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Food resource partitioning among Arctic sublittoral lysianassoid amphipods in summer

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Abstract Five species of lysianassoid amphipods (*Anonyx nugax*, *Anonyx sarsi*, *Onisimus caricus*, *Onisimus edwardsii*, *Orchomenella minuta*) co-occur in the shallow sublittoral of Kongsfjorden (Svalbard, Arctic), share similar functional attributes, and exploit a common food base. All species are known to be necrophagous; however, this study revealed through combination of gut-content analysis with the morphological characteristics of their mandibles and available information on feeding ecology, the complexity of their trophic strategies. Only mature individuals of *A. nugax* are true scavengers; immature individuals of this species feed on both animal and non-animal food. *A. sarsi* and *O. caricus* are scavengers and predators; the former prefers polychaetes, while the latter relies mostly on zooplankton. *O. edwardsii* is an omnivorous feeder, and the set of its primary food consists of carrion, crustaceans, and algae. *O. minuta* is a detrivorous–carnivorous species. These results indicate that niche overlap among these closely related species is reduced, not only by spatial segregation, but also by the exploitation of different components of food resources.

Keywords Lysianassoidea · Feeding ecology · Arctic

Introduction

The shallow sublittoral of the West Spitsbergen fjords is inhabited by at least eight species of necrophagous lysianassoid Amphipoda (Legeżyńska et al. 2000; Legeżyńska 2001). The co-occurrence of closely related members of the

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same functional guild (in this case, epibenthic mobile scavengers) may suggest some kind of resource partitioning which helps to reduce the potential for interspecific competition. Spatial segregation was a major factor contributing to the coexistence of necrophagic invertebrates in Admiralty Bay (South Shetland Islands, Antarctica) (Presler 1986). The clear depth and horizontal zonation of scavenging lysianassoid amphipods in Hornsund (77°N, West Spitsbergen, Arctic) was also described by Węsławski (1990) and Legeżyńska et al. (2000). Further studies carried out in Kongsfjorden (79°N, West Spitsbergen, Arctic) showed that the mosaic, but simultaneously zonal, distribution of these species resulted from a number of factors including hydrological and sedimentation regimes, depth, bottom type, and trophic conditions (Legeżyńska 2001, 2002).

Spatial and dietary separations are often coupled, which is another important factor leading to the reduction of competition between co-existing amphipod species. Both of them were observed by Sainte-Marie (1986) in four lysianassoid species occupying a shallow cold-water bay in the Saint Lawrence Estuary. Poltermann (2001) described subtle but important differences of the feeding strategies in four sympagic amphipods inhabiting the Arctic ice-pack. Recent studies on the morphology of their mouthparts and accessory feeding appendages combined with ecological observations led to the conclusion that trophic niche overlap among these amphipods is reduced substantially (Arndt et al. 2005).

Five amphipod species (*Anonyx nugax*, *Anonyx sarsi*, *Onisimus caricus*, *Onisimus edwardsii*, *Orchomenella minuta*) constituted nearly 95% of all scavenging animals collected with baited traps in Kongsfjorden (Legeżyńska 2001, 2002). Although all of them occupied the sublittoral zone (between 5 and 30 m), each species preferred a specific

microhabitat. Moreover, published data on *Anonyx* spp. (Sainte-Marie 1984, 1986) and the current author's preliminary data on *O. caricus*, *O. edwardsii*, and *O. minuta* indicate the pronounced differentiation of their feeding strategies (Legeżyńska 2001; Berge et al. 2007).

The aim of the current study was to evaluate the trophic niches of five co-existing scavenging amphipods that vary in size, mouthpart morphology, and distributional ecology in an Arctic fjord. The role of dietary separation as one of the major factors favoring co-existence is focused upon.

Materials and methods

Sampling

Kongsfjorden is an Arctic glacial fjord situated on the western coast of Spitsbergen (79°N, 12°E). The fjord opens into the Greenland Sea and is approximately 30 km long. Its inner basin is strongly affected by a complex of tidal glaciers. The Kongsfjorden area is the subject of extensive international study, and detailed information on the local ecosystem was reviewed by Svendsen et al. (2002) and Hop et al. (2002).

The amphipods used in the present study were collected during the summer seasons of 1998 (07–16 July) and 2000 (15–27 July). The individuals investigated were chosen randomly from material provided by traps with unavailable bait (≈300 g of beef) deployed between 5 and 30 m at three profiles in the inner, central, and outer fjord basins (Fig. 1). The detailed sampling techniques are as described by Legeżyńska (2001). These three sampling sites varied with respect to habitat conditions and species composition. *O. caricus* and *A. nugax* dominated materials collected at the

Fig. 1 Location of sampling stations

innermost profile situated in a glacial bay with massive freshwater discharge, heavy mineral sedimentation, and a floor composed of poorly consolidated mud. Traps in the central area of Kongsfjorden on the poorly diversified soft bottom with sparse drop-stones caught mostly *A. sarsi*. The same species, together with *O. minuta* and *O. edwardsii*, was collected on the hard bottom overgrown laminarian vegetation in the outer part of the fjord that is impacted significantly by the open sea (Legeżyńska 2001, 2002).

Gut content analysis

Gut content analysis was performed on 50 specimens of *O. caricus*, *O. edwardsii*, and *O. minuta* and on 20 *A. nugax* and *A. sarsi* fixed in 4% formaldehyde.

The amphipods were measured and dissected to remove the digestive tracts. Gut fullness (*C*) was coded with subjective scores (1, if <25% of the volume was filled; 2, 25–50%; 3, 50–75%; and 4, 75–100%). Food items were identified as precisely as possible and subsequently classified into several broad categories, following Sainte-Marie and Lamarche (1985), of carrion, polychaetes, detritus, algae (mainly diatoms, but also filamentous macroalgae), crustaceans, and unidentifiable amorphic organic matter (unidentifiable animal parts usually mixed with mineral grains). Due to their low-volumetric contribution, easily distinguished fish larvae, Hydrozoa, Halacaroidea, Molluca, Oligochaeta, Tintinnida, and Nematoda were assigned to the category "other". The frequency of occurrence of each food item (*F%*) was calculated for each species. The proportion of each food item (based on area covered) in single individuals was determined visually in a counting chamber. Afterwards, the relative volumetric contributions of each dietary category to the diet of a given species (*R%*) were expressed using the adopted points method, which takes into account gut fullness (Dauby et al. 2001).

The dietary compositions of the five scavenging species were compared to test the hypothesis that they would differ significantly from those of all other species, thus helping to reduce potential competition for food resources. Analysis of similarities (ANOSIM) and multi-dimensional scaling (MDS) were performed on the volumetric percentage share of the different dietary categories in individuals of the five scavenging species. The *R*-statistic values calculated for each pairwise comparison show the degree to which the species' diets were dissimilar. Values close to one imply that the dietary compositions of compared species were very different, whereas values close to zero demonstrate little or no dietary segregation (Clarke and Warwick 2001). The wide size range of animals examined within the species (except *O. edwardsii*) also permitted identifying some of the ontogenetic changes that occurred in the diets of the investigated species.
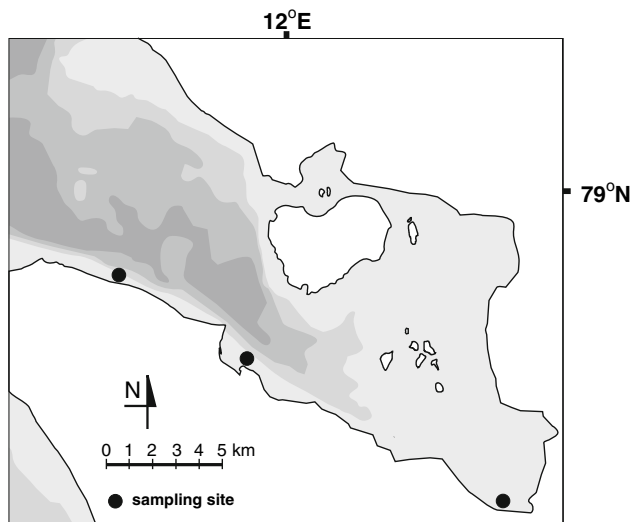
The feeding habits of amphipods have often been analyzed in relation to their mouthpart morphology (Sainte-Marie 1984; Poltermann 2001; Arndt et al. 2005). The mandibles of scavenging amphipods were divided roughly into two types: non-triturative and triturative, the former being characteristic of species highly adapted to carrion feeding and the latter possessed by generalist feeders. In the species investigated in the current study, the non-triturative types of mandibles were noted in the *A.* species (Sainte-Marie 1984; Steele and Steele 1993), while the triturative were noted in the *Onisimus* species and *O. minuta* (Sainte-Marie 1984). After the mandibles had been dissected, two parameters were measured under a stereomicroscope equipped with an Olympus DP-soft measurement system (x114): incisor width (in all species) and the area of the triturative molar surface (in species with well-developed triturative molars: *O. caricus*, *O. edwardsii*, and *O. minuta*). The results are presented in correlation with body size.

Results

Gut content analysis indicated that the fullness index was generally low, with mean values ranging from 1.65 in both *Anonyx* species to 2.90 in *O. minuta* (Table 1). The global ANOSIM test confirmed that the diet compositions of the five investigated species were significantly different (Global $R = 0.522$, $p < 0.001$). The R-statistic values for pairwise tests also revealed significant dietary segregation in all but one of the possible comparisons (Table 2). The results demonstrate, however, the different degrees of dissimilarity in the compositions of the diets. Of the five species, *O. edwardsii* showed the weakest food preference and its diet overlapped with those of the other species (see MDS plot, Fig. 2).

Carrion was a dominant food item in *A. nugax* ($R = 55\%$) comprising nearly 30% of the diets of *A. sarsi* and *O. edwardsii*. It was less important in the diet of *O. caricus* ($R = 10.4\%$) and never found in *O. minuta*. Crustacean remains were present in the guts of all the investigated species. Pelagic copepods predominated in *O. caricus* ($R = 53\%$) and together with mysids and euphausids, con-

Table 2 Analysis of similarity pairwise tests of the species' diets based on volumetric dietary data

	R	P
Global test	0.522	<0.001
Pairwise tests		
OM–AS	0.857	<0.001
OC–OM	0.854	<0.001
OC–AS	0.812	<0.001
OC–AN	0.648	<0.001
OM–AN	0.648	<0.001
OE–OM	0.437	<0.001
OC–OE	0.368	<0.001
AN–AS	0.279	<0.001
OE–AS	0.121	<0.006
OE–AN	0.023	<0.3

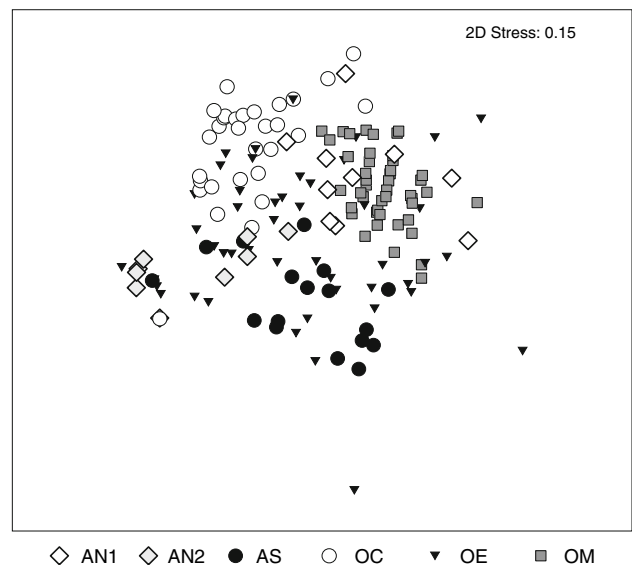*AN Anonyx nugax*, *AS Anonyx sarsi*, *OC Onisimus caricus*, *OE Onisimus edwardsii*, and *OM Orchomenella minuta*

Fig. 2 MDS plot of the species' diets based on volumetric dietary data. *AN1 Anonyx nugax* (10–20 mm), *AN2 Anonyx nugax* (35–40 mm), *AS Anonyx sarsi*, *OC Onisimus caricus*, *OE Onisimus edwardsii*, and *OM Orchomenella minuta*

stituted 72%, the total food volume of the species. Parts of amphipods, mysids, ostracods, and copepods (Harpacticoida and Calanoida) were also common food items in the guts of the rest of taxa, but they comprised, at most, about

Table 1 Gut content analysis: mean size of investigated amphipods, number and mean fullness-index of the guts, number of food categories, and frequency of mineral grains in the guts

Taxon	Mean size (mm) (±SD)	Number of guts examined	Mean fullness-index C	Number of food categories	Frequency of mineral grains (%)
Anonyx nugax	23.7 (±10.7)	20	1.65	7	0
Anonyx sarsi	15.9 (±5.3)	20	1.65	6	45
Onisimus caricus	15.34 (±4.6)	50	2.48	6	70
Onisimus edwardsii	9.75 (±1.04)	50	2.12	7	11
Orchomenella minuta	6.9 (±1.3)	50	2.9	6	16

20% of the food ingested. Polychaeta were consumed mostly by *A. sarsi* ($F = 80\%$, $R = 41\%$), but their share in the diets of the remaining species did not exceed 10%. Indistinguishable animal tissue and detritus were the main food items, in proportion as well as in occurrence, in the guts of *O. minuta* ($F = 92\%$, $R = 40\%$ and $F = 73\%$, $R = 25\%$, respectively). Both of these categories were of minor importance in the diets of the other species with maximum contributions made to the diet of *O. edwardsii* ($R = 10.5\%$ and $R = 10.2\%$). Algae were ingested to a great extent by O. *edwardsii* ($F = 50\%$, $R = 15\%$). The broad category of "others" comprised more than 8% of the diets in *A. nugax* (mainly fish larvae remains), *A. sarsi*, and *O. edwardsii* (mainly meiofaunal elements) (Fig. 3). Mineral grains were frequently noted in *O. caricus* and *A. sarsi*, while in contrast, they were either absent or found in <20% of individuals of the other species (Table 1).

Size-related changes in the diets of investigated species were observed only in the case of *A. nugax* and *O. caricus*. Juvenile *A. nugax* (10–20 mm) had a mixed diet, whereas large specimens (35–40 mm) relied mostly on carrion. A cohort of small *O. caricus* (6.5–10 mm) consumed more amorphous organic matter, detritus, algae, and meiofauna than did older specimens (10.5–20 mm) (Fig. 4).

Anonyx species possess wider incisors than other taxa of comparable size. The molars are especially well developed in *O. edwardsii.* In contrast, the much larger *O. caricus* has mandibles with weakly developed molars whose triturative surfaces are always smaller than those observed in *O. edwardsii* and *O. minuta* (Fig. 5).

Discussion

The lysianassoids attracted to baited traps in the Kongsfjorden sublittoral belong to three cold-water genera known for their scavenging life-style (Sainte-Marie 1984, 1986; Oliver and Slattery 1985; Legeżyńska et al. 2000). In general, shallow-water scavengers are more flexible in their feeding habits than their deep-sea counterparts. The contribution of carrion to their diets depends on the local and temporal availability of this kind of food and varies both between species and development stages (Vader and Romppainen 1985; Sainte-Marie 1986; Sainte-Marie and Lamarche 1985; Carey and Boudrias 1987; Poltermann 2001). Only a few shallow-water species does probably exclusively rely on carrion (e.g., *Orchomene nanus*; Kaiser and Moore 1999), for most others necrophagy is only a part of a wider feeding repertoire (Britton and Morton 1994).

Dietary composition of each species collected in Kongsfjorden differs significantly from each other. The present results and available information of feeding ecology indicate that within investigated species only mature, 35–40-mm

long, individuals of *A. nugax* can be considered as true scavengers. Their guts were either empty or filled with carrion, which contributed 88% of their diet. Immature specimens of the same species have more diversified diet (Fig. 4). Similar ontogenetic changes in the diets of six *Anonyx* spp. from the Saint Lawrence Estuary were observed by Sainte-Marie and Lamarche (1985). According to their study, juvenile specimens of *A. nugax*, *A. sarsi*, and *Anonyx makarovi* (<6 mm) consume relatively high amounts of detritus ($R = 23\%$), whereas larger specimens rely almost entirely on animal food ($R = 95\%$). Gut-content analysis of the Kongsfjorden specimens revealed that detritus and algae remain an important source of food for the immature 10–20-mm *A. nugax*. On the other hand, the high proportion of crustacean remains; the presence of fish larvae and the lack of mineral grains may indicate predatory behavior (Fig. 4, Table 1). Predation on copepods was predicted based on the fatty acid composition of *A. nugax* from the Barents Sea (Graeve et al. 1997). Specimens kept separately during laboratory observations demonstrated moderate interest in live zooplankton (Copepoda, *Themisto* spp., *Limancina helicina*) (Legeżyńska 2001), but Oliver and Slattery (1985) described dense swarms of *Anonyx* spp. that rapidly attacked not only stranded animals and fresh bait, but even "unsuspecting divers".

Anonyx sarsi exhibits both scavenging and predatory behavior (Sainte-Marie 1986; Ingolfsson and Agnarsson 1999; Werner et al. 2004). Results of the gut-content analysis of the species are in very good agreement with those of Sainte-Marie (1986), from the Saint Lawrence Estuary. In both localities carrion and polychaetes remain comprised about 70% of the food ingested, whereas the shares of Crustacea and detritus did not exceed 10% even though the Kongsfjorden individuals had a more diversified diet. Such similarity of diets in two geographically distinct populations indicates the invariability of feeding preferences of this species. Size-related changes in the *A. sarsi* diet were less pronounced than those observed in *A. nugax*. The main change in the diet of *A. sarsi* specimens as they increased in size was greater polychaete consumption (Fig. 4). Over time, this species probably evolves towards specialized predatory behavior. Ingolfsson and Agnarsson (1999) regarded *A. sarsi* as the main predator in the intertidal zone of Iceland. According to diver observations, the primary preys of *Anonyx* spp. are polychaete worms and crustaceans (Oliver and Slattery 1985). A high proportion of guts contained sediment particles (Table 1), which may result from feeding on infauna.

Onisimus caricus occupies the fine mud of the Kongsfjorden glacial bays and benefits from the "dead body rain" of zooplankton that die on osmotic shock in the low-salinity surface waters in glacier frontal zones during summer (Węsławski and Legeżyńska 1998; Zajączkowski and

Fig. 3 Frequency and mean volume percentage of different food items in the guts of studied species
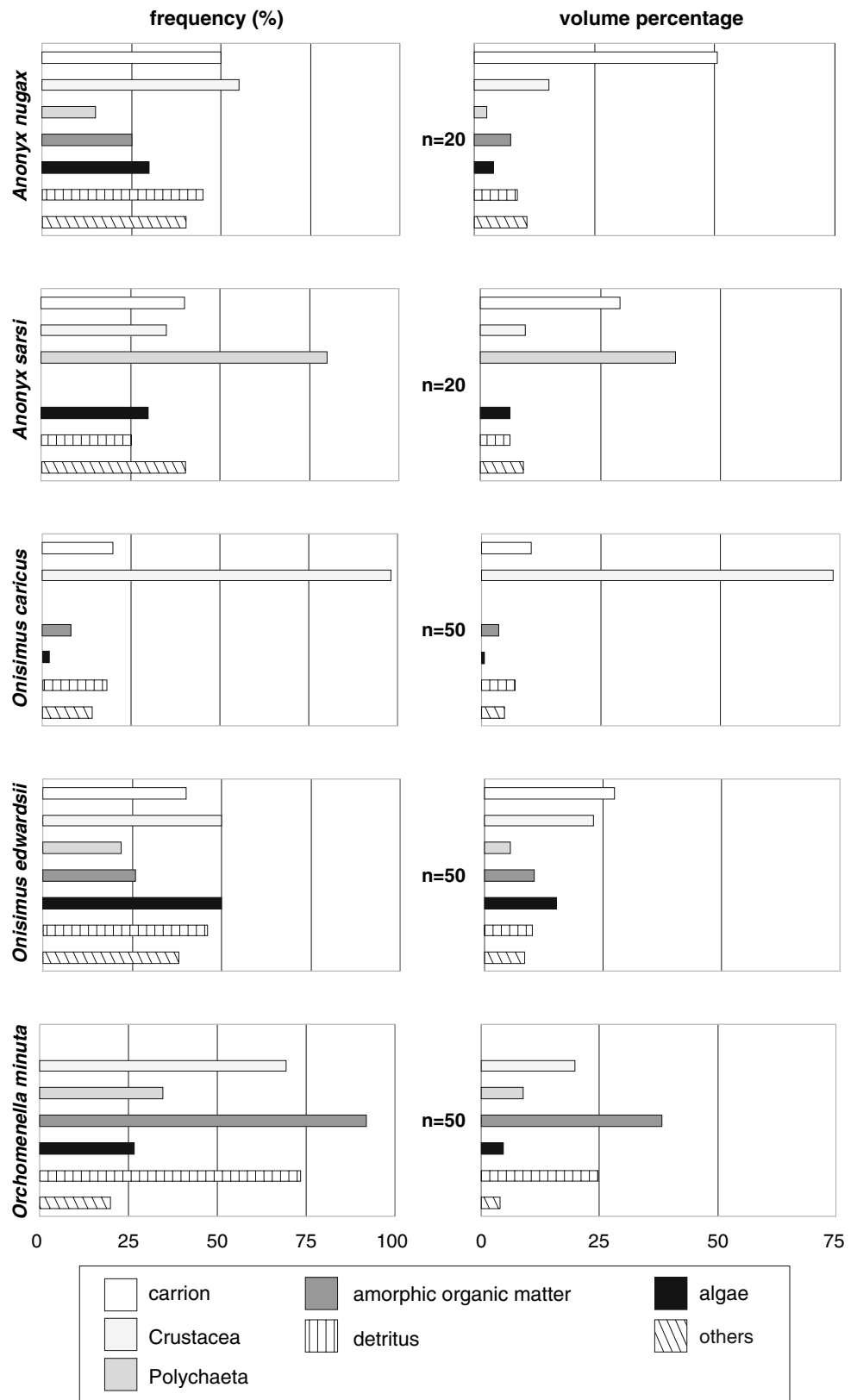
Legeżyńska 2001; Legeżyńska 2001). Pelagic crustaceans were its main food in proportion ($R = 72\%$) as well as in presence ($F = 98\%$) (Fig. 3). Small quantities of fine sediment grains were present in over 70% of the dissected guts, which suggested selective scavenging on the bottom as the most probable feeding mode. On the other hand, sediment

Fig. 4 Size related differences
in the diets of *A. nugax*, *A. sarsi*,
O. caricus, and *O. minuta*
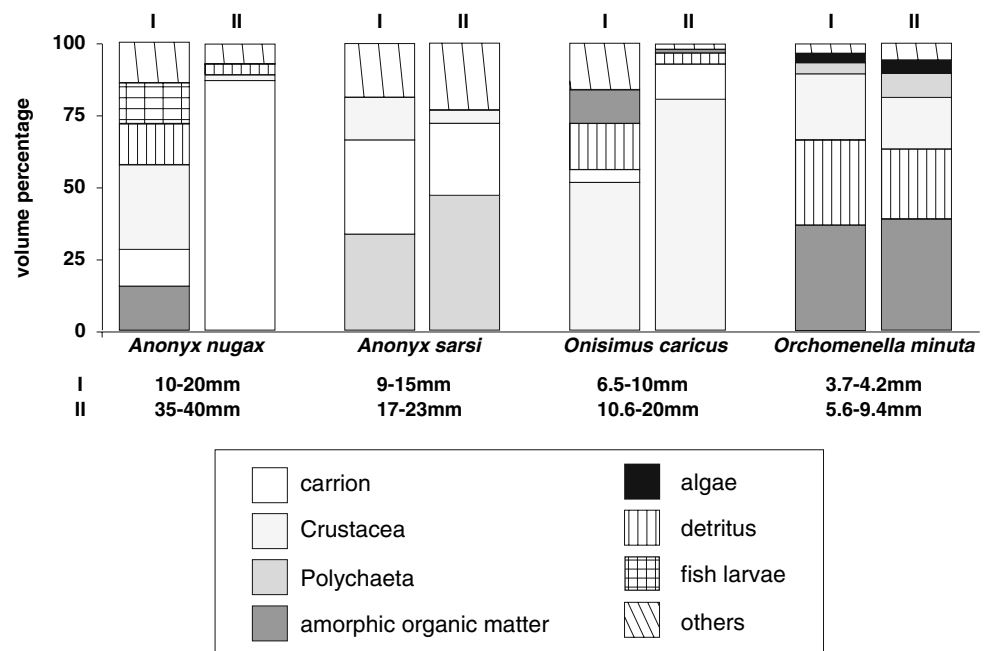
grains could have been consumed by animals preying in a
water column with a high content of inorganic suspension
or by preying on weakened specimens stranded on the bot-
tom, as was observed in the laboratory (Legeżyńska 2001).
The low contribution of carrion to the diet of *O. caricus* is
quite surprising as this species is a well-known scavenger
(Vader et al. 2005), it is attracted rapidly and in mass num-
bers to baited traps (up to 19,300 specimens in single trap
set for 6 h in Kongsfjorden; Zajączkowski and Legeżyńska
2001). Field and laboratory observations have also shown
that *O. caricus* is an eager carnivore that efficiently con-
sumes even considerable amounts of carrion (author's
unpublished data). This high feeding-efficiency may result
from the structure of its mandibles. Unlike its detrivore/
omnivore congeners (Sainte-Marie 1984; Arndt et al.
2005), *O. caricus* bears mandibles with weakly developed
molars (Fig. 5) suitable for cutting rather than for wasteful
and time-consuming grinding. The life history of *O. caricus*
is largely unknown, but taking into consideration its size
(up to 29 mm), mobility, behavioral, and morphological
features mentioned above, *O. caricus* seems to be well
adapted to explore occasional carrion resources. Therefore,
it is likely that zooplankton consumption is just a seasonal
feeding strategy of *O. caricus*.

Onisimus edwardsii is a relatively small species (up to
15 mm) that inhabits the mixed vegetated bottom of the
outer part of Kongsfjorden. The quantitative analysis of gut
content (Fig. 3) corroborates results of the preliminary, qual-
itative study that described *O. edwardsii* as a markedly
omnivorous feeder (Legeżyńska 2001). The species shows a
clear preference for animal food, but frequently also con-
sumes detritus and algae. Apart from feeding on large car-

rion ($R = 27.5\%$), *O. edwardsii* also consumed small
crustaceans and meiofauna. Again, it cannot be deducted
from the gut content whether they had been consumed alive,
scavenged dead from the sediment, or taken non-selectively
with detritus. Detritus has often been reported as an impor-
tant food source for some bait-attending *Onisimus* spp.
(Sainte-Marie 1986; Poltermann 2001; Arndt et al. 2005).
Despite high frequency, the volume percentage of detritus
was low ($R = 10\%$) in *O. edwardsii*. Sediment grains were
also rarely noted ($F = 11\%$, Table 1), which together with
the high proportion of animal food indicates a rather selec-
tive feeding mode. In contrast to the aggressive *Onisimus
litoralis*, which was observed feeding on live animals
(Sainte-Marie 1986; Legeżyńska 2001), *O. edwardsii* was
inactive and did not present interest when exposed to live
Calanus spp. during laboratory experiments (Legeżyńska
2001). Nevertheless, predation on much smaller organisms
commonly found in their guts, such as nauplii Copepoda,
Harpacticoida, Tintinnida, Halacaroidea, Nematoda, and
Oligochaeta cannot be excluded (Legeżyńska 2001). The
diet is supplemented with filamentous algae and diatoms,
which made a higher contribution to its diet than they did in
other species studied (Fig. 3). The opportunistic feeding
strategy of *O. edwardsii* is undoubtedly related to the abun-
dance and diversity of potential food noted in its habitat.
Hard bottoms overgrown with macroalgae offer a diversity
of microhabitats occupied by a rich set of planktonic and
benthic animals (Lippert et al. 2001; Kaczmarek et al.
2005). Similar to related species (Carey and Boudrias 1987;
Poltermann 2001; Arndt et al. 2005), *O. edwardsii* probably
modifies its diet according to the changing accessibility of
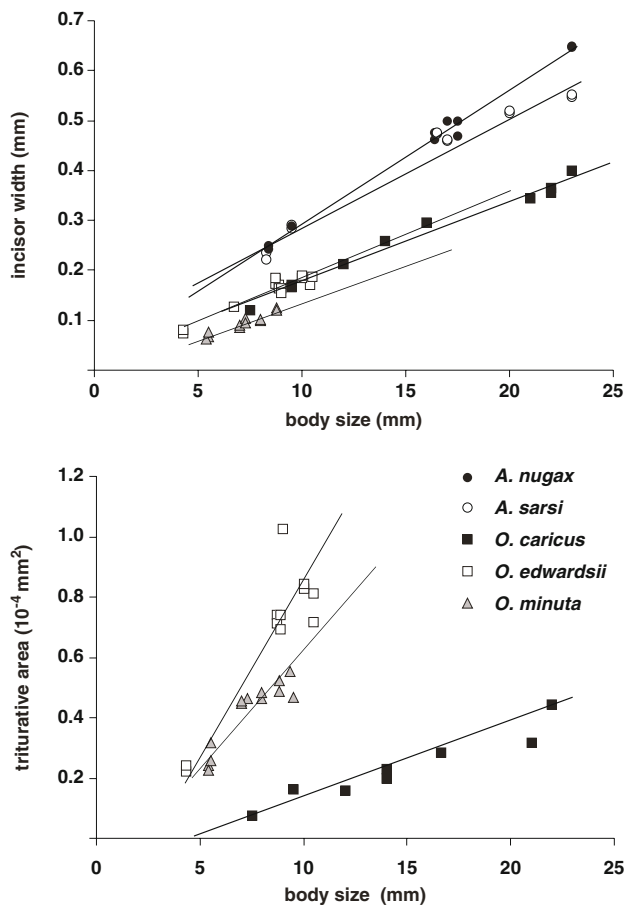different kinds of food throughout the year.

Fig. 5 Mandibular parameters in relation to total body size in *A. nugax*, *A. sarsi*, *O. caricus*, *O. edwardsii*, and *O. minuta*

The results of the gut-content analysis of *O. minuta* are especially difficult to interpret. Very few food items could be identified precisely owing to the small size of specimens and the grinding action of strong molars. The high fullness-index value indicates continuous feeding, which is characteristic of opportunistic feeders (Table 1). Animal remains prevailed in the dissected guts ($R = 70\%$), but detritus was also found in over 70% of them and contributed significantly to the diet ($R = 25\%$). Since *O. minuta* is known to prefer relatively old carcasses (Oliver and Slattery 1985), indistinguishable animal tissue, noted as the main food item, could have been derived from partly decomposed carrion. Since *O. minuta* is a small, weakly mobile species, it is most probably poorly prepared to compete for ephemeral large carrion, and relies on minute carcasses scavenged on the bottom or ingested as a part of detritus lumps. The importance of crustacean remains in its diet (mainly amphipods, harpacticoids, and ostracods) may also suggest selective micropredatory behavior.

All the studied species fed on carrion if the opportunity arose, but each of them also exploited a distinct selection of the components of accessible food. Since both depth

and horizontal zonation of scavenging amphipods was observed in West Spitsbergen fjords (Legeżyńska et al. 2000; Legeżyńska 2001), some differences in their diets can be explained by the natural food availabilities in their habitats. However, even species occupying the same habitats, for example *A. sarsi*, *O. edwardsii*, and *O. minuta*, have different diet compositions (Fig. 3). Similar dietary segregation led to a reduction in trophic niche overlap as was observed among four co-occurring, sympagic amphipods (Poltermann 2001; Arndt et al. 2005). The broad categories of food items used in the present study may not reflect the complexity of the feeding strategies of the examined species. As lysianassoids noted in the Kongsfjorden sublittoral vary with regard to size and mouthpart morphology (Table 1; Fig. 5), they may exploit different size fractions of the same food item. This, apart form overall differences in their diet, would further diminish potential for inter- and intraspecific competition among them.

The amphipods used for the present study were collected in summer when the fjord habitats provide relatively good feeding opportunities. Little is known about their trophic strategies during the remaining seasons, but considerable dietary shifts can be assumed. Under worse feeding conditions, some species occurring in the fjord would probably make use of all kinds of food available, while others would be able to rely on occasionally accessible large carrion. The first group would include relatively small, weakly mobile opportunistic species, such as *O. minuta* and *O. edwardsii*, while large *A. nugax*, able to withstand long periods of starvation (Christianasen and Diel-Christiansen 1993) would represent the second one. Although extensive sampling in Hornsund did not reveal any season-related changes in the composition of bait-attending lysianassoids (Legeżyńska et al. 2000), other studies provide good evidence that seasonal migrations towards the open sea can be another strategy exhibited by some species (or at least parts of their populations) in the case of food shortage. Werner et al. (2004) found males and juveniles of *A. sarsi* actively searching for food in the water column and at the underside of pack ice in the Barents Sea. Dissected guts contained macroalgal fibers, fish eggs and flesh from large carrion, and analysis of lipid biomarkers showed that some of the specimens had preyed on pelagic copepods. Carey and Boudrias (1987) described spring migrations of *O. litoralis*, an opportunistic scavenger typical of tidal waters, to the ice undersurface in the Beaufort Sea, where the species feeds on crustaceans and diatoms.

To determine overall trophic status of these amphipods more studies covering winter material and combination of the gut dissection with other methods [e.g. lipid and fatty acid analyses, which integrates feeding behavior over long periods of time (Graeve et al. 2001)] are needed.

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