates. The trace amounts of calanoid markers indicate that pelagic copepods do not comprise the bulk of the *R. aculeata* diet.

The species in group A are characterized by the distinct dominance of phytoplankton-derived FAs. Their isotopic signatures indicate they are primary consumers with TL estimates of between 2.2 and 2.6 in summer (this study). Gut content and FA analyses revealed diatoms are the main food source, with diatom markers of up to 48.7% in *Weyprechtia pinguis*. The large accumulation of lipid reserves is expected in animals fuelled by seasonally variable primary production. These species, however, store low to moderate lipid reserves (this study); therefore, their overwintering strategy probably includes a switch to omnivorous feeding and the use of all accessible resources. In summer, all group A species rely mostly on phytodetritus, although they also display different feeding modes and use different fractions of food available.

Pontoporeia femorata is a subsurface deposit-feeder that uses mainly phytodetritus from the upper 0–0.5 cm layer of sediment (Lopez & Elmgren, 1989; Byrén et al., 2006). Hill et al. (1992) reported small seasonal variation in lipid levels in the Baltic population of *P. femorata* with TAG consistently as the main lipid class. The same was observed in Spitsbergen specimens (this study). This species has no need to store lipids since it uses other food sources that are continually available in sediments such as microbial aggregations or meiofaunal organisms, and it can supplement its diet through predation on temporary meiofauna such as recently settled bivalves (Hill et al., 1992; Ejdung & Elmgren, 1998). In both seasons, FA profiles are dominated by diatom markers indicating these microalgae are the principal food sources of *Pontoporeia*. In winter, when primary production stops, these FAs can be derived through feeding on aged phytodetritus buried in sediments by bioturbators (Josefson et al., 2002). Feeding on this refractory material would explain the elevated levels of bacterial markers detected in winter specimens.

Weyprechtia pinguis is a shallow-water species, typically found on mixed bottoms overgrown with macroalgal vegetation (Just, 1970; Lippert et al., 2001; Kaczmarek et al., 2005). In winter, at least part of the population colonizes the ice underside using this temporary habitat as feeding and nursery grounds (Pike & Welch, 1990; Werner, 2006). The species is a grazer feeding on sea-ice algae and microphytobenthos, but it also consumes phytodetritus. Summer specimens contained in their guts not only the epiphyte *Licmophora gracilis*, but also *Nitschia frigida* and *Entomoneis* sp., both of which are typical sea ice species (Hop et al., 2002; J. Wiktor, personal comm.) and which must have been preserved in the sediments until July/August.

Other species from this group are generally considered as filtrators that rely either on sedimenting pelagic production or settled phytodetritus from bottom surfaces. As primarily tube dwellers, ampeliscid amphipods are generally dependent on organic matter that sinks through the water column or is transported horizontally from other locations. They can be classified as 'interface feeders' using their antennae that project outside their tubes to collect particles both from sediment surfaces and the water column (Enequist, 1949; Dauby et al., 2001). The balance between suspension feeding and surface detritus feeding depends on several factors such as species morphology, local/seasonal availability of suspended particulates in water columns and phases of tube formation (Enequist, 1949; Mills, 1971). *A. eschrichtii* and *H. tubicola* seem to exhibit both feeding modes. They are rich in phytoplankton markers and depleted in both isotopes, which indicates diets based on POM. At the same time, gut content analysis reveals that benthic elements such as diatoms, protist cysts and foraminiferans comprise a considerable portion of the food ingested.

Caprella septentrionalis is reported commonly on vegetated bottoms (Lippert et al., 2001; Włodarska-Kowalczuk et al., 2009). In spite of the great variety in feeding mechanisms reported for caprellids (Caine, 1977), an extensive study of their diets based on examinations of 743 species from all around world revealed that their major food source is detritus, while the consumption of planktonic elements such as diatoms and flagellates is extremely low (Guerra-Gracia & Tierno de Figueroa, 2009). In contrast, the examination of gut contents of *C. septentrionalis* indicated diatoms were the dominant food item. This, along with its typical upright posture, possession of densely setose antennae 2 and grooming behaviour, favour filter-feeding as its main nutritional strategy (Caine, 1977; Guerra-Gracia, 2002). Nevertheless, other strategies such as predation and scraping might also be possible as guts contained epiphytic diatoms, egg packets and the remains of crustaceans. The FA signature and the position of *C. septentrionalis* in the MDS plot suggest somewhat opportunistic feeding; this corresponds to general feeding observations reported for *Caprella* (Guerra-Gracia & Tierno de Figueroa, 2009). On the other hand, depleted isotopic signatures indicate that freshly sedimented phytodetritus is the main source of food.

Information on the biology and ecology of *Melita* and *Unciola* species occurring in the Arctic is sparse. In the Spitsbergen fjords, *Melita* is represented by three species with different habitat preferences: *M. formosa* is typical of muddy sediments, while *M. dentata* and *M. quadrispinosa* prefer mixed bottoms of the outer fjords (Legeżyńska & Węsławski, own data). They are free-swimming and free-crawling animals with robust gnathopods and powerfully developed limbs (Sainte-Marie & Brunel, 1985; Jarrett & Bousfield, 1996). The gut content of *M. formosa* and *M. quadrispinosa* is dominated by plankton-derived elements, but their enriched carbon isotopic signatures suggest they feed on deposits. Enequist (1949) observed *M. obtustata* collecting detritus near small irregularities in bottom surfaces using their second pairs of antennae and gnathopods. Similar feeding strategies are likely employed by *Melita* spp. that occur in Svalbard fjords, and this might be evidenced by the presence of very fine mineral particles in their guts. The FA profile of *M. formosa* concurs with a diet consisting mainly of phytodetritus. In addition to high amounts of diatoms and flagellate markers (over 50% of total FAs), levels of 16:0 are elevated which might be indicative of ingesting degraded macroalga material (Graeve et al., 2002) or high amounts of flagellates (Stübing & Hagen, 2003). Similarly, *M. nitida* have been observed feeding on microalgae, detritus and macroalga debris (Zimmerman et al., 1979).

Unciola leucopis typically inhabits the compacted soft sediments of outer deep fjord basins (Legeżyńska & Węsławski, own data). Gut content, FA and stable isotope signatures indicate that this species is fuelled mostly by primary production from the water column. The current results concur with general information on the feeding ecology of Corophiida, which are classified as filter-feeders that use setose appendages to trap organic particles from the water drawn through tubes by beating pleopods or that use second antennae to scrape settled phytodetritus from substrate surfaces (Myers & Lowry, 2003).

Conclusions

In conclusion, each method applied in this study provided valuable information on different aspects of amphipod feeding ecology, supporting the utility of applying multi-method approaches in trophic studies. Three main feeding strategies detected among the species studied included: scavenging/predatory, deposit-feeding/predatory and phytodetrivory. Benthic amphipods encompass three trophic levels with primary and secondary consumers being clearly separated by differences in $\delta\ ^{15}N$ signatures.

No evidence was found of major seasonal dietary shifts in the amphipods studied. The species set, however, was dominated by opportunistic deposit feeders and carnivores which utilize multiple food sources that are available in shallow polar waters year-round, and are thus not affected directly by variability in water column production. Winter material from the deep-sea would permit making comparisons of the overwintering strategies of amphipods inhabiting areas with different food supply regimes.

The current results support observations on the importance of a detrital food bank in supporting polar benthic communities. Further detailed studies concerning the role of different components of detritus, particularly ice- and macrophyte-derived material, in fuelling benthic fauna are essential to develop a better understanding of food web processes in Arctic fjords.

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