

Joanna LEGEŻYŃSKA

Instytut Oceanologii Polskiej Akademii Nauk
ul. Powstańców Warszawy 55
81-712 Sopot, POLAND
e-mail: zosia@iopan.gda.pl

Distribution patterns and feeding strategies of lysianassoid amphipods in shallow waters of an Arctic fjord

ABSTRACT: Scavenging fauna was sampled by means of baited traps in three different habitats of Kongsfjorden (Svalbard, Arctic). Lysianassoid amphipods, represented by nine species, made up 98.9% of the materials collected between 5 and 30 m. The dominant species were *Anonyx sarsi* and *Onisimus caricus*, which constituted 91.6% of collected individuals. The abundance of animals attracted to traps was variable and a gradual decrease in abundance with increasing depth was observed. Spatial segregation of species resulted from a number of factors ranging from depth, hydrological conditions, sedimentation regime, and bottom type to food accessibility. Gut contents analysis indicated that in summer *Onisimus caricus* relied on zooplankton sinking due to the osmotic shock in the glacial bay; *Onisimus edwardsi* had a diverse diet; and *Orchomenella minuta* fed mostly on small crustaceans. During laboratory experiments all species were observed feeding on dead or injured zooplankton, while preying on live planktonic organisms was never noted

Key words: Arctic, Svalbard, scavenging fauna, lysianassoid amphipods.

Introduction

Many species of the amphipod superfamily Lysianassoidea are well known for their scavenging behaviour. They are important members of many marine communities dominating the necrophagous fauna in the deep sea as well as in temperate and polar shallow-water environments (Thurston 1979, Oliver and Slattery 1985, Presler 1986, Sainte-Marie 1986, Slattery and Oliver 1986, Kaufmann 1992, Sainte-Marie 1992, Legeżyńska *et al.* 2000).

Although lysianassoids are generally recognised as scavengers, only some species possess the combination of morphological and behavioural traits which en-

ables them to rely on large carrion (Sainte-Marie 1986, 1992, Slattery and Oliver 1986). While large carrion is an uncommon and dispersed source of food, carcasses of relatively small benthic and pelagic animals are abundant and frequently accessible (Oliver and Slattery 1985, Presler 1986, Sainte-Marie 1986, Slattery and Oliver 1986, Dauby *et al.* 2001). Attraction to and feeding on plankton organisms settled on the bottom or dislodged and injured benthic animals was observed in the case of several lysianassoid species (Oliver and Slattery 1985, Slattery and Oliver 1986).

Fragments of planktonic organisms were often reported from diet studies on Lysianassoidea (Sainte-Marie and Lamarche 1985, Slattery and Oliver 1986, Dauby *et al.* 2001), but the direct link to natural zooplankton mortality was not shown. Mass mortality of marine zooplankton caused by the reduced salinity close to glacier cliffs during summer was observed in Kongsfjorden (Węślawski and Legeżyńska 1998). It was assumed that sinking zooplankton organisms (Copepoda, *Themisto* spp.) could create predictable food conditions and support scavenging fauna of glacial bays. However, while feeding preferences of *Anonyx nugax*, *A. sarsi* and *Onisimus litoralis* have been described (Sainte-Marie 1986, Carey and Boudrias 1987), there is no published information on the diet of *Onisimus caricus*, *Onisimus edwardsi* and *Orchomenella minuta*.

The aim of this study is to present distribution patterns of scavenging amphipods within an Arctic fjord and to relate these patterns to a variety of factors. Attention is paid to the role of dead zooplankton as a natural food base of scavenging amphipods, and preliminary data on the feeding habits of *Onisimus caricus*, *O. edwardsi* and *Orchomenella minuta* are presented.

Study area, materials, and methods

Kongsfjorden is a West Svalbard fjord with a surface area of about 210 km² (Fig. 1). The depths of the outer and central basins are influenced by the open sea and surpass 390 m, while the shallower, inner basin has a large glacial outflow and its maximum depths do not exceed 100 m. Bottom temperatures in summer range from 0.5°C to 3°C in the outer basin and from -1.5°C to 3°C in the inner basin. Salinity at the sea floor is relatively stable and fluctuates between 34.25 and 34.75 PSU. Detailed information on the hydrology of Kongsfjorden can be found in the papers by Ito and Kudoh (1997) and Svendsen *et al.* (unpubl.). Bottom sediments consisted of red fine-grained clay (80% of silt fraction) with boulders and rocks in the shallows of the fjord (Włodarska-Kowalczyk, pers. comm.)

Kongsfjorden carrion-feeding fauna was sampled during three summer seasons from 1998 to 2000. Samples were taken by cylindrical closed nets which were 70 cm in length and 40 cm in diameter. Traps had two conical entrances with 4 cm

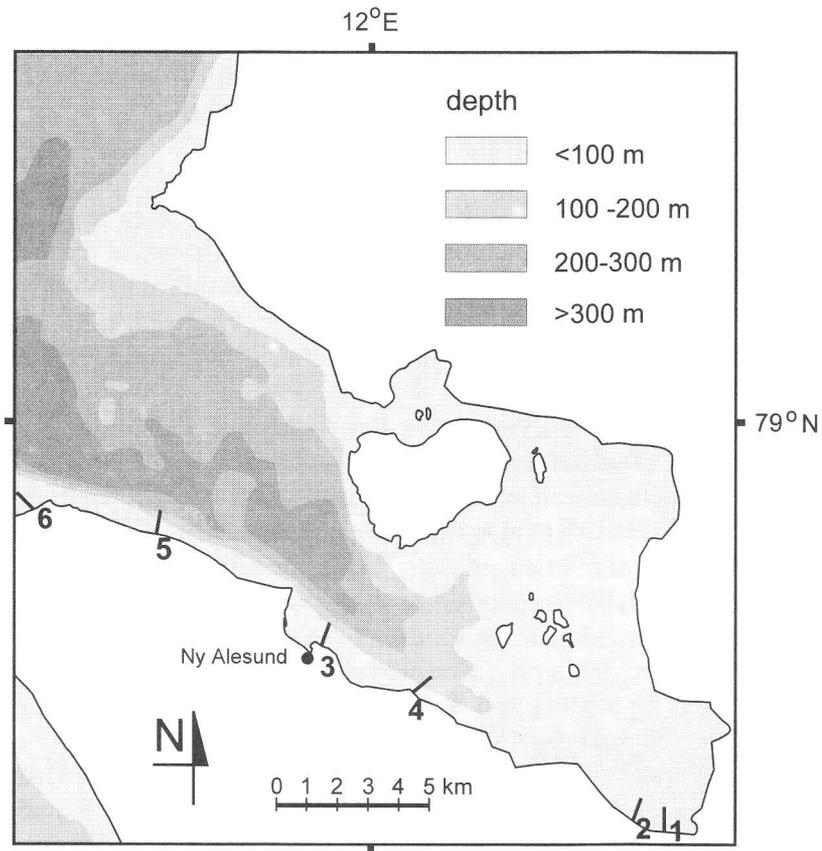


Fig. 1. Map of Kongsfjorden and the location of sampling stations.

diameter openings and 5 mm mesh. Traps were connected with a rope and fixed at one end to the shore. Approximately 0.3 kg of beef per trap was used as a bait .

Six sets of traps were deployed in the inner, central and outer fjord basins. (Fig. 1). Standard sampling depths were 5, 10, 20 and 30 meters and traps were set for 6 to 7.5 hours. Due to unsuccessful sampling at 30 m at stations 1 and 4, only twenty-two samples instead of twenty-four were collected.

Long-term investigations of scavengers in Kongsfjorden showed that the abundance of carrion feeding fauna in the traps is determined to a large extent by weather conditions which affect water dynamics. Due to considerable abundance differences, most likely caused by changeable weather conditions during sampling, it was decided to pool the numbers of animals from samples within each depth of the inner, central and outer stations.

Because of the lack of direct data, the densities of particular species may be only roughly estimated by adopting the catchability coefficients given by Sainte-Marie (1986) for *Orchomenella pinguides*, *Onisimus litoralis* and *Anonyx sarsi*

from the St. Lawrence Estuary. Assuming 7 m², 8 m², and 74 m² as the catchability coefficients of *Orchomenella minuta*, *Onisimus* spp. and *A. sarsi* respectively it is possible to estimate approximate densities of these species on the basis of the mean number of amphipods captured in the traps.

Additionally, parallel to stations 2, 3 and 5, where cylindrical traps were deployed, sets of small cages with the liophilised meat pieces of known weight (11–23 g of dry weight) were exposed. Renewed liophilization of the meat remains provided information about the amounts of carrion consumed by small scavengers and rates of consumption.

Collected animals were preserved in 4% formaldehyde and subsequently identified in the laboratory.

Guts content analysis was performed on 30 specimens of *Onisimus caricus*, 30 specimens of *O. edwardsi* and 10 specimens of *Orchomenella minuta* collected by means of traps with unavailable bait. Fullness index was estimated from 0 (empty) to 5 (full). Food items were identified through microscopic examination.

Experiments were carried out in the LSF laboratory in Ny-Alesund to measure the response of six lysianassoid species (*Anonyx nugax*, *A. sarsi*, *Onisimus caricus*, *O. litoralis*, *O. edwardsi* and *Orchomenella minuta*) to exposure to live and dead plankton. Collected amphipods were kept separately in plastic vials and acclimatised for 48 h in circulating aerated filtered seawater with no food supplied. Animals were starved for 5 days prior to exposure to plankton. Five individuals were placed in separate glass jars and were exposed to live or dead zooplankton (*Calanus* spp.). Two observations for each species were made. Responses were categorised as preying/ feeding / lack of interest.

Results

16 taxa were found in 22 traps deployed in Kongsfjorden (Table 1). Lysianassoid amphipods, represented by 9 species, comprised 98.9% of the 21338 collected individuals.

Two species of the family: *Anonyx sarsi* and *Onisimus caricus* made up 91.6% of the total abundance (D = 58.2% and D = 33.4% respectively). In terms of frequency, *A. sarsi* (F = 50%) was followed by *A. nugax* (F = 40.9%), *Anonyx* juv. (F = 36.4%), *Onisimus caricus*, *O. edwardsi* and *Orchomenella minuta* (F = 31.8%).

The abundance of animals attracted to traps varied considerably. Abundance and approximate densities of species estimated from catchability coefficients (Sainte-Marie 1986) are given in Table 2.

Average sample sizes were inversely correlated with depth ($r = -0.96$). This general pattern was also true for the central and outer stations. In the inner basin however, the highest abundance values were noted at 10 and 20 m depth stations (Fig. 2).

Table 1

Species list of the Kongsfjorden scavenging fauna. N – number of individuals collected, D – species domination values in the material, F – species frequency values in the material.

Species	N	D%	F%
<i>Anonyx laticoxae</i> Gurjanova, 1962	11	0.05	18.2
<i>Anonyx nugax</i> (Phipps, 1774)	197	0.92	40.9
<i>Anonyx sarsi</i> Steele and Brunel, 1968	12422	58.22	50.0
<i>Anonyx</i> juv.	452	2.12	36.4
<i>Onisimus caricus</i> Hansen, 1886	7119	33.36	31.8
<i>Onisimus edwardsi</i> (Krøyer, 1846)	349	1.64	31.8
<i>Onisimus litoralis</i> (Krøyer, 1845)	398	1.87	18.2
<i>Onisimus plautus</i> (Krøyer, 1845)	1	0.00	4.5
<i>Orchomenella minuta</i> (Krøyer, 1846)	348	1.63	31.8
<i>Gammarus setosus</i> Dementieva, 1931	25	0.12	4.5
<i>Paroediceros lynceus</i> (M. Sars, 1858)	5	0.02	13.6
<i>Eualus gaimardi</i> (Milne Edwards, 1837)	4	0.02	9.1
<i>Pagurus pubescens</i> (Krøyer, 1838)	2	0.01	4.5
<i>Hyas araneus</i> (Linné, 1766)	1	0.00	4.5
<i>Buccinum undatum</i> Linné, 1758	3	0.01	4.5
Echinoidea	1	0.00	4.5

Table 2

Abundance in the traps (r) and estimated densities (e, ind.m⁻²) of necrophagous amphipods in Kongsfjorden. C - catchability coefficient (m²) (Sainte-Marie 1986).

Species	C (m ²)	Depth (m)							
		5		10		20		30	
		r	e	r	e	r	e	r	e
<i>A. sarsi</i>	74	4–7842	0.05–105	4–2539	0.05–34	375	5	21	0.3
<i>O. caricus</i>	8	290	36	2800	350	4013	502	16	2
<i>O. edwardsi</i>	8	24–165	3–21	158	19.8	1	0.125	1	0.125
<i>O. litoralis</i>	8	7–288	0.88–36	2	0.25	0	0	0	0
<i>O. minuta</i>	7	8–72	1.14–10.3	5–257	0.7–36.7	0	0	2	0.3

Most pieces of liophilised meat were totally consumed during 7.5 h of exposition therefore it was impossible to determine differences in consumption rates at different fjord locations. Nevertheless, there were clear differences between the stations in terms of meat lost amounts (Table 3).

Necrophagous species were spatially segregated in Kongsfjorden (Fig. 2). *Onisimus caricus* made up 96% of all animals collected in the inner basin and was most abundant between 10 and 20 meters. *A. nugax* contributed significantly to the

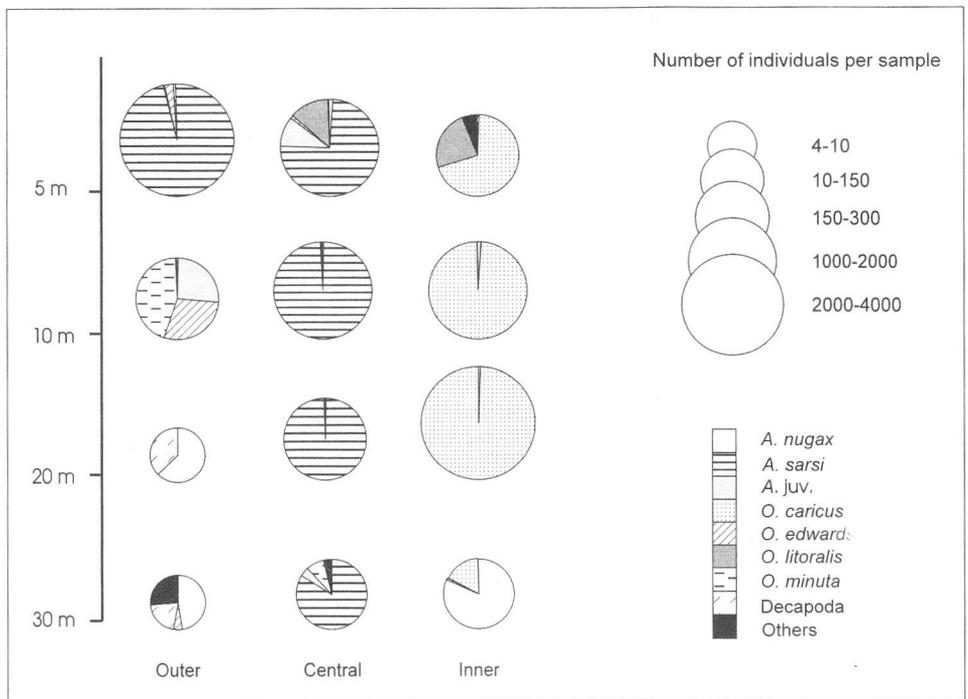


Fig. 2. Abundance in traps and shares of the most important species at the sampling stations.

total abundance at the deepest stations of the inner and outer basins. *A. sarsi* clearly predominated at all stations of the central basin and at the shallowest station of the outer basin. Bait-attending fauna of the outer part of the fjord was most diverse. Unlike the inner and central basins in the outer basin, non-amphipod species were attracted to the traps. Among the 12 taxa apart from lysianassoids, 3 species of Decapoda, one of Echinoidea, and one of Mollusca were found.

Examined guts were only partly filled with food (Table 4). Since all examined species possess triturative mandibles (Sainte-Marie 1984) food morsels found in their guts were small and very crushed. Crustacean parts were the most frequent food items in the guts of *Onisimus caricus* and *Orchomenella minuta* collected during the summer. *Onisimus caricus* fed mainly on pelagic Calanoida and mysids. Very few food particles from the guts of the small *Orchomenella minuta* could be identified precisely. Both amphipod species rarely fed on detritus. *Onisimus edwardsi* had a more diversified diet. It fed on meiofauna organisms such as Nematoda, Harpacticoida, Halacaridae, Tintinnoidea, Oligochaeta and Polychaeta. Filamentous algae and diatoms were present in 50% of the guts and detritus in 27%. Sediment grains were present in the guts of all species examined. Guts of *Onisimus caricus* contained significant admixtures of fine sediment grains, whereas the guts of the two other species contained small amounts of coarse-grained sediments.

Table 3

Amounts of liophilized meat consumed by scavenging amphipods in three different habitats of Kongsfjorden (g) and loss of meat (%).

		5 m	10 m	20 m	30 m
Inner	g	5.338	23.05	17.55	15.27
	%	39.28	100	100	100
Central	g	12.6	11.0	1.5404	9.3253
	%	100	100	13.51	54.85
Outer	g	19.98	19.56	0.4125	1.9548
	%	100	100	3.24	13.9

Table 4

Frequency of occurrence (% of N) of food items in the guts of *O. caricus*, *O. edwardsi* and *O. minuta* from Kongsfjorden.

	<i>O. caricus</i>	<i>O. edwardsi</i>	<i>O. minuta</i>
Algae	3.3	50.3	10
Amorphous material	13.3	46	100
Copepoda	100	36.6	
Other Crustacea	50	16.6	20
Detritus	13.3	26.6	20
Halacaridae		3.3	10
Nematoda		10	10
Oligochaeta		3.3	
Polychaeta		16.6	10
Tintinoidea		13.3	
Sediments	73.3	20	100
Mean fullness index	2.3	2.3	2.7
Guts examined (N)	30	30	10

In the laboratory feeding experiments all species were observed to feed on dead or injured zooplankton (Table 5). The introduction of dead zooplankton aroused moderate interest in *Anonyx nugax* and *A. sarsi*. The most voracious species was *Onisimus littoralis*, which was the most active taxon, attacking prey immediately, feeding on it and competing for different kinds of planktonic animals. A number of instances of fighting among *Onisimus littoralis* specimens was observed. Other *Onisimus* species and *Orchomenella minuta* attacked dead planktonic organisms within the first 5 minutes of their introduction into the jars and were feeding continuously for the duration of the experiments. Increased mobility of some species was observed after adding live zooplankton animals (Table 5). Preying on live plankton organisms was never noted. However, some specimens

Responses of six lysianassoid species exposed to live and dead zooplankton.

	<i>O. litoralis</i>	<i>O. edwardsi</i>	<i>O. caricus</i>	<i>A. sarsi</i>	<i>A. nugax</i>	<i>O. minuta</i>
T (min.)	Number of specimens feeding					
DEAD ZOOPLANKTON						
0	5	0	0	0	0	0
5	10	10	10	0	0	10
15	10	10	10	10	10	8
next 45	10	10	10	10	0	10
remarks	active, compete, feed on copepods, <i>Limacina helicina</i> , Ctenophora, <i>Themisto</i> spp.	feed continuously on copepods	active, feed continuously on copepods	moderate interest for copepods	moderate interest/lack of interest for copepods, <i>Limacina helicina</i>	feed continuously on copepods
LIVE ZOOPLANKTON						
remarks	increase of motility, compete for copepods <i>Limacina helicina</i> , Ctenophora, <i>Themisto</i> spp. stranded on the bottom	feed only on non-active copepods on the bottom	increase of motility, feed on copepods stranded on the bottom	increase of motility, feed on copepods stranded on the bottom	increase of motility, moderate interest for <i>Themisto</i> spp.	feed only on non-active copepods on the bottom

tried to catch them. All species attacked weak or injured planktoners as they fell to the bottom of the jars.

Discussion

Species list

Domination of lysianassoid amphipods among the organisms attracted to baited traps deployed in the shallow cold waters has been often observed (Busdosh *et al.* 1982, Presler 1986, Sainte-Marie 1986, Slattery and Oliver 1986, Legeżyńska *et al.* 2000). Sainte-Marie (1986) noted five species of lysianassoids making up 75 to 99.9% of total fauna collected in the Middle Saint Lawrence Estuary. A similar situation was reported by Legeżyńska *et al.* (2000) at Hornsund, a

southern Svalbard fjord where 6 species constituted 95% of the total number of animals caught. In comparison with the material from Kongsfjorden, Hornsund bait-attending fauna was more diverse, however, this may be related to the higher sampling effort and the extension of sampling down to 175 m.

Abundance of scavenging fauna

A gradual decrease in the abundance of the amphipod scavengers over increasing depth was clear in Kongsfjorden. The occurrence of scavenging amphipods in Kongsfjorden is restricted to depths of about 30 m (author's unpublished data), while in Hornsund and off Ellesmere Island they were still quite numerous in the traps deployed at 60 m and deeper (Legeżyńska *et al.* 2000). The abundance of the bait-attending amphipods in Kongsfjorden was generally higher than noted in Hornsund. In 77 Hornsund samples only 19475 individuals were encountered (with a maximum catch of 1784 per single trap), while average abundance in the 22 Kongsfjorden samples was nearly 1000 animals, with a maximum of 7476 specimens captured in a single trap. Busdosh *et al.* (1982) and Sainte-Marie (1986) reported far higher numbers of specimens collected by single traps in the Beaufort Sea and Saint Lawrence Estuary. Their investigation, however, was limited to the shallowest waters and bait was exposed for 24 h.

Estimation of lysianassoids' densities is difficult because their behaviour and high mobility makes them almost impossible to collect by dredges and grabs. In the large materials taken in Kongsfjorden by a Van Veen grab, as well as in the samples collected by means of a small dredge at the depths less than 50 m, only single specimens of lysianassoids were noted (author's unpublished data). The numbers of animals attracted to the traps in Kongsfjorden was considerable, but this did not provide information about lysianassoids' densities in the occupied habitats. Estimated densities of lysianassoids observed in different habitats in Kongsfjorden were extremely variable and are consistent with the direct data on endobenthic abundance of the Saint Lawrence Estuary species provided by Sainte-Marie (1986).

Utilisation and dispersal of carrion

As expected, the highest amounts of meat were consumed at the stations where the highest abundance of lysianassoids was noted (Table 3). Several authors (Stockton and DeLaca 1982, Sainte-Marie 1992) discussed the role played by scavenging amphipods in the dispersal of carrion. The efficiency of such dispersal, apart from the number of attracted animals, is also connected with the morphology of mouthparts and feeding behaviour of particular species. Although it couldn't be corroborated by a single observation, it is probable that dispersal of accessible carrion is greater in areas numerically dominated by *Onisimus* or *Orchomenella* species. According to Sainte-Marie (1992), due to their triturative mandibles they feed wastefully and slowly and food is processed continuously with low assimilation rates. Owing to their inefficient feeding and digestion, they can directly contribute

to the enrichment of local fauna, while *Anonyx* spp.'s contribution to the spread of carrion is low because they can consume and digest carrion very efficiently (Sainte-Marie 1992). The distribution patterns of lysianassoid species in Kongsfjorden indicate that, unlike other Arctic localities (Legeżyńska *et al.* 2000), these amphipods (in summer) are responsible for utilisation and dispersal of carrion only in relatively shallow water.

Distribution patterns

Spatial segregation of shallow water lysianassoids was observed in the Antarctic (Presler 1986, Slattery and Oliver 1986), boreal (Sainte-Marie 1986) and Arctic (Legeżyńska *et al.* 2000) nearshore environments. Considerable differences of the scavenging fauna composition in three areas of Kongsfjorden were observed as well. The distribution patterns of the scavenging fauna is influenced by a combination of diverse factors including depth, hydrological conditions, sedimentation regime, bottom type and food availability.

Glacial bays, in comparison with outer fjord basins influenced by the open sea, in general provide poor conditions for supporting pelagic and benthic life (Görlich *et al.* 1987, Włodarska-Kowalcuk *et al.* 1998). Due to the low availability of food, especially outside the summer season, scavengers occupying such habitats must be able to withstand long periods of starvation.

The idea of the dividing lysianassoid amphipods into two groups – one of them being a scavenger type of feeder well adapted to long starvation periods, like *Anonyx* spp., and the second group being feeding generalists not capable of enduring long starvation periods like the *Onisimus* and *Orchomenella* species – has been well established in literature (Sainte-Marie 1992). Laboratory observations, however, showed that the species ability to endure long periods of starvation is more size dependent than connected with differences in gut morphology and feeding behaviour (Christiansen and Diel-Christiansen 1993). Thus it is not astonishing that the largest representatives of the genus *Anonyx* and *Onisimus* dominate the glacial bay scavenging fauna (Fig. 2). *Onisimus caricus* and *Anonyx nugax* dominated in the inner basin and *Onisimus litoralis* and *Gammarus* spp., typical of brackish littoral waters (Węślawski 1991), made significant contributions to the total abundance only at the shallowest stations which are strongly influenced by freshwater outflow.

Onisimus caricus distribution was restricted exclusively to the glacial bay – the innermost location sampled. The same was observed in Hornsund, in Burgerbukta Bay, which is influenced by massive glacial outflows (Legeżyńska *et al.* 2000). In both localities similar frequency values (about 32%) of this species were noted: at the same time its contribution to the total abundance in Hornsund samples did not exceed 2%, whereas in Kongsfjorden it constituted 33% of all collected animals.

Concentration of the species, which occurs generally down to 200 m (Węślawski 1991) at the shallow sampling stations, might have a seasonal character and may be connected with the mass mortality of marine zooplankton caused by re-

duced salinity close to glacier cliffs during summer. Węśławski and Legeżyńska (1998) assumed that sinking zooplankton organisms (Copepoda, *Themisto* spp.) could create predictable food conditions and support the scavenging fauna of glacial bays. *Onisimus caricus*, which dominates in the glacial bay, might be one of the most important species taking advantage of this phenomenon (Zajączkowski and Legeżyńska 2001). The importance of zooplankton organisms in *O. caricus* diet was also confirmed by analysis of the gut contents of the specimens collected in Kongsfjorden (Table 4).

A. nugax whose share in the total abundance in the traps increased at the deepest stations of the inner and outer basins, was the largest lysianassoid species collected in Kongsfjorden. It can endure long periods without feeding (Christiansen and Diel-Christiansen 1993) and relies mostly on large carrion, but it was also suspected of preying on smaller suprabenthic and pelagic crustaceans (Sainte-Marie and Lamarche 1985). In contrast to Hornsund, where this species was dominant, especially in the inner, glacial bay (Legeżyńska *et al.* 2000) it was not of great importance in Kongsfjorden. The reason for this inverse composition of the two species dominating in glacial bays observed in Hornsund and Kongsfjorden remains unclear.

In comparison with the glacial bay, the remaining areas of the fjord are characterised by more stable and diverse bottom substrates and lower levels of sedimentation and disturbance, as well as better trophic conditions (Włodarska *et al.* 1996).

In the central area of Kongsfjorden 8 species were collected, with a dominant *A. sarsi* making up 88% of the collected animals. As in Hornsund, *A. sarsi* prefers waters less than 30 m in depth and at lower depths is replaced by *A. nugax*, which attains its maximal abundance between 30 and 60 m (Legeżyńska *et al.* 2000). The highest abundance values of *A. sarsi* were noted at shallow stations in the central and outer parts of Kongsfjorden. This pattern may be connected with the characteristics of the bottom. Rocks and diverse bottom substrate overgrown with laminarians and *Fucus* spp. prevail at these localities, providing favourable conditions for this species which is known for its preference for shaded areas (Sainte-Marie 1986). Furthermore such habitats provide good feeding opportunities as they contain a rich set of planktonic and benthic food (Hop *et al.* unpubl.).

Scavenging fauna inhabiting the shallow benches along south-western coast of Kongsfjorden (outer part of the fiord) is strongly affected by the open sea. Turbulence due to high seas might cause the odour plume to be dispersed, making it more difficult for amphipods to detect. Turbidity of water delays the animals' arrival at the traps, especially in the case of slow moving species like *Onisimus edwardsi* and *Orchomenella minuta*, for which attraction to bait deployed at 5 meters is strongly time dependent (correlation coefficients of 0.95 and 0.99 respectively, according to author's unpublished data). Large and mobile *A. sarsi* (Sainte-Marie 1986) reached the bait within the time of exposition even in turbulent hydrodynamic environments and dominated the shallowest localities sampled. *O. edwardsi*, *O.*

minuta and juvenile specimens of *Anonyx* spp. avoided extremely turbulent environments and were most concentrated at 10 m depth.

At 20 and 30 m of the outer area fewer amphipods (only the largest species: *A. nugax* and *A. laticoxae*) were sampled, while at the same time the contribution of decapods and *Buccinum undatum* to the total number of collected animals increased. The structure of scavenging fauna of the outer Kongsfjorden may be explained by the impact of hydrological factors; namely strong bottom currents penetrate the fjord along its south coast, but little is known about nearshore currents (Svendsen *et al.*, unpubl.). If they exist, they might make reaching bait difficult for relatively small amphipods. Predation by fish or larger invertebrates or competition for food might be other reasons for the low density of lysianassids in those areas.

Feeding

Parts of copepods and other pelagic crustaceans were often found in the guts of the large *Anonyx* species from the Saint Lawrence Estuary (Sainte-Marie and Lamarche 1985) and the Antarctic *Orchomenella pinguides* (Slattery and Oliver 1986). These fragments may come from predation on smaller crustaceans or feeding on dead or injured animals. Sainte-Marie and Lamarche (1985) pointed out that lysianassoid amphipods do not possess adaptations for predation, apart from having a high swimming speed. Preying on smaller crustaceans however, cannot be excluded. Field observations on necrophagous amphipods' feeding behaviour are still scarce. Feeding on injured or dead organisms was often reported (Oliver *et al.* 1984, Oliver and Slattery 1985, Slattery and Oliver 1986, Klages *et al.* 2001), but *A. sarsi* and *Onisimus litoralis* were also observed preying on live, active animals (Sainte-Marie 1986). During observations in aquaria specimens of several Antarctic lysianassoids were seen to kill living mysids, polychaetes or even small fish (when amphipods were present in large numbers) (Dauby *et al.* 2001).

The fact that in most guts of *Onisimus caricus* a considerable admixture of fine sediment grains was noted and that crustacean parts were torn to pieces (i.e. single appendages were found) suggests that planktoners were rather taken dead from bottom sediments than alive. Laboratory observations also revealed that *O. caricus*, like all *Onisimus* species, feeds on dead zooplankton organisms, while live ones are taken only when they were stranded near the bottom and non-active. Although there is no data on the feeding strategy of *O. caricus*, it can be assumed that it is flexible in its feeding habits like *O. litoralis*, which changes its diet depending on season (Carey and Boudrias 1987). Taking into consideration the size and mobility of *O. caricus*, it is possible that its population outside of the main melting season may be more dispersed and that it makes use of different food sources.

Preliminary analysis of gut contents indicated that *Onisimus edwardsi* is markedly opportunistic. Similarly to *O. litoralis* (Carey and Boudrias 1987), it takes animal as well as plant food. *Orchomenella minuta* fed mostly on crustaceans, which

were also frequently consumed by other small lysianassoid species, *Orchomenella pinguis* and *Psammonyx nobilis* (Scott and Croker 1976, Sainte-Marie 1986). At the same time, in contrast to these two species *O. minuta* from Kongsfjorden did not rely much on detritus. Neither *Onisimus edwardsi* nor *Orchomenella minuta* were observed to prey on active Calanoida (Table 5). Mostly parts of the much smaller crustaceans (e.g. harpacticoids, nauplii) were found in their guts however. It is not clear whether they were taken alive or scavenged from the sediment. Another question is whether or not minute food items were ingested selectively or without distinguishing them from detritus. It seems possible that the smallest food items (diatoms, Tintinnoidea, Oligochaeta) found in the guts of *O. edwardsi* were taken non-selectively since they also contained a considerable portion of detritus. *Orchomenella minuta*, whose guts contained almost exclusively crushed crustacean parts and little detritus, is probably a more selective species. Sediment grains contributed insignificantly to the total bulk of guts contents, but were noted much more frequently in the guts of examined taxa than in these of the Saint Lawrence Estuary species (Sainte-Marie and Lamarche 1985, Sainte-Marie 1986).

In conclusion, the distribution of scavenging fauna within Arctic fjords differs within and amongst fjords. Depth, bottom substrate, and proximity to glacial outflow appear to be important factors in determining the distribution patterns of species which differ in feeding mode, size, and mobility.

Acknowledgements. — The author is grateful to Dr M. Zajączkowski and Dr Maria Włodarska-Kowalczyk for their help and logistic support during sampling and experiments carried out at the LSF laboratory in Ny-Ålesund. Nina Karnovsky, Dr Józef Wiktor and Prof. Jan Marcin Weślowski kindly read and commented on the manuscript. Comments by Dr Claude De Broyer and Dr Jacek Siciński improved the manuscript. This study was supported by grants 6PO4E00517 of the Polish State Committee for Scientific Research and from Ny-Ålesund LSF.

References

- BUSDOSH M., ROBILLIARD G.A., TARBOX K. and BEEHLER C.L. 1982. Chemoreception in an Arctic amphipod crustacean: a field study. — *J. Exp. Mar. Biol. Ecol.*, 62: 261–269.
- CAREY A.G. and BOUDRIAS M.A. 1987. Feeding ecology of *Pseudalibrotus* (= *Onisimus*) *litoralis* Krøyer (Crustacea: Amphipoda) on the Beaufort Sea Inner Continental Shelf. — *Polar Biol.*, 8: 29–33.
- CHRISTIANSEN B. and DIEL-CHRISTIANSEN S. 1993. Respiration of lysianassoid amphipods in a subarctic fjord and some implications on their feeding ecology. — *Sarsia*, 78: 9–15.
- DAUBY P., SCAILTEUR Y. and DE BROYER C. 2001. Trophic diversity within the eastern Weddell Sea amphipod community. — *Hydrobiologia*, 443: 69–86.
- GÖRLICH K., WEŚLAWSKI J.M. and ZAJĄCZKOWSKI M. 1987. Suspension settling effect on macrobenthos biomass distribution in the Hornsund fjord, Spitsbergen. — *Polar Res.*, 5: 175–192.
- ITO H. and KUDOH S. 1997. Characteristics of water in Kongsfjorden, Svalbard. — NIPR Symposium on Polar Meteorology and Glaciology, No. 11, National Institute of Polar Research, Tokyo: 211–232.

- KAUFMANN R.S. 1992. The behavior, physiology and ecology of scavenging lysianassoid amphipods, with comparisons between shallow- and deep-water species, Ph.D. Thesis, University of California, San Diego.
- KINGES M., VOPEL K., BLUHM H., BREY T., SOLTEWDEL T. and ARNTZ W.E. 2001. Deep-sea food falls: first observation of a natural event. — *Polar Biol.*, 24: 292–295.
- LEGEŻYŃSKA J., WĘSŁAWSKI J.M. and PRESLER P. 2000. Benthic scavengers collected by baited traps in the high Arctic. — *Polar Biol.*, 23: 539–544.
- OLIVER J.S. and SLATTERY P.N. 1985. Destruction and opportunity on the sea floor: effects of gray whale feeding. — *Ecology*, 66: 1965–1975.
- OLIVER J.S., SLATTERY P.N., SILBERSTEIN M.A. and O'CONNOR E.F. 1984. Gray whale feeding on dense ampeliscid amphipod communities near Bamfield, British Columbia. — *Can. J. Zool.*, 62: 41–49.
- PRESLER P. 1986. Necrophagous invertebrates of the Admiralty Bay of King George Island (South Shetland Islands), Antarctica. — *Pol. Polar Res.*, 7: 25–61.
- SAINTE-MARIE B. 1984. Morphological adaptations for carrion feeding in four species of littoral or circalittoral lysianassid amphipods. — *Can. J. Zool.*, 62: 1668–1674.
- SAINTE-MARIE B. 1986. Feeding and swimming of lysianassid amphipods in a shallow cold-water bay. — *Mar. Biol.*, 91: 219–229.
- SAINTE-MARIE B. 1992. Foraging of scavenging deep-sea lysianassoid amphipods. In: Rowe G.T., Pariente V. (eds.) *Deep-sea food chains and the global carbon cycle*. — Kluwer Academic Publishers, Netherlands; 105–124.
- SAINTE-MARIE B. and LAMARCHE G. 1985. The diets of six species of the carrion-feeding lysianassid amphipod genus *Anonyx* and their relation with morphology and swimming behaviour. — *Sarsia*, 70: 119–126.
- SCOTT K.J. and CROKER R.A. 1976. Macroinfauna of northern New England marine sand. III. The ecology of *Psammonyx nobilis* (Stimpson, 1853) (Crustacea: Amphipoda). — *Can. J. Zool.*, 54: 1519–1529.
- SLATTERY P.N. and OLIVER J.S. 1986. Scavenging and other feeding habits of lysianassid amphipods (*Orchomene* spp.) from McMurdo Sound, Antarctica. — *Polar Biol.*, 6: 171–177.
- STOCKTON W.L. and DELACA T.E. 1982. Food falls in the deep sea: occurrence, quality and significance. — *Deep-Sea Res.*, 29 (2A): 157–169.
- THURSTON M.H. 1979. Scavenging abyssal amphipods from the Northeast Atlantic Ocean. — *Mar. Biol.*, 51: 55–68.
- WĘSŁAWSKI J.M. 1991. Malacostraca. — In: Klekowski R. and Węśłowski J.M. (eds.), *Atlas of the marine fauna of Southern Spitsbergen*, vol. 2, Invertebrates part I – IO Polish Academy of Sciences, Gdańsk 1991.
- WĘSŁAWSKI J.M. and LEGEŻYŃSKA J. 1998. Glaciers caused zooplankton mortality? — *J. Plankton Res.*, 20: 1233–1240.
- WŁODARSKA M., WĘSŁAWSKI J.M. and GROMISZ S. 1996. A comparison of the macrofaunal community structure and diversity in two Arctic glacial bays – a “cold” one off Franz Josef Land and a “warm” one off Spitsbergen. — *Oceanologia*, 38: 251–283.
- WŁODARSKA-KOWALCZUK M., WĘSŁAWSKI J.M. and KOTWICKI L. 1998. Spitsbergen glacial bays macrobenthos – a comparative study. — *Polar Biol.*, 20: 66–73.
- ZAJĄCZKOWSKI M. J. and LEGEŻYŃSKA J. 2001. Estimation of zooplankton mortality caused by an Arctic glacier outflow. — *Oceanologia*, 43: 341–351.