

MOUTHPART-ATLAS OF ARCTIC SYMPAGIC AMPHIPODS—TROPHIC NICHE SEPARATION BASED ON MOUTHPART MORPHOLOGY AND FEEDING ECOLOGY

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A B S T R A C T

The four amphipod species *Onisimus nansenii*, *O. glacialis* (Lysianassidae), *Gammarus wilkitzkii* (Gammaridae), and *Apherusa glacialis* (Calliopiidae) have been identified earlier as autochthonous sympagic organisms that spend the whole life cycle in close association with the Arctic ice pack. Even one and a half centuries after the discovery of the ice-bound ecosystem, the ecology of these amphipod species, and in particular of *Onisimus* spp. and *Apherusa glacialis*, is only poorly known. In this study we evaluate and separate the trophic niches of the four amphipod species by analysing the morphology of mouthparts and accessory feeding appendages and compiling all information available on species distribution and feeding ecology. Morphological features and ecological observations imply that interspecific trophic niche overlap among these four amphipod species is reduced; each species has evolved a specific trophic strategy in selecting a different set of primary and supplemental food sources: *O. nansenii* is detritivorous (necrophageous), *O. glacialis* is detritivorous (herbivorous), *G. wilkitzkii* is carnivorous (detritivorous), and *A. glacialis* is herbivorous (detritivorous). Food choice plasticity in general, and facultative detritivory in particular, can be interpreted as an adaptation to the highly variable and dynamic character of the ice ecosystem. There is evidence that in both *Onisimus* species, as well as in *A. glacialis*, niche separation is furthermore provided by their temporary absence from the sympagic environment, which questions the affiliation of these species to the group of autochthonous sympagic organisms.

The combined analysis of food type and morphological features of the mouthparts and accessory feeding appendages allows conclusions concerning food preference (Agrawal, 1965). Mouthpart morphology and feeding strategy have been studied from the ecological perspective by several authors on various amphipod families (e.g., Dennell (1933) on Haustoriidae; Nicolaisen and Kannevorff (1969) on Pontoperiidae; Caine (1974) on Caprellidae; Dahl (1979) on Lysianassidae; McGrouther (1983) on Hyalidae; Coleman (1987) on Acantonothozomatidae; Moore and Rainbow (1989) on Stegocephalidae; Morino *et al.* (2000) on Gammaridae). The present study examines the feeding ecology of four amphipod species, which belong to three different genera and three different families, but co-occur in sea ice. *Onisimus nansenii* (formerly *Pseudalibrotus nansenii*), *O. glacialis* (Lysianassidae), *Gammarus wilkitzkii* (Gammaridae) and *Apherusa glacialis* (Calliopiidae) have been identified as autochthonous sympagic organisms (Melnikov and Kulikov, 1980; Gulliksen and Lønne, 1989) that feed, reproduce, and release their offspring at the underside of sea ice. They are the major macrofaunal constituents of the sympagic ecosystem. Their co-occurrence in sea ice suggests some sort of resource partitioning and/or interspecific competition.

Even one and a half centuries after the discovery of the ice-bound ecosystem (Horner, 1976), the ecology of these four amphipod species, and in particular of *Onisimus* spp. and *Apherusa glacialis*, is only poorly known. The macrofaunal abundance in Arctic sea ice ranges from 0 to 490 ind. m⁻² corresponding to biomass values of over 20 g WM m⁻² (reviewed in Arndt and Lønne, 2002). *Gammarus wilkitzkii*

has the longest life span among sympagic amphipods, living up to six years (Beuchel and Lønne, 2002). Life spans range between two years for *A. glacialis* (Beuchel and Lønne, 2002) and three to four years for *O. nansenii* and *O. glacialis*, respectively (Arndt and Beuchel, in prep.).

Several studies have focused on diet and feeding behaviour of *G. wilkitzkii* and—to a minor extent—*A. glacialis* because these species are relatively more abundant than *Onisimus* spp. (Arndt and Lønne, 2002) and convenient to keep in the laboratory for feeding experiments (Poltermann, 2001; Arndt, 2002; Werner *et al.*, 2002). *Gammarus wilkitzkii* and *A. glacialis* clearly separate by food preference and acquisition (e.g., Poltermann, 2001; Werner *et al.*, 2002). *In situ* observations are almost impossible on *O. nansenii* and *O. glacialis* because these species are difficult to identify without dissecting them. As a consequence, they have been treated combined as *Onisimus* spp. in earlier studies (Gulliksen, 1984; Lønne and Gulliksen, 1991a, b; Werner, 1997a). Various methodological approaches are available for analyzing the feeding ecology of Crustacea: *in situ* observations, gut-content analysis, lipid analysis, stable isotope analysis, descriptions of mouthpart morphology, feeding experiments in the laboratory. Few studies have examined the morphology of mouthparts and their functional role in sympagic amphipods (Poltermann, 2001; Arndt, 2002). We therefore present herein the complete description of the mouthparts and accessory feeding appendages of autochthonous sympagic amphipods. The purpose of this study is to evaluate the trophic niches of the four co-occurring species by combining morphological peculiarities with a review of available information on species distribution and feeding ecology.

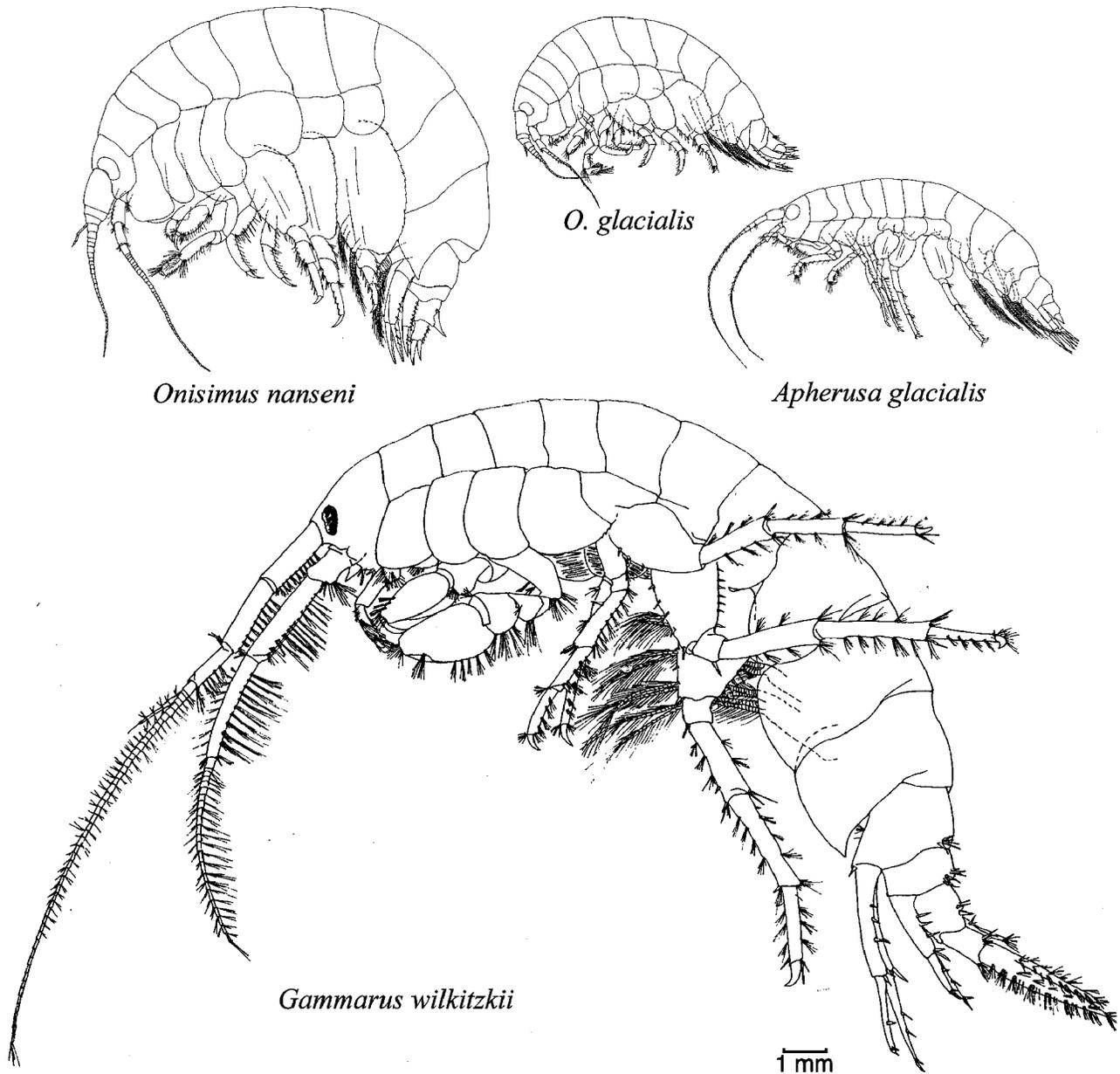


Fig. 1. Habitus illustration and size relationships of the four autochthonous sympagic amphipod species.

MATERIALS AND METHODS

All amphipods were sampled in the High Arctic ice pack north of Svalbard (Norway). The mouthparts and accessory feeding appendages of ethanol-preserved specimens were dissected and figured. Some of the extracted appendages were then placed in an ultrasonic cleaner to remove debris clinging to the amphipod. For scanning electron microscopy (SEM: LEO 15 25), the appendages were dehydrated through an alcohol series and dried using liquid carbon dioxide as the exchange medium, then critical point dried and sputter-coated with gold.

RESULTS

Onisimus nanseni (Sars, 1900)

Material Examined.—14 specimens, 81.5°N 19.2°E, 14 Sept 1998; 9 spec., 80.7°N 15.0°E, 17 Sept 1998; 28 spec., 80.1°N 0.3°E, 20 Sept 1998; 5 spec., 81.2°N 15.8°E, 22 Sept 2000; 16 spec., 81.1°N 31.1°E, 25 Sept 2000; 34

spec., 80.3°N 7.3°E, 27 Sept 2000; 41 spec., 81.2°N 1.3°E, 14 Sept 2002; 5 spec., 80.3°N 4.4°E, 28 Sept 2002; all samples collected on RV *Jan Mayen*.

Description.—Mature female (Fig. 1), body length 23.5 mm, 81.1°N 31.1°E, 25 Sept 2000, RV *Jan Mayen*.

Mouthpart bundle (Fig. 2a): Subquadrate.

Labrum: Well developed, lower edge rounded, covered with setulae.

Mandible (Fig. 2b, c): Body bowl-shaped, incisors symmetrical, with slightly convex margins; left lacinia mobilis present as robust peg, slightly bifurcate; accessory spine row absent; molar columnar with fully tritulative surface, partly surrounded by ring of dense short setae; palp opposite to molar, 3-articulate, second and third article with long simple setae.

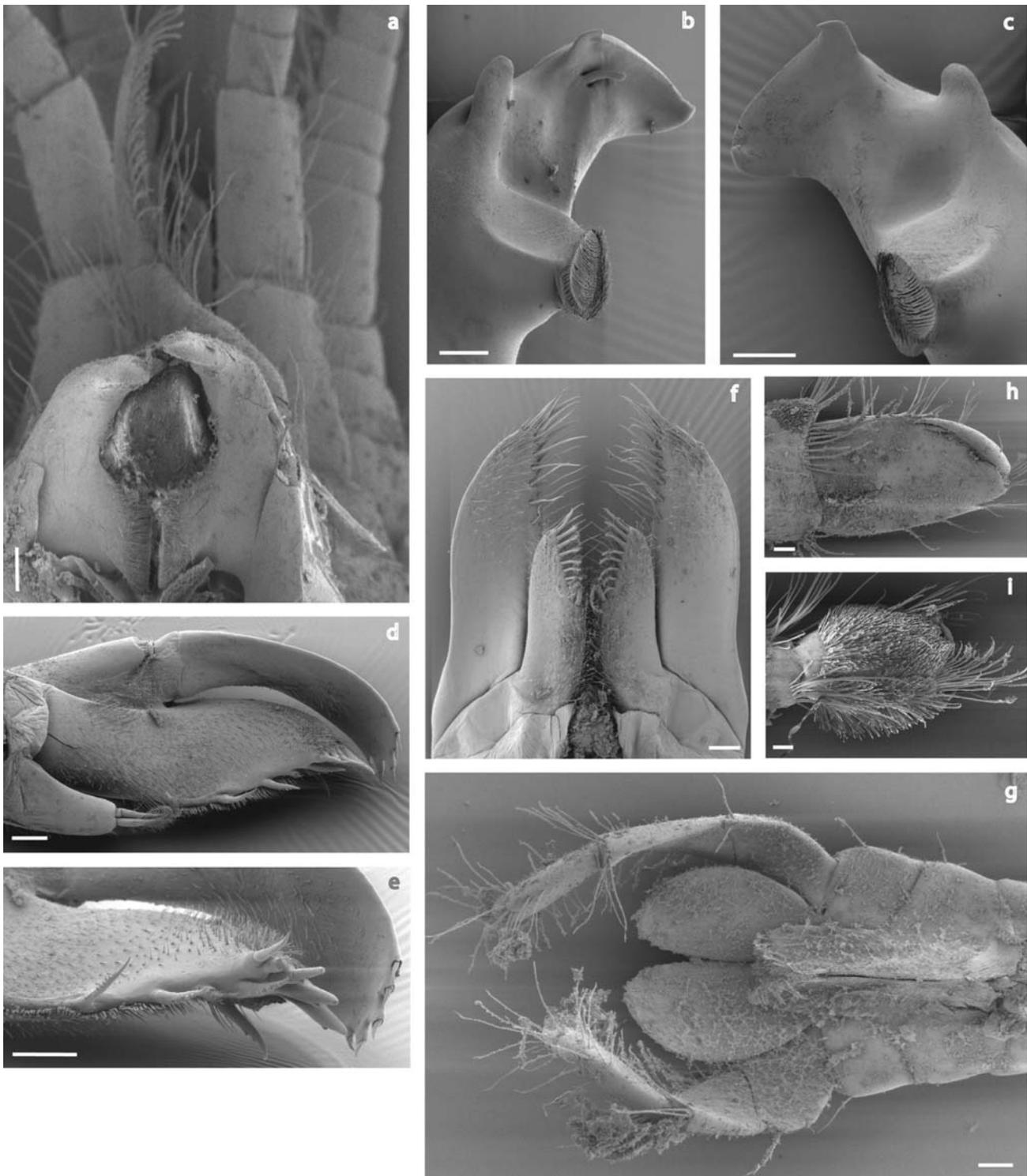


Fig. 2. Mouthparts of *Onisimus nansenii* (female). a, buccal area in ventral view (maxillipeds and maxilla 1 and 2 removed); b, left mandible; c, right mandible; d, maxilla 1; e, outer plate and palp of maxilla 1; f, maxilla 2; g, maxillipeds; h, gnathopod 1; i, gnathopod 2; scale bar: 100 μ m.

Paragnath: 2-lobed, with setulae.

Maxilla 1 (Fig. 2d, e): Inner plate short and narrow, with 2 plumose apical setae; outer plate setose with 11 setal-teeth in 7/4 crown-arrangement, cuspidate, basal row of short simple setae; palp large, setose, 2-articulate, article 2

multifurcate distally, with 6 robust setae and 1 simple flag seta.

Maxilla 2 (Fig. 2f): Inner plate slender and short, outer plate broad; inner plate setose, with 1 plumose, 6 pappose, and 8 cuspidate setae arranged in 2 rows, rows separated by

row of short simple setae; outer plate setose, with long simple and pappose setae along medial and apical margin.

Maxillipeds (Fig. 2g): Outer plate slender, short, with pappose and simple setae along medial and apical margins; inner plate large, crescent shaped, with 1 apical simple seta in line with nodular setae; palp strongly exceeding outer plate, with bunches of long setae; dactylus well developed, with subterminal setae.

Gnathopod 1 (Fig. 2h): Subchelate, palm oblique; propodus with long setae; dactylus stout, with inner edge minutely serrate with stout, short spine; palm with rows of small setae.

Gnathopod 2 (Fig. 2i): Subchelate, palm transverse; propodus rectangular-shaped, with dense comb-like setae, 2 bunches of long simple setae inserting near joint and tip of dactylus, short fan-like setae at joint of dactylus; dactylus claw-like; palm obtuse.

Onisimus glacialis (Sars, 1900)

Material Examined.—1 specimen, 81.5°N 19.2°E, 14 Sept 1998; 5 spec., 80.7°N 15.0°E, 17 Sept 1998; 23 spec., 80.1°N 0.3°E, 20 Sept 1998; 2 spec., 81.2°N 15.8°E, 22 Sept 2000; 25 spec., 81.1°N 31.1°E, 25 Sept 2000; 2 spec., 80.3°N 7.3°E, 27 Sept 2000; 3 spec., 81.2°N 1.3°E, 14 Sept 2002; 7 spec., 81.6°N 18.5°E, 19 Sept 2002; 31 spec., 80.3°N 4.4°E, 28 Sept 2002; 17 spec., 77.8°N 4.3°E, 30 Sept 2002; all samples collected on RV *Jan Mayen*.

Description.—Mature male (Fig. 1), body length 14.0 mm, 80.3°N 4.4°E, 28 Sept 2002, RV *Jan Mayen*.

Mouthpart bundle (Fig. 3a): Subquadrate.

Labrum: Well developed, lower edge rounded, with setulae.

Mandible (Fig. 3b, c): Body bowl-shaped, incisors symmetrical, with slightly convex margins; left lacinia mobilis present as robust peg, slightly toothed; accessory spine row absent; molar columnar with fully tritritative surface, partly surrounded by ring of dense short setae; palp inserts opposite molar, 3-articulate, second and third article with long simple setae.

Paragnath: 2-lobed, with setulae.

Maxilla 1 (Fig. 3d): Inner plate short, narrow, with 2 plumose apical setae; outer plate setose with 11 setal-teeth in 7/4 arrangement, cuspidate, basal row of short simple setae; palp large, setose, 2-articulate, article 2 multifurcate distally, with 5 robust setae and 1 simple flag seta.

Maxilla 2 (Fig. 3e, f): Inner plate slender, short, outer plate broad; inner plate setose, with 1 plumose, 4 pappose, and 5 cuspidate setae arranged in 2 rows, rows separated by row of short simple setae; outer plate setose, with long simple and cuspidate setae along medial and apical margin.

Maxillipeds (Fig. 3g): Outer plate slender, short, with pappose and simple setae along medial and apical margins; inner plate large, crescent shaped, with 1 apical simple seta in line with nodular setae; palp strongly exceeding outer plate, with bunches of long setae; dactylus well developed, with subterminal setae.

Gnathopod 1 (Fig. 3h): Subchelate, palm oblique; propodus with long setae; dactylus stout, with inner edge minutely serrate, with stout, short spine; palm with rows of small setae.

Gnathopod 2 (Fig. 3i, j): Chelate, palm transverse; propodus oval-shaped, pointed, with dense comb-like setae,

1 bunch of long simple setae and short fan-like setae inserting near joint of dactylus; dactylus small, tweezers-like; palm obtuse.

Gammarus wilkitzkii (Birula, 1897)

Material Examined.—601 specimens, 81.5°N 19.2°E, 14 Sept 1998; 544 spec., 80.7°N 15.0°E, 17 Sept 1998; 255 spec., 80.1°N 0.3°E, 20 Sept 1998; 44 spec., 81.2°N 15.8°E, 22 Sept 2000; 99 spec., 81.1°N 31.1°E, 25 Sept 2000; 54 spec., 80.3°N 7.3°E, 27 Sept 2000; 110 spec., 81.2°N 1.3°E, 14 Sept 2002; 12 spec., 81.6°N 18.5°E, 19 Sept 2002; 83 spec., 80.3°N 4.4°E, 28 Sept 2002; 5 spec., 77.8°N 5.3°E, 30 Sept 2002; all samples collected on RV *Jan Mayen*.

Description.—Mature male (Fig. 1), body length 42.5 mm, 80.3°N 4.4°E, 28 Sept 2002, RV *Jan Mayen*.

Mouthpart bundle (Fig. 4a): Subquadrate.

Labrum: Well developed, lower edges rounded, apical setulae.

Mandible (Fig. 4b–d): Cutting edges asymmetrical; left incisor 5-toothed, right 4-toothed; left lacinia mobilis 4-toothed, right bifurcate, with 5 + 2 teeth; setal row well developed, strong cuspidate and pappose setae; molar columnar with fully tritritative surface, partly surrounded by dense, short setae; palp inserts opposite setal row, 3-articulate, all articles with long pappose setae.

Paragnath: 2-lobed, medial and apical setulae.

Maxilla 1 (Fig. 4e, f): Inner plate oval, setose, with dense row of long plumose setae along medial margin; outer plate robust, setose, 11 strong cuspidate setae in 2 parallel rows; palp 2-articulate, first article short, second article with 6 apical spines, 1 flag seta, and 5 long simple setae, medial row of 5 long simple setae.

Maxilla 2 (Fig. 4g): Inner plate large, inflated, setose, medial row of long plumose setae along medial margins, terminal setae cuspidate, setae in second layer pappose and cuspidate; outer plate large, plane, setose, apical setae long and cuspidate.

Maxillipeds (Fig. 4h): Inner plate slender, setose, medial margin with long pappose setae, apical margin with 3 strong terminal spines and 2 rows of long simple setae and long pappose setae; outer plate large, crescent shaped, setose, medial and apical margins with strong spines and long pappose setae; palp robust, exceeding outer plate, with bunches of strong simple setae; at base of dactylus long pappose setae; dactylus robust, with long subterminal setae.

Gnathopod 1 (Fig. 4i): Subchelate, palm oblique; propodus stout, robust, with bunches of long setae facing dactylus; dactylus strong, claw-like; palm with lamellar crest and rows of simple setae and single spines.

Gnathopod 2: Subchelate, palm transverse; morphology equal to gnathopod 1.

Apherusa glacialis (Hansen, 1888)

Material Examined.—471 specimens, 81.5°N 19.2°E, 14 Sept 1998; 357 spec., 80.7°N 15.0°E, 17 Sept 1998; 285 spec., 80.1°N 0.3°E, 20 Sept 1998; 170 spec., 81.2°N 15.8°E, 22 Sept 2000; 217 spec., 81.1°N 31.1°E, 25 Sept 2000; 519 spec., 80.3°N 7.3°E, 27 Sept 2000; 23 spec., 81.2°N 1.3°E, 14 Sept 2002; 31 spec., 81.6°N 18.5°E, 19 Sept 2002; 46 spec., 80.3°N 4.4°E, 28 Sept 2002; all samples collected on RV *Jan Mayen*.

Description.—Mature female (Fig. 1), body length 13.0 mm, 81.6°N 18.5°E, 19 Sept 2002, RV *Jan Mayen*.

Mouthpart bundle (Fig. 5a): Subquadrate

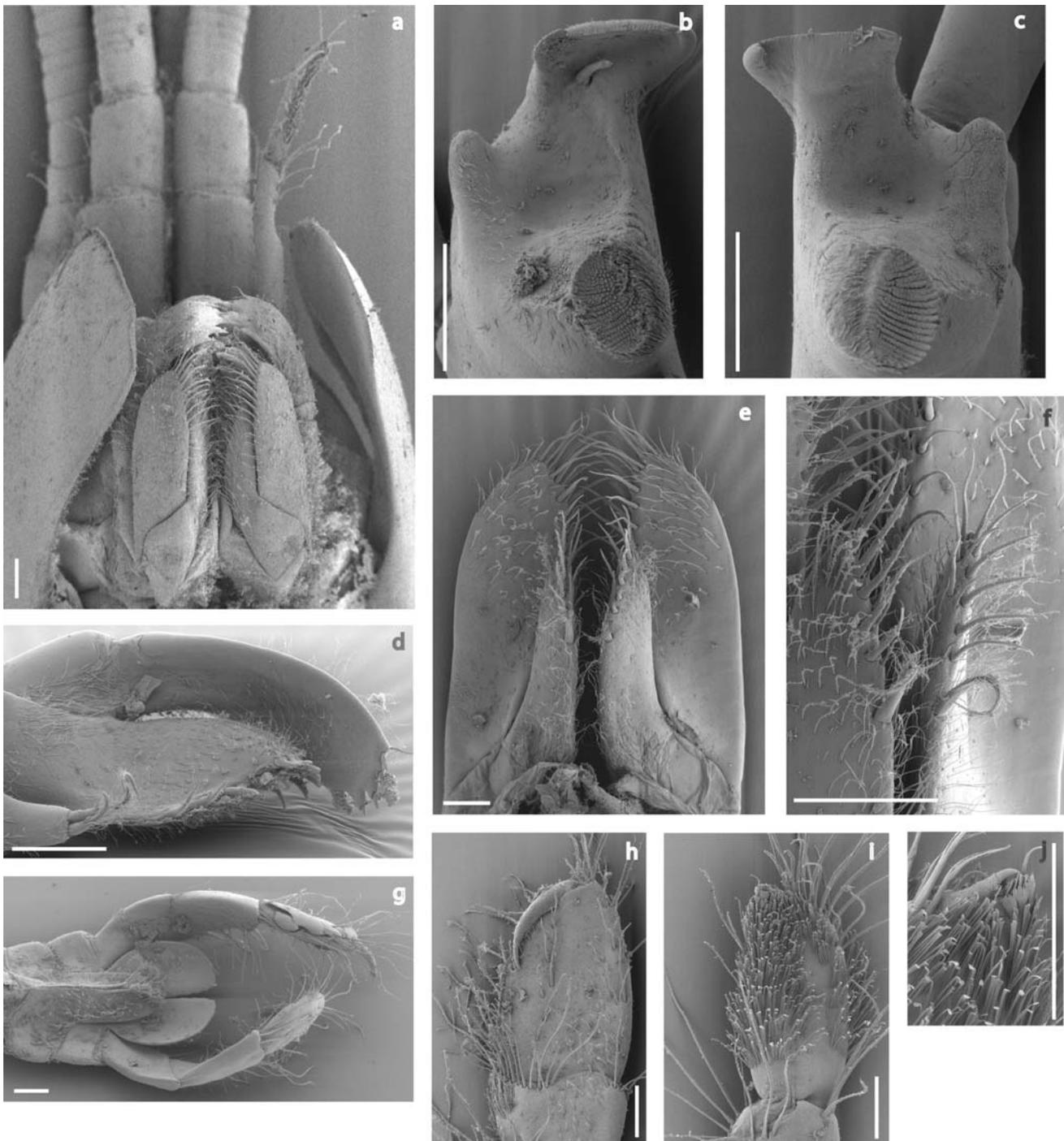


Fig. 3. Mouthparts of *Onisimus glacialis* (male). a, buccal area in ventral view (maxillipeds and maxilla 2 removed); b, left mandible; c, right mandible; d, maxilla 1; e, maxilla 2; f, inner plate of maxilla 2; g, maxillipeds; h, gnathopod 1; i, gnathopod 2; j, dactylus of gnathopod 2; scale bar: 100 μ m.

Labrum: Well developed, lower edges rounded, apical setulae.

Mandible (Fig. 5b–d): Incisors symmetrical, 6-toothed; both laciniae mobilis present, articulate, left robust, as long as incisor, 3-toothed, right slender, short, 3-fucate; setal row strong cuspidate and pappose setae; molar columnar, only distal part with triturative surface, partly surrounded by ring of dense short setae; palp 3-articulate, first article short, second and third equal in length, with long simple setae along medial margins.

Paragnath: 2-lobed, medial and apical setulae.

Maxilla 1 (Fig. 5e): Inner plate well developed, crescent shaped, setose, medial margin with long plumose setae; outer plate narrow, rectangular, apical margin with 8 strong cuspidate setae in 2 parallel rows; palp 2-articulate, setose, first article short, second large, with long simple setae along medial and apical margin.

Maxilla 2 (Fig. 5f): Inner plate long, narrow, setose, medial and apical margins with long plumose setae, terminal

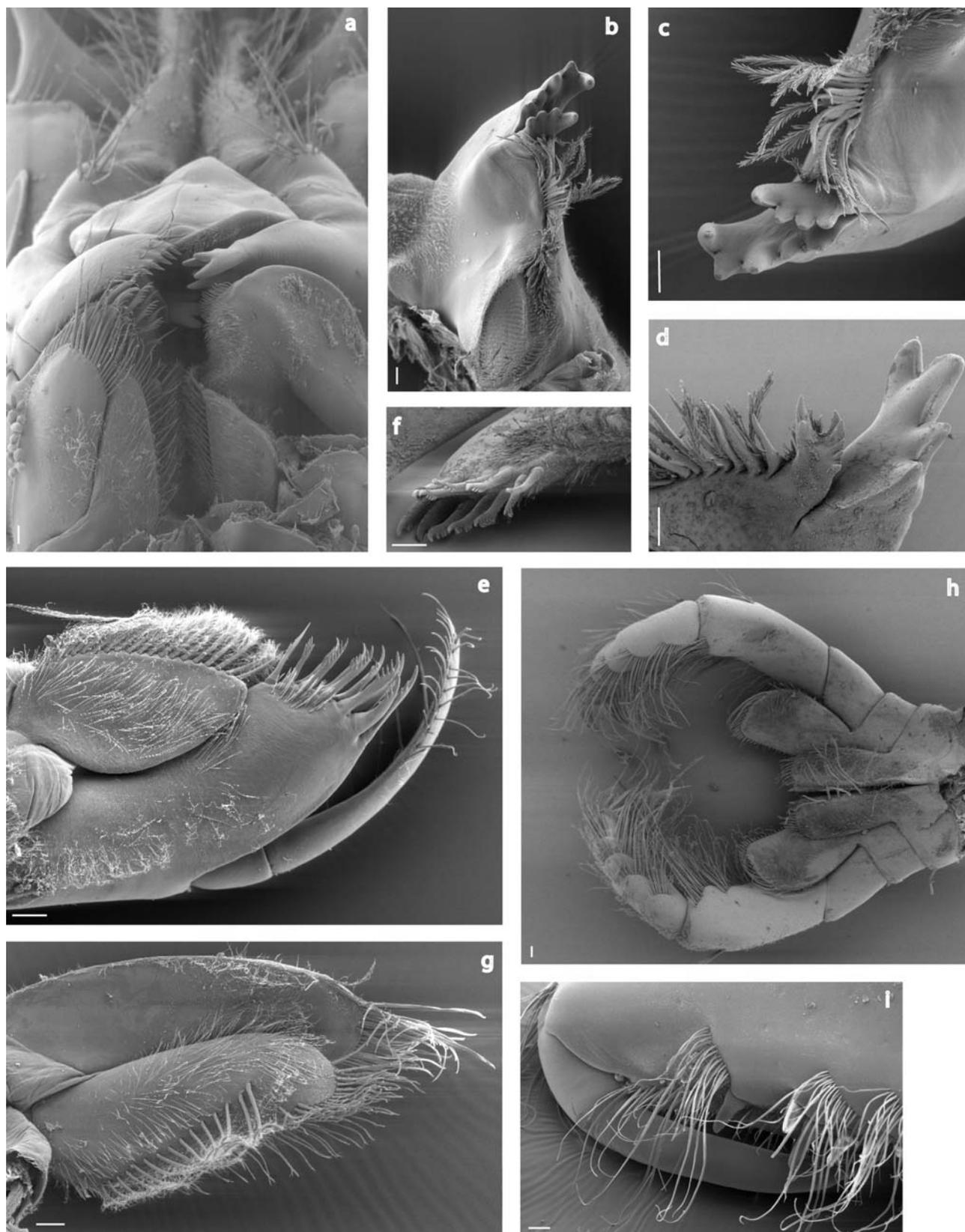


Fig. 4. Mouthparts of *Gammarus wilkitzkii* (male). a, buccal area in ventral view (maxillipeds, maxilla 2 and right maxilla 1 removed); b, right mandible; c, incisor and lacinia mobilis of right mandible; d, incisor and lacinia mobilis of left mandible; e, maxilla 1; f, apical spines on outer plate of maxilla 1; g, maxilla 2; h, maxillipeds; i, gnathopod 1; scale bar: 100 μ m.

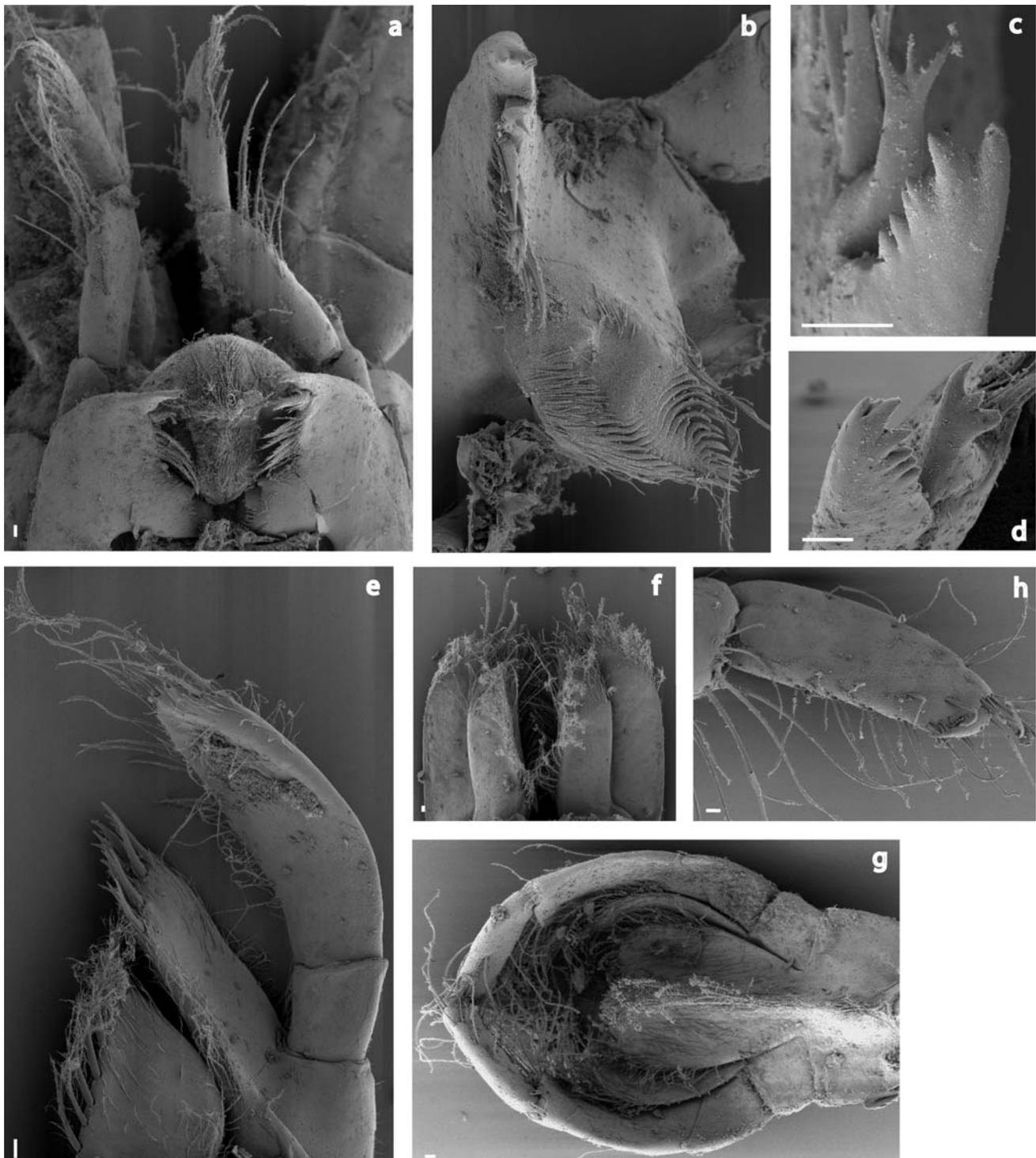


Fig. 5. Mouthparts of *Apherusa glacialis* (female). a, buccal area in ventral view (maxillipeds and maxillae 1 and 2 removed); b, right mandible; c, incisor and lacinia mobilis of the right mandible; d, incisor and lacinia mobilis of the left mandible; e, maxilla 1; f, maxilla 2; g, maxillipeds; h, gnathopod 1; scale bar: 20 μm .

setae cuspidate; outer plate slightly exceeding inner plate, setose, medially with long cuspidate setae, apical margin with plumose setae.

Maxillipeds (Fig. 5g): Inner plate large, crescent shaped, setose, apical margin with long pappose setae, medial row of

long simple setae; outer plate slightly larger than inner plate, setose, medially with long pappose setae, apical margin with single spines and pappose and simple setae; palp strongly exceeding outer plate, with bunches of long simple setae; tip of dactylus rounded, with terminal simple setae.

Gnathopod 1 (Fig. 5h): Subchelate, palm transverse; propodus with long simple setae along medial and apical margins; dactylus serrate; palm obtuse with single spines.

Gnathopod 2: Equal to gnathopod 1 in size and morphology.

DISCUSSION

Not only morphological peculiarities but also species distribution, *in situ*, and tank observations suggest large differences in the feeding ecology of the four sympatric amphipod species examined in this study, leading to the separation of their trophic niches.

Both *Onisimus* species have been collected by means of handnet and suction pump underneath different ice types in the High Arctic ice pack as well as in seasonally ice-covered subarctic seas (Table 1). Highest abundance values have been observed in the multiyear ice near Franz Josef Land (Averintzev, 1993; Poltermann, 1998). Baited traps deployed underneath sea ice generally attracted *O. nansenii*, and only few individuals of *O. glacialis* were captured (Barnard, 1959; George and Paul, 1970; Poltermann, 1997; Broms *et al.*, 2004; pers. obs.). The family Lysianassidae is known as a taxon that includes necrophagous scavengers, which are equipped with a sensitive olfactory apparatus to find carrion from great distances (Dahl, 1979; Sainte-Marie, 1992). By comparing trap data with divers-evaluated abundance data it has been recently demonstrated that *O. nansenii* is attracted from much greater distance than *O. glacialis*, indicating its strong preference for carrion (Broms *et al.*, 2004). Indeed, not all *Onisimus* species are typical scavengers but often feeding generalists (Sainte-Marie, 1992; Vader *et al.*, 2005). Predatory and even cannibalistic behaviour was explicitly observed in *O. nansenii* (George and Paul, 1970) (Table 2). It is likely that other studies that did not identify *Onisimus* to species level but described its carnivorous life style based on lipid analysis (Scott *et al.*, 1999) and feeding experiments (Werner, 1997a), were actually considering *O. nansenii*. The gut of *O. glacialis* contained crustacean parts in minor proportions (Poltermann, 2001). Crustacean remains, such as exuvias, can be ingested as part of detritus lumps. Detritivory has been suggested for both *Onisimus* species (Poltermann, 2001). In the laboratory, *Onisimus* spp. were observed to form large, mucous aggregates of different organic material (pers. obs.). The acquisition and ingestion of ice algae and phytoplankton (phytodetritus), however, has been described only for *O. glacialis* based on gut content analysis (Bradstreet and Cross, 1982; Poltermann, 2001). Because abundance values are generally low for both *Onisimus* species, spatial preferences on the ice floe are not yet clear. Their apparent preference for gathering underneath the ice rather than at the ice edges has been suggested but without statistical evidence (Poltermann, 1998). Herbivorous species such as *A. glacialis* (see below) prevail along the ice edges.

The mouthpart bundles of both *Onisimus* species bear typical characteristics of the family Lysianassidae (e.g., Dahl, 1979). Morphological differences are small between the two sympatric *Onisimus* species. The bowl-shaped mandibles are suitable for processing the food particles that

are precisely cut with the sharp cutting blades, the incisors, and ground by strong molars. Only number and type of setation differ slightly on maxilla 1 and 2 in the two species. The major difference is the morphology of gnathopod 2. The forceps-like dactylus allows *O. glacialis* to selectively pick small particles such as diatoms. Size dimensions of the very abundant ice alga *Navicula* sp. (> 10 µm) in Arctic sea ice (Horner, 1989) suits the opening between dactylus and propodus of gnathopod 2. It is likely that the abundant and strong simple and comb-like setae on the propodus help in working on the ice and retrieving the algal cells. In contrast, gnathopod 2 is larger and claw-like in *O. nansenii* and may be used when holding firm live prey or animal remains.

We hypothesise that mouthpart morphology differs little between related amphipod species, but greater changes are encountered in the morphology of accessory feeding appendages as a consequence of trophic specialization. The data presented herein very much support this hypothesis; despite differences in trophic specialization between the two *Onisimus* species, mouthpart morphology seems highly conservative. Different morphological adaptations in gnathopod 2 (rather than the buccal appendages), however, clearly separate these two species and reflect their different feeding ecology.

Gammarus wilkitzkii has also been sampled by means of baited traps (Barnard, 1959; George and Paul, 1970; Poltermann 1997; pers. obs.) (Table 1), suggesting a necrophagous feeding behaviour. Tank observations, however, indicate that *G. wilkitzkii* is not attracted by biochemical cues such as described for scavengers (e.g., Dahl, 1979; Sainte-Marie, 1992), because it does not show any search patterns or directional motion (Arndt, 2002). Legezyska *et al.* (2000) found *Gammarus* species in traps deployed on Svalbard (Norway) but never observed them feeding on carrion. Lipid analysis, feeding experiments, and gut-content analysis clearly identify *G. wilkitzkii* as a carnivorous species (Bradstreet and Cross, 1982; Poltermann, 1997, 2001; Scott *et al.*, 2001; Arndt, 2002; Werner *et al.*, 2002) that feeds on chaetognaths, copepods, and other crustacea including conspecifics (Table 2). Based on gut-content analysis it has been furthermore suggested that this amphipod feeds on diatoms, microflagellates, and filamentous algae (Bradstreet and Cross, 1982; Poltermann, 2001). In tank experiments, *G. wilkitzkii* in fact ingested diatoms that were frozen into sea ice (Werner, 1997a; Arndt, 2002), but mouthparts and feeding appendages only worked on the ice to liberate food particles when these reached the ice-water interface (Arndt, 2002). The amphipods' pronounced grooming behaviour, the dense and long setae on both pairs of antennae and the mouthparts, and the presence of a lamellar crest on the gnathopods suggest suspension feeding as a supplementary mode of food acquisition (Poltermann, 1997; Arndt, 2002). Detritivory was proposed by Poltermann (2001) on the basis of gut-content analysis. In particular perennial sea ice contains high concentrations of detritus throughout the year (Melnikov, 1997). However, gut-content analysis of field-sampled animals only has limited value because it may underestimate the overall importance of algal material (Quigley and Vanderploeg,

Table 1. List of information available on the biogeographic distribution of the four sympagic amphipod species including study site, ice type, and sampling method; handnet and (suction) pump are generally diver-operated tools.

Location	Method/depth (ice type)*	Reference
<i>Onisimus nansenii</i>		
Polar Ocean	traps, handnet/(MY-P)	Barnard, 1959; Melnikov and Kullkov, 1980
Barents Sea	pump/(MY-P); traps/(MY-P)	Gulliksen, 1984; Poltermann, 1977; Hop <i>et al.</i> , 2000; Broms <i>et al.</i> , 2004; Arndt and Pavlova, in prep.
Greenland Sea	traps/(MY-P)	Poltermann, 1997
Franz Josef Land/Russia	pump/(FY-F)	Poltermann, 1998
Laptev Sea/Russia	traps, handnet/(FY-P)	Poltermann, 1997
Pond Inlet/Canada	handnet/(FY-F)	Cross, 1982
Foxe Basin/Canada	handnet/(FY-F)	Grainger, 1962
Ungava Bay/Canada	handnet/(FY-F)	Dunbar, 1954
<i>Onisimus glacialis</i>		
Polar Ocean	handnet/(MY-P)	Melnikov and Kulikov, 1980
	vertical plankton net/130–50 m; deep water	Sars, 1900; Griffith and Dillinger, 1981
Barents Sea	pump, traps/(MY-P)	Hop <i>et al.</i> , 2000; Poltermann, 1997; Arndt and Pavlova, in prep.
Franz Josef Land/Russia	pump/(FY-F)	Poltermann, 1998
Laptev Sea/Russia	traps, handnet/(FY-P)	Poltermann, 1997
Pond Inlet/Canada	handnet/(FY-F)	Cross, 1982
Foxe Basin/Canada	handnet/(FY-F)	Grainger, 1962
Ungava Bay/Canada	handnet/(FY-F)	Dunbar, 1954
<i>Onisimus spp.</i>		
Barents Sea	pump, handnet/(FY-P, MY-P)	Lønne and Gulliksen, 1991a, b; Arndt and Lønne, 2002
Greenland Sea	imaging/(MY-P)	Werner, 1997a
Laptev Sea/Russia	imaging/(FY-P)	Werner, 1997a
<i>Gammarus wilkitzkii</i>		
polar Ocean	traps/(MY-P)	Barnard, 1959
	handnet/(MY-P)	Melnikov and Kulikov, 1980
Barents Sea	pump, handnet/200–0 m (FY-P, MY-P); traps/(MY-P)	Lønne and Gulliksen, 1991a, b; Poltermann, 1977; Hop <i>et al.</i> , 2000; Arndt and Lønne, 2002; Arndt <i>et al.</i> , 2005.; Arndt and Pavlova, in prep.
Greenland Sea	imaging/(MY-P); traps/(MY-P)	Werner, 1997a; Poltermann, 1977
Franz Josef Land/Russia	handnet, pump/(FY-F)	Aveintzev, 1993; Poltermann, 1998
Laptev Sea/Russia	imaging/(FY-P); traps/(MY-P)	Werner, 1997a; Poltermann, 1997
Pond Inlet/Canada	handnet/(FY-F)	Cross, 1982
Frobisher Bay/Canada	coring/surface (FY-F)	Grainger <i>et al.</i> , 1985
Foxe Basin/Canada	handnet/(FY-F)	Grainger, 1962
Ungava Bay/Canada	handnet/(FY-F)	Dunbar, 1954
<i>Apherus glacialis</i>		
Polar Ocean	vertical plankton net/2500–0 m; handnet/(MY-P)	Barnard, 1959; Melnikov and Kullkov, 1980
Barents Sea	pump, handnet/(FY-P, MY-P)	Lønne and Gulliksen, 1991a, b; Hop <i>et al.</i> , 2000; Arndt and Lønne, 2002; Arndt and Pavlova, in prep.
Greenland Sea	imaging/(MY-P); trawl/1000 m; trawl/100 m	Werner, 1997a; pers. obs. J. Berge; Arndt and Pavlova, in prep.
Laptev Sea/Russia	imaging/(FY-P); traps/(FY-P)	Werner, 1997a; Poltermann, 1977
Franz Josef Land/Russia	handnet, pump/(FY-F)	Gollikov and Scarlato, 1973; Averintzev, 1993; Poltermann, 1998
Narwhal Island/Alaska	coring, handnet/(FY-P)	Carey, 1992
Resolute Bay/Alaska	obs./deep water	Siferd <i>et al.</i> , 1997
Frobisher Bay/Canada	coring/(FY-F)	Grainger <i>et al.</i> , 1985
Pond Inlet/Canada	handnet/(FY-F)	Cross, 1982
Foxe Basin/Canada	handnet/(FY-F)	Grainger, 1962
Ungava Bay/Canada	handnet/(FY-F)	Dunbar, 1954

*FY-F: first year fast ice.
FY-P: first year pack ice.
MY-F: multiyear pack ice.

1991). Moreover, the differentiation of fresh algae (as consumed by herbivorous species) from fresh phytodetritus and “aged” detritus (as consumed by detritivorous species) in the gut is often intricate (pers. obs.).

Mouthpart morphology indicates for *G. wilkitzkii* an opportunistic feeding mode as a generalist omnivore such as described for other *Gammarus* species (e.g., Kelly *et al.*, 2002). It is the availability and the encounter with a food

Table 2. List of information available on the feeding ecology of the four sympagic amphipod species.

Diet	Prey	Method	Reference
<i>Onisimus nansenii</i>			
necrophageous	animal carcass	baited traps	Barnard, 1959; George and Paul, 1970; Poltermann, 1997; Broms <i>et al.</i> , 2004
detrivorous	phytodetritus/crustacean remains	gut analysis	Poltermann, 2001
carnivorous (predatory)	crustaceans	gut analysis	Poltermann, 2001
(cannibalistic)	conspecifics	lab. observation	George and Paul, 1970
<i>Onisimus glacialis</i>			
necrophageous	animal carcass	baited traps	Poltermann, 1997
herbivorous	diatoms/phytodetritus	gut analysis	Bradstreet and Cross, 1982; Poltermann, 2001
detrivorous	phytodetritus/crustacean remains	gut analysis	Poltermann, 2001
carnivorous	crustaceans	gut analysis	Poltermann, 2001
<i>Onisimus</i> spp.			
carnivorous (predatory)	calanoid copepods	lipid analysis	Scott <i>et al.</i> , 1999
	copepods; other crustaceans	feeding experiments	Werner, 1997a; pers. obs. C. Arndt
(cannibalistic)	conspecifics	feeding experiments	Werner, 1997a; pers. obs. C. Arndt
herbivorous	diatoms	feeding experiments	Werner, 1997a
	—	lipid analysis	Scott <i>et al.</i> , 1999
<i>Gammarus wilkitzkii</i>			
necrophageous	animal carcass	baited traps	Poltermann, 1997
carnivorous (predatory)	pteropods	<i>in situ</i> observation	Gulliksen and Lønne, 1989
	copepods; other crustaceans	lipid analysis	Scott <i>et al.</i> , 1999
	—	feeding experiment	Werner <i>et al.</i> , 2002
	—	gut analysis	Bradstreet and Cross, 1982; Poltermann, 2001
(cannibalistic)	conspecifics	feeding experiment	Poltermann, 1997; Werner, 1997a; Arndt, 2002
detrivorous		gut analysis	Poltermann, 2001
herbivorous	diatoms/microflagellates/filamentous algae	gut analysis	Bradstreet and Cross, 1982; Poltermann, 2001
	—	feeding experiment	Werner, 1997b; Arndt, 2002
suspension feeder	microparticles	morpholog. features; behavioural obs.	Poltermann, 1997; Arndt, 2002
<i>Apherusa glacialis</i>			
herbivorous-phytodetrivorous	diatoms/filamentous algae	lipid analysis	Scott <i>et al.</i> , 1999
detrivorous	phytodetritus/crustacean remains	gut analysis	Poltermann, 2001
herbivorous	diatoms/microflagellates/filamentous algae	gut analysis	Bradstreet and Cross, 1982; Poltermann, 2001
	—	feeding experiment	Werner, 1997b
	—/phytoplankton	<i>in situ</i> spec. distribution	Hop <i>et al.</i> , 2000

item that governs the diet of *G. wilkitzkii* (Arndt, 2002). Its feeding plasticity is reflected in its mouthpart morphology. The mouthparts of *G. wilkitzkii* are interpreted as being able to cope with firm body walls as well as with microparticles. The roughly toothed cutting edges of the incisors and laciniae mobilis imply that the food item is torn apart rather than cut. *Gammarus wilkitzkii* feeds wastefully, suggesting no specialised handling and, therefore, no optimized utilisation of the food source (Arndt, 2002). The strong molars enable *G. wilkitzkii* to reduce the food morsels to small pieces and to crack and grind even hard particles such as the shells of diatoms. The strong apical spines on maxilla 1 may help to loosen food particles from the ice or larger food objects, and the strong setation on maxillae 2 and maxillipeds probably serve as a retrieving chamber for food particles or as grooming devices for the antennae. Both pairs of gnathopods are strong and bear robust dactyli that enable *G. wilkitzkii* to cling to objects, either prey or other food items, or its mate. Tank observations suggest a multipurpose use of the gnathopods in food acquisition (pers. obs.).

Apherusa glacialis was mainly sampled by different types of nets but was only once attracted by baited traps (Table 1). Several observations confirm its occurrence in deeper water, for example, this amphipod species was collected in vertical net tows from 2500 m to the surface in the Polar Ocean (Barnard, 1959) and by depth-restricted multinet tows at 1000 m in the Greenland Sea (pers. obs. J. Berge) but also in shallow waters far off the ice edge (Arndt and Pavlova, in prep.). Like *O. glacialis* (Sars, 1900; Griffiths and Dillinger, 1981; Melnikov, 1997) *A. glacialis* also was observed in deeper water down to the abyss in Resolute Bay (Canada) (Siferd *et al.*, 1997). In sea ice, *A. glacialis* is one of the most abundant species (e.g., reviewed in Arndt and Lønne, 2002) and inhabits fast seasonal as well as multiyear pack ice. Abundance values are highest in multiyear ice, which also shows highest concentrations of Chl *a* (Melnikov *et al.*, 2002) and detritus (i.e., particulate organic matter (Melnikov, 1997)). Small-scale distribution analysis confirm higher densities along the ice edges (Hop *et al.*, 2000) and underneath thin, translucent ice floes (Poltermann, 1998).

Here, the onset of primary production takes place. The guts contained diatoms, microflagellates, and filamentous algae (Bradstreet and Cross, 1982; Poltermann, 2001) but also amorphous material and occasionally crustacean remains that may derive from ingested detritus and algal lumps (Poltermann, 2001) (Table 2). In feeding experiments, *A. glacialis* harvests algal cells from the ice (Werner, 1997b). Biochemical signatures in body lipids confirm that *A. glacialis* preferably feeds on ice and filamentous algae (Scott *et al.*, 1999). Its occurrence in deeper water, however, may indicate a more (phyto-)detritivorous diet on organic material that derives from the euphotic zone. Whether this shift in diet from herbivory to detritivory is seasonally triggered by the availability of food type or by spatial separation from the primary producers in the surface waters is not clear. It has been suggested earlier that *A. glacialis* descends to the abyss with the onset of polar night (Barnard, 1959). This assumption yet needs verification because it questions the concept of autochthonous *versus* allochthonous species in the sympagic ecosystem (Gulliksen and Lønne, 1989). If it is an allochthonous species, *A. glacialis* avoids habitat and, thus, resource partitioning for at least parts of the year.

Mouthpart morphology of *A. glacialis* supports the feeding on small particles such as algal cells. Incisors and laciniae mobilis on the left and right mandibles are multitoothed and strong and probably assist in working on the ice to loosen the algal material. The triturative molar has a relatively large surface that is capable of grinding hard structures such as diatom shells. The apical spines on maxilla 1 probably co-operate with the apical edges of the mandibles in loosening the ice algae. The pronounced setation on both pairs of maxillae and maxillipeds form a chamber to retrieve the loosened material or filter phytoplankton cells from the water column. The role of the two pairs of identical gnathopods is not known. Because *A. glacialis* clings to the ice substrate in ventral position, the gnathopods may assist in holding the amphipod firm to the ice substrate. Related *Apherusa* species sampled in the littoral of subarctic and boreal seas graze on sea weeds, where they are subjected to continuous swell and wave action (Krapp-Schickel and Kulla, 2002).

The review of the morphological features concomitant with ecological observations allow the conclusion that trophic niche overlap among the four co-occurring sympagic amphipods is reduced; each species has evolved a certain trophic strategy for selecting a different set of primary and supplemental food sources:

- *O. nanseni* is detritivorous (necrophageous)
- *O. glacialis* is detritivorous (herbivorous)
- *G. wilkitzkii* is carnivorous (detritivorous)
- *A. glacialis* is herbivorous (detritivorous).

Food choice plasticity is high in sympagic amphipods. An opportunistic feeding strategy can be seen as an adaptation to a highly variable environment. Food type and availability of “fresh” food changes seasonally and as a consequence, so does concentration and accessibility of different food items. Food particles tend to accumulate in the sea ice matrix. Freeze and thaw cycle, swell, and ice deformation liberates organic matter that has been encapsulated in the ice

interior. All four sympagic amphipod species are primarily or facultatively detritivorous. Sea ice literally stores ice algae and (phyto-)detritus all year round like vegetables in a freezer. It is thus believed that food shortage is no issue in the sympagic environment at any time of the year (e.g., Gradinger *et al.*, 1999; Poltermann, 2001).

As already discussed for *A. glacialis*, habitat and hence (ice-associated) resource partitioning is reduced for parts of the year if the amphipod species seasonally descends to deeper waters. Also, for both *Onisimus* species, their belonging to the autochthonous group among sympagic organisms has recently been questioned (Arndt and Beuchel, in prep.). The evidence that the autochthonous and allochthonous species concept is no longer valid for at least some ice amphipod species should be addressed in further studies by monitoring interseasonal changes in the sympagic ecosystem as well as in the underlying waters.

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