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Arctic pelagic amphipods: lipid dynamics and life strategy

ANGELINA KRAFT[1], MARTIN GRAEVE[1]*, DIETER JANSSEN[1], MICHAEL GREENACRE[2,3] AND STIG FALK-PETERSEN[2,4]

[1]ALFRED-WEGENER-INSTITUTE HELMHOLTZ-CENTRE FOR POLAR- AND MARINE RESEARCH, AM HANDELSHAFEN 12, 27570 BREMERHAVEN, GERMANY, [2]AKVAPLAN-NIVA, FRAM CENTRE, 9296 TROMSØ, NORWAY, [3]DEPARTAMENT D'ECONOMIA I EMPRESA, UNIVERSITAT POMPEU FABRA, AND BARCELONA GRADUATE SCHOOL OF ECONOMICS, RAMON TRIAS FARGAS 25-27, 08005 BARCELONA, SPAIN AND [4]DEPARTMENT OF ARCTIC AND MARINE BIOLOGY, FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS, UIT THE ARCTIC UNIVERSITY OF NORWAY, 9037 TROMSØ, NORWAY

*CORRESPONDING AUTHOR: martin.graeve@awi.de

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Polar regions are characterized by a strong seasonality in primary production and distinct fluctuations in food supply. The storage of energy in the form of lipids is expected to follow a seasonal pattern; however, year-round observations are lacking. The seasonal variations of lipid classes and fatty acid compositions of four pelagic amphipods have been investigated. Individuals were collected at various depths during summer and winter expeditions to the Fram Strait and Svalbard archipelago (78°–81°N). Our results show a year-round dominance of wax esters and triacylglycerols over phospholipids for *Themisto abyssorum*, *Themisto libellula*, *Themisto compressa* and *Cyclocaris guilelmi*. High levels of the *Calanus*-marker fatty acids 20:1 and 22:1 (both isomers) during summer and winter indicated that all four species are part of the *Calanus*-based food web. Specific fatty acid trophic markers for diatoms and flagellates indicated that the lipid-based energy transfer could be traced back to the respective algal sources. We found a distinct difference between animals collected from very deep and shallow waters, which indicates that the lipid reservoir of these amphipods and their biochemical modifications seem to buffer seasonal variations in available prey and to allow an active, predatory life-style year-round in Arctic waters.

KEYWORDS: pelagic amphipods; trophic relationships; lipids; fatty acids; polar night

INTRODUCTION

Pelagic amphipods are an important part of the Arctic marine food chain, transferring energy from herbivorous *Calanus* species to higher trophic levels (Conover, 1988; Scott *et al.*, 1999; Falk-Petersen *et al.*, 2009a). Hyperiid amphipods of the genus *Themisto* are important food items for capelin (*Mallotus villosus*), cod (*Gadus morhua*), polar cod (*Boreogadus saida*), ringed seal (*Phoca hispida*), harp seal (*Phoca

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groenlandica) and sea birds (Bradstreet and Cross, 1982; Lønne and Gulliksen, 1989; Lydersen *et al.*, 1989; Dalpadado *et al.*, 2000, 2001, 2008; Hobson *et al.*, 2002; Dalpadado and Bogstad, 2004; Noyon *et al.*, 2009; Wold *et al.*, 2011). Analysis of the lipid composition of zooplankton has been used to address food web relationships in marine ecosystems and for studying the life-cycle strategy of Arctic pelagic animals. With seasonality being a crucial feature in structuring plankton communities, the investigation of temporal influences in the lipid-based energy flux at high latitudes is of fundamental importance (e.g. Falk-Petersen *et al.*, 2000, 2007; Leu *et al.*, 2006). In this context, the dominance of biomarkers in lipid class and fatty acid compositions can provide trophic information over a time scale of several weeks to months (Graeve *et al.*, 1994a, 2005). Thus, this technique is considered to produce a prolonged understanding of trophic structure and contrasts with snapshot insights provided by the classical approaches such as gut content analysis (e.g. Stübing *et al.*, 2003). Pelagic zooplankton represent an extensively studied group with regard to their lipid and biochemical composition (e.g. Graeve *et al.*, 1994a; Falk-Petersen *et al.*, 1999; Lee *et al.*, 2006; Mayzaud *et al.*, 2007). Especially, the composition and function of lipids in the life-cycle of calanoid copepods and krill are well documented in polar waters (Sargent and Henderson, 1986; Hagen *et al.*, 1996; Falk-Petersen *et al.*, 2000, 2009b; Pond and Tarling, 2011).

Three hyperiid amphipod species comprise the genus *Themisto* in northern latitudes: *T. libellula*, a large Arctic species associated with cold, polar water masses, its subarctic congener *T. abyssorum*, which is transported to the Arctic by inflowing North Atlantic water masses and *T. compressa*, a North Atlantic species with its major distribution area in the southern Norwegian Sea (Kraft *et al.*, 2011). *Themisto libelulla* and *T. abyssorum* have been studied over the past decade with regard to their food sources, variations in distribution, reproductive strategies, abundances and summer lipid compositions, while little is known about the deepwater species *Cyclocaris guilelmi* (Bousfield, 1951; Percy, 1993; Koszteyn *et al.*, 1995; Auel *et al.*, 2002; Dalpadado *et al.*, 2008; Marion *et al.*, 2008; Noyon *et al.*, 2009, 2011, 2012; Kraft *et al.*, 2011, 2012, 2013b).

Investigations of the lipid class compositions of *T. abyssorum* and *T. libellula* during Arctic summer in the Fram Strait, Svalbard Fjords and central Arctic Ocean, indicated that dominant lipid classes in both species consisted of wax esters and triacylglycerols (Auel *et al.*, 2002; Dale *et al.*, 2006; Noyon *et al.*, 2011). Both lipid classes represent the major energy storage in most Arctic calanoid copepods (Falk-Petersen *et al.*, 2009a). However, few studies from the polar night as well as from deepwater exist from high Arctic waters. To understand the life strategy of these in amphipods, living in the high Arctic, it is important to understand the seasonal migration as well as seasonal lipid dynamics and feeding mode. The aim of this study was to investigate the feeding strategies of three epipelagic and one deepwater species associated with different depth zones. Specimens from summer and winter from different depths were analyzed for length–frequency distribution, dry weight, total lipids, lipid class, fatty acid and fatty alcohol composition. The seasonal information of the lipid dynamic is expected to provide a new understanding of the life strategy of these free-swimming predators.

METHOD

Study area

Sampling sites were located around the archipelago of Svalbard and in the Fram Strait. Both areas are characterized as transition zones between Atlantic and Arctic water masses (Fig. 1). The Fram Strait, a sea-passage with a mean depth of ~2600 m, located west of Svalbard, represents the only deep connection between the central Arctic Ocean and its surrounding seas. Already the early pioneers in physical oceanography recognized the complex oceanographic characteristics of this area, featuring the meridional hydrographic fronts of the cold polar current on the Greenland side and the warm Atlantic current west of Svalbard (Helland-Hansen and Nansen, 1909). The northward flowing West Spitsbergen Current, located over the upper shelf slope in the eastern Fram Strait, transports relatively warm Atlantic water into the Arctic Ocean, while the southward flowing East Greenland Current, with a core over the western shelf slope, exports colder and less-saline Arctic waters out of the Arctic basin (Schauer *et al.*, 2008). In the Fram Strait, below the relatively warm Atlantic water layer, low-temperature waters prevail, namely the Arctic Intermediate Water and Norwegian Sea Deep Water, the latter modified by polar origin deepwater masses (Schlichtholz and Houssais, 2002).

Net sampling

In general, the animals from the "R/V *Polarstern* ARK" summer cruises were from depths of 600–2000 m, the IMR summer cruises from the upper 100 m and ARCTOS winter cruises from the upper 200 m, except for one sample at Sofiadjupet. Pelagic amphipods were sampled during four cruises onboard the research vessels R/V *Polarstern* and R/V *Helmer Hanssen* at a total of 53 stations in the coastal waters of Svalbard and across the Fram Strait (Table I, Fig. 1). During summer, sampling took place from the surface to 2000 m water depth at 24 stations along a 78°50′N transect and at the long-term

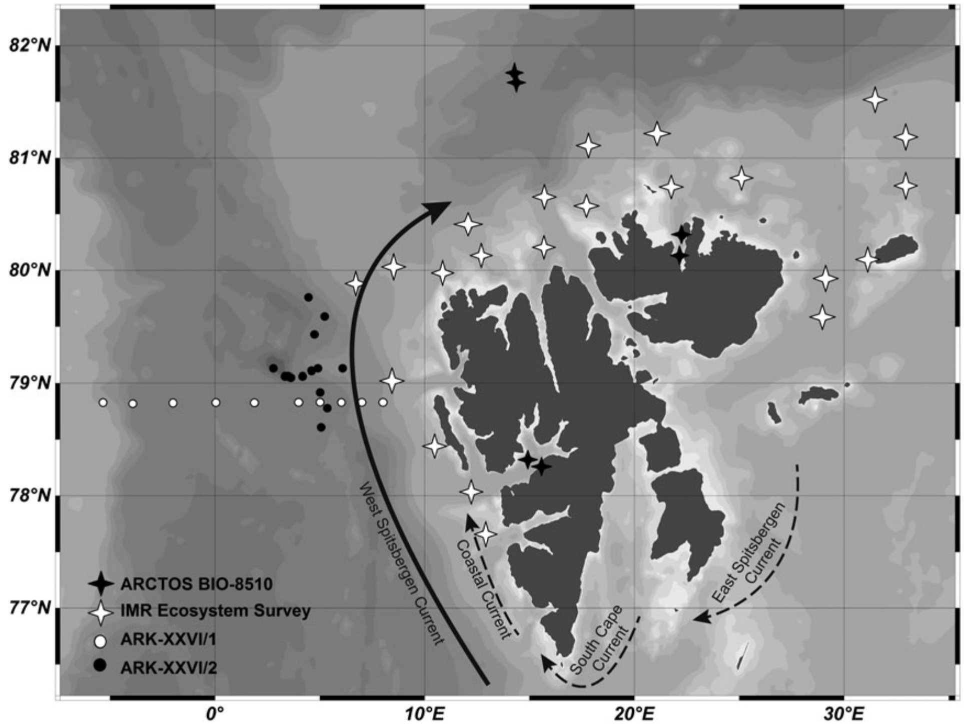

Fig. 1. Map of sampling stations in the eastern and across the central Fram Strait and around Svalbard, Arctic Ocean. Black stars: stations during the ARCTOS BIO winter cruise in January 2012; white stars: stations during the IMR Ecosystem Survey cruise in August 2011; black circles: stations during the ARK-XXVI/2 expedition to the long-term observatory HAUSGARTEN in July and August 2011 the eastern Fram Strait; white circles: sampling stations on a 78°50′N transect across the central Fram Strait (ARK-XXVI/1) in June and July 2011.

Table I: Station and sampling information during four research cruises to the Fram Strait and Svalbard in summer 2011 (ARK-XXVI/1, ARK-XXVI/2, IMR Ecosystem Survey) and winter 2012 (ARCTOS BIO-8510)

Cruise	ARCTOS BIO-8510	IMR Ecosystem Survey	ARK-XXVI/1	ARK-XXVI/2
Number of stations	6	22	10	15
Month/year	1/2012	8/2011	6 and 7/2011	7 and 8/2011
Bottom depth (m)	2417	−850	2736	5578
Gear	MIK-net 1500 μm	Pelagic fish trawl 10 000 μm	Multinet 1000 μm	Multinet 1000 μm

observatory HAUSGARTEN (Fig. 1). For sample collection, a large multinet (HYDRO-BIOS type Maxi with an aperture of 0.5 m^2 and nine 1000 μm net bags) was hauled at 0.8 m/s with stops at 1500, 1000, 800, 600, 400, 200, 100 and 50 m. At shallower stations, the sampling depth was adapted accordingly. The volume of water filtered in each stratum varied from 344 to 1449 m^3. Additionally, particularly large specimens of *T. libellula* (≥40 mm) were caught in August 2011 around Spitsbergen on the R/V *Helmer Hanssen* during the "IMR Ecosystem survey" cruise with a pelagic fish trawl, with an opening of 9 m and 10 mm mesh in the cod end. Winter samples of *Themisto* and the deepwater amphipod *C. guilelmi* were obtained during the ARCTOS "polar night" research cruise with R/V *Helmer Hanssen* at six sampling sites located around Svalbard (Rijpfjorden, Sofiadjupet and Isfjorden) in January 2012. During the winter cruise, sampling took place with a Methot Isaac Kidd (MIK; 3.14 m^2 opening and 1.5 mm mesh size) by trawling the net for 10 min with a speed of ~1.5 knots at three different depth intervals (20, 75 and 225 m in Rijpfjorden and 30, 60 and 225 m in Isfjorden). Owing to ice cover, no MIK tow was possible at Sofiadjupet. Instead, samples were collected with a vertically hauled WP3 net (1 m^2, 1.0 mm mesh size, at 600−2000 m).

All materials collected were immediately transferred into buckets with cold seawater and brought to a cooling container or cold room (4°C). All amphipods were sorted, determined to species level, counted and measured for their total body length (accuracy 1.0 mm, from the front of the head to the tip of the longest uropod (Dunbar, 1957)). Maturity was determined by the examination of secondary sexual characters: females were identified by the presence of oostegites among the inner coxal margin of the anterior walking legs; males were identified by the presence of penal papillae on the ventral side of the last segment of the thorax and a segmented, elongated second antenna (Dalpadado *et al*., 2008). Small individuals without recognizable sexual features were recorded as juveniles. Following identification, the specimens were quickly rinsed with Milli-Q water and deep-frozen alive at −80°C for lipid analyses.

Analyses of dry mass and total lipid content

For the determination of dry mass (DM) and length–frequency, specimens of *Themisto abyssorum* (summer: $n = 118$, winter: $n = 30$), *T. libellula* (summer: $n = 89$, winter: $n = 13$), *T. compressa* (summer: $n = 9$, winter: $n = 2$) and *C. guilelmi* (summer: $n = 47$, winter: $n = 5$) were lyophilized for 24 h and their weight determined on a microbalance (Sartorius micro 4504 MP8; accuracy 0.01 mg). Lipid classes and fatty acids were analyzed for a total of 52 amphipods, including the species *T. abyssorum* ($n = 12$), *T. compressa* ($n = 10$), *T. libellula* ($n = 21$) and *C. guilelmi* ($n = 9$). For lipid analysis, adult specimens with fully developed sexual characters (the presence of fully developed oostegites in females and a segmented, elongated second antenna in males) were used. Samples originated from water depths of 0–400 m (*Themisto* spp.) and 800–2000 m (*C. guilelmi*).

Total lipids were extracted after Folch *et al.* (Folch *et al.*, 1957) three times with 3 mL dichloromethane:methanol (2:1, v/v) from single, lyophilized (24 h) and homogenized individuals using a Potter homogenizer (Sartorius, Göttingen, Germany). The solvent was washed with 2 mL 0.88% KCl solution before the mixture was centrifuged at low speed (2000 rpm). The lipid containing organic phase was separated and evaporated under nitrogen. The lipid extract was re-dissolved in dichloromethane and taken for analysis. All extracts were kept at −20°C for further analysis. The lipid classes were separated and identified according to Graeve and Janssen (Graeve and Janssen, 2009) on a monolithic silica column (Chromolith®Performance-Si) using high-performance liquid chromatography (HPLC, LaChromElite HPLC system) with an evaporative light scattering detector (ELSD). A gradient program with combination of three solvent mixtures was used: eluent A consisted of isooctane:ethylacetate (99.8:0.2, v/v), eluent B was a mixture of acetone and ethyl acetate (2:1, v/v) containing acetic acid (0.02% (v/v)) and eluent C 2-propanol–water (85:15, v/v) (with acetic acid and ethanolamine, each 0.05% (v/v)). Total lipid content in terms of percent DM was calculated using the sum of neutral and polar lipids.

For the gas–liquid chromatographic analyses of the fatty acids and fatty alcohols, aliquots of the total lipid extract were taken. Methyl esters of fatty acids were prepared by transesterification under nitrogen atmosphere with 3% concentrated sulfuric acid in methanol for 4 h at 80°C. The resulting fatty acid methyl esters and free fatty alcohols were extracted with hexane and their composition determined with a Hewlett Packard 6890 gas liquid chromatograph on a 30 m wall-coated capillary column (i.d. 0.25 mm, film thickness: 0.25 µm; liquid phase DB-FFAP) using temperature programing according to Kattner and Fricke (Kattner and Fricke, 1986). Fatty acids and alcohols were quantified with an internal tricosanoic acid methylester standard (FAME, Sigma-Aldrich, USA) and identified by comparing the retention time with those of known standard mixtures. Based on fatty acid compositions, four biomarker ratios were calculated. These included the ratio of PUFA/SFA (polyunsaturated versus saturated fatty acids) and the quotient of the fatty acid isomers 18:1(n−9)/18:1(n−7). Both are used as relative indicators of carnivory in marine zooplankton (e.g. Graeve *et al.*, 1997; Falk-Petersen *et al.*, 2000; Nelson *et al.*, 2001; Auel *et al.*, 2002, Legezynska *et al.*, 2012). To further differentiate between a diatom- and a flagellate-based diet composition, the ratios of EPA/DHA (eicosapentaenoic versus docosahexaenoic acid, 20:5(n−3)/22:6(n−3)) and 16:1(n−7)/16:0 were calculated (Graeve *et al.*, 1994a; Nelson *et al.*, 2001; Auel *et al.*, 2002) (Table II).

In order to assess the differences in the compositions between different species and depths, joint ordination of the three compositional data matrices of fatty acids, fatty alcohols and lipid classes was performed using correspondence analysis (CA) (Greenacre, 2007; Greenacre and Primicerio, 2013). Computations were carried out using the package ca (Nenadić and Greenacre, 2007) in R (R core team, 2014). CA has been shown to be suitable for compositional data in the presence of a large number of zeros (Greenacre, 2010, 2011). Because of the small sample sizes, distribution-free univariate permutation tests were conducted, using the R function oneway_test in the package coin (Hothorn *et al.*, 2008), and multivariate permutation tests using function permutest in the package vegan (Oksanen *et al.*, 2011). When several tests were performed jointly, the multiple comparison procedure of Benjamini and Hochberg (Benjamini and Hochberg, 1995) was used to control the false discovery rate.

Table II: Trophic markers and ratios commonly determined in fatty acid profiles [Graeve et al. 1994a, 1994b, 1997 (a); Falk-Petersen et al., 1987, 1999 (b); Auel et al., 2002 (c); Scott et al., 2002 (d); Legezynska et al., 2012 (and references therein) (e)]

Fatty acid	Trophic marker
16:0	Carnivory (a,b,c)
16:1(n−7)	Spring bloom (diatoms) (a,b)
16:4(n−1)	Diatoms/ice-algae (a,b)
18:1(n−9)	Carnivory (a,b)
18:2(n−6)	Chlorophytes or cyanobacteria (a,b,c,d,e)
20:1(n−9)	*Calanus* spp.
20:5(n−3)	Diatoms (a,b)
22:1(n−11)	*Calanus* spp. (a,b)
22:6(n−3)	Flagellates, e.g. the presence of *P. pouchetii* in the diet of *Calanus* (a,b,c)
Fatty acid ratios	
18:1(n−9)/ 18:1(n−7)	High values (>3) as indicator for increasing carnivory in marine zooplankton (d,e)
20:5(n−3)/ 22:6(n−3)	High ratio—diatom-originated diet; low ratio—flagellate-based diet (c,d,e)
PUFA/SFA	Increasing value may be used as an indicator for dominance of carnivorous versus herbivorous feeding; however also increases under starvation conditions (c.d.e)
Fatty alcohol ratio	
22:1(n−11)/ 20:1(n−9)	Indicates different copepod species in diets of carnivore zooplankton; e.g. ∼2:1 refers to *C. hyperboreus* and ∼1.1:1 or less to *C. finmarchicus* (a,b)

RESULTS

DM and length–frequency analysis

Biometric measurements were taken of different stages (females, males and juveniles) of the pelagic amphipods *T. abyssorum*, *T. compressa*, *T. libellula* and *C. guilelmi*. Relationships between DM and length and the length–frequency distribution are shown in Fig. 2. For *T. abyssorum* and *C. guilelmi*, the relationship of dry weight to total body length is modeled significantly higher in winter than in summer ($P = 0.001$ and 0.047, respectively), whereas for *T. libellula*, the relationship is significantly lower in winter ($P = 0.024$). For *T. libellula*, the slope of the winter relationship is also significantly steeper than for summer ($P = 0.045$). The low sample sizes for the summer and winter samples for *T. compressa* do not support any significant differences. A cumulative frequency analysis (Fig. 3) showed that the *T. libellula* population consisted of 3 year classes, while *T. abyssorum* consisted of 2 year classes. We found a similar mean total body length and DM of *Themisto* spp. females and males during summer and winter. For *T. abyssorum*, juvenile individuals were smaller in summer samples than in winter samples (*P*-values for difference in total body length and dry weight are $P = 0.0002$ and $P < 0.0001$, respectively). Large adult *T. libellula* were sampled in pelagic fish trawls during August 2011. The DM of adult males and females was high, ∼84 and 70 mg, respectively (Tables III and IV).

Total lipid and lipid classes

Mean percentages of the seasonal total lipid content as a percentage of DM (TL%) of adult specimens ranged from a modest 8.0–13.3% in *T. abyssorum*, 6.9–29.0% in *T. compressa* and 7.9–23.5% in *T. libellula* to a substantial 27.2–27.6% in *C. guilelmi* (Fig. 4). The individual total lipid content of the amphipods investigated ranged from 0.3 to −18.5%, showing the overall range of lipid accumulation according to species, stages and season. However, almost no differences in the share of total lipids in summer and winter samples of *C. guilelmi* were observed. *Themisto libellula* collected on the IMR summer cruise had a high lipid content (mean 23.5%) with relatively low variance, significantly above the other summer as well as winter values. These results probably reflected the larger size of these animals rather than season. No significant differences were observed between adult males and females during both seasons. Based on the multiple comparison procedure, there was only one inter-species significant difference found in TL%, between *C. guilelmi* and *T. abyssorum* (means are 27.3 and 10.6, respectively ($P = 0.002$)). There was no significant relationship observed between TL% and DM. TL% in *T. abyssorum* and *T. compressa* was higher during the winter period, with a mean of 13.3% for *T. abyssorum* and 29.0% of *T. compressa* (Table IV), whereas TL% was on average lower in the winter samples for *T. libellula*, but these differences are not statistically significant according to the univariate permutation tests.

The lipid class compositions showed inter-specific similarities: wax esters comprising the major lipid class in summer and winter samples of *T. libellula* (mean 50.5–76.7%) and *C. guilelmi* (mean 60.4–84.0%), as well as in summer samples of *T. compressa* (mean 46.1%). Triacylglycerols were the second most abundant lipid component in these three species. In *T. abyssorum*, triacylglycerols represented the most prominent lipid class (mean 39.0–59.8%) during summer and winter. Polar lipids including the membrane components phosphatidylethanolamine and phosphatidylcholine accounted for the third most abundant lipid class (mean 2.2–12.2%, with the highest values found in winter samples of *T. libellula*), followed by free fatty acids (mean 1.0–10.2%) and cholesterol (0.2–3.8%). The cell membrane component phosphatidylcholine dominated the polar lipid composition in all species, with high proportions in summer

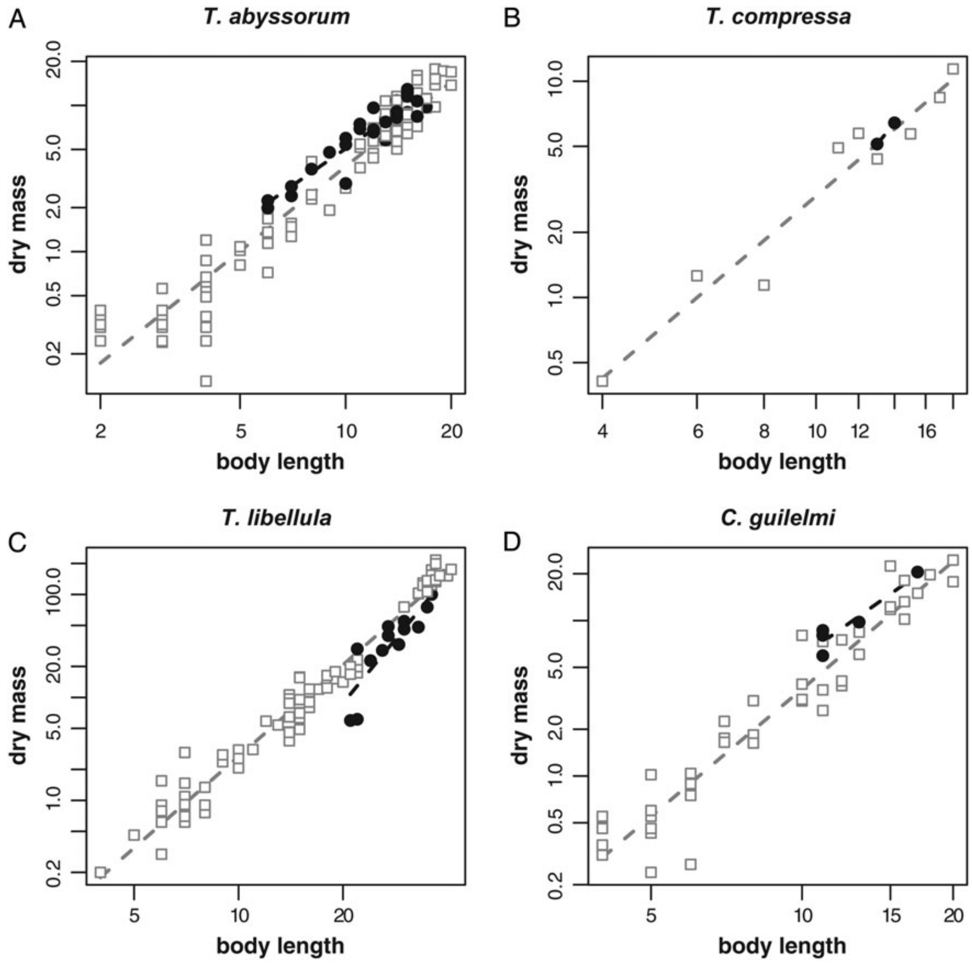

Fig. 2. Allometric relationships between dry mass (mg) and total body length (mm) and the respective length–frequency distribution (proportion, %) of *T. abyssorum* (**A**), *T. compressa* (**B**), *T. libellula* (**C**) and *C. guilelmi* (**D**) collected during four research cruises to the Fram Strait and Svalbard. Logarithmic scales on both axes. Summer: open squares, winter: solid circles.

samples of *T. abyssorum* (mean 10.7%) and winter samples of *T. libellula* (mean 9.9%). Other phospholipid classes, e.g. cardiolipine, phosphatidylserine, phosphatidylinositol, phosphatidic acid could be detected, but close to detection limit, and therefore omitted for further calculations.

Fatty acids, biomarkers and fatty alcohol composition

In all species and seasons, the typical membrane fatty acids DHA (22:6(n−3)) and EPA (20:5(n−3)) represented the two major PUFAs (mean 2.3–13.3% and 2.3–13.5% of total fatty acids, respectively) (Table V). Another PUFA frequently found in the samples was the flagellate marker 18:4(n−3), with a mean contribution of 1.2–7.0%. The share of most identified PUFAs including DHA and EPA was higher in winter samples. The most frequent monounsaturated fatty acids (MUFAs) included 20:1(n−9) (mean 9.9–22.2% of total fatty acids), 18:1(n−9) (7.6–21.5%) and 16:1(n−7) (4.2–9.1%). For the species *T. abyssorum*, *T. compressa* and *C. guilelmi*, the proportion of MUFAs was higher during the summer season. The principal SFAs in all samples were 16:0 (mean 6.6–21.3% of total fatty acids), 14:0 (2.3–8.9%) and 18:0 (0.7–2.8%). The overall SFAs contribution of *Themisto* was lower in winter (Table V).

The observed EPA/DHA ratio was low (0.6–1.6), with no significant difference between summer and winter samples. Values, which were found in the summer samples of *T. libellula* (Table V), seem to be higher compared with winter samples. In general, *T. libellula* had the highest EPA/DHA ratios (0.8–1.6) (Table V). A strong seasonal gradient between summer and winter ratios of the 18:1(n−9)/18:1(n−7) biomarker in all four species could be observed, showing higher values in summer

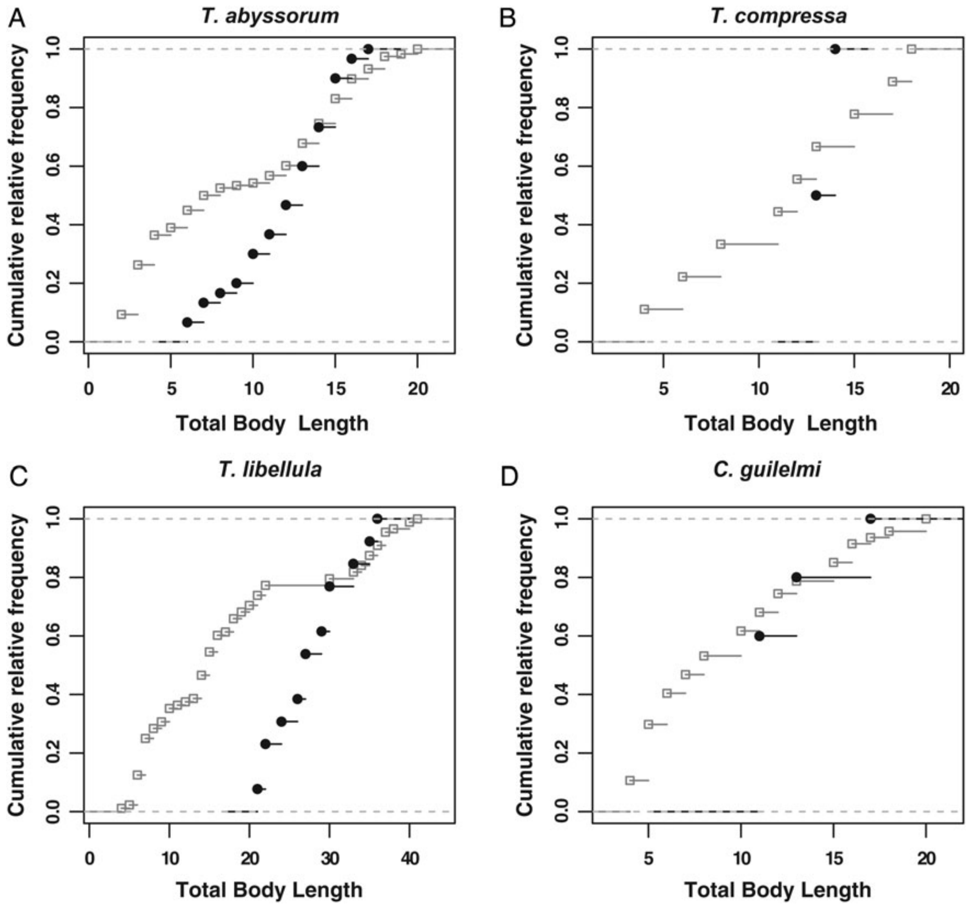

Fig. 3. Cumulative distributions of the samples for each species of the pelagic amphipods *T. abyssorum* (**A**), *T. compressa* (**B**), *T. libellula* (**C**) and *C. guilelmi* (**D**), for summer and winter seasons in each case (summer: open squares, winter: solid circles). The seasonal differences for *T. abyssorum* and *T. libellula* are observed, with many more summer individuals at earlier growth stages than winter ones. The cumulative curves meet at ~80% frequency, above which there is no seasonal differences. The winter samples for *T. compressa* and *C. guilelmi* are too small to make any conclusions.

(6.8–8.0), whereas the IMR summer samples were comparable with the winter individuals (Table V). The reverse pattern was found with regard to the PUFA/SFA ratio, with higher values in *Themisto* and *C. guilelmi* in the winter (2.0–2.3) versus the summer (0.9–1.6) samples, except for the IMR samples. For the 16:1(n−7)/16:0 ratios, no seasonal trend could be observed.

The fatty alcohol composition of the amphipods investigated consisted mainly of the long-chain monounsaturated 22:1(n−11) (mean 37.6–62.7% of total fatty alcohols) and 20:1(n−9) (21.0–38.3%). Interestingly, the high 22:1(n−11)/20:1(n−9) ratio in *T. abyssorum* (2.0), *T. compressa* (1.8) and the high ratio in *C. guilemi* (2.6 summer and 1.7 winter) collected at depths of 600–2000 m strongly indicates that *Calanus hyperboreus* is most likely the main prey in the deeper part of the Fram Strait. For animals collected from the upper 200 m in the Fram Strait and on the Svalbard shelf, the ratio varied between 1.0 and 1.5 for the *Themisto* species, indicating that *Calanus finmarchicus* and *Calanus glacialis* are the main prey. Short-chain saturated moieties such as 14:0 and 16:0 contributed with means of 1.7–18.0% and 5.9–15.7%, respectively, to the total fatty alcohol composition. In *T. abyssorum*, the short-chain fatty alcohols showed strong seasonal variations with a higher proportion in summer samples (14:0 and 16:0) (Table V).

Correspondence analysis

The three compositional datasets, of 27 fatty acids, 7 fatty alcohols and 6 lipid classes, were jointly analyzed by CA to discriminate between the nine species-by-season groups. The late summer shallow samples of large *T. libellula* (IMR Ecosystem Cruise) were kept separate here to show empirically that they are similar to the winter samples. To improve legibility, the resulting joint ordination has been separated into two plots: Fig. 5A (for the individuals) and Fig. 5B (for the variables, i.e. fatty

Table III: Allometric characteristics of the four pelagic amphipod species T. abyssorum, T. compressa, T. libellula *and* C. guilelmi *sampled during summer 2011 (ARK-XXVI/1+2, IMR Ecosystem Survey) and winter 2012 (ARCTOS BIO-8510) research cruises to the Fram Strait and Svalbard*

Species	Stage	*n*	Total body length (mm ± SD)	DM (mg ± SD)	Allometric relationships *y* (log DM) versus *x* (log TBL)
T. abyssorum					
ARK-XXVI/1 + 2 Summer	Juvenile	64	4.1 ± 1.8	0.7 ± 0.7	$y = 1.243x - 3.329$; $R^2 = 0.704$
	Female	40	14.9 ± 2.6	9.5 ± 4.2	$y = 2.464x - 6.458$; $R^2 = 0.794$
	Male	16	14.3 ± 1.5	7.9 ± 1.7	$y = 1.275x - 1.919$; $R^2 = 0.420$
ARCTOS Winter	Juvenile	4	7.2 ± 1.1	3.0 ± 1.0	$y = 2.469x - 5.554$; $R^2 = 0.958$
	Female	14	13.2 ± 2.1	8.3 ± 2.6	$y = 1.738x - 3.483$; $R^2 = 0.632$
	Male	10	13.5 ± 1.7	8.6 ± 1.6	$y = 1.020x - 0.743$; $R^2 = 0.486$
T. compressa					
ARK-XXVI/1 + 2 Summer	Juvenile	3	6.0 ± 1.6	0.9 ± 0.4	$y = 1.560x - 4.199$; $R^2 = 0.764$
	Female	3	12.0 ± 0.8	5.0 ± 0.6	$y = -0.673x + 4.728$; $R^2 = 0.169$
	Male	3	16.7 ± 1.3	8.5 ± 2.3	$y = 3.678x - 11.89$; $R^2 = 0.978$
ARCTOS Winter	Juvenile	–	–	–	–
	Female	1	13.0	5.1	–
	Male	1	14.0	6.4	–
T. libellula					
IMR Ecosystem Survey Summer	Juvenile	–	–	–	–
	Female	20	26.4 ± 11.8	84.1 ± 78.0	$y = 2.932x - 8.147$; $R^2 = 0.958$
	Male	19	26.9 ± 8.2	70.2 ± 54.6	$y = 3.158x - 9.306$; $R^2 = 0.953$
ARK-XXVI/1 + 2 Summer	Juvenile	32	7.3 ± 1.6	1.3 ± 0.9	$y = 2.317x - 6.616$; $R^2 = 0.694$
	Female	18	17.8 ± 4.2	13.2 ± 10.2	$y = 2.932x - 8.679$; $R^2 = 0.922$
	Male	–	–	–	–
ARCTOS Winter	Juvenile	–	–	–	–
	Female	6	29.8 ± 3.9	51.3 ± 24.3	$y = 2.986x - 9.065$; $R^2 = 0.738$
	Male	7	26.1 ± 4.7	33.1 ± 22.4	$y = 4.464x - 16.35$; $R^2 = 0.717$
C. guilelmi					
ARK-XXVI/1 + 2 Summer	Juvenile	25	5.6 ± 1.3	0.9 ± 0.7	$y = 0.138x - 1.484$; $R^2 = 0.610$
	Female	19	13.3 ± 3.1	9.4 ± 6.6	$y = 2.727x - 7.189$; $R^2 = 0.724$
	Male	3	17.0 ± 0.8	16.0 ± 2.7	$y = 3.382x - 9.840$; $R^2 = 0.949$
ARCTOS Winter	Juvenile	–	–	–	–
	Female	4	11.5 ± 0.9	8.1 ± 1.4	$y = 1.610x - 2.674$; $R^2 = 0.412$
	Male	1	17.0	20.5	–

The sample sizes (*n*), total body length (mm ± standard deviation (SD)), DM (mg ± SD) and allometric relationships between DM and total body length (TBL) are reported, as are the coefficients of determination (R^2).

acids, fatty alcohols and lipid classes). In Fig. 5A, it can be seen that the second (vertical) ordination axis, accounting for 33.1% of the variability, coincides almost exactly with the winter (shallow)–summer (deep) contrast, noting again that the IMR summer samples of large *T. libellula* are shallow. The first (horizontal) axis, accounting for 43.4%, reveals an opposition within the summer samples, contrasting *C. guilelmi* and *T. libellula* on the left versus *T. compressa* and *T. abyssorum* on the right. In Fig. 5A, the group means are connected to the individuals, showing the different levels of within-group variability, for example the low variability of the summer samples of *C. guilelmi* and *T. libellula* compared with the generally higher variability of *T. compressa* and *T. abyssorum* summer samples.

The corresponding ordination of the variables in Fig. 5B, shown using the contribution coordinate scaling (Greenacre, 2013), explains the separation of the species/season groups observed in Fig. 5A. In this plot, the further away a variable is away from the center, the more it contributes to the two-dimensional solution. There are 16 variables (out of the 40) that contribute more than average to the solution, shown in larger font. Variables that contribute less than average but which are still highly correlated with the solution (usually, these are variables with lower percentage values) are shown in smaller font, whereas low-contributing and low-correlating variables, whose positions are near the center and unimportant to the interpretation, are omitted. Thus, in the upper left,

Table IV: DM, lipid content and lipid class composition (mean ± SD) of the amphipods T. abyssorum, T. compressa, T. libellula *and* C. guilelmi, *sampled during summer 2011 and winter 2012 research cruises to the Fram Strait and Svalbard*

	Sampling depth (m)	DM (mg)	Total lipid (mg)	Total lipid (% DM)	Wax esters (% TL)	Sterols (% TL)	Free fatty acids (% TL)	Triacylglycerols (% TL)	PE (% TL)	PC (% TL)
T. abyssorum										
ARK-XXVI/1+2 Summer ($n = 6$; $L = 14.0$)	800–200	9.0 ± 1.1	0.7 ± 0.3	8.0 ± 3.3	37.3 ± 15.3	3.8 ± 3.5	8.3 ± 3.6	39.0 ± 22.9	0.9 ± 0.9	10.7 ± 9.1
ARCTOS Winter ($n = 6$; $L = 13.0$)	200–0	8.3 ± 0.9	1.1 ± 0.5	13.3 ± 6.1	32.4 ± 19.7	1.2 ± 0.7	2.6 ± 2.0	59.8 ± 20.7	0.8 ± 0.6	3.1 ± 1.1
T. compressa										
ARK-XXVI/1+2 Summer ($n = 8$; $L = 12.5$)	600–100	5.4 ± 3.4	0.4 ± 0.3	6.6 ± 3.6	46.1 ± 20.4	0.8 ± 1.7	4.7 ± 4.2	39.3 ± 19.7	1.5 ± 2.4	7.7 ± 6.3
ARCTOS Winter ($n = 2$; $L = 13.5$)	200–0	5.8 ± 0.9	0.7 ± 0.5	29.0 ± 25.2	67.0 ± NA	1.1 ± NA	4.0 ± NA	25.7 ± NA	0.5 ± NA	1.7 ± NA
T. libellula										
IMR Summer ($n = 12$; $L = 26.3$)	50–0	77.4 ± 67.9	18.5 ± 16.3	23.5 ± 5.5	60.5 ± 6.8	0.4 ± 0.3	1.7 ± 2.0	34.9 ± 8.1	0.5 ± 0.5	2.0 ± 1.8
ARK-XXVI/1+2 Summer ($n = 3$; $L = 22.0$)	600–200	20.1 ± 2.9	2.3 ± 1.0	11.1 ± 4.5	76.7 ± 4.6	0.7 ± 0.2	4.9 ± 1.7	14.6 ± 2.7	0.2 ± 0.3	2.9 ± 0.7
ARCTOS Winter ($n = 6$; $L = 30.2$)	200–0	57.9 ± 25.9	4.7 ± 3.4	7.9 ± 4.6	50.5 ± 24.2	1.6 ± 2.0	1.0 ± 2.1	34.8 ± 33.5	2.3 ± 2.4	9.9 ± 6.4
C. guilelmi										
ARK-XXVI/1+2 Summer ($n = 6$; $L = 14.0$)	2000–1000	11.8 ± 5.1	2.9 ± 1.8	27.2 ± 14.7	84.0 ± 11.4	0.4 ± 0.6	2.7 ± 1.3	10.7 ± 11.4	0.3 ± 0.3	2.0 ± 1.5
ARCTOS Winter ($n = 3$; $L = 12.0$)	1200–600	8.8 ± 0.9	2.1 ± 1.3	23.6 ± 15.4	60.4 ± 28.6	0.2 ± 0.3	10.2 ± 3.2	25.9 ± 22.3	0.3 ± 0.3	3.0 ± 2.5

n, number of samples; *L*, total body length of analyzed individuals; DM, dry mass; TL, total lipid content; PE, phosphatidylethanolamine; PC, phosphatidylcholine.

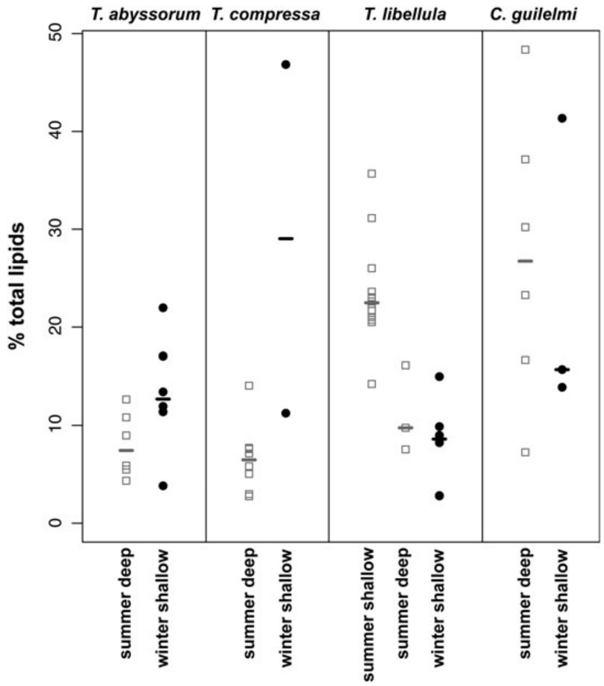

Fig. 4. Seasonal variation of the proportion of lipids per DM (% mass percentage) in the pelagic amphipods *T. abyssorum*, *T. libellula*, *T. compressa* and *C. guilelmi*. Median values are shown by horizontal bars.

fatty acids 20:4(n−3), 18:4(n−3) and fatty alcohol 20:1(n−9) are higher in the winter and summer samples of the large *T. libellula* and the single winter sample of *T. compressa*. Triacylglycerols and the 22:6(n−3) fatty acid are generally higher in the *T. abyssorum* winter samples. Similarly, the typical wax ester fatty acid and alcohol 22:1(n−11) are higher than average for the *C. guilelmi* and *T. libellula* summer samples, bottom left, while fatty acids 18:1(n−9), 16:0, fatty alcohols 14:0 and 16:0, and lipid classes PC and FFA are on average higher in *T. compressa* and *T. abyssorum* summer samples.

Using the multivariate permutation test, the differences between the seasons and between the species were found to be highly significant ($P < 0.001$ in both cases), but there was no significant season−species interaction, i.e. the differences between the species are found to be the same in each season, or equivalently phrased, the seasonal differences are the same across the species.

DISCUSSION

Lipids are of fundamental importance within high-latitude pelagic animals. Storage lipids serve as energy sources during the polar winter and reproduction periods, and provide hydrostatic uplift. This study presents a first evaluation of the influence of seasonality on lipid compositions in four free-swimming amphipods from varying ecological backgrounds, comparing Arctic (*T. libellula*), sub-Arctic (*T. abyssorum*), North Atlantic (*T. compressa*) and deepwater (*C. guilelmi*) species. In all species, the reliance on lipid reserves was high, and storage lipids such as wax esters and triacylglycerols dominated the lipid composition (Table IV). We discuss the trophic status of these free-swimming predators below.

Allometry and total lipid content

In polar waters, lipids in crustaceans contribute as much as 48% of the DM (Hagen *et al.*, 2001), with high potential shares of neutral storage lipids such as wax esters or triacylglycerols (Falk-Petersen *et al.*, 1987, 1999). The relative amount and composition of storage lipids may depend on the type of food, feeding history and life-cycle strategy of the respective species, as well as their biosynthesis from either dietary fatty acids or dietary proteins, carbohydrates or lipids (Pond *et al.*, 2000; Pond, 2012). So far no species-specific differences of the four species between seasons were detected. The observed DM of adult *T. abyssorum* and *T. libellula* agreed with previous summer studies from the Fram Strait (Auel *et al.*, 2002).

The deepwater *C. guilelmi* had a lipid content of 27–28% in summer and winter, in line with the findings of Lee (Lee, 1975) (22% total lipid) from the central Arctic, where the author represented the only published data on lipid class and fatty acid compositions of *C. guilelmi*. The lack of species-specific differences in the total lipid content of *C. guilelmi* between seasons indicated that their metabolic demands were sustained by year-round dietary input and the biochemical modification of internal reserves. Evidence of active winter feeding on copepods by *Themisto* during the polar night has also been documented (Kraft *et al.*, 2013b).

Lipid classes

In all amphipods, we observed an outstanding dominance of storage lipids (particularly wax esters and triacylglycerols) over phospholipids. This phenomenon is frequently found among zooplankton from polar regions. Especially, wax esters are important sources of metabolic energy and an adaptation to a highly seasonal food supply (e.g. Sargent and McIntosh, 1974; Falk-Petersen *et al.*, 1987; Lee *et al.*, 2006; Noyon *et al.*, 2011). While we cannot rule out that the amphipods investigated might be able to synthesize wax esters themselves, previous investigations of gut contents from summer and winter (e.g. Dalpadado *et al.*, 2008; Marion *et al.*, 2008; Kraft *et al.*, 2013b) have shown that *Themisto* spp. mainly feed on

Table V: Fatty acid and alcohol composition of the four amphipods T. abyssorum, T. compressa, T. libellula *and* C. guilelmi *sampled during summer 2011 and winter 2012*

	T. abyssorum		*T. compressa*		*T. libellula*			*C. guilelmi*	
	ARK-XXVI/1 + 2 Summer (*n* = 6)	ARCTOS Winter (*n* = 6)	ARK-XXVI/1 + 2 Summer (*n* = 8)	ARCTOS Winter (*n* = 2)	IMR Summer (*n* = 12)	ARK-XXVI/1 + 2 Summer (*n* = 3)	ARCTOS Winter (*n* = 2)	ARK-XXVI/1 + 2 Summer (*n* = 6)	ARCTOS Winter (*n* = 3)
Fatty acids									
14:0	6.0 ± 2.7	5.1 ± 1.9	5.2 ± 2.1	4.9 ± 4.5	6.4 ± 1.9	8.9 ± 2.7	3.6 ± 1.2	2.3 ± 1.9	3.2 ± 0.4
15:0	0.0 ± 0.0	0.2 ± 0.1	0.2 ± 0.4	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.2	0.2 ± 0.1	0.0 ± 0.0	0.1 ± 0.0
16:0	17.1 ± 5.0	11.6 ± 1.2	20.3 ± 6.6	11.8 ± 0.2	9.9 ± 2.0	16.5 ± 3.5	11.3 ± 1.2	6.6 ± 2.2	10.6 ± 5.2
16:1(n−7)	6.5 ± 1.8	6.1 ± 0.6	6.1 ± 2.7	4.2 ± 1.3	8.8 ± 2.6	5.2 ± 0.8	5.6 ± 1.9	9.1 ± 5.4	8.3 ± 1.1
16:1(n−5)	0.3 ± 0.2	0.4 ± 0.2	0.2 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.3 ± 0.2	0.3 ± 0.1	0.2 ± 0.1	0.5 ± 0.2
16:2(n−4)	0.4 ± 0.2	0.5 ± 0.1	0.3 ± 0.3	0.5 ± 0.2	0.5 ± 0.2	0.3 ± 0.1	0.1 ± 0.1	0.3 ± 0.2	0.4 ± 0.0
17:0	0.4 ± 0.2	0.4 ± 0.1	0.5 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.1	0.2 ± 0.2	0.0 ± 0.0	0.1 ± 0.0
16:3(n−4)	0.5 ± 0.1	0.7 ± 0.2	0.4 ± 0.2	0.3 ± 0.1	0.6 ± 0.2	0.5 ± 0.1	0.4 ± 0.2	0.3 ± 0.2	0.3 ± 0.0
16:4(n−1)	0.2 ± 0.2	0.3 ± 0.2	0.1 ± 0.2	0.2 ± 0.3	1.0 ± 0.6	0.6 ± 0.1	0.9 ± 0.5	0.5 ± 0.4	0.2 ± 0.1
18:0	1.7 ± 0.2	1.2 ± 0.5	2.2 ± 0.7	1.3 ± 0.5	0.7 ± 0.3	0.9 ± 0.2	1.0 ± 0.3	0.7 ± 0.2	0.8 ± 0.3
18:1(n−9)	20.9 ± 1.4	11.1 ± 2.1	20.0 ± 9.0	10.6 ± 2.7	7.6 ± 1.3	13.2 ± 0.7	14.9 ± 3.4	21.5 ± 6.8	14.4 ± 1.2
18:1(n−7)	2.7 ± 0.6	2.2 ± 0.6	2.5 ± 0.6	2.6 ± 2.1	1.8 ± 0.4	2.0 ± 0.4	3.1 ± 0.9	2.8 ± 0.9	2.9 ± 1.0
18:2(n−6)	1.2 ± 0.3	1.6 ± 0.4	1.2 ± 0.8	1.7 ± 0.3	1.4 ± 0.3	0.9 ± 0.7	2.2 ± 0.2	1.5 ± 0.3	2.0 ± 1.1
18:3(n−3)	0.8 ± 0.3	1.7 ± 0.4	0.8 ± 0.9	2.0 ± 1.8	1.3 ± 0.8	0.5 ± 0.5	0.9 ± 0.6	0.6 ± 0.3	1.5 ± 1.4
18:4(n−3)	1.4 ± 0.8	6.0 ± 2.7	1.3 ± 2.1	7.2 ± 8.6	7.0 ± 3.3	1.8 ± 2.3	3.0 ± 1.8	2.4 ± 3.8	5.7 ± 3.3
20:1(n−11)	3.7 ± 1.8	2.6 ± 1.3	3.3 ± 1.8	2.2 ± 0.3	2.5 ± 1.1	6.1 ± 0.0	3.4 ± 1.6	4.6 ± 3.2	2.4 ± 0.7
20:1(n−9)	9.9 ± 3.3	11.2 ± 3.0	10.4 ± 5.1	12.9 ± 4.8	16.0 ± 6.3	22.2 ± 0.8	14.3 ± 3.1	14.8 ± 4.1	11.6 ± 4.6
20:1(n−7)	0.7 ± 0.2	1.9 ± 0.7	0.6 ± 0.4	0.9 ± 0.0	0.9 ± 0.1	0.7 ± 0.2	1.0 ± 0.2	1.7 ± 0.6	1.5 ± 0.5
20:4(n−6)	0.3 ± 0.2	0.6 ± 0.2	0.3 ± 0.4	1.2 ± 0.3	0.5 ± 0.3	0.0 ± 0.1	0.5 ± 0.3	0.4 ± 0.1	0.5 ± 0.1
20:4(n−3)	0.4 ± 0.3	1.1 ± 0.2	0.2 ± 0.3	6.6 ± 8.7	5.0 ± 5.4	0.2 ± 0.2	4.7 ± 4.9	0.4 ± 0.3	0.7 ± 0.2
20:5(n−3)	7.7 ± 4.6	13.5 ± 2.8	7.1 ± 6.1	8.5 ± 6.1	11.8 ± 3.5	2.3 ± 1.6	8.5 ± 2.6	4.4 ± 2.3	9.0 ± 1.9
22:1(n−11)	6.0 ± 2.8	4.3 ± 1.3	5.9 ± 3.2	4.7 ± 5.9	4.5 ± 3.2	10.2 ± 0.7	6.2 ± 5.8	15.7 ± 5.4	9.4 ± 4.3
22:1(n−9)	1.4 ± 0.8	1.5 ± 0.5	1.6 ± 1.4	0.9 ± 0.9	0.8 ± 0.7	2.4 ± 0.7	1.1 ± 1.1	3.5 ± 1.3	3.2 ± 1.1
22:1(n−7)	0.2 ± 0.2	0.3 ± 0.3	0.2 ± 0.1	0.2 ± 0.2	0.9 ± 2.3	0.4 ± 0.3	0.1 ± 0.1	0.4 ± 0.1	0.4 ± 0.1
22:5(n−3)	0.2 ± 0.2	0.7 ± 0.5	0.1 ± 0.2	0.4 ± 0.2	0.7 ± 0.1	0.2 ± 0.3	0.2 ± 0.2	0.6 ± 0.4	0.8 ± 0.4
24:1(n−9)	0.7 ± 0.2	0.4 ± 0.3	0.9 ± 0.7	0.4 ± 0.0	0.5 ± 0.1	0.9 ± 0.2	0.7 ± 0.5	0.8 ± 0.5	0.6 ± 0.2
22:6(n−3)	8.7 ± 5.0	12.8 ± 3.3	7.9 ± 7.2	13.3 ± 1.6	8.1 ± 2.5	2.3 ± 1.7	12.0 ± 4.1	4.1 ± 2.2	9.0 ± 2.7
	Summer (*n* = 6)	Winter (*n* = 6)	Summer (*n* = 8)	Winter (*n* = 2)	Summer (*n* = 6)	Summer (*n* = 8)	Winter (*n* = 2)	Summer (*n* = 6)	Winter (*n* = 3)
$\sum$ PUFA	21.8 ± 10.2	39.5 ± 6.2	19.0 ± 17.0	42.0 ± 11.6	38.1 ± 5.6	9.5 ± 7.4	33.4 ± 4.2	15.5 ± 8.9	30.1 ± 8.6
$\sum$ MUFA	53.0 ± 6.3	42.0 ± 6.2	51.8 ± 11.9	39.8 ± 15.5	44.6 ± 8.8	63.6 ± 2.7	50.6 ± 4.5	74.9 ± 10.5	55.1 ± 10.3
$\sum$ SFA	25.3 ± 7.6	18.5 ± 2.4	28.4 ± 8.1	18.2 ± 4.0	17.3 ± 4.1	26.9 ± 6.5	16.1 ± 1.2	9.6 ± 4.1	14.8 ± 5.7
Fatty acids ratios									
16:1(n7/16:0	0.4 ± 0.3	0.5 ± 0.0	0.3 ± 0.2	0.4 ± 0.1	1.0 ± 0.5	0.3 ± 0.1	0.5 ± 0.2	1.5 ± 0.8	0.9 ± 0.6
18:1(n−9)/18:1(n−7)	7.9 ± 1.4	5.4 ± 1.7	8.0 ± 3.0	5.4 ± 3.4	4.6 ± 1.4	6.8 ± 1.3	5.0 ± 0.9	7.9 ± 1.8	5.3 ± 1.3
EPA/DHA	0.9 ± 0.2	1.1 ± 0.1	0.0 ± NA	0.6 ± 0.4	1.6 ± 0.7	1.0 ± 0.1	0.8 ± 0.3	1.1 ± 0.2	1.0 ± 0.1
PUFA/SFA	1.0 ± 0.8	2.2 ± 0.5	0.9 ± 0.8	2.3 ± 0.1	2.3 ± 0.4	0.4 ± 0.4	2.1 ± 0.3	1.8 ± 1.0	2.2 ± 0.9
Fatty alcohols									
14:0	18.0 ± 11.2	5.5 ± 3.3	13.0 ± 16.0	9.3 ± 8.6	2.6 ± 0.7	1.7 ± 0.6	2.4 ± 1.8	2.3 ± 1.5	5.3 ± 2.8
16:0	15.7 ± 6.4	9.2 ± 3.2	14.0 ± 11.4	11.6 ± 0.6	8.2 ± 3.2	6.8 ± 0.7	7.1 ± 4.3	5.9 ± 1.9	8.9 ± 2.5
16:1(n−7)	0.5 ± 0.6	0.6 ± 0.7	0.9 ± 1.5	1.5 ± 2.1	2.7 ± 1.4	1.2 ± 0.3	1.6 ± 0.9	0.7 ± 0.5	1.6 ± 0.6
18:1(n−9)	1.2 ± 0.7	3.7 ± 1.1	2.0 ± 2.1	2.5 ± 3.5	2.8 ± 1.2	2.2 ± 0.3	2.2 ± 0.5	2.4 ± 2.0	2.2 ± 0.5

18:1(n−7)	1.4 ± 1.3	2.5 ± 1.0	1.1 ± 1.7	0.8 ± 1.1	1.4 ± 0.4	1.0 ± 0.0	1.4 ± 0.1	1.5 ± 1.1	2.0 ± 0.7
20:1(n−9)	21.0 ± 5.3	38.3 ± 4.5	25.2 ± 8.9	36.8 ± 0.7	35.8 ± 4.6	35.5 ± 1.5	36.8 ± 2.1	24.5 ± 4.1	30.1 ± 3.2
22:1(n−11)	42.2 ± 13.4	40.2 ± 7.7	43.8 ± 19.0	37.6 ± 1.9	46.5 ± 7.8	51.7 ± 1.6	48.6 ± 5.0	62.7 ± 7.6	50.0 ± 6.2
Fatty alcohol ratio									
22:1(n−11)/20:1(n−9)	2.0 ± 0.3	1.1 ± 0.3	1.7 ± 0.4	1.0 ± 0.1	1.3 ± 0.4	1.5 ± 0.1	1.3 ± 0.2	2.7 ± 0.8	1.7 ± 0.3

The sample sizes (*n*) and mean fatty acid and fatty alcohol composition (in percent ± SD) are reported.
PUFA, polyunsaturated fatty acids; MUFA, monounsaturated fatty acids; SFA, saturated fatty acids.

copepods of the genus *Calanus*, which accumulate high amounts of wax esters. The wax esters analyzed in this study contain the long-chain MUFAs 20:1(n−9) and 22:1(n−11) fatty acids and alcohols that are not found in phytoplankton (e.g. Pascal and Ackman, 1976; Hagen, 1988; Albers *et al.*, 1996). A dominance of wax esters within the genus *Themisto* was previously described by Auel *et al.* (Auel *et al.*, 2002). The authors found wax ester proportions of 41–43% of total lipid content in both *T. libellula* and *T. abyssorum*. In the fjords Kongsfjorden and Rijpfjorden (Svalbard, Norway), Noyon *et al.* (Noyon *et al.*, 2011) observed proportions of wax esters ranging from 24.4 to 48.5% for adult *T. libellula*. In our study, the wax ester proportions of *T. libellula* were even higher, with means of 60.5–76.7 and 50.5% during summer and winter, respectively. Other studies also reported high proportions of wax esters within *Themisto*, e.g. 46% for *T. abyssorum* collected in April from Ullsfjord (~70°N), Norway (Falk-Petersen *et al.*, 1987). Noyon *et al.* (Noyon *et al.*, 2011) proposed that varying shares of wax esters have an important function fueling reproduction during late winter as part of the life-cycle strategy of *Themisto*. A limited number of investigations of *T. compressa* suggested a free-swimming life-style, with sporadic occurrences in North Atlantic water masses in sub-arctic regions (Brandt, 1997; Weigmann-Haass, 1997; Dalpadado *et al.*, 2001; Dalpadado, 2002). Since 2004, we regularly observed this species in the Fram Strait, with its northernmost distribution at 81°N (Kraft *et al.*, 2011, 2012). *Themisto compressa* from the Fram Strait had very high wax esters (up to 67.0% of total lipids) and, to our knowledge, these lipid class and fatty acid compositions are the first to be published for individuals from Arctic waters.

Triacylglycerols were the dominant lipid class in *T. abyssorum*, with higher proportions in winter (mean 59.8%) compared with summer (39.0%) (Table IV). Similar proportions of triacylglycerols were recorded by Auel *et al.* (Auel *et al.*, 2002) in the Fram Strait (23.0%) and in the central Arctic Ocean (31.9%). Next to wax esters, triacylglycerols are the dominant form of metabolic energy storage in polar zooplankton groups including copepods (e.g. *Calanus propinquus*, Pond, 2012), krill (e.g. *Euphausia superba*, *Themisto raschii*, Falk-Petersen *et al.*, 2000) and amphipods (e.g. *Anonyx nugax*, Legezynska *et al.*, 2012). Being less sensitive to pressure changes, Pond (Pond, 2012) suggested that triacylglycerols represent the preferred form of storage by zooplankton species occupying the epipelagic zone, such as *C. propinquus*. This species does not undergo diapause and maintains an active lifestyle throughout the winter.

The short-term availability of triacylglycerols is an advantage for migrating hyperiid amphipods. For example, *T. abyssorum* performs vertical migration from the surface

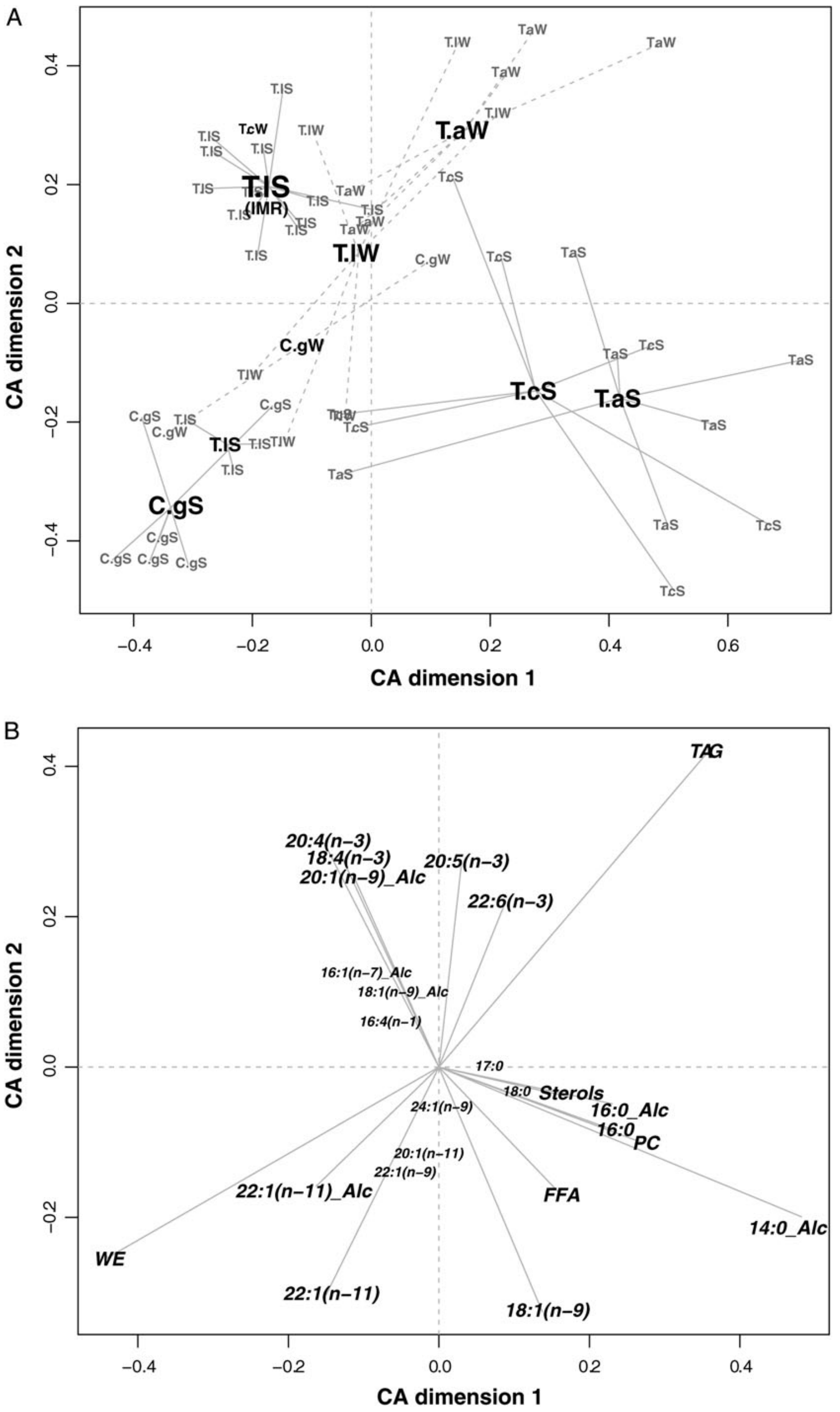

Fig. 5. Two-dimensional CA ordination of the investigated species *T. abyssorum*, *T. compressa*, *T. libellula* and *C. guilelmi* according to individuals (**A**) and three sets of compositional variables, fatty acids, fatty alcohols and lipid classes (**B**). In B only those variables with above average contributions to the ordination (large font) or below average contributions but high correlations with the solution (small font) are shown. WE, wax esters; FFA, free fatty acids; TAG, triacylglycerols; PE, phosphatidylethanolamine; PC, phosphatidylcholine. A 76.5% of variance is explained by the two ordination axes.

to 3000 m (Vinogradov *et al.*, 1996). A different life-cycle strategy with a later start of the reproduction period for *T. abyssorum* (May to July) than for *T. libellula* (February to May) (Koszteyn *et al.*, 1995; Dalpadado, 2002; Weslawski *et al.*, 2006, Kraft *et al.*, 2012) might be connected to the higher share of triacylglycerols in *T. abyssorum*. Consequently, triacylglycerols seem to be of high importance for readily accessible short-term energy storage of hyperiid amphipods.

For the deepwater amphipod *C. guilelmi*, we expected no significant seasonal differences in the lipid class composition; *C. guilelmi* inhabits the meso- and bathypelagic zones of the northern Fram Strait and has a year-round reproductive cycle (Kraft *et al.*, 2013a). While its total lipid content was similar in summer and winter, we observed a decrease of their wax ester proportion from 84.0% in summer to 60.4% in winter (Table IV). The proportion of wax esters in *C. guilelmi* in summer was obviously higher than the only data recorded for *C. guilelmi* (54%, Lee, 1975) and other published results of free-swimming amphipods in Arctic waters (Scott *et al.*, 1999; Auel *et al.*, 2002; Noyon *et al.*, 2011; Prokopowicz, 2011; Legezynska *et al.*, 2012). The decrease in wax esters during winter was associated with high amounts of 20:5(n−3) (Tables IV and V). This observation points to changes in the diet of *C. guilelmi* in winter as a response to a shift in food availability. We conclude that wax esters of copepod origin are important as a year-round long-term energy reserve for demanding metabolic processes such as reproduction and might serve as buoyancy aids (Pond, 2012) in *Themisto* spp. and *C. guilelmi*.

Fatty acids, fatty alcohols and biomarker ratios

Fatty acid profiles reflect a time-averaged feeding history of consumers (Table II) and can be further modified by species-specific metabolic processes (Dalsgaard *et al.*, 2003). Few studies have included data on fatty acid compositions of Arctic zooplankton in winter. Pelagic amphipods are commonly known for a mixed diet related to season, vertical and geographical distribution and prey abundance (e.g. Auel *et al.*, 2002; Dale *et al.*, 2006; Dalpadado *et al.*, 2008; Kraft *et al.*, 2013a, b). We expected their fatty acid profiles to consist of a mixture of accumulated and *de novo* synthesized fatty acids of their prey. Summer versus winter as well as deep versus shallow profiles indicated that all species studied were part of the *Calanus*-based food web. This was shown by high levels of the *Calanus* biomarkers 20:1(n−9) and 22:1(n−11) in fatty acid and alcohol compositions (Sargent and Henderson, 1986; Kattner and Hagen, 1995; Hagen *et al.*, 2000; Dalsgaard *et al.*, 2003). Further, *T. abyssorum*, *T. compressa* and *C. guilemi* collected at great depths in the Fram Strait had a high ratio of 22:1(n−11)/20:1(n−9) fatty alcohols indicating that the large and lipid-rich *C. hyperboreus* is their main prey, while the animals collected in the upper water masses or on the shelf had a ratio of 22:1(n−11)/20:1(n−9) similar to that found in *C. glacialis* and *C. finmarchicus* (Falk-Petersen *et al.*, 2009b). C20 and C22 long-chain monoenes are typical components of herbivorous *Calanus* and are accumulated during brief, pronounced ice-algae and phytoplankton blooms in Arctic spring and summer, and consequently allow copepods to survive long periods of food shortage (Falk-Petersen *et al.*, 1999, 2009b). The fatty alcohol compositions during all seasons were clearly dominated by the monounsaturated *Calanus* markers 20:1(n−9) and 22:1(n−11). Based on our results we suggest an intense feeding on copepods as the primary food source of *Themisto* and *Cyclocaris* during winter and a more diverse diet during summer. Consequently, our findings imply a vertical migration of *Themisto* during winter, as this hyperiid amphipod follows its main prey into deeper waters.

In addition to the individual contribution of specific fatty acid markers, fatty acid ratios are commonly used to address the trophic status of a species (Table II). For example, a high 18:1(n−9)/18:1(n−7) ratio is considered an indicator of carnivory, and the respective increase of the 18:1(n−9)/18:1(n−7) biomarker ratio (Table V) from June to August implies stronger carnivory during summer and fall for all observed amphipods.

Arctic spring blooms in cold, nutrient-rich waters have a high potential to support good nutritional quality that shows in high levels of PUFAs in the fatty acid composition (Leu *et al.*, 2006, 2011; Søreide *et al.*, 2008, 2010). The classical "spring bloom" may occur under the ice, along the ice-edge as the sea-ice recedes during summer and autumn, or in openings in the ice cover any time between late March and October (Zenkevitch, 1963; Falk-Petersen *et al.*, 2007, Leu *et al.*, 2011). During our study we observed an increase of flagellate (22:6(n−3) and 18:4(n−3)) and diatom (particularly 20:5(n−3) fatty acid trophic markers in winter samples of *Themisto* spp. and *C. guilelmi* (Table V). High DHA contents have been related to an increased share of dinoflagellates and *Phaeocystis pouchetii* in the diet of *Calanus* (Scott *et al.*, 2002). Consequently, the seasonality of phytoplankton biomarkers in the summer and winter fatty acid profiles of pelagic amphipods could be influenced by different phytoplankton diets of their preferred prey, *Calanus* copepods. Furthermore, our results imply that the typical high Arctic diatom system (Horner *et al.*, 1992 and references therein) and a flagellate (*P. pouchetii)* dominated photosynthetic system (Sargent *et al.*, 1985) are capable of providing the baseline energy reserves for higher trophic predators such as pelagic amphipods.

In summary, the lipid class, detailed fatty acid and fatty alcohol compositions reveal minor seasonal and interspecific differences in feeding behavior and food sources of the species investigated. In contrast to most herbivorous or omnivorous zooplankton, which enter a state of dormancy or face starvation, *Themisto* spp. and *C. guilelmi* are pelagic predators which follow a "business-as-usual" life strategy during the polar winter. This overwintering strategy was first described by Torres *et al.* (Torres *et al.*, 1994) and is characterized by the absence of a reduction of the metabolic rate and an active feeding behavior throughout this season.

CONCLUSION

The lipid classes and fatty acid profiles of *Themisto* and *Cyclocaris* indicated that both genera are predominantly carnivorous predators during summer and winter in the *Calanus*-based Arctic food web, with *Calanus* as their main food source. Seasonal and depth differences characterized their fatty acid composition, with increasing contributions of polyunsaturated fatty acids during winter in surface waters. As a part of the *Calanus*-based food web, the population dynamics of *T. abyssorum*, *T. compressa*, *T. libellula* and *C. guilelmi* might be vulnerable to shifts in abundance and distribution of *Calanus* species. Seasonal shifts and vertical distribution of these copepods are also reflected in their gut content and fatty alcohol profile, with *C. hyperboreus* as the preferred prey of *Themisto* in deep water in the northern Fram Strait during summer and *C. fimarchicus* and *C. glacialis* as the major food sources on shelf regions and upper water masses north of Svalbard during winter. Consequently, pelagic predators such as *Themisto* spp. might be affected by climate-induced changes in the copepod community composition, seasonal vertical migration behavior and timing in reproduction of *Calanus* copepods. This highlights the importance of a future match between primary producers (either ice-algae or phytoplankton bloom or both), copepod life-cycles and their respective availability as a key food source for pelagic amphipods.

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REFERENCES

Albers, C. S., Kattner, G. and Hagen, W. (1996) The compositions of wax esters, triacylglycerols and phospholipids in Arctic and Antarctic copepods: evidence of energetic adaptations. *Mar. Chem.*, **55**, 347–358.

Auel, H., Harjes, M., da Rocha, R., Stübing, D. and Hagen, W. (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. *Polar Biol.*, **25**, 374–383.

Benjamini, Y. and Hochberg, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. Roy. Stat. Soc. B*, **57**, 289–300.

Bradstreet, M. S. W. and Cross, W. E. (1982) Trophic relationships at high Arctic ice edges. *Arctic*, **35**, 1–12.

Bousfield, E. L. (1951) Pelagic amphipoda of the Belle Isle Strait region. *J. Fish. Res. Board Can.*, **8**, 134–163.

Brandt, A. (1997) Suprabenthic Peracarida (Crustacea, Malacostraca) sampled at 75 degrees N off East Greenland. *Polar Biol.*, **17**, 462–464.

Conover, R. J. (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high-latitudes of the northern hemisphere. *Hydrobiologia*, **167**, 127–142.

Dale, K., Falk-Petersen, S., Hop, H. and Fevolden, S. E. (2006) Population dynamics and body composition of the Arctic hyperiid amphipod *Themisto libellula* in Svalbard fjords. *Polar Biol.*, **29**, 1063–1070.

Dalpadado, P. (2002) Inter-specific variations in distribution, abundance and possible life-cycle patterns of *Themisto* spp. (Amphipoda) in the Barents Sea. *Polar Biol.*, **25**, 656–666.

Dalpadado, P. and Bogstad, B. (2004) Diet of juvenile cod (age 0-2) in the Barents Sea in relation to food availability and cod growth. *Polar Biol.*, **27**, 140–154.

Dalpadado, P., Borkner, N., Bogstad, B. and Mehl, S. (2001) Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator-prey interactions. *ICES J. Mar. Sci.*, **58**, 876–895.

Dalpadado, P., Ellertsen, B., Melle, W. and Dommasnes, A. (2000) Food and feeding conditions of Norwegian spring spawning herring (*Clupea harengus*) through its feeding migrations. *ICES J. Mar. Sci.*, **58**, 876–895.

Dalpadado, P., Yamaguchi, A., Ellertsen, B. and Johannessen, S. (2008) Trophic interactions of macro-zooplankton (krill and amphipods) in the Marginal Ice Zone of the Barents Sea. *Deep-Sea Res. II*, **55**, 2266–2274.

Dalsgaard, J., St John, M., Kattner, G., Müller-Navarra, D. and Hagen, W. (2003) Fatty acid trophic markers in the pelagic marine environment. *Adv. Mar. Biol.*, **46**, 225–340.

Dunbar, M. J. (1957) The determination of production in the northern seas: a study of the biology of *Themisto libellula* Mandt. *Can. J. Zool.*, **35**, 797–819.

Falk-Petersen, S., Hagen, W., Kattner, G., Clarke, A. and Sargent, J. (2000) Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill. *Can. J. Fish. Aquat. Sci.*, **57**, 178–191.

Falk-Petersen, S., Haug, T., Hop, H., Nilssen, K. T.. and Wold, A. (2009a) Transfer of lipids from plankton to blubber of harp and hooded seals off East Greenland. *Deep-Sea Res. II*, **56**, 2080–2086.

Falk-Petersen, S., Mayzaud, P., Kattner, G. and Sargent, J. R. (2009b) Lipids and life strategy of Arctic *Calanus*. *Mar. Biol. Res.*, **5**, 18–39.

Falk-Petersen, S., Sargent, J. R., Lønne, O. J. and Timofeev, S. (1999) Functional biodiversity of lipids in Antarctic zooplankton: *Calanoides acutus*, *Calanus propinquus*, *Thysanoessa macura* and *Euphausia crystallorophias*. *Polar Biol.*, **21**, 37–47.

Falk-Petersen, S., Sargent, J. R. and Tande, K. S. (1987) Lipid composition of zooplankton in relation to the sub-arctic food web. *Polar Biol.*, **8**, 115–120.

Falk-Petersen, S., Timofeev, S., Pavlov, V. and Sargent, J. R. (2007) Climate variability and possible effects on Arctic food chains. The role of *Calanus*. In Ørbæk, J.-B., Tombre, T., Kallenborn, R., Hegseth, E. N., Falk-Petersen, S. and Hoel, A. H. (eds), *Arctic-Alpine Ecosystems and People in a Changing Environment*. Springer, Berlin, pp. 147–166.

Folch, J., Lees, M. and Sloane-Stanley, G. H. (1957) A simple method for isolation and purification of total lipids from animal tissue. *J. Biol. Chem.*, **226**, 497–509.

Graeve, M., Albers, C. and Kattner, G. (2005) Assimilation and biosynthesis of lipids in Arctic *Calanus* species based on feeding experiments with a 13C labelled diatom. *J. Exp. Mar. Biol. Ecol.*, **317**, 109–125.

Graeve, M., Hagen, W. and Kattner, G. (1994a) Herbivorous or omnivorous? On the significance of lipid composition as trophic markers in Antarctic copepods. *Deep-Sea Res. I*, **41**, 915–924.

Graeve, M., Hagen, W. and Kattner, G. (1994b) Diet-induced changes in the fatty acids composition of Arctic herbivorous copepods: experimental evidence of trophic markers. *J. Exp. Mar. Biol. Ecol.*, **182**, 97–110.

Graeve, M. and Janssen, D. (2009) Improved separation and quantification of neutral and polar lipid classes by HPLC-ELSD using a monolithic silica phase: application to exceptional marine lipids. *J. Chromatogr. B. Analyt. Technol. Biomed. Life Sci.*, **877**, 1815–1819.

Graeve, M., Kattner, G. and Piepenburg, D. (1997) Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? *Polar Biol.*, **18**, 53–61.

Greenacre, M. (2007) *Correspondence Analysis in Practice*, 2nd edn. Chapman & Hall/CRC, Boca Raton, FL.

Greenacre, M. (2010) Power transformations in correspondence analysis. *Comp. Stat. Data Anal.*, **53**, 3103–3106.

Greenacre, M. (2011) Measuring subcompositional incoherence. *Math. Geosci.*, **43**, 681–693.

Greenacre, M. (2013) Contribution biplots. *J. Comput. Graph. Stat.*, **22**, 107–122.

Greenacre, M. and Primicerio, R. (2013) *Multivariate Analysis of Ecological Data*. BBVA Foundation, Bilbao. http://www.multivariatestatistics.org (last accessed 28/2/2015).

Hagen, W. (1988) Zur Bedeutung der Lipide im antarktischen Zooplankton. *Ber. Polarforsch.*, **49**, 1–129.

Hagen, W., Kattner, G. and Friedrich, C. (2000) The lipid compositions of high-Antarctic notothenioid fish species with different life strategies. *Polar Biol.*, **23**, 785–791.

Hagen, W., Kattner, G., Terbrüggen, A. and Van Vleet, E. S. (2001) Lipid metabolism of the Antarctic krill *Euphausia superba* and its ecological implications. *Mar. Biol.*, **139**, 95–104.

Hagen, W., Van Vleet, E. S. and Kattner, G. (1996) Seasonal lipid storage as overwintering strategy of Antarctic krill. *Mar. Ecol. Prog. Ser.*, **134**, 85–89.

Helland-Hansen, B. and Nansen, F. (1909) *The Norwegian Sea, its physical oceanography. Based on the Norwegian researches 1900–1904*. Report on Norwegian Fishery and Marine-Investigations, Vol. 11, Bergen, Norway.

Hobson, K. A., Fisk, A., Karnovsky, N., Holst, M., Gagnon, J.-M. and Fortier, M. (2002) A stable isotope (δ13C, δ15N) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. *Deep-Sea Res. II*, **49**, 5131–5150.

Horner, R., Ackley, S. F., Dieckmann, G. S., Gulliksen, B., Hoshiai, T., Legendre, L., Melnikov, I. A., Reeburgh, W. S. *et al.* (1992) Ecology of sea ice biota. 1. Habitat, terminology, and methodology. *Polar Biol.*, **12**, 417–427.

Hothorn, T., Hornik, K., van de Wiel, M. A. and Zeileis, A. (2008) Implementing a class of permutation tests: the coin package. *J. Stat. Softw.*, **28**, http://www.jstatsoft.org/v28/i08/paper.

Kattner, G. and Fricke, H. S. G. (1986) Simple gas-liquid chromatographic method for the simulataneous determination of fatty acids and alcohols in wax esters of marine organisms. *J. Chromatogr.*, **361**, 263–268.

Kattner, G. and Hagen, W. (1995) Polar herbivorous copepods – different pathways in lipid biosynthesis. *ICES J. Mar. Sci.*, **52**, 329–335.

Koszteyn, J., Timofeev, S., Weslawski, J. M. and Malinga, B. (1995) Size structure of *Themisto abyssorum* Boeck and *Themisto libellula* (Mandt) populations in the European Arctic Seas. *Polar Biol.*, **15**, 85–92.

Kraft, A., Bauerfeind, E. and Nöthig, E.-M. (2011) Amphipod abundance in sediment trap samples at the long-term observatory

HAUSGARTEN (Fram Strait, ∼79°N/4°E) - variability in species community patterns. *Mar. Biodiv.*, **41**, 353–364.

Kraft, A., Bauerfeind, E., Nöthig, E.-M. and Bathmann, U. V. (2012) Size structure and life-cycle patterns of dominant pelagic amphipods collected as swimmers in sediment traps in the eastern Fram Strait. *J. Mar. Sys.*, **95**, 1–15.

Kraft, A., Bauerfeind, E., Nöthig, E.-M., Klages, M., Beszczynska-Möller, A. and Bathmann, U. V. (2013a) Amphipods in sediment traps of the eastern Fram Strait with focus on the life-history of the lysianassoid *Cyclocaris guilelmi*. *Deep-Sea Res. I*, **73**, 62–72.

Kraft, A., Berge, J., Varpe, Ø. and Falk-Petersen, S. (2013b) Feeding in Arctic darkness: mid-winter diet of the pelagic amphipods *Themisto abyssorum* and *T. libellula*. *Mar. Biol.*, **160**, 241–248.

Lee, R. F. (1975) Lipids of arctic zooplankton. *Comp. Biochem. Phys. B*, **51**, 263–266.

Lee, R. F., Hagen, W. and Kattner, G. (2006) Lipid storage in marine zooplankton. *Mar. Ecol. Prog. Ser.*, **307**, 273–306.

Legezynska, J., Kedra, M. and Walkusz, W. (2012) When season does not matter: summer and winter trophic ecology of Arctic amphipods. *Hydrobiologia*, **684**, 189–214.

Leu, E., Falk-Petersen, S., Kwasniewski, S., Wulff, A., Edvardsen, K. and Hessen, D. O. (2006) Fatty acid dynamics during the spring bloom in a High Arctic fjord: importance of Abiotic factors versus community changes. *Can. J. Fish. Aquat. Sci.*, **63**, 2760–2779.

Leu, E., Søreide, J. E., Hessen, D. O., Falk-Petersen, S. and Berge, J. (2011) Consequences of changing sea ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity, and quality. *Prog. Oceanogr.*, **90**, 18–32.

Lønne, O. J. and Gulliksen, B. (1989) Size, age and diet of polar cod, *Boreogadus saida* (Lepechin, 1773) in ice covered waters. *Polar Biol.*, **9**, 187–191.

Lydersen, C., Gjertz, I. and Weslawski, J. M. (1989) Stomach contents of autumn-feeding marine vertebrates from Hornsund, Svalbard. *Polar Record*, **25**, 107–114.

Marion, A., Harvey, M., Chabot, D. and Brethes, J. C. (2008) Feeding ecology and predation impact of the recently established amphipod, *Themisto libellula*, in the St. Lawrence marine system, Canada. *Mar. Ecol. Prog. Ser.*, **373**, 53–70.

Mayzaud, P., Laureillard, J., Merien, D., Brinis, A., Godard, C., Razouls, S. and Labat, J. P. (2007) Zooplankton nutrition, storage and fecal lipid composition in different water masses associated with the Agulhas and Subtropical Fronts. *Mar. Chem.*, **107**, 202–213.

Nelson, M. M., Mooney, B. D., Nichols, P. D. and Phleger, C. F. (2001) Lipids of Antarctic Ocean amphipods: food chain interactions and the occurrence of novel biomarkers. *Mar. Chem.*, **73**, 53–64.

Nenadić, O. and Greenacre, M. (2007) Correspondence analysis in R, with two- and three-dimensional graphics: the ca package. *J. Stat. Softw.*, **20**. http://www.jstatsoft.org/v20/i03 (last accessed 28/2/2015).

Noyon, M., Gasparini, S. and Mayzaud, P. (2009) Feeding of *Themisto libellula* (Amphipoda Crustacea) on natural copepods assemblages in an Arctic fjord (Kongsfjorden, Svalbard). *Polar Biol.*, **32**, 1559–1570.

Noyon, M., Narcy, F., Gasparini, S. and Mayzaud, P. (2011) Growth and lipid class composition of the Arctic pelagic amphipod *Themisto libellula*. *Mar. Biol.*, **158**, 883–892.

Noyon, M., Narcy, F., Gasparini, S. and Mayzaud, P. (2012) Ontogenic variations in fatty acid and alcohol composition of the pelagic amphipod *Themisto libellula* in Kongsfjorden (Svalbard). *Mar. Biol.*, **159**, 805–816.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P. *et al.* (2011) vegan: Community Ecology Package. R package version 2.0-2. http://CRAN.R-project.org/package=vegan (last accessed 28/2/2015).

Pascal, J. C. and Ackman, R. G. (1976) Long chain monoethylenic alcohol and acid isomers in lipids of copepods and capelin. *Chem. Phys. Lipids*, **16**, 219–223.

Percy, J. A. (1993) Reproduction and growth of the Arctic hyperiid amphipod *Themisto libellula* Mandt. *Polar Biol.*, **13**, 131–139.

Pond, D. W. (2012) The physical properties of lipids and their role in controlling the distribution of zooplankton in the oceans. *J. Plankton Res.*, **34**, 443–453.

Pond, D. W., Gebruk, A., Southward, E., Southward, A., Fallick, A., Bell, M. and Sargent, J. (2000) Unusual fatty acid composition of storage lipids in the bresilioid shrimp *Rimicaris exoculata* couples the photic zone with MAR hydrothermal sites. *Mar. Ecol. Prog. Ser.*, **198**, 171–179.

Pond, D. W. and Tarling, G. A. (2011) Phase transitions of wax esters adjust buoyancy in diapausing *Calanoides acutus*. *Limnol. Oceanogr.*, **56**, 1310–1318.

Prokopowicz, A. J. (2011) *Écophysiologie de l'amphipode Themisto libellula sur le plateau du Mackenzie et dans la Polynie du Cap Bathurst (mer de Beaufort, océan Arctique)*. Ph.D. thesis, Départment de Biologie, Université Laval, Québec.

R core team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/ (last accessed 28/2/2015).

Sargent, J. R., Eilertsen, H. C., Falk-Petersen, S. and Taasen, J. P. (1985) Carbon assimilation and lipid production in phytoplankton in northern Norwegian fjords. *Mar. Biol.*, **85**, 109–116.

Sargent, J. R. and Henderson, R. J. (1986) Lipids. In Corner, E. D. S. and O'Hara, S. C. M. (eds), *The Biological Chemistry of Marine Copepods*. Clarendon Press, Oxford, pp. 491–531.

Sargent, J. R. and McIntosh, R. (1974) Studies on the mechanism of biosynthesis of wax esters in *Euchaeta norvegica*. *Mar. Biol.*, **25**, 271–277.

Schauer, U., Beszczynska-Möller, A., Walczowski, W., Fahrbach, E., Piechura, J. and Hansen, E. (2008) Variation of measured heat flow through the Fram Strait between 1997 and 2006. In Dickson, R. R., Meincke, J. and Rhines, P. (eds), *Arctic–Subarctic Ocean Fluxes*. Springer, Netherlands, pp. 65–85.

Schlichtholz, P. and Houssais, M. N. (2002) An inverse modeling study in Fram Strait. Part II: water mass distribution and transports. *Deep-Sea Res. II*, **46**, 1137–1168.

Scott, C. L., Falk-Petersen, S., Sargent, J. R., Hop, H., Lønne, O. J. and Poltermann, M. (1999) Lipids and trophic interactions of ice fauna and pelagic zooplankton in the marginal ice zone of the Barents Sea. *Polar Biol.*, **21**, 65–70.

Scott, C. L., Kwasniewski, S., Falk-Petersen, S. and Sargent, J. R. (2002) Species differences, origins and functions of fatty alcohols and fatty acids in the wax esters and phospholipids of *Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus* from Arctic waters. *Mar. Ecol. Prog. Ser.*, **235**, 127–134.

Søreide, J. E., Falk-Petersen, S., Hegseth, E. N., Hop, H., Carroll, M. L., Hobson, K. A. and Blachowiak-Samolyk, K. (2008) Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region. *Deep-Sea Res II*, **55**, 2225–2244.

Søreide, J. E., Leu, E., Berge, J., Graeve, M. and Falk-Petersen, S. (2010) Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Global Change Biol.*, **16**, 3154–3163.

Stübing, D., Hagen, W. and Schmidt, K. (2003) On the use of lipid biomarkers in marine food web analyses: An experimental case study on the Antarctic krill, *Euphausia superba*. *Limnol. Oceanogr.*, **48**, 1685–1700.

Torres, J. J., Donnelly, J., Hopkins, T. L., Lancraft, T. M., Aarset, A. V. and Ainley, D. G. (1994) Proximate composition and overwintering strategies of Antarctic micronektonic Crustacea. *Mar. Ecol. Prog. Ser.*, **113**, 221–232.

Vinogradov, M. E., Volkov, A. F. and Semenova, T. N. (1996) *Hyperiid Amphipods (Amphipoda, Hyperidea) of the World Oceans*. Science Publishers Inc., Lebanon, USA.

Weigmann-Haass, R. (1997) Verbreitung von Makrozooplankton in der Grönlandsee im Spätherbst 1988 (Crustacea: Ostracoda, Hyperiidea [Amphipoda], Euphausiacea). *Helgoländer Meeresuntersuch.*, **51**, 69–82.

Weslawski, J. M., Kwasniewski, S., Stempniewicz, L. and Blachowiak-Samolyk, K. (2006) Biodiversity and energy transfer to top trophic levels in two contrasting Arctic fjords. *Pol. Polar Res.*, **27**, 259–278.

Wold, A., Jaeger, I., Hop, H., Gabrielsen, G. W. and Falk-Petersen, S. (2011) Arctic seabird food chains explored by fatty acid composition and stable isotopes in Kongsfjorden, Svalbard. *Polar Biol.*, **34**, 1147–1155.

Zenkevitch, L. (1963) *Biology of the Seas of the USSR*. Georg Allen and Unwin, London.