



# The amphipod scavenging guild in two Arctic fjords: seasonal variations, abundance and trophic interactions

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**ABSTRACT:** Scavenging amphipods are important for the circulation and dispersal of organic material in the marine environment. Despite their dominance in the scavenging guild and importance in the food web, little is known about Arctic amphipods and their feeding preferences. We studied the amphipod scavenging guild using baited traps for one full year to increase our understanding of its seasonal variations. Two Arctic fjords with contrasting hydrographical conditions were studied: Adventfjorden, which is influenced by Atlantic water inflow, and Rijpfjorden, which is dominated by cold Arctic water masses. The species composition clearly differed between the 2 fjords. *Onisimus caricus*, followed by *Anonyx laticoxae*, were the dominant species in Adventfjorden. In Rijpfjorden, the species diversity was higher, particularly for *Anonyx* spp. In both fjords, a clear depth zonation in species distribution was detected, with a seasonal dynamic in species composition. A seasonal pattern in catch sizes was observed in both fjords. The timing of this pattern varied, likely because of the climatic differences between the fjords. Lipid content, lipid classes and fatty acid composition were analyzed for *A. nugax*, *O. caricus*, *O. littoralis*, *O. nansenii* and *O. glacialis*, and stable isotopes were also analyzed for the all these species except *O. glacialis*. A clear difference in the fatty acid and stable isotope composition was found among species. *O. glacialis* and *O. littoralis* were primarily omnivorous-herbivorous, while the other species were predominantly carnivorous. *O. nansenii* and *A. nugax* preyed extensively on calanoid copepods (*Calanus* spp.) whereas *O. caricus* did not.

**KEY WORDS:** Scavenger · Lysianassoid amphipods · *Onisimus* spp. · *Anonyx* spp. · Seasonality · Lipid content · Fatty acid composition · Stable isotope analysis

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## INTRODUCTION

Scavenging animals feed on dead organisms and play a key role in circulating and dispersing organic material from food falls (Britton & Morton 1994). In the marine environment, only a few species show adaptations suitable for an obligate scavenging feeding mode, as carrion are a scarce food source in comparison to the vast area of the oceans (Britton & Morton 1994, Dauby et al. 2001, De Broyer et al. 2004).

Thus, most marine necrophagous species are facultative scavengers with an omnivorous diet, also being predators or detritivores (Sainte-Marie 1984, Slattery & Oliver 1986, Sainte-Marie et al. 1989, Legeżyńska 2001, 2008). Lysianassoid amphipods are a species-rich group that appears to be especially important as scavengers in polar and cold waters, as well as in the deep sea (Vader & Romppainen 1985, Legeżyńska et al. 2000, De Broyer et al. 2004, Premke et al. 2006). Many of the deep-sea lysianassoid amphipods are

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especially adapted to scavenging, with specialized mouthparts and an alimentary tract suited for accumulation and storage of food (Dahl 1979, De Broyer et al. 2004). However, shallow-water lysianassoid amphipods seem to be less specialized and are likely to have broader diets (Sainte-Marie 1984, Slattery & Oliver 1986).

In the Arctic, lysianassoid amphipods dominate the necrophagous fauna (Legeżyńska et al. 2000). In Svalbard fjords, lysianassoid amphipods dominate the invertebrate macrofauna; for example, on tidal flats *Onisimus litoralis* constitute up to 95% of the total macrofauna density (Węsławski et al. 2000). Several studies have focused on species distribution, feeding behavior and life history traits of scavenging amphipods both in the deep sea and in shallow coastal areas (e.g. Węsławski et al. 1991, Legeżyńska et al. 2000, Legeżyńska 2001, 2008, Węsławski & Legeżyńska 2002, Premke et al. 2006), but few studies have had a year-round sampling approach and thus comprehensive information on seasonality in the amphipod scavenging guild is lacking.

Although scavenging fauna are expected to be omnivorous and thus not directly dependent on highly seasonal primary production, processes related to the life history of scavenger species might imply seasonal variation in baited trap catches. Ontogenic processes among the different lysianassoid amphipods, such as timing of the life cycle, increased activity prior to mating, reduced appetite among egg-carrying females or brood release (e.g. Sainte-Marie et al. 1989, 1990, Conlan 1991, Nygård et al. 2009), can influence not only catch sizes, but also species composition in the samples in different seasons. Moore & Wong (1995) report a seasonal pattern in abundance of *Orchomene nanus* in baited traps from Scotland, with the highest abundance in autumn. In a study from Antarctica, Smale et al. (2007) found large differences in the scavenging guild between winter and summer, especially in the abundance of amphipods, suggesting a seasonal change in feeding behavior. No such large variations have been reported from the Arctic, even though sampling has been conducted year-round (Legeżyńska et al. 2000). In the present study, we attempt to describe seasonal variation in the amphipod scavenging guild by using a high temporal resolution in sampling.

Amphipods form a key component in polar food webs, transferring and recycling organic material to higher trophic levels (TLs, Jarre-Teichmann et al. 1997, Dauby et al. 2003). Despite their importance in the food web, feeding preferences of polar, and especially Arctic, amphipods are not well known.

Traditional methods such as *in situ* observations, gut content analyses and feeding experiments, have provided some information on short-term feeding behavior (Sainte-Marie 1986, 1987, Dauby et al. 2001, Legeżyńska 2001, 2008). Recently, techniques such as fatty acid composition and stable isotope analyses have broadened our understanding, integrating feeding patterns over a longer period. Fatty acid composition can be utilized to trace certain fatty acid trophic markers (FATM) that are specific for certain groups (reviewed by Dalsgaard et al. 2003), while the ratios of stable carbon ( $\delta^{13}\text{C}$ ) and stable nitrogen ( $\delta^{15}\text{N}$ ) can be used to trace the organisms' major carbon sources and to estimate their TL, respectively (Hobson & Welch 1992, Søreide et al. 2006a). These methods have provided new information on feeding patterns and trophic structure of Antarctic amphipods (Graeve et al. 2001, Nyssen et al. 2005), but our knowledge about feeding patterns in Arctic amphipod assemblages is still restricted. By studying the feeding preferences of different scavenging amphipods, we wanted to increase understanding of the Arctic food web structure and the ecological significance of amphipods. Further, our aim was to investigate how the amphipods' feeding behavior affects their attraction to bait.

We studied the amphipod scavenging guild in 2 contrasting Arctic fjords in Svalbard, Norway: Adventfjorden and Rijpfjorden, differing both in hydrology and climate (Zajączkowski et al. 2010, Ambrose et al. 2006, Berge et al. 2009). As the conditions are different in the 2 fjords, we expected a different set of scavenging amphipods in each fjord, but a similar seasonality in catch sizes. Our hypothesis was that the seasonal variation in species composition is relatively low and that the co-existence of several amphipod species is possible due to these species' opportunistic feeding strategies and high flexibility in diet, which is influenced by amphipod size, habitat and season.

## MATERIALS AND METHODS

### Study area

Sampling was performed in Adventfjorden (78° 13.5' N, 15° 40.5' E) and Rijpfjorden (80° 13.3' N, 22° 26.0' E), both fjords located in the Svalbard archipelago, Norway (Fig. 1). In addition, some samples of the sympagic species for lipid and fatty acid analyses were collected in the pack ice north of Svalbard (81° 05' N, 14° 54' E).

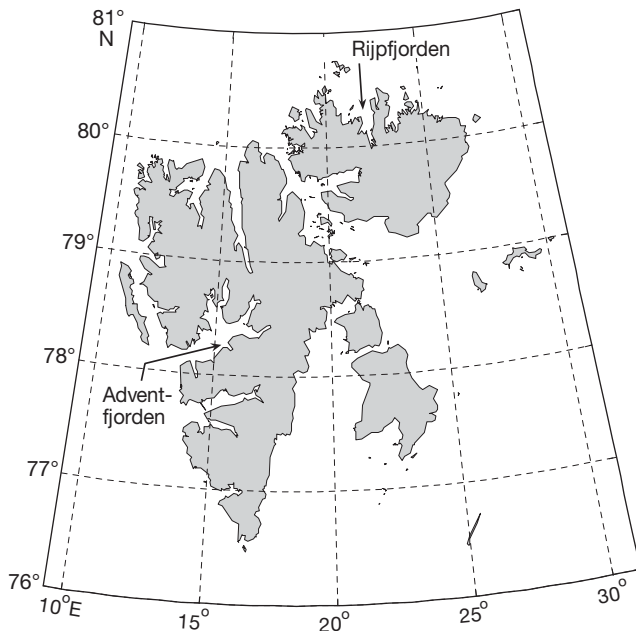


Fig. 1. Svalbard archipelago, Norway, showing the study fjords, Adventfjorden and Rijpfjorden

Adventfjorden is a branch of the Isfjorden system on the western side of Spitsbergen. Isfjorden is influenced by the West Spitsbergen Current that brings warm Atlantic water into the fjord and creates a rather mild climate in the area (Svendsen et al. 2002). The temperature in Adventfjorden varies at 30 m depth from around  $-1^{\circ}\text{C}$  in April to around  $5^{\circ}\text{C}$  in July (Zajączkowski et al. 2010). No sea ice formed during our study period 2006 to 2007. Adventfjorden is influenced by 2 rivers, Adventelva and Long-yearrelva, which transport melt water from glaciers located several kilometers inland from the shore. The surface salinity in the fjord decreases to less than 5 psu during the approximately 120 d long melting period during summer (Zajączkowski et al. 2010, Węśławski et al. 1999). The rivers also bring a lot of suspended terrigenous particles, increasing the turbidity in the water during the melt period. The sedimentation rate of inorganic particles is  $60$  to  $80\text{ g m}^{-2}\text{ d}^{-1}$  (Zajączkowski et al. 2010) and as a result the bottom in the fjord consists mainly of silt (Pawłowska et al. 2011). In the outer part of Adventfjorden the sedimentation rate of suspended particles is reduced and the sediment is coarser (Zajączkowski 2008).

Rijpfjorden is a north-facing fjord located on Nord-austlandet and is characterized by Arctic surface water (Ambrose et al. 2006, Berge et al. 2009). The fjord is ice-covered 6 to 8 mo per year (Wallace et al. 2010). In 2007, ice formed in early February and the ice cover started to break up in the end of June and

had totally disappeared by mid-July (Søreide et al. 2010). The hydrography in the fjord was monitored continuously from August 2006 to August 2008 by a mooring (Wallace et al. 2010). During the period when the fjord was ice-covered, the water column had a homogenous temperature of around  $-1.8^{\circ}\text{C}$ ; in the open period the surface layer warmed up to  $4^{\circ}\text{C}$ , while the bottom water remained cold (Søreide et al. 2010). Although one large glacier feeds the fjord with melt water, the influence of melt water in the sampling area is comparatively small. The bottom substrate in the sample area consisted mainly of gravel, in contrast to the soft sediments in Adventfjorden.

### Sampling

Sampling was performed using baited traps with similar-sized pieces of chicken meat as bait packed in a fine mesh bag, preventing the animals from feeding on the bait (Nygård et al. 2009). In both fjords, 3 transects with 5 traps each were regularly deployed. The transects started close to shore at depths of around 1 to 2 m and extended outwards with 50 m between the traps, typically ending at a depth of 20 to 40 m. The traps were deployed for approximately 24 h at a time. In Adventfjorden sampling was carried out regularly from September 2006 until August 2007, in Rijpfjorden from February to October 2007 with an additional sampling campaign in April 2008 (for sampling dates see Tables S1 and S2 in the supplement at [www.int-res.com/articles/suppl/b014p247\\_supp.pdf](http://www.int-res.com/articles/suppl/b014p247_supp.pdf)). In Rijpfjorden samples were also taken from deeper parts of the fjord (maximum depth 180 m) and from traps mounted directly under the sea ice (hereafter called 'ice traps'). The ice traps were used in both shallow ( $<40$  m) and deep ( $>40$  m) areas in Rijpfjorden.

The samples were sorted under a stereomicroscope and identified to species level/nearest taxa. *Anonyx* species were determined according to the key in Steele & Brunel (1968), and *Onisimus* species according to Vader et al. (2005) and Berge et al. (2007). In addition, the length of the first pereonal segment (Ls), which can be used as a trustworthy proxy for total length (Arndt and Beuchel 2006, Nygård et al. 2009), was measured on the *Onisimus* species for life cycle estimation. Length measurements on *O. brevicaudatus* were made with 2 different stereomicroscopes that, unfortunately, did not have the same magnification; resulting in uneven measurement intervals. Replicate samples of each species were taken for lipid and stable isotope analyses each

month except for the June, July and October samples of *O. glacialis* (see Tables 4 and S4). Samples were packed in aluminum foil and shock-frozen in liquid nitrogen immediately after collection and then stored at  $-80^{\circ}\text{C}$  until further analysis.

### Lipid and fatty acid analyses

Wet and dry weight (DW), lipid class and fatty acid composition were determined for *Anonyx nugax*, *Onisimus glacialis*, *O. nanseni*, *O. littoralis* and *O. caricus*. Fatty alcohols were also analyzed for the wax ester-rich species *O. glacialis*, *O. nanseni* and *O. littoralis*. For *A. nugax*, all lipid samples were from Rippfjorden, except for February when samples from Adventfjorden were used. Samples of *O. glacialis* and *O. nanseni* were collected in Rippfjorden and additionally in September from the pack ice north of Svalbard. All *O. littoralis* and *O. caricus* specimens for lipid and stable isotope analyses were collected in Adventfjorden. A sample consisted of a single individual, except for *O. glacialis* where 2 individuals were pooled in order to get enough material for the analyses. Samples for lipid class and fatty acid data for *A. nugax* were collected from the fast ice in Rippfjorden in April 2007 ( $n = 4$ ) and 2008 ( $n = 3$ ). A *t*-test did not reveal differences in any lipid class or fatty acid between the years and hence these samples were pooled.

Lipid classes, fatty acids and fatty alcohols were analyzed at UNILAB, Tromsø, Norway. Prior to analysis, the samples were wet weighed and freeze-dried to obtain the DW. The dried samples were homogenized in chloroform:methanol 2:1 (v/v), and total lipid was extracted, following Folch et al. (1957), and weighed.

Sub-samples of the total lipid extract were used to analyze the lipid class and fatty acid composition of the polar and neutral lipid fraction, separated using solid bond extraction-fractionation as described by Kaluzny et al. (1985). A known amount of the fatty acid 21:0 was added as an internal standard to both fractions and an acid-catalyzed transesterification was carried out with 1% sulphuric acid in methanol (Christie 1982). The relative (%) compositions of fatty acid methyl esters and fatty alcohol acetates were determined on an Agilent 6890 N gas chromatograph, equipped with a fused silica, wall-coated capillary column with an Agilent 7683 injector and flame ionization detection. Hydrogen was used as the carrier gas with an oven thermal gradient from an initial  $60$  to  $150^{\circ}\text{C}$  at  $30^{\circ}\text{C min}^{-1}$ , and then to a final temperature of  $230^{\circ}\text{C}$  at  $1.5^{\circ}\text{C min}^{-1}$ . Individual components were identified by comparing them to known stan-

dards and were quantified using HPChemStation software (Hewlett-Packard).

The presence of 20:1 and 22:1 fatty acids and fatty alcohols are used as FATM for feeding on calanoid copepods (Sargent & Falk-Petersen 1988), while the sum of C16 polyunsaturated fatty acids, 16:1 n-7 and 20:5 n-3 fatty acids are used as an indicator for diatom feeding (Dalsgaard et al. 2003). A high ratio of 18:1 n-9/n-7 is used as an indicator of carnivory and necrophagy (Sargent & Falk-Petersen 1981, Bühring & Christiansen 2001).

### Stable isotope analysis

Stable carbon and nitrogen isotope analyses were performed at the Institute for Energy Technology, Kjeller, Norway as described in Søreide et al. (2006b), which includes removal of both inorganic carbon and lipids before analyses. All samples consisted of a single amphipod individual.

TL was calculated by using a stepwise enrichment factor of  $3.4\text{‰}$   $\delta^{15}\text{N}$  per level (Søreide et al. 2006a) and setting the baseline level (TL = 1) at  $\delta^{15}\text{N} = 3.6\text{‰}$  during the ice-covered season (April–June) in Rippfjorden (mean value for ice algae in Rippfjorden April 2007; Leu et al. 2010), and  $\delta^{15}\text{N} = 4.0\text{‰}$  (mean value for phytoplankton in Svalbard waters; Søreide et al. 2006a) during the open water season (July–October) in both for Rippfjorden and for all samples from Adventfjorden.

### Statistical analyses

The trap samples were divided into depth zones (0–5, 5–20, 20–40, 40–100 and  $>100$  m) and a catch per unit effort (CPUE) value was calculated separately for each depth zone and month. The catch was expressed as the number of individuals and 1 trap deployed for 24 h was taken as 1 unit of effort.

Constrained correspondence analysis (CCA) was used to obtain a graphical representation of the depth and fjord allocation of amphipod species. CCA is a  $\chi^2$  distance-based ordination method, where a community data matrix is constrained by a matrix of explanatory variables (ter Braak 1986). Fjord and the depth zone data (pooling the 40–100 m and  $>100$  m depth zones) was used as the explanatory matrix. CPUE data for each trap was  $\log(x + 1)$  transformed and entered into the community data matrix. Empty traps and *Ischyrocerus anguipes* (only 1 specimen was found) were removed from the dataset. The

analysis was performed using R-statistical environment (R Development Core Team 2010) and Vegan (Oksanen 2011). Depth contour was fitted to the CCA model using a generalized additive model (GAM, 'ordisurf' command in Vegan). In addition, samples were tested for difference between fjords, depth zones and months using the PERMANOVA+ package (Anderson et al. 2008) for PRIMER v6 (Clarke & Gorley 2006). The PERMANOVA analysis uses the Bray-Curtis similarity index and performs a permutation test to judge the similarities between chosen factors. For calculating the Bray-Curtis similarity index the data was square-root transformed and a dummy variable of 0.0001 was added. This was necessary to include the variability of using baited traps for sampling, as many traps were empty. Factors used in the PERMANOVA analysis were fjord, depth zone and month. In cases where the number of unique permutations was <100 the Monte Carlo p-value was chosen (Anderson et al. 2008). The significance level was set to 0.05. For the pairwise PERMANOVA tests a Holm-Bonferroni correction for multiple comparisons was applied (Holm 1979), thus lowering the critical significance level. PRIMER was also used for calculating Shannon-Wiener's diversity index and Pielou's evenness index (Clarke 1993).

A principal component analysis (PCA) was performed using CANOCO for Windows v4.5 to investigate the dominant patterns in the fatty acid composition among species (ter Braak & Smilauer 2002). Only fatty acids contributing more than 1% were included in the analysis and the compositional data was not transformed prior to analysis. Ordination techniques and rules of interpretation of PCA ordination plots are summarized by ter Braak (1995) and ter Braak & Smilauer (2002). In short, the closer the samples are clustered together the more similar fatty acid composition they have. The fatty acids (shown as arrows) are standardized and centered and point in the direction of maximum change. Projecting samples perpendicularly to the arrows indicates their relative amount of these fatty acids. The angle between arrows indicates their correlation, i.e. they are uncorrelated if they are perpendicular to each other and highly correlated (positive or negative) if the angle is small. The lengths of the arrows indicate the importance of the fatty acid in describing the variability.

The lengths-frequencies of *Onisimus edwardsii* and *O. brevicaudatus* were plotted in R-statistical environment (R Development Core Team 2010). Kernel densities were obtained using the default values in the 'density' function, except for band-width, which was set to 0.04.

## RESULTS

### Species composition

A total of 8 amphipod species (in addition to the decapod *Eualus gaimardii* in September) were collected in the samples from Adventfjorden, whereas 19 amphipod species were recorded in Rjippfjorden (see Tables S1 and S2 in the supplement at [www.int-res.com/articles/suppl/b014p247\\_supp.pdf](http://www.int-res.com/articles/suppl/b014p247_supp.pdf)). The average (mean  $\pm$  SD) species richness in the samples was  $3.8 \pm 1.7$  in Adventfjorden and  $5.1 \pm 2.2$  in Rjippfjorden ( $t = 0.012$ ). In terms of diversity, a lower Shannon-Wiener index (mean  $\pm$  SD) was observed in Adventfjorden,  $0.57 \pm 0.42$ , compared to  $1.06 \pm 0.40$  in Rjippfjorden ( $t < 0.001$ ). Pielou's evenness index (mean  $\pm$  SD) showed a stronger dominance of few species in Adventfjorden ( $0.46 \pm 0.29$ ), while a more even distribution of species was observed in Rjippfjorden ( $0.68 \pm 0.18$ ,  $t = 0.002$ ).

The CCA plot shows clear differences in the species composition of the amphipod scavenging guild between the fjords and among depth layers (Fig. 2). Axis 1 mainly explains the differences in species distribution between the fjords, indicating the importance of *Onisimus caricus* in Adventfjorden and showing a higher diversity in the scavenging guild in Rjippfjorden. Axis 2 demonstrates the depth zonation in species distribution. Depth contours, fitted to the CCA model (estimated degrees of freedom = 5.85, generalized cross validation score = 1.30), assist the interpretation of the species' depth preferences (Fig. 2).

Similarly, based on the Bray-Curtis similarity index, the species composition in the baited trap samples was significantly different between the 2 studied fjords (PERMANOVA: pseudo- $F = 48.186$ ;  $p < 0.001$ ) and among the depth zones (PERMANOVA: pseudo- $F = 9.911$  and  $4.957$  for Adventfjorden and Rjippfjorden, respectively;  $p < 0.001$ ). In Adventfjorden the 0–5 m depth zone was significantly different from both the 5–20 and 20–40 m depth zones ( $t = 3.536$  and  $3.701$ , respectively;  $p < 0.001$ ), whereas the species composition was similar in the 5–20 and 20–40 m depth layers. In Rjippfjorden the depth layers deeper than 20 m showed similarities, whereas the 2 shallower depth zones differed significantly from each other and the deeper layers. Moreover, a difference in species composition between months was observed both in Adventfjorden and in Rjippfjorden (PERMANOVA: pseudo- $F = 3.329$  and  $7.591$ , respectively;  $p < 0.001$ ). In Adventfjorden, the species composition observed in the 5–20 m depth layer, in the spring months April and May, differed from that found in the



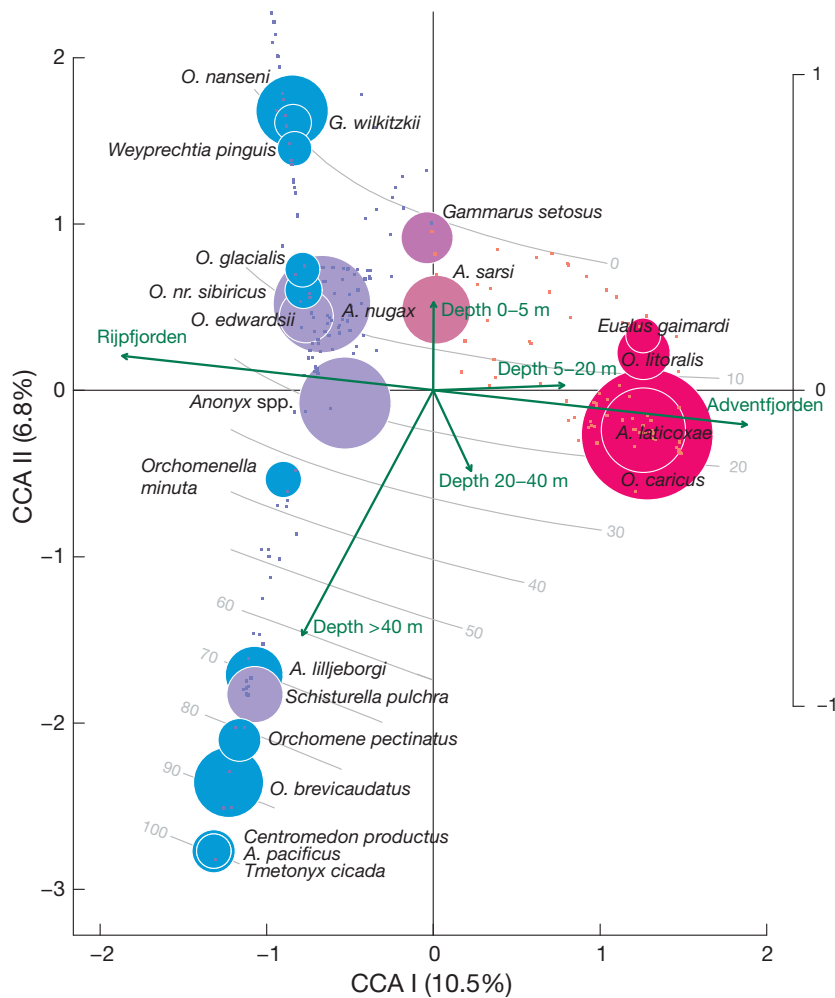


Fig. 2. Constrained correspondence analysis (CCA) plot illustrating the distribution of amphipod species in baited trap samples collected from Adventfjorden and Rijpfjorden in the Svalbard archipelago. Each species is represented by a filled circle whose diameter corresponds to the mean catch per unit effort (CPUE) of the species. Red and blue circles indicate species collected in Adventfjorden and Rijpfjorden respectively. Shades of purple indicate that the species were encountered in both fjords. Shades closer to red indicate higher occurrence in Adventfjorden, while shades closer to blue indicate higher occurrence in Rijpfjorden. The arrows indicate the explanatory variables. Small red and blue dots represent the samples collected in Adventfjorden and Rijpfjorden, respectively. Axis 1 mainly explains the distribution between fjords, whereas Axis 2 mainly explains the depth distribution of the species. Fitted depth contours are plotted in grey

late autumn months October and November (Table 1). In Rijpfjorden, species composition in the June and July samples was different than in other months (Table 1). In February, the species composition in the 20–40 m depth layer significantly differed from that in March and April at the same depth (Table 1).

In Adventfjorden, the most common species in the traps was *Onisimus caricus* (Table S1). Except in September, it was by far the most abundant species. It was present in all depth layers with highest abundance at depths deeper than 5 m. *O. litoralis* and *Gammarus setosus* were frequently found in the shallowest traps (0–5 m). In Adventfjorden, 3 species of *Anonyx* were recorded, the most common being *A. laticoxae*. This species occurred in all depth layers, but it was more abundant in the deeper ones. *A. sarsi* occurred mostly in the shallowest traps, while *A. nugax* was mainly found deeper. Compared to the high number of juvenile *Anonyx* spp. recorded in Rijpfjorden, very few were found in Adventfjorden. In September, when the traps were placed at a slightly different place, *A. laticoxae* was the most

abundant species recorded. *O. edwardsii* and the decapod *Eualus gaimardii* were only found in September.

In Rijpfjorden, the scavenging amphipod fauna was heavily dominated by *Anonyx* species (Table S2). *A. nugax* and *Anonyx* spp. juveniles were abundant in all depth layers, except in June and July when the overall catches were small. Other *Anonyx* species recorded in Rijpfjorden were *A. sarsi* in the shallow traps, *A. lilljeborgi* in the deeper traps, as well as *A. laticoxae* and *A. pacificus* that were only infrequently recorded. Five species of *Onisimus* were recorded in Rijpfjorden. *O. brevicaudatus* was almost only present in the deep traps, and sometimes in high numbers (>900 ind. in one trap), while *O. edwardsii* and *O. nr. sibiricus* (see Berge et al. 2007) were only present in the shallower traps. In addition, a few specimens of the sympagic species *O. nanseni* and *O. glacialis* were caught in the traps on the bottom. *O. nanseni* was recorded in traps at 20–40 m depth in March and April, while *O. glacialis* was caught in the traps at 5–20 m depth in April. In July both these sympagic species were collected close to shore at

Table 1. Significant *t*-values and *p*-values from the pairwise PERMANOVA test of differences in species composition of amphipods in 2 Arctic fjords between months and depth layers. Following a Holm-Bonferroni correction for multiple comparisons the critical significance level was set to 0.0012 in Adventfjorden and to 0.0033 (depths 0–5 and 5–20 m) and 0.0050 (20–40 m) in Rjipfjorden

Tested months	Depth (m)	<i>t</i>	<i>p</i>
<b>Adventfjorden</b>			
October, April	5–20	3.773	<0.001
October, May	5–20	2.796	<0.001
November, April	5–20	3.440	<0.001
November, May	5–20	2.683	0.001
<b>Rjipfjorden</b>			
February, March	20–40	1.971	0.004
February, April	20–40	2.216	0.003
February, June	5–20	2.844	<0.001
February, June	20–40	3.527	0.002 <sup>a</sup>
February, July	0–5	2.555	<0.001
February, July	5–20	2.810	<0.001
March, June	0–5	3.038	0.002 <sup>a</sup>
March, June	5–20	2.523	0.002
March, July	0–5	2.132	0.003
March, July	5–20	2.647	<0.001
April, June	20–40	1.826	0.002
April, July	0–5	1.997	0.001
April, July	5–20	2.575	<0.001
June, July	0–5	3.489	<0.001
July, October	0–5	2.383	<0.001
July, October	5–20	2.671	<0.001

<sup>a</sup>Indicates Monte-Carlo *p*-values

depths of 0–5 m. *Orchomenella minuta* was frequently recorded in low numbers in Rjipfjorden in all depth layers, while *Orchomene pectinatus*, *Schisturella pulchra* and *Centromedon productus* were mostly recorded in the deeper traps. *Gammarus setosus* was also frequently found in the shallowest traps.

In the ice traps attached directly under the sea ice in Rjipfjorden, a total of 8 species were recorded, all of which have been previously recorded in the sea ice habitat (e.g. Melnikov & Kulikov 1980). The ice traps placed in shallow waters contained primarily benthic species such as *Gammarus setosus*, *Ischyrocerus anquipes*, *Weyprechtia pinguis* and *Anonyx* spp. (Table S3). The sympagic species *Onisimus Nanseni*, *O. glacialis* and *G. wilkitzkii* were mainly found under the ice over deep water. Of these, *O. nanseni* showed a highly patchy distribution. In April 2007 almost all *O. nanseni* were collected in a small area below sea ice, where the water depth was 180 m, with >200 ind. per trap, while in other areas on deep water most of the ice traps were completely empty. In April 2008 the most abundant species in the ice traps was *A. nugax*. This species was regularly present in the ice traps, whereas only a few individuals of the sympagic am-

phipods were collected. In total 908 ind. of *A. nugax* were caught in the ice traps in April 2008, of which 227 random ind. were sexed: 158 (70%) were mature males, 13 (6%) were immature males, 53 (23%) were immature females and 3 (1%) were juveniles.

In general, more amphipods were caught in the winter months compared to the summer months (Fig. 3). In Adventfjorden, the peak in catch size was in November, after which the catch size decreased continuously through the winter. In April, almost no amphipods were caught shallower than 20 m, and in May very few amphipods were caught in total. In June the catch size increased again, mainly at depths >5 m (Table S1). In Rjipfjorden, the mean CPUE was highest in February, after which the catch size decreased during spring. In June and July CPUE was very low compared to the rest of the year. The large number of juvenile *Anonyx* spp. in the traps in September indicate that recruitment to the population had occurred. In October, the shallowest traps caught a very low number of amphipods, probably due to a storm creating wave action and thus disturbing the shallow sampling (Table S2).

#### Length-frequency distribution of *Onisimus edwardsii* and *O. brevicaudatus*

New data on length-frequency distributions are only presented for *Onisimus edwardsii* and *O. brevicaudatus* in this study. For the more numerous species the length frequency has been described elsewhere (Boudrias & Carey 1988, Węślawski et al. 2000, Arndt & Beuchel 2006, Nygård et al. 2009, 2010) and will be referred to in the discussion.

The smallest individuals of *Onisimus edwardsii* were recorded in February and March and measured 0.25 mm (Ls). The largest individuals were observed in both February and April and measured 0.98 mm (Ls) (Fig. 4). Based on the length-frequency distribution and kernel densities, the occurrence of 3 separate cohorts seems likely, which suggests that *O. edwardsii* has a 2 yr life cycle.

*Onisimus brevicaudatus* was almost exclusively recorded in the deep traps and the only month with sufficient length data was April (Fig. 5). The smallest individuals measured 0.25 mm (Ls), while the largest individuals measured 1.11 mm (Ls). Based on the length-frequency distribution and kernel densities, 3 cohorts seem likely, assuming that the smallest individuals, despite few observations, formed a separate cohort. This suggests that *O. brevicaudatus* also has a 2 yr life cycle.

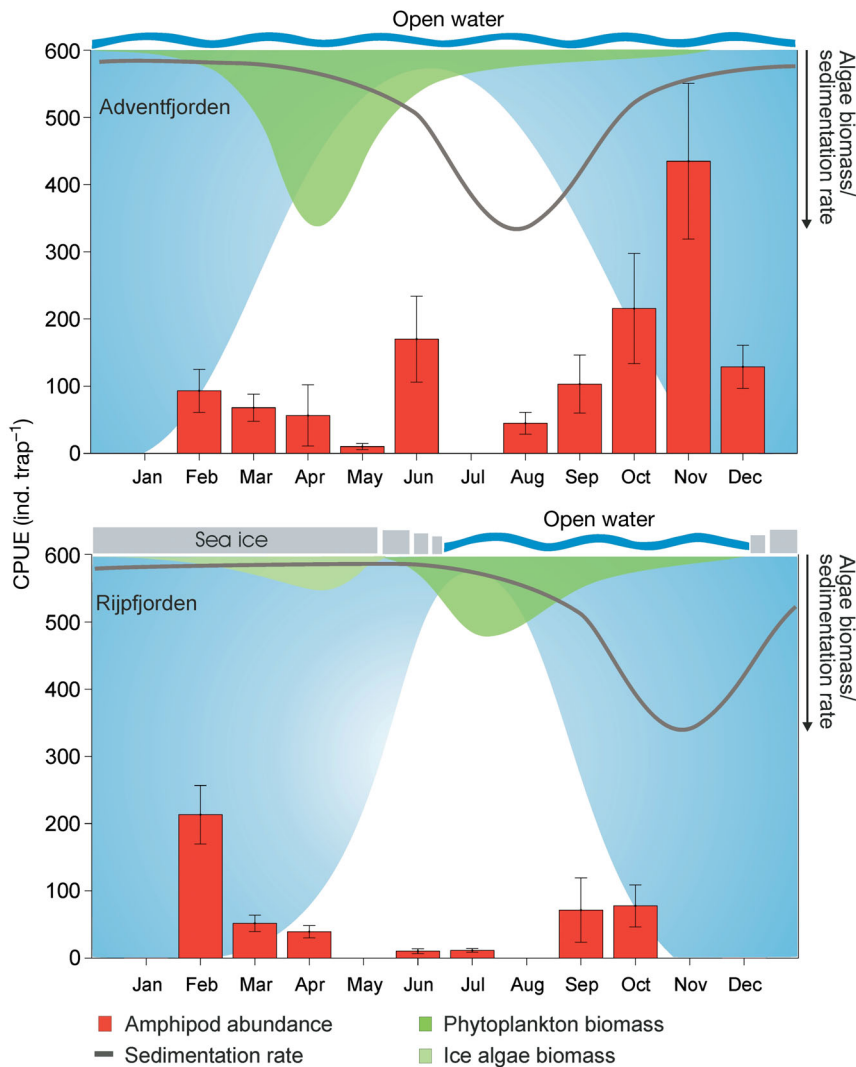


Fig. 3. Seasonal variation in amphipod trap catches in different depth zones in Adventfjorden and Rijpfjorden. Error bars indicate standard error. Note that amphipod abundances in September to December in Adventfjorden are from 2006, while all other data is from 2007. Data on phytoplankton and sedimentation rates in Adventfjorden are based on Zajaczkowski et al. 2010, while ice algae and phytoplankton curves in Rijpfjorden are based on Søreide et al. 2010. The sedimentation rate for Rijpfjorden is based on data from sediment traps placed at 100 m depth on a mooring (J. Berge et al. unpubl.) and is thus not directly comparable to sedimentation rates shown for Adventfjorden. The white areas represent incoming light

### Total lipid and lipid classes

The highest lipid contents were found in *Onisimus glacialis*, *O. nanseni* and *O. littoralis* (Table 2). In these species the lipid content was generally between 15 and 30% of DW, with the highest values observed in summer and autumn. In *Anonyx nugax*, the lipid content of samples collected from the bottom was between 11 and 19% of DW, compared to only 6 to 9% of DW in samples from the ice traps. *O. caricus* had low lipid content compared to the other *Onisimus* species (Table 2).

In all species, triacylglycerols made up the largest proportion of the lipids (Table 2). Wax esters were important in *Onisimus nanseni*, especially during the spring when >40% of total lipids were wax esters. Wax esters were also important in *O. glacialis*, while this lipid class seems to be of minor importance

(<15%) for the other studied species. The remaining lipids were to a large extent phospholipids.

### Fatty acid composition

More than 70% of the total fatty acid variability is shown in the 2-dimensional PCA plot, suggesting strong and consistent patterns in fatty acid composition in the 94 samples comprising 5 different amphipod species (Fig. 6). The strongest gradient, Axis 1, explains close to 50% of the total fatty acid variability and shows a gradient from mainly herbivorous-omnivorous to carnivorous, as indicated by the change from elevated levels of the typical algae FATMs 20:5 n-3, and C16 and C18 polyunsaturated fatty acids, to elevated levels of the typical carnivore FATM 18:1 n-9 (Fig. 6). The second gradient, Axis 2,



mainly shows a gradual change from typical diatom FATMs to typical calanoid copepod FATMs (i.e. 20:1 and 22:1).

Based on the 5 species' fatty acid composition, *Onisimus glacialis* and *O. litoralis* were those with the most herbivorous diet (Fig. 6, Table S4). The 3 other species were predominantly carnivorous during all seasons with *O. nanseni* and *Anonyx nugax* seasonally having high proportions of *Calanus* FATMs (up to 37 and 30%, respectively; Table S4). *O. caricus* had a particularly high proportion of the carnivore FATM 18:1 n-9 (30–48%).

In *Anonyx nugax*, the level of 18:1 n-9 was elevated during winter, while the lowest values for this fatty acid were observed in the ice traps in spring. *Onisimus litoralis* also showed seasonal variation in this carnivorous FATM, with the lowest values recorded in summer (overall mean 13.7%). *O. glacialis* had consistently low proportions of 18:1 n-9 (overall mean, spring to autumn, 14.2%; winter values not available).

The calanoid copepod FATMs, 20:1 and 22:1, were particularly important in *Onisimus nanseni*, where the sum of these fatty acids comprised almost 35% during spring (Table S4). In *Anonyx nugax* these fatty acids were elevated in April, and again in August to September. *O. glacialis* had moderate levels of 20:1 and 22:1 fatty acids (max. 18.5% in October), whereas these fatty acids were of little importance for *O. litoralis* (mean 8.2%) and *O. caricus* (mean 3.9%). Levels of 20:1 and 22:1 fatty alcohols were high in *O. nanseni* and considerable in *O. glacialis* (Table 3).

The diatom FATMs 16:1 n-7 and 20:5 n-3 were particularly important in *Onisimus glacialis* and *O. litoralis*, with the highest values recorded in summer. Other important fatty acids were 16:0 (in all studied species), and 22:6 n-3 (especially in *Anonyx nugax*).

### Stable isotopes

Based on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values no clear seasonal pattern in trophic position could be seen for *Anonyx nugax* (Table 4). The trophic position of this species seemed to be stable at a high TL (3.3–3.5) throughout the year. *Onisimus caricus* had a trophic position between 2.9 and 3.3, whereas *O. nanseni* (2.6–2.9) and *O. litoralis* (1.8–2.8) had the lowest trophic positions, with particularly low values in July (Table 4).

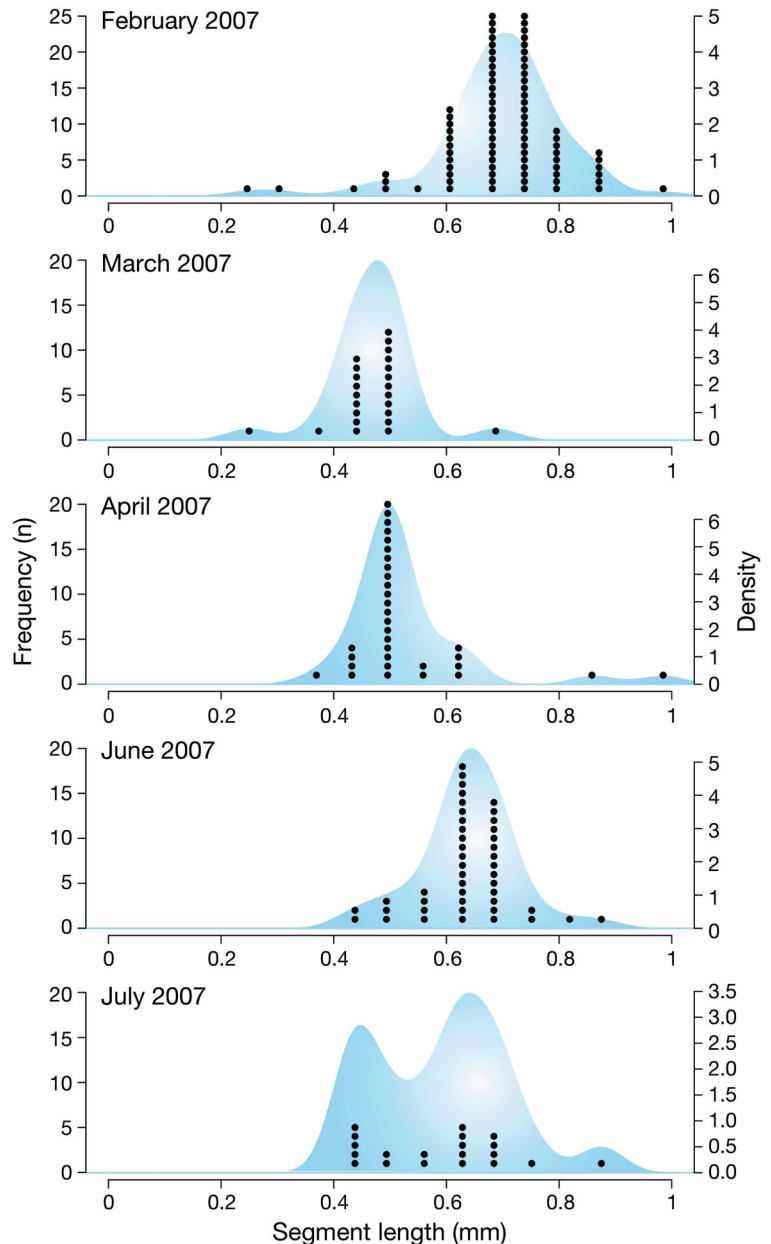


Fig. 4. *Onisimus edwardsii*. Length-frequency distribution (black dots; n = no. of individuals) and kernel density distribution (blue background) in samples collected in Rijpfjorden in April 2007

## DISCUSSION

### The amphipod scavenging guild

There was a clear difference in the species composition between the 2 fjords, which was as expected, given their differing environmental conditions. As seems to be common in Arctic coastal waters (Sainte-Marie 1986, Legeżyńska et al. 2000), the 2 genera *Anonyx* and *Onisimus* co-occurred and

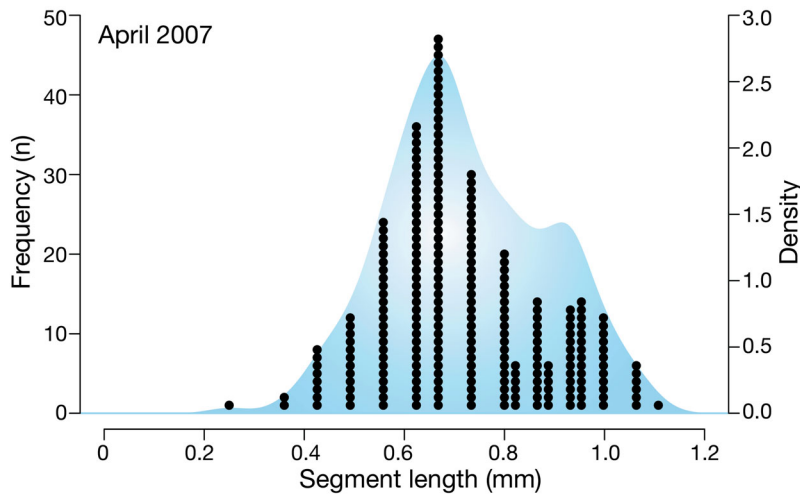


Fig. 5. *Onisimus brevicaudatus*. Length-frequency distribution (black dots; n = number of individuals) and kernel density distribution (blue background) in samples collected in Rijpfjorden in April 2007

dominated the scavenging guild also in our study. However, different sets of species from these genera were found in the 2 fjords, with different species showing different habitat preferences.

The high-Arctic Rijpfjorden opens directly towards the Arctic Ocean with drifting sea ice influencing the fjord environment (Hop & Pavlova 2008). The presence of the true ice fauna *Onisimus nanseni*, *O. glacialis* and *Gammarus wilkitzkii* in Rijpfjorden underlines the strong influence of pack ice from the Arctic Ocean; none was detected in the more Atlantic influenced fjords on Svalbard, such as Adventfjorden (this study) or Kongsfjorden (Legeżyńska 2001). In both Adventfjorden and Rijpfjorden, the

Table 2. Wet weight (WW), dry weight (DW), total lipid content and lipid classes of lysianassoid amphipods in Adventfjorden and Rijpfjorden. See 'Materials and methods' for details of sampling locations. WE: wax esters; TAG: triacylglycerol; C: cholesterol; DAG: diacylglycerol; MAG: monoacylglycerol; GAL: galactocerebroside; CL: cardiolipin; PL: phospholipids. Dashes indicate no data

		WW (mg)	DW (mg)	Lipid content (% of DW)	Lipid classes (% of total lipid)							
					WE	TAG	C	DAG	MAG	GAL	CL	PL
<i>Anonyx nugax</i>	Feb	479.7	–	–	–	–	–	–	–	–	–	–
	Mar	322.2	–	–	–	–	–	–	–	–	–	–
	Apr	914.8	259.9	16.4	2.5	87.4	1.8	1.0	0.0	0.4	0.2	6.6
	Apr <sup>a</sup>	1301.6	272.7	9.1	6.2	55.5	5.3	0.2	0.0	1.9	0.1	30.9
	Jun <sup>a</sup>	1070.1	217.7	5.8	9.4	35.7	7.6	0.8	0.0	2.6	0.0	43.9
	Aug	2465.9	576.5	18.6	1.7	88.4	1.7	1.1	0.0	0.5	0.3	6.2
	Sep	1333.5	352.3	17.6	11.1	76.0	1.8	0.9	0.0	0.6	0.0	9.5
	Oct	1328.1	305.4	11.2	2.9	73.8	2.3	0.9	0.0	0.9	0.0	19.2
<i>Onisimus glacialis</i>	May <sup>a</sup>	15.1	4.4	–	8.7	79.4	1.3	1.6	4.4	0.0	0.0	4.5
	Jun <sup>a</sup>	21.7	6.4	23.4	15.7	58.3	1.9	1.4	8.7	1.0	0.0	13.0
	Jul <sup>a</sup>	22.8	6.9	29.0	26.6	59.5	1.6	1.1	5.4	0.8	0.0	4.9
	Aug	26.8	7.4	24.9	14.1	70.4	2.0	0.3	3.2	0.3	0.0	9.6
	Sep <sup>b</sup>	34.6	9.8	18.1	6.5	80.0	1.2	1.6	3.1	0.0	0.0	7.5
	Oct	13.8	3.7	30.4	30.5	56.1	3.5	0.0	0.0	0.0	0.0	9.8
<i>O. nanseni</i>	Apr <sup>a</sup>	60.8	20.1	29.1	43.6	46.8	1.1	2.0	2.0	0.8	0.3	3.2
	May <sup>a</sup>	49.6	16.9	19.2	40.9	49.5	1.0	1.7	1.7	0.7	0.3	4.1
	Jun <sup>a</sup>	86.2	20.3	23.8	27.5	56.4	1.8	2.5	4.0	1.1	1.0	5.7
	Jul	90.5	23.7	26.7	12.7	75.2	1.9	1.4	2.1	0.7	0.3	5.6
	Aug	125.2	39.6	24.2	20.0	71.3	0.9	0.9	0.0	0.3	0.0	6.6
	Sep	115.1	34.6	21.6	16.8	69.3	1.5	2.2	1.4	0.7	0.3	7.9
	Sep <sup>b</sup>	96.7	25.0	15.7	19.8	48.1	2.9	3.2	10.4	1.3	1.2	13.1
	Oct	92.2	28.7	13.6	22.3	48.5	2.6	2.2	1.6	1.2	0.7	20.9
<i>O. littoralis</i>	Apr	44.2	11.4	–	14.3	49.6	4.3	1.8	6.7	3.1	0.0	20.2
	May	49.9	12.2	15.2	6.5	74.0	2.4	1.9	3.3	1.0	0.0	10.9
	Jun	52.9	13.2	19.7	7.4	77.6	1.9	2.6	1.1	1.8	0.0	7.6
	Jul	58.7	17.5	32.2	9.3	85.4	1.2	1.2	0.0	0.0	0.0	2.8
	Aug	120.3	30.1	26.8	5.4	90.0	1.0	1.0	0.0	0.0	0.0	2.7
	Nov	126.3	21.8	–	12.9	16.1	9.7	0.0	8.4	4.0	4.8	44.1
<i>O. caricus</i>	Feb	272.0	70.6	5.8	3.1	60.0	3.6	3.2	4.5	1.0	0.0	24.7
	Jun	185.5	51.8	11.7	7.8	86.8	1.3	0.0	0.0	0.0	0.0	4.1
	Nov	280.3	74.0	8.5	2.0	78.5	2.2	2.1	1.3	0.7	0.4	12.9

<sup>a</sup>Individuals collected in ice traps; <sup>b</sup>samples collected in the pack ice north of Svalbard

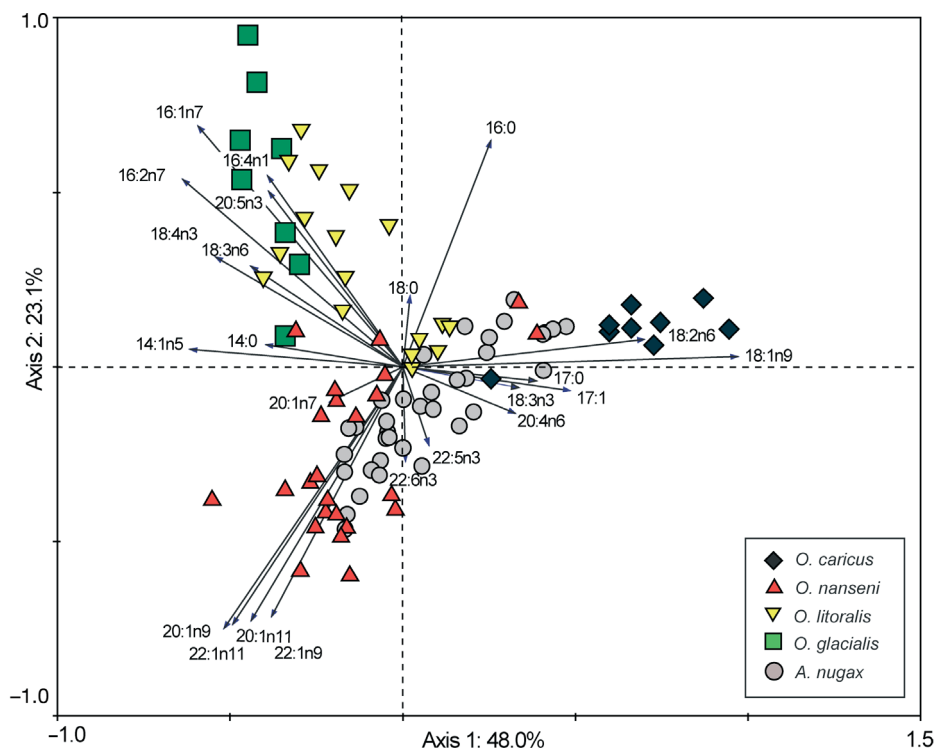


Fig. 6. Principal component analysis of the fatty acids contributing >1% of the total lipid composition in the studied amphipods, showing 3 distinct groupings. Axis 1, explaining 48% of the total variability, shows a gradient from herbivory on the left side to carnivory/scavenging on the right side, whereas Axis 2 (explaining 23% of the total variability) shows a gradient from diatom fatty acid trophic marker (FATM) in the upper part to *Calanus* FATM in the lower part of the figure. See 'Materials and methods' for further explanation

scavenging guild was dominated by typical cold-water species, similar to results from other Arctic areas (Legężyńska et al. 2000); even though the difference in the temperature regime between the 2 fjords was pronounced, temperature probably had less influence on the species composition than did sea ice. While sympagic fauna drifting out in the Fram Strait is believed to be lost to the pelagial and benthos when the ice melts (Werner et al. 1999,

Arndt & Pavlova 2005, Hop & Pavlova 2008), the fate of these species when they are released from ice melting in shallow, seasonally ice-covered areas is not fully understood. There are indications that sympagic amphipods can survive ice-free periods in the benthic habitat and re-colonize the ice when it is reformed (Arndt et al. 2005b, Nygård et al. 2007). Based on ice charts, drift ice was present in Rippfjorden in autumn 2006 from the end of September to

Table 3. *Onisimus nanseni*, *O. glacialis* and *O. littoralis*. Fatty alcohols as percent of total lipid content. n: number of replicate samples. When 3 replicates were measured, results are shown as mean ± SD, when 2 replicate samples were measured, the range is shown, and when 1 sample was measured the single value is shown

Species, site	Month	n	FA-OH							Ratio 22:1 / 20:1
			14:0	16:0	16:1 n-7	18:1 n-9	20:1 n-9	22:1 n-11	22:1 n-9	
<i>O. nanseni</i>										
Rippfjorden	Apr	3	0.1 ± 0.0	0.4 ± 0.1	0.1 ± 0.0	0.2 ± 0.0	5.1 ± 0.9	9.2 ± 2.9	0.8 ± 0.1	1.98
	May	1	0.2	0.5	0.1	0.3	4.3	6.4	0.8	1.69
	Jun	3	0.1 ± 0.0	0.3 ± 0.1	0.1 ± 0.1	0.1 ± 0.0	2.3 ± 0.8	4.2 ± 2.0	0.6 ± 0.3	2.12
	Jul	2	0.1	0.2–0.4	0.0–0.2	0.1	1.1–1.4	1.5–1.7	0.4	1.58
	Aug	2	0.0–0.1	0.1–0.3	0.0–0.1	0.2–0.3	1.3–2.3	2.3–7.8	0.3–1.0	3.22
	Sep	3	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	1.4 ± 0.4	2.9 ± 1.5	0.6 ± 0.0	2.45
	Sep	3	0.0 ± 0.0	0.2 ± 0.2	0.1 ± 0.0	0.1 ± 0.1	2.2 ± 1.6	2.4 ± 1.9	0.3 ± 0.2	1.26
Pack ice	Sep	3	0.0 ± 0.0	0.2 ± 0.2	0.1 ± 0.0	0.1 ± 0.1	2.2 ± 1.6	2.4 ± 1.9	0.3 ± 0.2	1.26
Rippfjorden	Oct	3	0.2 ± 0.1	0.6 ± 0.3	0.1 ± 0.1	0.2 ± 0.1	2.5 ± 1.6	2.0 ± 0.8	0.9 ± 0.4	1.17
<i>O. glacialis</i>										
Rippfjorden	Jun	1	0	0.2	0.1	0.1	1.5	1.8	0.2	1.38
	Jul	1	0.2	0.6	0.2	0.2	2.7	4.6	0.6	1.89
	Aug	1	0.1	0.2	0.1	0.1	1.2	1.8	0.3	1.77
	Oct	1	0.1	0.6	0.1	0.3	4	4.7	0.7	1.36
<i>O. littoralis</i>										
Adventfjorden	Jul	2	0.0–0.1	0.2–0.4	0.1–0.2	0.1–0.2	1.1–2.1	1.2–2.6	0.2–0.4	1.34

Table 4. *Anonyx nugax*, *Onisimus nanseni*, *O. littoralis* and *O. caricus*. Stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope values (mean  $\pm$  SD) and trophic levels *A. nugax* and *O. nanseni* were collected in Rijpfjorden, *O. littoralis* and *O. caricus* in Adventfjorden. n: number of replicate samples

Species	Month	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Trophic level
<i>A. nugax</i>	Apr	4	$-21.6 \pm 0.4$	$12.0 \pm 0.7$	3.5
	Jun	4	$-20.7 \pm 0.5$	$11.6 \pm 0.6$	3.4
	Jul	3	$-21.5 \pm 0.6$	$11.8 \pm 0.3$	3.3
	Aug	3	$-21.6 \pm 0.6$	$12.0 \pm 1.5$	3.3
	Sep	4	$-21.4 \pm 0.4$	$11.7 \pm 1.1$	3.3
	Oct	6	$-20.8 \pm 0.4$	$12.7 \pm 0.8$	3.5
<i>O. nanseni</i>	Apr	5	$-22.6 \pm 0.5$	$9.6 \pm 0.6$	2.8
	May	4	$-22.3 \pm 0.4$	$10.1 \pm 0.1$	2.9
	Jun	7	$-22.3 \pm 0.7$	$9.2 \pm 0.8$	2.6
	Jul	3	$-21.8 \pm 0.7$	$9.7 \pm 0.9$	2.7
	Aug	5	$-21.6 \pm 0.4$	$10.1 \pm 0.7$	2.8
<i>O. littoralis</i>	Apr	3	$-21.6 \pm 0.3$	$9.9 \pm 0.4$	2.7
	Jul	3	$-22.4 \pm 0.5$	$6.8 \pm 1.7$	1.8
	Aug	11	$-21.1 \pm 1.2$	$10.0 \pm 0.9$	2.8
	Sep	5	$-22.7 \pm 1.0$	$8.9 \pm 0.7$	2.5
	Oct	5	$-22.6 \pm 0.6$	$8.0 \pm 0.2$	2.2
<i>O. caricus</i>	Feb	5	$-21.8 \pm 0.4$	$11.5 \pm 0.7$	3.2
	Apr	3	$-21.9 \pm 0.6$	$10.5 \pm 1.6$	2.9
	Jun	3	$-20.6 \pm 0.6$	$12.0 \pm 0.7$	3.3

early November (<http://polarview.met.no/>), but from then on the fjord was ice free until land-fast ice formed in early February 2007 (Leu et al. 2010). Since the land-fast ice prohibited drift ice entering the fjord, the ice amphipods collected in our study probably originated from the ice that drifted in during autumn, or even earlier. After the ice melt in July 2007, and still in September, *O. nanseni* could be collected with hand nets nearshore, showing that it can survive outside the ice habitat at least for some months (H. Nygård pers. obs.). A further interesting observation was the high abundance of *Anonyx nugax* in the ice traps even over depths of 200 m and kilometers away from shallow areas. *A. nugax* has been sporadically found in ice (e.g. Melnikov & Kulikov 1980), but the high abundances of it in ice in the present study suggest that it might utilize the sea-ice habitat more actively than thought.

The difference in the bottom substrate should also be kept in mind when comparing the species composition in the 2 fjords. *Onisimus caricus*, a species known to inhabit inner fjords disturbed by glacial outflow (Legeżyńska 2001), dominated the scavenging guild on the soft substrate in Adventfjorden, whereas *Anonyx* spp. dominated on the coarser substrate in Rijpfjorden. A similar pattern, with *Onisimus* species dominating in inner parts and *Anonyx* species in outer parts of the fjord, was found in

Kongsfjorden (Legeżyńska 2001). The September samples from Adventfjorden, which were mainly collected in the outer part of the fjord on a substrate more comparable to that in Rijpfjorden, were dominated by *Anonyx* species. However, the species composition in the September samples from Adventfjorden clusters together with the other Adventfjorden samples, indicating that there is a difference in species composition between the 2 fjords that is not fully explained by differences in type of substrate. The differing temperature and production regimes in the 2 fjords (Søreide et al. 2010, Zajaczkowski et al. 2010), resulting from differences in seasonal ice cover, probably constrain the species that can thrive in each fjord.

The clear difference in species composition between depth zones, found in both fjords, can be explained by the depth preferences of different species. This pattern is in accordance with Legeżyńska et al. (2000), who found a depth separation between different *Anonyx* and *Onisimus* species: *A. nugax* and *O. caricus* occurred mainly at depths greater than 30 m while *A. sarsi* was found mainly in shallower waters; *O. edwardsii* peaked at 15 m and *O. littoralis* was most abundant at 5 m depth (Legeżyńska et al. 2000).

In the present study, 2 species that have not been recorded earlier in Svalbard waters were found (Palerud et al. 2004). Both *Anonyx pacificus* and *Onisimus* nr. *sibiricus* were found in Rijpfjorden, an area that until now has not been thoroughly studied. *A. pacificus* has its main distribution area in the northwest Atlantic (Steele & Brunel 1968), whereas *O. sibiricus* has until now been found only in the Russian Arctic seas (Berge et al. 2007).

### Seasonality in the trap catches

A clear seasonal difference in the baited trap catches was evident in both Rijpfjorden and Adventfjorden, with, in general, larger catches in winter than in summer. Interestingly, this seasonal variation was not synchronized in the 2 fjords. The highest catches were retrieved in Adventfjorden in November, while in Rijpfjorden the highest abundance was recorded in February. The samples collected in spring, April and May, in Adventfjorden, and early summer, June and July, in Rijpfjorden, contained very few amphipods compared to the samples collected during the rest of the year. The earlier peak and the earlier decrease of amphipods in the traps in Adventfjorden compared to Rijpfjorden can be related to the different environmental conditions i.e.

the earlier seasonal development of the system in Adventfjorden, with an earlier primary production bloom due to the lack of sea ice (Fig. 3; Søreide et al. 2010, Zajaczkowski et al. 2010). This pattern can be compared to the timing of primary production described on a latitudinal gradient by Leu et al. (2011).

Changes in the amphipods' feeding behavior or preferences influence the baited trap catches (Smale et al. 2007). Thus, the seasonality in the catches does not reflect real differences in the abundances of scavenging amphipods in the fjords. During the winter, food resources are presumably scarce in the fjords, thus a baited trap is likely to be attractive for the amphipods. In contrast, during spring and summer, when primary production and settling of organic material peak, there is an excess of potential food and the amphipods might not be so strongly attracted to the smell of bait. Legeżyńska (2008) suggests a seasonal feeding strategy for *Onisimus caricus*, i.e. that this species consumes mainly zooplankton carcasses in summer, when they are highly abundant in glacial bays (Zajaczkowski & Legeżyńska 2001). Additionally, during summer, a large proportion of the amphipod populations consist of newly released juveniles that might have different feeding preferences than older stage amphipods (Nygård et al. 2009).

Processes connected to reproduction influence the attractiveness to bait. Mature males increase their swimming activity prior to the mating season and might therefore be more prone to enter traps (Sainte-Marie 1986, Sainte-Marie et al. 1990, Conlan 1991). Based on earlier observations on brood carrying females, mating in the studied species generally occurs in early winter (Węśławski & Legeżyńska 2002, Nygård et al. 2009, 2010). The delay of the phytoplankton spring bloom in Rjipfjorden due to the sea ice cover might alter the scheduling of the life cycles in Rjipfjorden compared to Adventfjorden. As the egg sizes in *Onisimus* and *Anonyx* species are approximately the same (Sainte-Marie et al. 1990, Węśławski & Legeżyńska 2002), the embryo development time should be comparable between the species, and thus the main mating period of these species is probably around 2 mo earlier in Adventfjorden compared to Rjipfjorden. In many species, males die shortly after the mating period (Sainte-Marie et al. 1990, Nygård et al. 2009), which could also be reflected in decreased catches. Sainte-Marie et al. (1990) noted that pregnant females of *A. sarsi* carrying eggs in their brood pouches contract their gut and stop feeding actively; consequently they would not be attracted to baited traps. Sainte-Marie & Lamarche (1985) suggest that species attracted to

traps while brooding are iteroparous, while semelparous species do not feed while brooding.

A final factor that could have an impact on the behavior or habitat choice of the amphipods is predation pressure, or rather avoidance of predators. As these amphipods are quite large they are probably easy prey for visual predators if they expose themselves to brightly lit areas. In Adventfjorden, the decrease in the catches, especially in the shallow traps, coincides with the time of the year when the light increases and migrating birds return. Seabirds (black guillemots *Cephus grylle*, Arctic terns *Sterna paradisea*, eider ducks *Somateria mollissima*) feed on amphipods (Węśławski et al. 1994, Byers et al. 2010), as do shore-birds (purple sandpiper *Calidris maritima*) in the inter-tidal zone (Luukkonen 2009). Interestingly, there is an increase in the trap catches again in June, when the melting season has started and the fjord is receiving high loads of suspended particles. Reduced visibility in the water complicates the foraging of visual predators and may provide favorable conditions for the amphipods to return to the shallower areas. However, this explanation can not explain the decrease in the catches in Rjipfjorden in June, since the fjord was still ice covered and therefore predation from birds is not expected. However, in July, Arctic terns were actively foraging near-shore in Rjipfjorden, probably catching amphipods (H. Nygård pers. obs.). The predation pressure on amphipods by fish and seals (Labansen et al. 2007) remains unknown in our study area.

### Feeding patterns

Based on the stable isotope analyses we were able to assign a trophic position to 4 of the investigated amphipods. *Anonyx nugax* was the highest positioned species in the food web with a TL of 3.3 to 3.5, followed by *Onisimus caricus* (2.9–3.3) and *O. nanseni* (2.6–2.9). *O. littoralis* was the species closest to a herbivore (1.8–2.8) with a clearly herbivorous trophic position (1.8) in July. It should however be noted that whole individuals were used for the stable isotope analyses, which probably underestimates their true trophic level (Søreide & Nygård 2011).

The stable isotope results strongly support the pattern found in the fatty acid composition, where 3 main groups were identified: (1) a herbivorous/omnivorous group including *Onisimus glacialis* and *O. littoralis*; (2) a carnivorous/scavenging group comprising *O. caricus*, and (3) a *Calanus* predating group including primarily *O. nanseni*. *Anonyx nugax* was situated between groups 2 and 3 (Fig. 6).



The trophic position of *Anonyx nugax*, indicated by its isotope signature, fits well with diet signals as interpreted by lipid composition. That it has a carnivorous/necrophagous diet is revealed by its high 18:1 n-9/n-7 ratio (Sargent & Falk-Petersen 1981, 1988). *Anonyx* species show typical adaptations necessary for scavenging feeding: the same mouth part characteristics as typical scavenging amphipods in the deep sea (Sainte-Marie 1984, Sainte-Marie & Lamarche 1985), large size for increased motility (Sainte-Marie 1984), efficient feeding, and large gut size and ability to withstand starvation (Sainte-Marie 1984, Sainte-Marie et al. 1989). Legeżyńska (2008) identified a size-dependant scavenging mode, where immature individuals of *A. nugax* fed on a variety of food and only mature individuals were true scavengers. Even though *A. nugax* is ill-equipped for predation, it seems to predate on pelagic crustaceans (Sainte-Marie & Lamarche 1985). Based on fatty acid analyses, Graeve et al. (1997) showed that *A. nugax* probably feeds on calanoid copepods. Similarly, in our study, levels of the typical *Calanus* FATM were elevated in the autumn, indicating a predatory behavior. These markers, however, decreased in the winter, possibly indicating a more scavenging behavior, as the 18:1 n-9/n-7 ratio was elevated. Thus, the PCA analysis, showing *A. nugax* positioned between the mainly scavenging *Onisimus caricus* and the mainly *Calanus*-feeding *O. nansenii*, confirms that *A. nugax* is an omnivorous scavenger that seasonally broadens its diet by predated on *Calanus*. Another interesting feature of the fatty acid composition is the high levels of 22:6 n-3, a well known dinoflagellate FATM (Dalsgaard et al. 2003). The origin of this fatty acid in *A. nugax* remains unknown for the time being.

The individuals collected from the sea ice under-surface had markedly lower lipid content and a reduced proportion of triacylglycerols, indicating that these individuals had a poor nutritional status. As most of the specimens collected in the ice traps were mature males, these could be individuals that, after the reproduction in winter, are about to die, or are actively trying to replenish their energy stores. However, their fate remains unknown for the time being. Similarly, *Anonyx sarsi* collected below drifting sea ice in the Barents Sea had low lipid content and mostly empty guts, indicating that they migrated to the ice in search for food (Werner et al. 2004).

Both *Onisimus glacialis* and *O. nansenii* have been described in earlier studies as detritivores, which reduce their niche overlap by using different food sources, with *O. glacialis* primarily using algal material and *O. nansenii* mainly animal remains (Poltermann

2001, Arndt et al. 2005a). Based on our fatty acid results, *O. glacialis* is clearly separated from *O. nansenii* in having a high content of the diatom marker 16:1 n-7, while *O. nansenii* is rich in the *Calanus* markers 20:1 n-9 and 22:1 n-11. A seasonal feeding pattern was found in *O. glacialis*, with a switch from a diet based on diatoms in summer and autumn to a diet including calanoid copepods in winter. In contrast *O. nansenii* appears to feed year-round on calanoid copepods (Werner & Auel 2005, present study). As shown by Arndt et al. (2005a) *O. glacialis* shows morphological adaptations to feeding on small particles like diatoms, having a forceps-like dactylus on the second gnathopod, while in *O. nansenii* the dactylus on the second gnathopod is more claw-like and suitable for holding live prey or animal remains. The  $\delta^{15}\text{N}$  ratio in *O. nansenii* also supports carnivory. Unfortunately we do not have stable isotope values for *O. glacialis*, but Hobson & Welch (1992) and Søreide et al. (2006a) placed this species on a TL of 2.2 to 2.7, slightly lower than our results for *O. nansenii* (2.6–2.9).

*Onisimus litoralis* is closely grouped with *O. glacialis* in the PCA analysis; the 2 species being mostly herbivorous/omnivorous. *O. litoralis* has been shown to utilize the spring bloom intensively, while it probably switches to a more omnivorous diet outside the phytoplankton bloom period (Carey & Boudrias 1987, Gradinger & Bluhm 2010). In a feeding experiment, *O. litoralis* was found to actively feed on dead zooplankton as well as living zooplankton stranded on the bottom (Legeżyńska 2001). Based on its lipid dynamics, Nygård et al. (2010) concluded that *O. litoralis* feeds year-round. In Adventfjorden this species seems to feed on the spring bloom, showing an increased content of the diatom marker 16:1 n-7 in summer, while the amount of the marker for carnivory, 18:1 n-9, decreases. Consequently the  $\delta^{15}\text{N}$  value is lowest in July, when it indicates a trophic level of 1.8, which confirms a predominantly herbivorous diet.

*Onisimus caricus* seems, based on fatty acid and stable isotope data, to have a rather regular diet during the year. It has constantly a high ratio of 18:1 n-9/n-7, which indicates necrophagy (Bühning & Christiansen 2001). Legeżyńska (2008) studied the gut contents of *O. caricus* and found a high proportion of crustacean parts in their guts. However, it remains unclear if they were caught by predation or if they were eaten dead from the bottom, as the guts also contained a lot of sediment grains. In a feeding experiment *O. caricus* fed actively on dead copepods, while it only fed on live copepods if they were stranded on the bottom of the aquaria (Legeżyńska

2001). The structure of its mandibles suggests an efficient consumption of carrion (Legeżyńska 2008) and it is likely that zooplankton is only seasonally important as a food source (Zajączkowski & Legeżyńska 2001, Legeżyńska 2008, Nygård et al. 2009). In our study, the level of *Calanus* FATM was quite low in *O. caricus*. However, as we have fatty acid composition data on *O. caricus* only from February, June and November, seasonal feeding on copepods could have been overlooked.

### Life cycles

Generally, Arctic amphipods have a single brood per year and brood release is synchronized with the most favorable conditions, which often is at the onset of the spring algal bloom (Węśławski & Legeżyńska 2002). Thus, it can be assumed that distinct size classes represent cohorts and by studying the length-frequency distribution of populations, life spans and life cycles can be retrieved. Alternatively, species could have multiple broods per year, but this is very rare in the Arctic (Węśławski & Legeżyńska 2002, Tandberg et al. 2010).

Life cycles of *Onisimus* species have been described in a number of publications (Boudrias & Carey 1988, Węśławski et al. 2000, Węśławski & Legeżyńska 2002, Arndt & Beuchel 2006, Nygård et al. 2009, 2010). Based on these studies it appears that *O. littoralis* and *O. nanseni* have the shortest life cycles (2 yr) and the highest growth rate. In comparison, *O. glacialis* and *O. caricus* have prolonged life cycles (3–5 yr) and a slower growth rate. The differences in growth rate could be explained by different feeding strategies. Based on our fatty acid composition data, *O. nanseni* seems to be a predator on calanoid copepods in addition to necrophagous feeding (Arndt et al. 2005a), while *O. glacialis* is more herbivorous and thus more affected by the seasonality in primary production; although Werner & Auel (2005) suggest the latter species switches to a *Calanus* diet in winter. *O. littoralis* is also herbivorous-omnivorous, but it has been shown to feed year-round (Nygård et al. 2010). As a predominantly scavenger species, *O. caricus* is probably the most dependent on sporadic food falls and may therefore have the most unpredictable food source. Thus, *O. nanseni* and *O. littoralis* have feeding strategies that allow them to grow continuously throughout the year, and complete their life cycles in 2 to 2.5 yr. Although *O. glacialis* also feeds on detritus and *Calanus* in winter (Arndt et al. 2005a, Werner & Auel

2005), it is probably mostly a seasonal feeder on ice algae. It therefore needs to build up lipid reserves (30% of DW in October) for overwintering and can not afford continuous growth. *O. caricus* has an unpredictable food source and thus also needs to prioritize survival until the next feeding opportunity, instead of investing energy in growth. These trade-offs most likely restrict the growth rate of *O. glacialis* and *O. caricus*, so that these species require longer life spans in order to complete their life cycles.

The length-frequency distribution of *Onisimus edwardsii* indicates 3 cohorts, resulting in a 2 yr life cycle, similar to that earlier suggested for this species (Węśławski & Legeżyńska 2002). The smallest individuals recorded in February are assumed to be newly hatched, which is surprising since the brood release could be expected to happen during the most productive time of the year. Unfortunately, we did not observe egg-carrying females, but ovigerous females have previously been reported in the period November to May (Węśławski & Legeżyńska 2002). *O. edwardsii* is an opportunistic omnivore, feeding on carrion, algae, detritus, meiofauna and crustaceans (Legeżyńska 2001, 2008). Thus, this species probably feeds year-round and does not need to build up energy reserves, and could be expected to have a similar life strategy to *O. littoralis* (Węśławski & Legeżyńska 2002, Nygård et al. 2010).

For *Onisimus brevicaudatus* the length-frequency distribution suggests the presence of 3 separate cohorts, implicating a 2 yr life cycle. There is, however, some uncertainty here as we only have sufficient data from one month and the cohorts seem to overlap widely. The wide length span of the cohort, peaking around 0.65 mm (Fig. 5), could indicate an unsynchronized brood release in this species or large differences in individual growth rates. Alternatively, this cohort could actually consist of 2 cohorts, which we were unable to separate because we had too few observations. In the latter case, a 3 yr life cycle would be suggested. Unfortunately we do not have any information on the feeding strategy of *O. brevicaudatus*, but considering that it was mainly found in deeper parts of Rjippfjorden, it most likely exhibits omnivorous scavenging or predatory behavior. Assuming a scavenging feeding strategy, the growth rate of *O. brevicaudatus* could be comparable to the growth rate of *O. caricus*, which could indicate a 3 yr life cycle. However, further studies on *O. brevicaudatus* are needed to confirm this.

The high abundance of *Anonyx* spp. juveniles in the September traps reflects the brood release earlier that summer. As we did not catch any egg-carrying

females in this study, and the overall catches were small in the summer months, we do not have any information on the timing of the brood release for these species. In Adventfjorden, *Anonyx* spp. juveniles were almost exclusively collected in September. *A. nugax* is reported to have at least a 4 yr life cycle (Sainte-Marie et al. 1990, Węśławski & Legeżyńska 2002). It has large eggs (1.6 mm in diameter) and carries brood between November and June (Węśławski & Legeżyńska 2002). *A. sarsi* has been described as having a 2 yr life cycle in the Saint Lawrence Estuary (Sainte-Marie et al. 1990), while it has at least a 3 yr life cycle in Svalbard waters (Węśławski & Legeżyńska 2002). In Svalbard, it has large eggs (1.3 mm in diameter) and has been found to be brood-carrying between November and April (Węśławski & Legeżyńska 2002). Sainte-Marie et al. (1990) found that the embryo development took ~4 mo in the Saint Lawrence Estuary, but the eggs here were smaller (1.0 mm in diameter) than in Svalbard waters and thus probably developed faster (Steele & Steele 1975).

### Conclusions

A clear difference in the species composition of the amphipod scavenging guild was observed between Adventfjorden and Rijpfjorden. The influence of sea ice was observed in Rijpfjorden with presence of sympagic amphipods, whereas these were not found in Adventfjorden. Another factor contributing to the differences in species composition was the sediment quality, favoring the occurrence of *Onisimus* species in Adventfjorden on soft substrate and the higher abundance of *Anonyx* species in Rijpfjorden on coarser substrate.

The baited trap catches varied seasonally in both Adventfjorden and Rijpfjorden, but the timing of the peak in abundance differed. The variations were probably due to ontogenic processes, feeding behavior and/or predator avoidance. The differences in climate between the fjords regulate both the productive period and the timing of life history events in the amphipods.

Three main feeding strategies were observed among the collected amphipods: (1) a herbivorous-omnivorous group, consisting of *Onisimus glacialis* and *O. littoralis*, with high proportions of diatom markers (17–41 %) combined with relatively low  $\delta^{15}\text{N}$  values (mean 8.7 ‰); (2) a carnivorous/scavenging group, consisting of *O. caricus*, with particularly high proportion of the fatty acid 18:1n-9 (39–40 %) combined with high  $\delta^{15}\text{N}$  values (mean 11.3 ‰), and (3)

a *Calanus*-feeding group, consisting of *O. nanseni*, characterized by high proportion of *Calanus* markers (13–35 %) combined with moderate  $\delta^{15}\text{N}$  values (mean 9.7 ‰). The fatty acid and stable isotope composition of *Anonyx nugax* indicated an omnivorous-carnivorous diet. Differences in feeding strategies influence growth rates in the amphipods and thus also life history strategies.

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