RESEARCH/REVIEW ARTICLE

Kelp forest as a habitat for mobile epifauna: case study of *Caprella septentrionalis* Kröyer, 1838 (Amphipoda, Caprellidae) in an Arctic glacial fjord

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Abstract

Distribution and abundance of the amphipod *Caprella septentrionalis* in relation to environmental conditions and habitat preferences were investigated in a kelp forest in Hornsund, Spitsbergen. Three sampling sites differed in hydrodynamics, organic and inorganic suspension concentration, and sedimentation rates. None of these abiotic factors or species of a macroalgal host appeared to have a significant influence on *C. septentrionalis* abundance and size range. An apparent preference towards the blade parts of the algal thalli was observed. These results support the idea of *C. septentrionalis* as a generalist Arctic–boreal species that takes advantage of the protective nature of kelp forests.

In the high-latitude glacial Arctic fjord, Hornsund, an extensive kelp forest develops on hard bottom, from about 5 to 25 m. The kelp community is dominated by three perennial species: *Alaria esculenta*, *Laminaria digitata* and *Saccharina latissima* (Tatarek et al. 2012). The overall biomass of these species may reach up to 3443 g wet weight m^{-2} (Tatarek et al. 2012). Apart from being important primary producers and habitat formers (Christie et al. 2009), kelps are also ecosystem engineers that change the environmental properties by altering water flow and sedimentation (Jones et al. 1994) and constitute hot spots of diversity in temperate and cold-water regions of the Northern Hemisphere (Graham et al. 2007). Diverse communities of sessile and mobile invertebrates find food, physical substratum and shelter from predators in the kelp forests of Spitsbergen fjords (Lippert et al. 2001; Ronowicz et al. 2008; Włodarska-Kowalczuk et al. 2009).

Caprella septentrionalis Kröyer, 1838 (Amphipoda, Caprellidae) is one of the most common species associated with macroalgae in Spitsbergen fjords (Węsławski 1990; Lippert et al. 2001; Włodarska-Kowalczuk et al. 2009). It is a taxon noted in boreal and Arctic regions of the North Atlantic—Greenland, the Barents Sea, the White Sea, Svalbard, Faroe Islands, north Scotland, Iceland, Baffin Bay and the Gulf of Maine (Vasilenko 1974; Guerra-García 2002). The species plays an important role in the food web of the White Sea, where its mass occurrence on macroalgal, poriferan and hydrozoan substrata attracts many fishes including the commercially exploited *Gadus morhua* (Geptner 1963; Marfenin & Belorusceva 2006). Limited information is available concerning its biology and ecology. The species occurs at temperatures between 0 and 7.9°C (Larsen 1998), typically in shallow waters (McCain 1968; Vasilenko 1974; Węsławski 1990), but it has also been recorded at 1026 m depth by Larsen (1998). According to Węsławski & Legeżyńska (2002), *C. septentrionalis* in Hornsund requires more than two years to complete its life cycle. Its typical upright posture and possession of densely setose second antennae used for filtering particles out of the water column and grooming behaviour indicate suspension feeding is its main feeding strategy (Guerra-García 2002; Legeżyńska et al. 2012).

The main goal of this study was to investigate the population structure (body size distribution, sex ratio) and patterns of distribution and abundance of *C. septentrionalis* in relation to hydrodynamics, glacier-induced

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environmental conditions (inorganic sedimentation rate, inorganic suspension concentration) and macroalgal host species.

Study area and methods

The study was carried out in Hornsund (76°56′–77°03′N; 15°28′–16°45′E), in south-western Spitsbergen, in July 2003 (Fig. 1). Hornsund is a typical glacial fjord with 14 tidal glaciers discharging high loads of freshwater and inorganic suspensions to the system in summer. A detailed description of the Hornsund physical features can be found in Swerpel (1985), Węsławski et al. (1995) and Włodarska-Kowalczuk et al. (2009).

The material was collected by SCUBA divers at three sites with different physical characteristics: Isbjørnhamna and Hyrneodden, situated close to glacier outflows, and Gåshamna, situated far from the glacier outflows (Fig. 1). The highest mineral and organic sedimentation rates, and mineral and organic suspended matter concentrations were observed in Isbjørnhamna, while the lowest values were noted in Gåshamna, which is less affected by glacier-induced disturbance (Ronowicz et al. 2008). Secchi disc transparency, which indicates water transparency, was much higher in Gåshamna (about 10 m) compared to the two other sites (1.6 m in Isbjørnhamna and 1.77 in Hyrneodden; Ronowicz et al. 2008). Isbjørnhamna and Hyrneodden are more exposed sites while Gåshamna is sheltered from wave action (Ronowicz et al. 2008).

At each site, the three most common kelp species—*Laminaria digitata*, *Saccharina latissima* and *Alaria esculenta*—and the understory macroalga *Desmarestia aculeata* together with associated fauna, were collected at two depths of 5 and 10 m. Each algal specimen was cut from the substratum with a knife and placed in a bag. A total of 372 algal samples were collected and fixed in buffered 4% formaldehyde. In the laboratory *C. septentrionalis* specimens were removed from the kelp, counted and measured from the tip of the head to the end of the telson to the nearest 0.1 mm. Caprellid abundance is given as the number of individuals per alga. The frequency of occurrence of *Caprella* was estimated as the percentage of algal samples in which the amphipod occurred in the total number of algae collected. Sex was determined using the presence of genital papillae for identifying males and the presence of oostegites for identifying females. If no sexual characteristics were observed, a specimen was considered juvenile. Sex ratio was calculated as the proportion of males to females. Environmental parameters such as current velocity, water transparency, sedimentation rate and suspension concentration are described by Ronowicz et al. (2008).

The differences between abundance and size of *C. septentrionalis* among different algal species and among sites were tested using the nonparametric Kruskal–Wallis test. All statistical analyses were conducted with Statsoft's Statistica software version 6.

Results

The mean number of *Caprella septentrionalis* individuals varied from 2.0 ± 2.9 (mean $\pm$ SD) in Isbjørnhamna to 3.6 ± 7.4 in Gåshamna (Table 1). The abundance did not differ significantly between the three sites

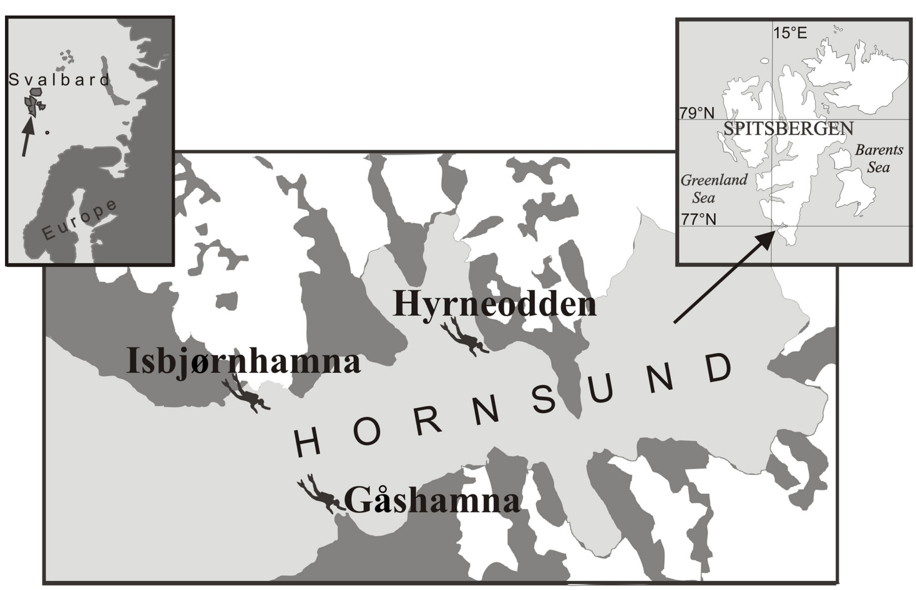

Fig. 1 Location of the sampling sites. Glaciers are indicated by the white areas.

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Table 1 Mean abundance of *Caprella septentrionalis* per algal sample with minimum and maximum values in brackets at different sites (*N*, number of algae collected; *F*, frequency of caprellid occurrence on algal hosts). The frequency of occurrence (*F*) was estimated as the percentage of algal samples in which *Caprella* occurred in the total number of algae collected.

	Site						Total		
	Gåshamna		Hyrneodden		Isbjørnhamna				
Algae	Mean	*N*	Mean	*N*	Mean	*N*	Mean	*N*	*F* (%)
A. esculenta	5.5 (1–32)	48	6.2 (1–25)	36	3.3 (1–14)	38	4.9 (1–32)	122	21
L. digitata	1	26	1.3 (1–2)	32	1.6 (1–4)	21	1.4 (1–4)	79	11
S. latissima	(1–2)	45	(1–1)	42	1.3 (1–2)	68	1.3 (1–2)	155	9
D. aculeata	0	3	2.2 (1–4)	12	0	1	2.2 (1–4)	16	37
Total	3.6 (1–32)	122	3.1 (1–25)	122	2 (1–14)	128	2.9 (1–32)	372	15

(Kruskal–Wallis test: $H = 4.14$, $p = 0.53$). There was also no difference in the size range of amphipods between different sites (Kruskal–Wallis test: $H = 8.27$, $p = 0.14$).

C. septentrionalis was present in 15% of 372 collected algal samples. The abundance and body length did not differ significantly among different algal hosts (Kruskal–Wallis test for abundance: $H = 5.97$, $p = 0.11$; and body length: $H = 1.377$, $p = 0.71$). The highest number of individuals was recorded on *A. esculenta* (up to 32 per algal sample at Gåshamna, mean 5.5 ± 7.1), while on other host species the number of caprellids did not exceed four specimens per algal sample. *C. septentrionalis* occurred more frequently on the alga *D. aculeata* ($F = 37\%$) than on kelp species *A. esculenta, L. digitata* and *S. latissima* (Table 1).

A total of 156 individuals were collected. Body length of the animals ranged from 2.9 to 25 mm with a mean value of 12.8 mm (± 5.7 SD). Juveniles comprised 23%, males 45% and females 32% of specimens. There was a male predominance (sex ratio = 1.3). Mean body length of juveniles was 4.8 mm (± 1.5 SD). Adult males were generally larger than females (Fig. 2). Body length of males ranged from 5.7 to 24.8 mm (mean 14.9 ± 5.4 mm), while in females it varied from 6 to 20 mm (mean 13.8 ± 2.6 mm). Three ovigerous females were found.

Discussion

Caprella septentrionalis has been found to be the dominant mobile crustacean associated with kelp beds in Hornsund, making up to 43% of the total crustacean abundance (Włodarska-Kowalczuk et al. 2009). However, little is known about its population structure in the Arctic. The present study shows the predominance of males in July (sex ratio = 1.3). This result differs from what is reported in other studies. An earlier study from Hornsund showed predominance of females (sex ratio = 0.76; Węsławski & Legeżyńska 2002). However, that earlier material was collected in several seasons and was not limited to summer only, as in this study. Geptner (1963) reported that the sex ratio of the White Sea population of *C. septentrionalis* changed during the year. He observed that females dominated in June (sex ratio = 0.7). Later in the year, young individuals predominated

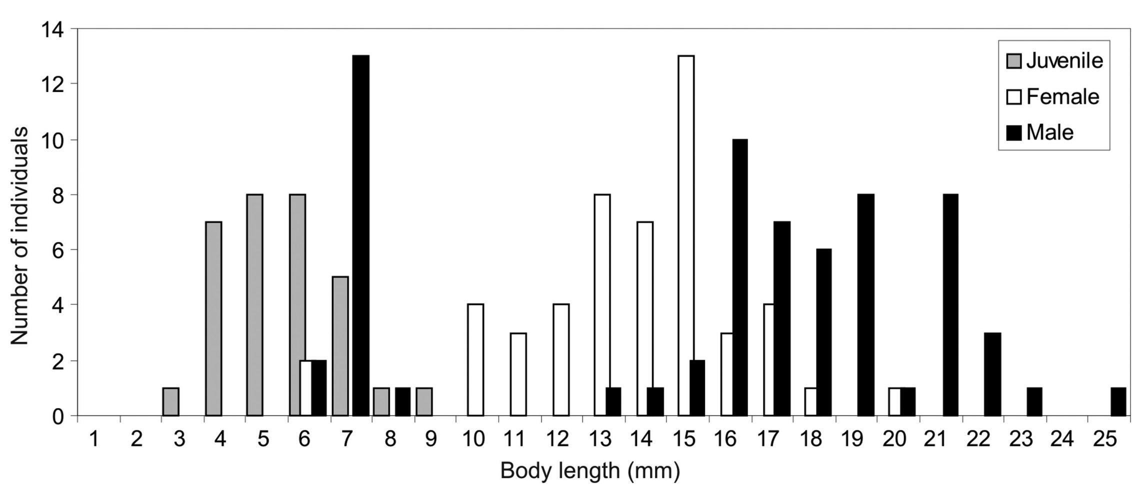

Fig. 2 The population structure of *Caprella septentrionalis* in July.

due to adult mortality after breeding. Later, there was no clear pattern of dominance of any sex. This finding differs from our July material when juveniles, males and females were represented by comparably large numbers of individuals. There are probably two age cohorts of males: small males up to 8 mm of length that hatched in spring the same year and big males 13–25 mm long that are one or two years old. Our results do not suggest mortality of adults in July. It is possible that the life cycle in the colder waters of Svalbard is delayed compared to the White Sea, and adult mortality occurs in late summer. We found three ovigerous females in July. Węsławski & Legeżyńska (2002) showed that *C. septentrionalis* in Hornsund incubates eggs in winter, releases its offspring in May and females with empty marsupia are found in July. Since our material only comprised three ovigerous individuals, we cannot speculate about this difference.

This study indicates that *C. septentrionalis* should be considered a substratum generalist since its distribution was patchy and it occurred on different algal species with no statistically important preference. Studies from other regions showed the use of various substrata, such as brown, green and red algae, seagrass, sponges, hydrozoans, alcyonarians, bryozoans and tunicates (Geptner 1963; McCain 1968). In Kongsfjorden, located further north in Spitsbergen, the species occurred on soft and hard bottom, but dominated in a benthic community associated with kelp species (Kaczmarek et al. 2005). In the same fjord, Lippert et al. (2001) observed that *C. septentrionalis* preferred the alga *D. aculeata* which offered good structures for attachment and a high degree of camouflage. In our study, *C. septentrionalis* reached the highest frequency of occurrence on the highly branched *D. aculeata* but was less abundant on this alga than on the kelp *A. esculenta*. The lower abundance of caprellids on *D. aculeata* was probably due to the much smaller size of this alga compared to the large kelp species.

Underwater observations enabled us to detect a clear preference of *Caprella* towards the uppermost part of the host algal species. The amphipods were mainly observed clinging to algal fronds (Fig. 3), using them as a physical support that lifts them up into the water column where they can access sufficient water flow (Hirst 2007).

The results suggest that *C. septentrionalis* is not particularly vulnerable to high loads of mineral suspension concentration and high sedimentation rates in near-glacier areas. As this caprellid is assumed to be a suspension feeder (Guerra-García 2002; Legeżyńska et al. 2012), some effect of sediment disturbance on the caprellid distribution in localities adjacent to glacier fronts was expected. In areas exposed to high sediment stress, suspension-feeding organisms suffer damage resulting from burial or clogging of the filtering apparatus (Moore 1977; Ronowicz et al. 2011). However, recent studies of gut contents of *C. septentrionalis* (Legeżyńska et al. 2012) revealed the possibility of other means of feeding such as predation and scraping (Legeżyńska et al. 2012). Employment of different feeding strategies by *C. septentrionalis* may be the adaptation to survive in a sediment-impacted environment.

Fig. 3 *Caprella septentrionalis* Kröyer, 1838 on the frond of kelp showing its typical vertical position. Photo by P. Kukliński.

The abundance and size distribution of *C. septentrionalis* did not vary between the three sites with different hydrodynamics. Comparisons of fauna associated with macroalgae in the areas of high and low wave exposure showed that in sites affected by strong water dynamics abundance of the total fauna was much lower, while clinging animals, such as mobile amphipods predominated (Hagerman 1966; Fenwick 1976). The caprellid domination at exposed sites is explained by its ability to hold onto algae firmly with its strong grasping appendages (Hagerman 1966) to avoid dislodgment by wave action (Guerra-García & García-Gómez 2001).

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Therefore, water hydrodynamics is not a key factor determining their distribution.

Kelp forests provide favourable conditions for *C. septentrionalis* by shielding its populations from the direct impacts of sedimentation and wave action and offering a relatively stable substrate that allows for effective feeding. Warming of the Arctic, with global climate change (IPCC 2007), will likely have a positive impact on the kelp forests in Arctic coastal seas due to longer ice-free periods and decreasing ice cover extent (Krause-Jensen et al. 2012). We can expect that kelp-associated fauna with a wide temperature tolerance—including the species studied here—will not be threatened by climate change but will broaden its distribution in step with the expanded kelp forest distribution.

Conclusions

Caprella septentrionalis does not show any preference between kelp species hosts. The physical factors of sedimentary regime and wave action do not affect its distribution in a glacial Arctic kelp forest. Our results indicate that *C. septentrionalis* is an opportunistic species taking advantage of the protective attributes of its habitat in the Arctic glaciated fjord of Hornsund.

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