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# The malacostracan fauna of two Arctic fjords (west Spitsbergen): the diversity and distribution patterns of its pelagic and benthic components

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**Summary** This study examines the performance of pelagic and benthic Malacostraca in two glacial fjords of west Spitsbergen: Kongsfjorden, strongly influenced by warm Atlantic waters, and Hornsund which, because of the strong impact of the cold Sørkapp Current, has more of an Arctic character. The material was collected during 12 summer expeditions organized from 1997 to 2013. In all, 24 pelagic and 116 benthic taxa were recorded, most of them widely distributed Arctic-boreal species. The advection of different water masses from the shelf had a direct impact on the structure of the pelagic Malacostraca communities, resulting in the clear dominance of the sub-arctic hyperiid amphipod *Themisto abyssorum* in Kongsfjorden and the great abundance of Decapoda larvae in Hornsund. The taxonomic, functional and size compositions of the benthic malacostracan assemblages varied between the two fjords, and also between the glacier-proximate inner bays and the main fjord basins, as a result of the varying dominance patterns of the same assemblage of species. There was a significant drop in species richness in the strongly disturbed glacial bays of both fjords, but only in Hornsund was this accompanied by a significant decrease in density and diversity, probably due to greater isolation and poorer quality of sediment organic matter in its innermost basin. Our results suggest that the diversity and distribution of benthic malacostracans in these two fjords are only distantly related to the different hydrological regimes; rather, they are governed by

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locally acting factors, such as depth, sediment type, the variety of microhabitats and the availability and quality of food.

## 1. Introduction

Malacostracan crustaceans are widespread across a broad range of Arctic habitats from intertidal (Węsławski et al., 1993) and sea ice (Macnaughton et al., 2007) to deep ocean basins (Brandt, 1997). They can locally dominate the benthic (Conlan et al., 2013; Grebmeier et al., 1989) and plankton (Hirche et al., 2015; Huenerlage et al., 2015) biomass. The total number of bottom-dwelling malacostracan species noted in the Arctic Ocean surpasses 800, while about 50 planktonic forms are known (Sirenko, 2001). They contain both mobile and sessile forms, exhibit a variety of life strategies and hold crucial positions within food-webs, acting as conduits of nutrients and energy to higher trophic levels such as fish, birds and mammals (e.g. Highsmith and Coyle, 1990). The wide functional diversity exhibited by polar crustaceans results from the large species pool, but also from the considerable potential of ontogenetic niche shifts due to the relatively long life cycles and distinct size differences between juveniles and adults (Węsławski et al., 2010). Functional roles within populations are dynamic since different age or sex cohorts may vary considerably in terms of motility, microhabitat choice and food preferences (Carey and Boudrias, 1987; Hopkins et al., 1993; Legeżyńska, 2008; Sainte-Marie, 1986).

Svalbard crustaceans have been studied extensively over the last 150 years and are known to have the greatest species diversity of all the macrozoobenthic taxa (Palerud et al., 2004). Planktonic malacostracans being relatively large and mobile, are not target organisms of standard zooplankton sampling nets (WP-2, mesh 180-$\mu$m), therefore they are rarely included in routine plankton surveys. Sampling with specialized equipment (e.g. Tucker trawl or Isaacs-Kidd net with mesh size >1 mm) has shown that euphausiids (*Thysanoessa inermis*, *Thysanoessa raschii* and *Thysanoessa longicaudata*) and amphipods (*Themisto libellula* and *Themisto abyssorum*) are prominent members of the zooplankton communities in Svalbard fjords (Buchholz et al., 2010; Dalpadado et al., 2016; Hirche et al., 2015; Hop et al., 2002). Identification of the epifaunal components of Svalbard benthic communities is still not comprehensive, but investigations using dredges, baited traps and materials collected by SCUBA divers have recorded dense populations of malacostracan crustaceans, especially in the littoral (Nygård et al., 2010; Węsławski et al., 1993) and shallow sublittoral (Berge et al., 2009; Kaczmarek et al., 2005; Laudien et al., 2007; Legeżyńska, 2001; Nygård, 2011; Voronkov et al., 2013). Estimating their density, however, is complicated because of their motility and also the difficulty of taking quantitative samples on the heterogeneous substrates overgrown with macroalgae often found in shallow waters. Grabs operated from on board ship are suitable for catching infauna and small epifauna on soft sediments below 30 m but are much less efficient in the case of large, mobile and rare epifaunal species. Typically, therefore, crustaceans are poorly represented in grab samples and have been overlooked in the majority of subtidal benthic studies from Spitsbergen (e.g. Włodarska-Kowalczuk and Pearson, 2004; Włodarska-Kowalczuk et al., 2012; Włodarska-Kowalczuk and Węsławski, 2008).

Understanding ongoing processes in the Arctic ecosystem requires a better knowledge of the specific life-histories and functional traits of the available species pool (Cochrane et al., 2012; Węsławski et al., 2011). Here we summarize knowledge of planktonic and benthic Malacostraca based on samples collected during 12 summer expeditions organized from 1997 to 2013 by the Institute of Oceanology PAN to two Spitsbergen fjords: Kongsfjorden and Hornsund. The fjords have been frequently used as model oceans (Buchholz et al., 2010), because they have the same physical and biological processes as the adjacent seas, but are ecosystems of manageable size. The two fjords compared are eminently suitable for observations on the possible effects of climate change on the functioning of the Arctic ecosystem. Because of the sea currents on the Spitsbergen shelf they are differently exposed to present-day warming and can be regarded as representing two phases in the course of global warming: a cold one (Hornsund) and a warm one (Kongsfjorden). Furthermore, both fjords have secluded inner glacial bays, which are strongly influenced by the surrounding glaciers. One of the key effects of glacier activity is the considerable accumulation of fine-grained sediments, which is causing bottom habitat heterogeneity in the glacial bays to decline. It has been predicted, however, that glacier retreat in the coming decades will cause the homogenization of the seafloor over large areas of the coastal Arctic and will pose a major threat to species richness, diversity and the trophic structure of bottom communities in the Arctic (Węsławski et al., 2011). Therefore, surveys in the glacial bays may help to assess the changes that, in the future, are likely to take place across seafloor biota on a larger scale.

Our main aims were to update the checklist of malacostracan taxa from Hornsund and Kongsfjorden, and to explore and compare the distribution, abundance and diversity patterns of species in both fjords and their glacial bays and outer basins. We also examined the functional roles and size structure within the crustacean community. Our results provide baseline information for further monitoring research on climate-change-induced effects on the crustacean fauna of the European Arctic.

## 2. Study area

Hornsund and Kongsfjorden are similarly-sized glacial fjords situated on the west coast of Spitsbergen (Svalbard archipelago; Fig. 1). Both fjords are open to the Greenland Sea

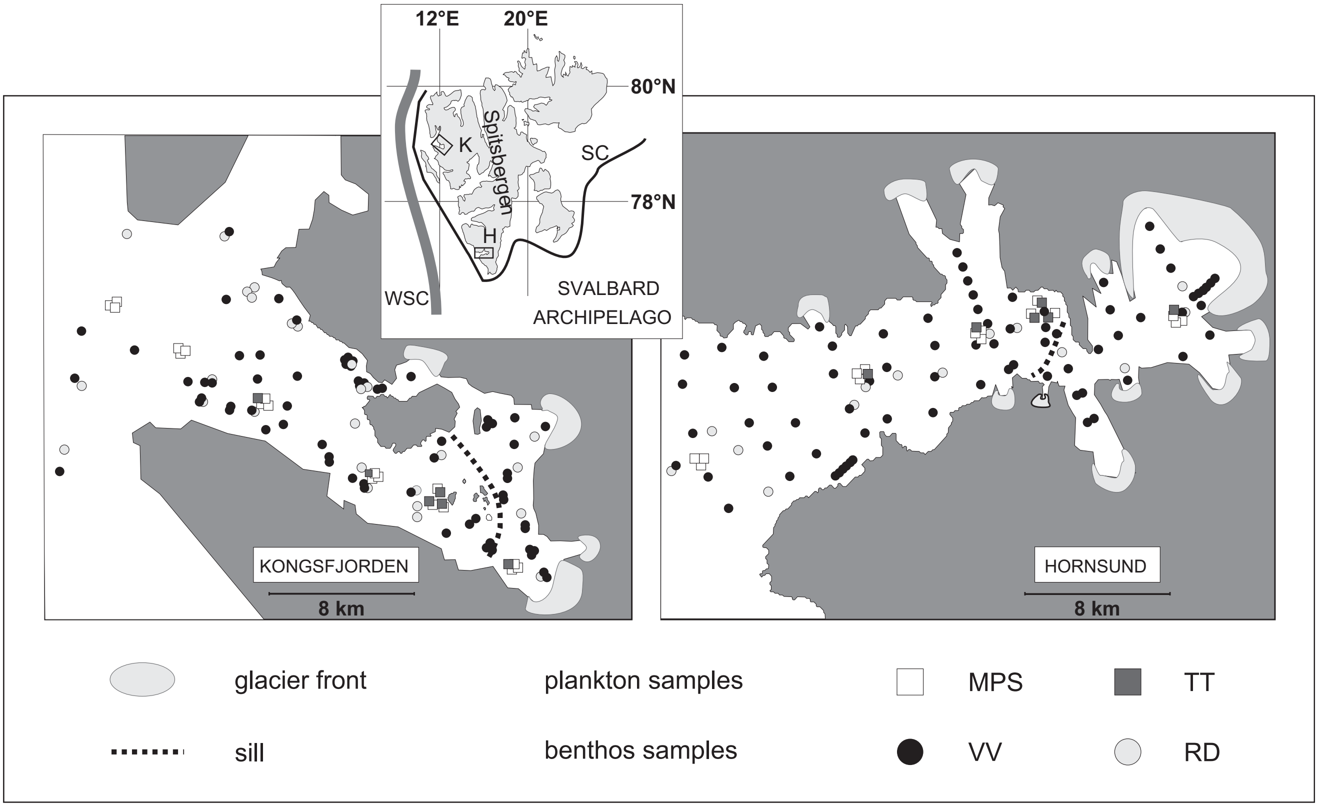

**Figure 1** Sampling stations in Kongsfjorden (K) and Hornsund (H); WSC — West Spitsbergen Current; SC — Sørkapp Current; gear used: MPS — multinet; TT — Tucker trawl; VV — van Veen grab; RD — rectangular dredge.

(no entrance sills), but contain well-marked and partially isolated shallower inner basins. The water mass composition in the fjords results from the balance between the Atlantic and Arctic waters flowing along the shelf of west Spitsbergen (West Spitsbergen Current, WSC; $T > 3.0°C$ and Sørkapp Current, SC; $-1.5°C < T < 1.0°C$, respectively) and varies seasonally and year-on-year (Cottier et al., 2005; Svendsen et al., 2002). The bottom topography of northernmost Kongsfjorden (79°N) favours the inflow of Atlantic waters, so this fjord has a more Atlantic-like character than Hornsund (77°N) (Walczowski, 2013). The Hornsund mouth area is shallower, and the strong polar front between the WSC stream and the Sørkapp Current reduces the influence of warm Atlantic waters in that fjord (Walczowski, 2013). The numerous glaciers terminating in the fjords have a great impact on their hydrography. In Kongsfjorden the main disturbance is due to the front formed by the three glaciers situated at the head of the fjord (Kongsvegen, Kronebreen and Kongsbreen); a fourth glacier on the northern coast is less active. In Hornsund the shoreline of the innermost bay (Brepollen) is formed almost entirely by the cliffs of five tidal glaciers; another eight glaciers terminate in the lateral bays on either side of the fjord. The glacial inflows peak in summer, creating steep gradients in turbidity, salinity and mineral sedimentation along the fjords' axes (Svendsen et al., 2002; Włodarska-Kowalczuk et al., 2005; Włodarska-Kowalczuk and Węsławski, 2008). The high concentrations of suspended mineral particles severely limit the depth of the euphotic zone, thereby reducing primary production in the innermost parts of the fjords (Piwosz et al., 2009; Svendsen et al., 2002). With increasing distance from the active glaciers the magnitude of the glacial effects diminishes: concentrations of suspended mineral particles and accumulation rates decline, while sediment stability, the extent of the euphotic zone and primary production all display considerable increases (Piwosz et al., 2009; Svendsen et al., 2002; Włodarska-Kowalczuk and Pearson, 2004; Zajaczkowski, 2008). Subtidal sediments throughout the fjords are dominated by glacio-marine deposits, which are mostly silt and clay (Włodarska-Kowalczuk et al., 2005; Włodarska-Kowalczuk and Węsławski, 2008), but the shallow bottom boasts a diversity of substrata (Kaczmarek et al., 2005; Tatarek et al., 2012; Włodarska-Kowalczuk, 2007; Włodarska-Kowalczuk et al., 2009). The organic carbon concentration in Kongsfjorden sediments decreases significantly with distance up the fjord (Kędra et al., 2010; Włodarska-Kowalczuk and Pearson, 2004), but in Hornsund a clear pattern of change in organic carbon concentration along the fjord axis has not emerged (Drewnik et al., 2016). The environmental characteristics of both fjords are summarized in Table 1.

## 3. Material and methods

The material was collected during 12 summer expeditions of r/v *Oceania* to the Spitsbergen fjords (1997—2013). Zooplankton was sampled with two different types of sampling gear: a multi plankton sampler (MPS, Hydro-Bios) consisting of five closing nets with a 0.25 $m^2$ square opening and a

**Table 1** Characteristics of the environmental conditions in Kongsfjorden and Hornsund.

| | Kongsfjorden | | Hornsund | |
|---|---|---|---|---|
| Location | 78°58′–79°03′N<br>11°23′–11°36′E | | 76°54′–76°59′N<br>15°14′–15°23′E | |
| Length [km] | 26 | | 27 | |
| Width [km] | 10 | | 12 | |
| Surface [km$^2$] | 231 | | 275 | |
| Volume [km$^3$] | 29.4 | | 23 | |
| | **Kongsfjorden** | | **Hornsund** | |
| | Inner basin | Outer basin | Inner basin | Outer basin |
| Max depths [m] | 100 | 394 | 180 | 260 |
| Summer bottom temperature [°C] | −1.3 to 0.5 | −0.5 to 3.5 | −1.6 to 0.5 | −0.8 to 3.5 |
| Summer bottom salinity | 34.10–34.50 | 34.1–34.90 | 34.30–34.55 | 34.10–34.85 |
| Sediment accumulation rate [cm y$^{-1}$] | Up to 10[3]<br>6–9[4] | 0.4[2] | 0.7[1] | 0.5[1]<br>0.22[2] |
| Summer primary production [mgC m$^{-2}$ h$^{-1}$] | 2.47[5] | 4.48[5] | <14.00[5] | 86.65[5] |
| Organic carbon content [%] | 0.1–1.2[9]<br>0.2–1.8[10]<br>0.28[11] | 1–3.4[9]<br>0.5–2.9[10]<br>1.25[11]<br>1.38[8] | 0.8–1.8[6]<br>2[7] | 0.8–1.8[6]<br>1.4[7]<br>1.65[8] |

References in superscripts: 1, Szczuciński et al. (2006); 2, Zaborska et al. (2016); 3, Elverhøi et al. (1983); 4, Trusel et al. (2011); 5, Piwosz et al. (2009); 6, Drewnik et al. (2016); 7, Koziorowska et al. (2016); 8, Winkelmann and Knies (2005); 9, Zaborska et al. (2006); 10, Kędra et al. (2010); 11, Kuliński et al. (2014).

180 $\mu$m mesh size to collect mesozooplankton, and a Tucker trawl (TT) net (1 m$^2$ opening area) equipped with a 1 mm mesh net to catch macrozooplankton. Both types of nets were hauled vertically from the bottom to the surface. The samples were preserved with 4% formaldehyde solution in seawater buffered with borax. In the laboratory they were analyzed qualitatively and quantitatively, following the standard procedure described in Postel et al. (2000). All zooplankton abundances are given as water column averages expressed by the number of individuals per 100 m$^3$. The material consisted of 34 samples collected at 15 stations (Fig. 1, Table 2).

Benthic samples were taken with a van Veen grab (VV, catching area: 0.1 m$^2$) and a rectangular dredge (RD, opening: 0.8 m × 0.3 m, 1 mm net mesh size, hauled at a speed of 1.5—1.8 kn for 15 min). A total of 323 samples were collected at 202 stations (Fig. 1, Table 2). On board ship, the samples were rinsed carefully with seawater through a 500 $\mu$m mesh screen and preserved in 4% formaldehyde solution. In the laboratory the animals were sorted, identified under a stereoscopic microscope to the lowest possible taxonomic level and counted. Benthic densities are stated as the number of individuals per 0.1 m$^2$ (VV samples) or the number of specimens per sample (RD samples).

The specific names and taxonomic classification follow the World Register of Marine Species (http://www.marinespecies.org/index.php). In some cases, correct identification to species level was not possible. This applied particularly to tiny cumaceans and tanaids: only some of the specimens belonging to the genus *Leucon* and the order Tanaidacea were identified to species level, so we combined them as *Leucon* spp. and Tanaidacea indet. in the subsequent analyses. Nevertheless, it is worth noting that *Leucon* spp. contained at least four species: *Leucon (Leucon) nasica*, *L(L). fulvus*, *L(L). nasicoides* and *L(L). nathorstii* (our own data), whereas tanaids were represented by at least three species, identified by Prof. M. Błażewicz-Paszkowycz (University of Łódź) as *Typhlotanais mixtus*, *Pseudotanais (Pseudotanais) forcipatus* and *Akanthophoreus gracilis* (Błażewicz-Paszkowycz and Sekulska-Nalewajko, 2004; our own data).

To compare the benthic species richness between the fjords, the species accumulation curves for the number of observed species ($S_{obs}$) and *Chao2* estimator were computed with 95% confidence intervals (Chao, 2004; Colwell, 2013) and plotted as a function of the sampling effort (pooled for VV and RD samples, presence/absence data). *Chao2* is a non-parametric estimator that is calculated on the basis of presence/absence data. Taking into account rare species and the total number of species observed in the sample ($Chao2 = S_{obs} + Q_1^2/2Q_2$, where $Q_1$ is the number of species recorded in just one sample and $Q_2$ is the number of species that occurred in exactly two samples), it is used to predict species richness under the assumption that not every species present has been captured.

All benthic taxa were assigned to a size class and functional traits (containing information on their motility, food sources and feeding modes) according to published records (e.g. Błażewicz-Paszkowycz et al., 2012; Enequist, 1949; Hessler and Stromberg, 1989; Legeżyńska et al., 2012; Macdonald et al., 2010; Sainte-Marie and Brunel, 1985). Seven size classes were distinguished on the basis of published information on the maximum size of species: 1 — 0—5 mm, 2 — 6—10 mm, 3 — 11—15 mm, 4 — 16—20 mm, 5 — 21—25 mm, 6 — 26—30 mm and 7 — >30 mm. The guilds considered were combinations of two mobility types (discretely motile — the species can move, but movement is not necessary for feeding; motile — the species moves actively, especially while feeding), two food sources (surface, subsurface pool) and four feeding modes (suspension feeder, deposit feeder, microalgae grazer and carnivore) (Cochrane et al.,

**Table 2** Sampling effort.

| | Years | $N/N_M$ | Depth [m] |
|---|---|---|---|
| **Kongsfjorden** | | | |
| Plankton MPS | 2007, 2012, 2013 | 16/16 | 0—320 |
| Plankton TT | 2013 | 6/6 | 0—350 |
| Benthos VV | 1997, 1998, 2006, 2011 | 136/125 | 27—380 |
| Benthos RD | 1997, 1999, 2000, 2011 | 27/27 | 35—350 |
| **Hornsund** | | | |
| Plankton MPS | 2007, 2012, 2013 | 15/15 | 0—170 |
| Plankton TT | 2013 | 6/6 | 0—220 |
| Benthos VV | 2002, 2003, 2005, 2007, 2011 | 145/122 | 50—244 |
| Benthos RD | 2003, 2005, 2011 | 15/13 | 79—203 |

$N$, number of samples taken; $N_M$, number of samples containing Malacostraca; MPS, multinet; TT, Tucker trawl; VV, van Veen grab; RD, rectangular dredge.

2012; Macdonald et al., 2010). Taxa were coded on the basis of the prevailing feeding type: species employing two types of feeding were coded with both, and species with more possible feeding types as omnivores.

The dataset was divided a priori according to the sampling gear used (i.e. MPS, TT, VV and RD) and station position (two fjords: Hornsund and Kongsfjorden). The large number of samples collected with VV permitted subdivision of the VV dataset containing samples collected in two zones of the fjords (the inner and outer basins of each fjord). The frequency of occurrence and dominance were calculated for each taxon. The number of rare species (i.e. unique taxa occurring in just one sample and singletons — taxa represented by just one specimen) was assessed in each dataset. All statistical analyses were performed with the PRIMER v. 6 software package and PERMANOVA (Anderson et al., 2008; Clarke and Gorley, 2006). Calculations of the pseudo-$F$ and $p$ values were based on 999 permutations of the residuals under a reduced model. The significance level for all the statistical tests was $p = 0.05$.

The univariate descriptors — the number of individuals ($N$), number of species ($S$), Shannon—Wiener $\log_e$-based index ($H$) and Hurlbert index [ES(50)] — were assessed in each sample and the differences were analyzed using two-way (VV dataset) or one-way (MPS, TT and RD datasets) PERMANOVA on a Euclidean similarity matrix. Taxonomic distinctness indices (avTD — average taxonomic distinctness and varTD — variation in taxonomic distinctness) were also compared in the case of the quantitative benthic samples (VV). The average taxonomic distinctness describes the average taxonomic distance (the "path length" between two species following Linnean taxonomy) of all the species in the association. Variation in taxonomic distinctness is defined as the variance of the taxonomic distances between all pairs of species in the association. Five taxonomic levels were used in calculations: species, genus, family, suborder, order and superorder, and equal step levels between successive taxonomic levels were assumed (Clarke and Gorley, 2006). The multivariate differences in taxonomic composition, size structure and functional traits (percentages of individuals representing a certain species, size class or functional guild in the total number of specimens in each sample) were tested using one-way (RD dataset) or two-way (VV dataset) PREMANOVA on a Bray—Curtis similarity matrix based on square-root-transformed data. Constrained analysis of principal coordinates (CAP) was used to visualize the differences in the taxonomic composition of malacostracan assemblages between the two fjords (MPS, TT, RD datasets) or among the four basins distinguished (inner Kongsfjorden, outer Kongsfjorden, inner Hornsund, outer Hornsund, VV sets). Spearman's rank correlation vectors of taxonomic composition with two canonical axes were overlain on the CAP plots. SIMPER analysis was applied to identify the species that were the most important in creating the observed patterns.

## 4. Results

### 4.1. Plankton

Members of 5 malacostracan orders were recorded in the plankton samples (Fig. 2). Isopoda represented only by parasitic forms (numerous in MPS samples) were excluded from the subsequent analyses. Nineteen taxa were identified to species/genus level and five to a higher taxonomic level. Data on dominance and frequency for each taxon are listed in Table 3. The material included larvae of six Decapoda species and three juvenile stages of Euphausiacea, of which the furcilla was by far the most abundant and frequent (Table 3). The composition of the taxa varied significantly in both plankton datasets (MPS and TT) between the fjords (one-way PERMANOVA, MPS: pseudo-$F$ 3.40, $p = 0.001$; TT pseudo-$F$ 2.39, $p < 0.05$) (Fig. 3). The Kongsfjorden planktonic fauna was dominated by the amphipod *T. abyssorum* (MPS: 63.1% and TT: 67.9% of total abundance) and Euphausiacea larvae (20.3% and 15.3%, respectively). In Hornsund Euphausiacea larvae (MPS: 48.8%; TT: 29.4%) and *Pagurus pubescens* larvae (25.2% and 27.4%, respectively) were the most numerous. *Themisto libellula* was frequently noted (in 73—100% of all samples depending on the gear and the fjord), but generally, it did not contribute much to the total abundance, making up only 3—8% of a total number of specimens. Other commonly recorded but less abundant species included *T. inermis*, *T. abyssorum* and *Hyas araneus* larvae in Hornsund and *T. inermis* and *T. raschii* in Kongsfjorden (Table 3, Fig. 3). MPS samples from Kongsfjorden and Hornsund did not differ significantly with respect to the average number of species per sample (Kongsfjorden: 5.4 ± 2.2, Hornsund: 6.0 ± 2.4) or

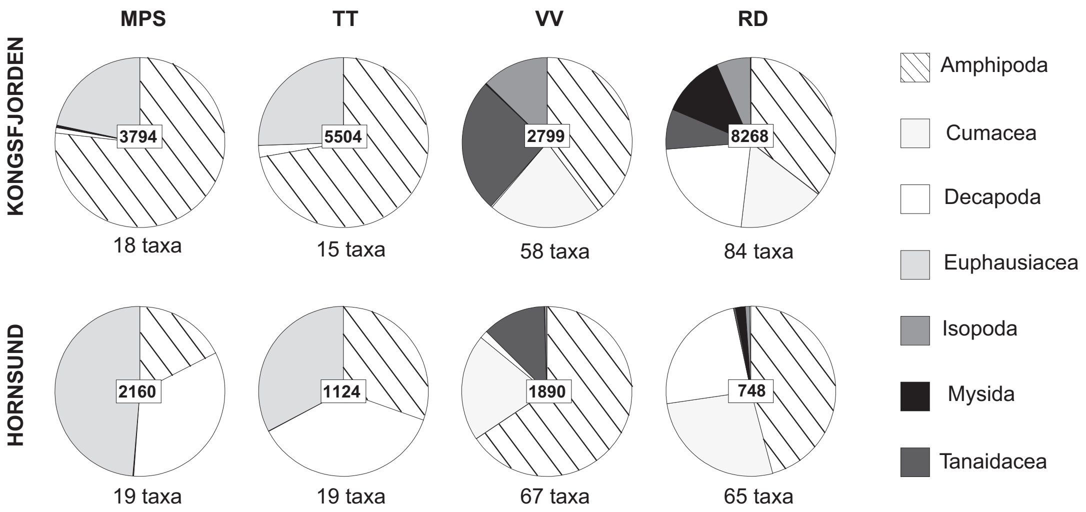

**Figure 2** Percentages of malacostracan taxa in the total number of animals collected with four types of sampling gear in Kongsfjorden and Hornsund: MPS — multinet, TT — Tucker trawl, VV — van Veen grab, and RD — rectangular dredge. The numbers of taxa collected in each fjord and with each type of sampling gear are given below the pie charts, while the total numbers of malacostracans collected are shown in the centre of the charts.

the number of individuals per sample (237.1 ± 222.7 and 144.1 ± 100.3, respectively). Mean values of the Shannon—Wiener index and Hurlbert index were significantly higher in Hornsund (1.2 ± 0.4 and 5.2 ± 1.7, respectively) than in Kongsfjorden (0.8 ± 0.4 and 3.9 ± 1.4, respectively) (one-way PERMANOVA, pseudo-*F* 5.5, $p < 0.05$). TT samples did not differ between the fjords with respect to species richness (Kongsfjorden: 9.2 ± 0.8, Hornsund: 10 ± 2.9) or Hurlbert indices (7.4 ± 1.7 and 5.4 ± 1.6, respectively). Higher numbers of individuals per sample were noted in Kongsfjorden than in Hornsund (879.2 ± 662.1 and 174 ± 64, respectively) (one-way PERMANOVA, pseudo-*F* 2.6, $p < 0.05$), while values

**Table 3** Planktonic Malacostraca of Kongsfjorden and Hornsund.

| | Kongsfjorden MPS | | | Hornsund MPS | | | Kongsfjorden TT | | Hornsund TT | |
|---|---|---|---|---|---|---|---|---|---|---|
| | avN | min—max | *F* | avN | min—max | *F* | avN | *F* | avN | *F* |
| Amphipoda indet. | **4.4** | 0—21 | 38 | **7.1** | 0—97 | 20 | **0.3** | 33 | **0.2** | 17 |
| *Boreomysis arctica* | **0.8** | 0—12 | 13 | | | | **0.2** | 17 | | |
| *Caridion* sp. zoea | | | | | | | | | **0.2** | 17 |
| Decapoda larva indet. | **0.3** | 0—3 | 19 | **0.2** | 0—3 | 7 | | | **4.0** | 83 |
| *Eualus gaimardi* zoea | | | | | | | **0.5** | 17 | **0.2** | 17 |
| Euphausiacea calyptopsis | | | | **2.8** | 0—38 | 13 | | | | |
| Euphausiacea furcilla | **43.3** | 0—336 | 75 | **48.7** | 0—184 | 80 | **134.2** | 100 | **51.2** | 100 |
| Euphausiacea nauplii | **4.9** | 0—40 | 13 | **18.7** | 0—193 | 20 | | | | |
| *Hyas araneus* megalopa | | | | **0.4** | 0—3 | 20 | | | | |
| *Hyas araneus* zoea | | | | **5.4** | 0—25 | 60 | | | **8.5** | 83 |
| *Hyperia galba* | | | | **0.3** | 0—5 | 7 | | | **0.2** | 17 |
| *Hyperoche medusarum* | **17.1** | 0—232 | 13 | **1.2** | 0—18 | 7 | | | **0.5** | 33 |
| *Meganyctiphanes norvegica* | **0.4** | 0—7 | 6 | **0.1** | 0—2 | 7 | **6.8** | 50 | | |
| *Mysis oculata* | **0.1** | 0—2 | 6 | **0.2** | 0—3 | 7 | | | | |
| *Pagurus pubescens* megalopa | **1.3** | 0—14 | 19 | **0.3** | 0—4 | 7 | **6.5** | 83 | **0.8** | 33 |
| *Pagurus pubescens* zoea | **0.2** | 0—1 | 19 | **36.0** | 0—104 | 93 | **6.0** | 67 | **46.8** | 83 |
| *Pandalus borealis* zoea | **0.6** | 0—6 | 25 | **0.5** | 0—3 | 27 | **8.0** | 100 | **1.7** | 67 |
| *Pseudomma truncatum* | **0.2** | 0—1 | 19 | **0.0** | 0—0 | 0 | **0.3** | 33 | **0.3** | 33 |
| *Sabinea septemcarinata* zoea | **0.1** | 0—1 | 6 | **2.4** | 0—15 | 40 | **0.2** | 17 | **2.3** | 67 |
| *Thysanoessa longicaudata* | **0.5** | 0—5 | 19 | | | | **3.7** | 100 | **1.2** | 67 |
| *Thysanoessa raschii* | **0.4** | 0—2 | 31 | **0.3** | 0—4 | 7 | **22.8** | 100 | **0.3** | 33 |
| *Themisto abyssorum* | **149.6** | 51—447 | 100 | **10.9** | 0—70 | 60 | **596.8** | 83 | **32.7** | 100 |
| *Themisto libellula* | **11.1** | 0—59 | 81 | **5.9** | 0—23 | 73 | **23.5** | 100 | **14.0** | 100 |
| *Thysanoessa inermis* | **1.8** | 0—17 | 44 | **2.5** | 0—13 | 47 | **69.5** | 100 | **9.0** | 83 |

MPS, multinet samples; TT, Tucker trawl samples; avN, average number of ind. 100 $m^{-3}$; min, minimum abundance; max, maximum abundance; *F*, frequency of occurrence.

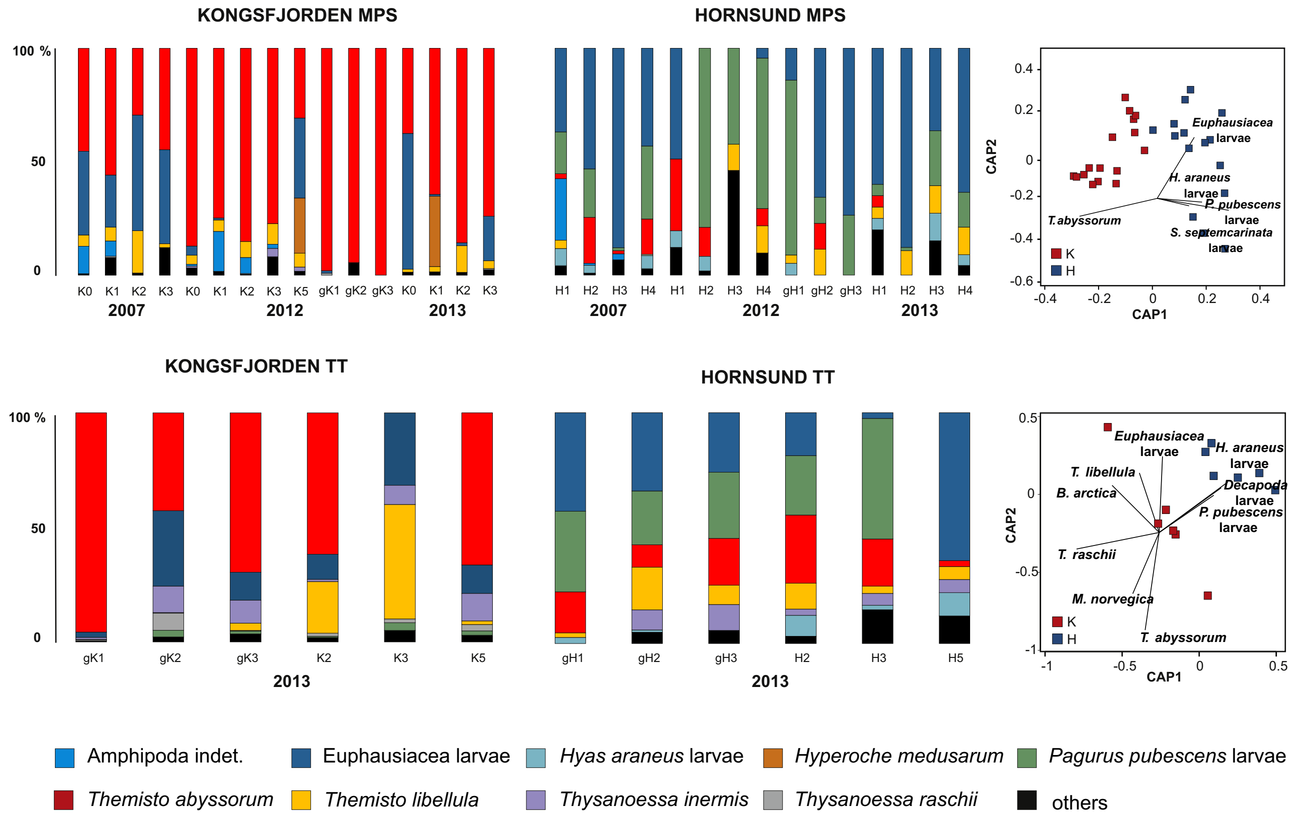

**Figure 3** Species composition in pelagic samples collected with MPS — multinet and TT — Tucker trawl in Kongsfjorden and Hornsund. Results of CAP analysis based on Bray—Curtis similarity of species composition in pelagic samples. Taxa with Spearman rank correlations with CAP axes >0.6 are shown. Full species names can be found in Table 4.

of the Shannon—Wiener index were higher in Hornsund than in Kongsfjorden (1.0 ± 0.4 and 1.5 ± 0.2, respectively) (one-way PERMANOVA, pseudo-$F$ 2.7, $p < 0.01$).

## 4.2. Benthos

Benthic sampling in Kongsfjorden and Hornsund yielded 13 706 specimens belonging to seven orders of Malacostraca (Fig. 2). Typical planktonic elements such as hyperiids, euphausiids, mysids and Decapoda larvae were not included in the analysis of the VV material. A total of 116 benthic taxa were identified in both fjords (Table 4). Species-accumulation curves failed to approach asymptotes for the observed number of species ($S_{\mathrm{obs}}$), but tended to stabilize in the case of the *Chao2* estimators (Fig. 4). The total numbers of species recorded were lower than the estimated ones, but 0.95 CI values overlapped slightly with 0.95 CI of the *Chao2* estimator. After analysing approximately 160 samples from each

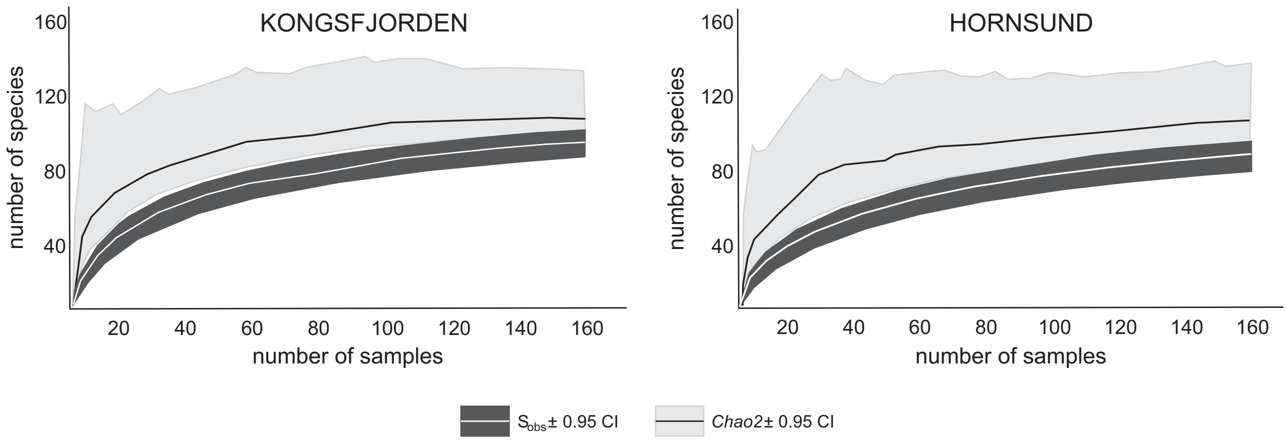

**Figure 4** Species accumulation curves plotted for the number of species observed ($S_{\mathrm{obs}}$) and the true number of species estimated with *Chao2* based on VV and RD presence/absence data sets. $S_{\mathrm{obs}}$ and *Chao2* are plotted with 0.95 confidence intervals.

**Table 4** List of Malacostraca species recorded in Kongsfjorden and Hornsund.

| Taxon | | Order | Group | Distribution | | | | | | | | | | Habitat of occurrence | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Large scale distribution | | | | Kongsfjorden and Hornsund records | | | | | | Depth [m] | | | | | Bottom type | | | Fjord basins | |
| | | | | I | II | III | IV | K_L | K_C | K_T | H_L | H_C | H_T | <50 | 50—100 | 100—200 | 200—300 | >300 | Soft | Hard | Algae | In | Out |
| *Acanthonotozoma inflatum* | (Krøyer, 1842) | A | B | | | x | x | | x | x | | x | x | | 11 | 11 | 11 | | | | | | 11 |
| *Acanthonotozoma serratum* | (Fabricius, 1780) | A | B | x | x | x | x | | x | x | | x | x | | | 11 | 11 | 11 | | | | | 11 |
| *Acanthostepheia malmgreni* | (Goës, 1866) | A | B | | x | x | x | | | | 1, 2 | x | x | 1, 7 | 1, 11 | | | | 1, 11 | | | 1, 11 | |
| *Aceroides (Aceroides) latipes* | (Sars, 1883) | A | B | x | x | x | x | | | | | x | x | 7 | 11 | 11 | | | | | | | 11 |
| *Aeginina longicornis* | (Krøyer, 1843) | A | B | x | x | x | x | | | | 2 | | x | | | | | | | | | | |
| *Ampelisca eschrichtii* | Krøyer, 1842 | A | B | x | x | x | x | 2 | x | x | 1, 2 | x | x | | 1, 11 | 1, 11 | 11 | 11 | 1, 11 | | | | 1, 11 |
| Amphilochidae indet. | Boeck, 1871 | A | B | | | | | | | | | x | x | | | 11 | | | 11 | | | | 11 |
| *Andaniexis lupus* | Berge & Vader, 1997 | A | B | x | | x | x | 2 | | x | | | | | | | | | | | | | |
| *Anonyx laticoxae* | Gurjanova, 1962 | A | B | | | x | x | 6 | | x | 1, 3 | | x | 3, 6 | 1 | | | | 1, 6 | | | | 6 |
| *Anonyx nugax* | (Phipps, 1774) | A | B | x | x | x | x | 7, 8, 6 | x | x | 1, 2, 3 | x | x | 1, 3, 7, 8, 6 | 1, 3, 11 | | 11 | | 1, 3, 7, 8, 6, 11 | | 1, 7 | 1, 3, 11 | 1, 3, 7, 8, 6, 11 |
| *Anonyx sarsi* | Steele & Brunel, 1968 | A | B | x | | x | x | 7, 6 | x | x | 1, 2, 3 | | x | 1, 3, 7, 6, 9 | 3, 11 | | | | 1, 3, 7, 6 | | 1, 3, 7, 6 | 7, 6, 9 | 3, 7, 6, 9, 11 |
| *Apherusa bispinosa* | (Bate, 1857) | A | B | x | x | x | | | | | | x | x | | | | 11 | | | | | | 11 |
| *Apherusa corbeli* | Lagardère, 1968 | A | B | | | | x | 9 | | x | | | | 9 | | | | | | 9 | | 9 | 9 |
| *Apherusa glacialis* | (Hansen, 1888) | A | C | | x | x | x | 7, 9, 11 | | x | 1, 2 | x | x | 1, 9 | | 11 | | | 11 | 9 | | 11 | 11 |
| *Apherusa jurinei* | Milne Edwards, 1830 | A | B | x | | x | | 5, 9 | | x | | | | 5 | | | | | | | 5 | | 5 |
| *Apherusa megalops* | (Buchholz, 1874) | A | B | | | x | | | x | x | | | | 11 | | | | | | | | | 11 |
| *Apherusa sarsi* | Shoemaker, 1930 | A | B | x | | x | x | 7, 9 | x | x | 1, 2 | | x | 1, 7, 9 | 11 | | | | | 1, 7, 9 | 1 | | 1, 9, 11 |
| *Apherusa* sp. | Walker, 1891 | A | B | | | | | | | | | x | x | | | | | | | | | | |
| *Aristias tumidus* | (Krøyer, 1846) | A | B | x | x | x | x | | | | 2 | | x | | | | | | | | | | |
| *Arrhinopsis longicornis* | Stappers, 1911 | A | B | | | x | x | | x | x | | | | 7 | | 11 | | | 11 | | | | 11 |
| *Arrhis phyllonyx* | (Sars, 1858) | A | B | x | x | x | x | 7, 2 | x | x | 1, 2 | x | x | 1, 7, 11 | 11 | 11 | 11 | 11 | 1, 7, 11 | | | 1, 11 | 1, 11 |
| *Atylus carinatus* | (Fabricius, 1793) | A | B | x | | x | | 9 | | x | 1, 2 | | x | 1, 9 | | | | | 1 | 9 | 1 | | 1, 9 |
| *Bathymedon obtusifrons* | (Hansen, 1883) | A | B | x | x | x | x | 9 | x | x | | x | x | 9 | | 11 | | | 11 | 9 | | | 9, 11 |
| *Byblis gaimardii* | (Kröyer, 1846) | A | B | x | x | x | x | 2 | | x | 1, 2 | x | x | 1 | 11 | 11 | | | 1, 11 | | | | 1, 11 |
| *Calliopius laeviusculus* | (Krøyer, 1838) | A | B | x | | x | x | 9, 2 | | x | 1, 2, 3 | | x | 1, 9 | | | | | | 9 | 1 | | 1, 9 |
| *Caprella septentrionalis* | Krøyer, 1838 | A | B | x | | x | x | 7, 5, 9 | x | x | 1, 2, 3 | | x | 1, 7, 5, 9, 11 | | | | | 7, 9 | 7, 9 | 1, 7, 5, 9 | 9 | 1, 5, 9, 11 |
| *Centromedon productus* | (Goës, 1866) | A | B | | | x | x | | x | x | | | | 11 | | | | | | | | | 11 |
| *Centromedon pumilus* | (Lilljeborg, 1865) | A | B | x | | x | x | 2 | | x | | | | | | | | | | | | | |
| *Crassicorophium crassicorne* | (Bruzelius, 1859) | A | B | x | | x | x | 7, 8 | | x | 2 | | x | 7, 8 | | | | | 8 | | | | 8 |
| *Deflexilodes norvegicus* | (Boeck, 1860) | A | B | x | | x | x | 9 | | x | | | | 9 | | | | | | 9 | | 9 | 9 |
| *Deflexilodes tesselatus* | (Schneider, 1884) | A | B | x | | x | x | 9, 2 | | x | | | | 9 | | | | | | 9 | | | 9 |
| *Deflexilodes tuberculatus* | (Boeck, 1871) | A | B | x | | x | x | 9 | | x | | | | 9 | | | | | | | 9 | 9 | 9 |
| *Gammarellus homari* | (Fabricius, 1779) | A | B | x | | x | x | 7, 5, 9 | | x | 1, 2, 3 | | x | 1, 3, 7, 5, 9 | | | | | | | 1, 7, 5, 9 | 9 | 1, 7, 5, 9 |
| *Gammaropsis melanops* | G.O. Sars, 1883 | A | B | x | | x | | | | | | x | x | | | * | | | 11 | | | | 11 |
| *Gammarus oceanicus* | Segerstråle, 1947 | A | B | x | | x | x | 9 | | x | 1, 2, 3 | x | x | 1, 3, 7, 9 | | | | | 1 | 1, 9 | 1 | | 1, 9, 11 |
| *Gammarus setosus* | Dementieva, 1931 | A | B | x | | x | x | 7, 6, 9 | | x | 1, 2, 3 | | x | 1, 3, 7, 6, 9 | | | | | 1, 9 | 1, 9 | 1 | 1, 6, 9 | 1, 6, 9 |
| *Gammarus wilkitzkii* | Birula, 1897 | A | C | | | x | x | 9 | | x | 1, 2 | x | x | 1, 7, 9 | | | 11 | | | 9 | | 9 | 9, 11 |
| *Gitanopsis arctica* | Sars, 1895 | A | B | x | x | x | x | 9 | | x | | | | 9 | | | | | | 9 | | | 9 |
| *Gitanopsis inermis* | (Sars, 1883) | A | B | x | x | x | x | 5, 9 | | x | | x | x | 5, 9 | 11 | | | | | 9, 11 | 5 | 9 | 5, 9, 11 |
| *Goesia depressa* | (Goës, 1866) | A | B | | | x | x | | x | x | 1, 2 | x | x | 7 | 1, 11 | 1, 11 | | 11 | 1, 11 | | | | 1, 11 |
| *Gronella lobata* | (Chevreux, 1907) | A | B | | | x | x | 2 | | x | | | | | | | | | | | | | |
| *Guernea (Prinassus) nordenskioldi* | (Hansen, 1888) | A | B | | | | | 9 | | x | | | | 9 | | | | | | 9 | | | 9 |
| *Halirages fulvocinctus* | (M. Sars, 1858) | A | B | x | x | x | x | 7, 5, 9, 2 | x | x | 1, 2 | x | x | 1, 7, 5, 9, 11 | 1, 11 | 11 | 11 | 11 | 7, 9 | | 1, 7, 5, 9 | 1, 7, 9 | 1, 7, 5, 9, 11 |
| *Haploops tubicola* | Liljeborg, 1856 | A | B | x | x | x | x | 2 | x | x | 1, 2 | x | x | | 1, 11 | 1, 11 | 11 | 11 | 1, 11 | | | | 1, 11 |

**Table 4** (*Continued*)

| Taxon | | Order | Group | Distribution | | | | | | | | | | Habitat of occurrence | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Large scale distribution | | | | Kongsfjorden and Hornsund records | | | | | | Depth [m] | | | | | Bottom type | | | Fjord basins | |
| | | | | I | II | III | IV | K_L | K_C | K_T | H_L | H_C | H_T | <50 | 50–100 | 100–200 | 200–300 | >300 | Soft | Hard | Algae | In | Out |
| *Harpinia plumosa* | (Krøyer, 1842) | A | B | x | x | x | x | | | | 2 | | x | | | | | | | | | | |
| *Harpinia propinqua* | Sars, 1891 | A | B | x | x | x | x | | | | | | | | | | | | | | | | |
| *Harpinia serrata* | G.O. Sars, 1879 | A | B | x | x | x | x | | | | 1, 2 | | x | | 1 | 1 | | | 1 | | | | 1 |
| *Harpinia* sp. | Boeck, 1876 | A | B | | | | | | x | x | | | | | | | | 11 | | | | | 11 |
| *Hippomedon holbolli* | (Linnaeus, 1758) | A | B | x | x | x | x | 2 | | x | | | | | | | | | | | | | |
| *Hyperia galba* | (Kröyer, 1838) | A | P | | | x | x | | | | | x | x | | | | | | | | | | |
| *Hyperoche medusarum* | (G.O. Sars, 1877) | A | P | | | x | x | | x | x | | x | x | | | | | | | | | | |
| *Idunella aequicornis* | Sars, 1870 | A | B | x | x | x | x | 2, 11 | | x | | | | | 11 | | 11 | 11 | 11 | | | | 11 |
| *Ischyrocerus anguipes* | (Boeck, 1871) | A | B | x | | x | x | 5, 9, 2 | | x | 1, 2, 3 | | x | 1, 7, 5, 9 | | | | | 9 | 9 | 1, 5, 9 | 1, 9 | 1, 5, 9 |
| *Ischyrocerus megacheir* | Sars, 1894 | A | B | x | x | x | x | 9 | | x | | | | 9 | | | | | | 9 | | | 9 |
| *Ischyrocerus megalops* | Krøyer, 1838 | A | B | x | | x | x | 8 | | x | | x | x | 8 | | 11 | | | 8 | | | 11 | 8 |
| *Ischyrocerus* sp. | Leach, 1814 | A | B | | | | | | x | x | | x | x | 7, 9, 11 | 11 | 11 | | | 7, 9 | 7, 9 | 7, 9 | 7, 9, 11 | 7, 9, 11 |
| *Lepidepecreum umbo* | Sars, 1869 | A | B | x | x | x | x | | x | x | 1, 2 | x | x | 11 | 1, 11 | 1, 11 | 1, 11 | | 1, 11 | | | 11 | 11 |
| *Liljeborgia fissicornis* | (Sars, 1858) | A | B | x | x | x | x | | x | x | | | | | | | 11 | 11 | | | | | 11 |
| *Maera danae* | Stimpson, 1853 | A | B | | | | | 9 | | x | | | | 9 | | | | | | 9 | | | 9 |
| *Megamoera dentata* | (Krøyer, 1842) | A | B | x | | x | x | 7, 9 | x | x | 1, 2 | | x | 1, 7, 9, 11 | | 7, 11 | 11 | | 1, 9 | | 7, 9, 11 | 9 | 1, 9, 11 |
| *Melphidippa goesi* | Stebbing, 1899 | A | B | x | x | x | x | | x | x | 1, 2 | x | x | | 11 | | 11 | 11 | | | | | 11 |
| *Melphidippa* sp. | Boeck, 1871 | A | B | | | | | | x | x | | x | x | | | | | | | | | | |
| *Menigrates obtusifrons* | (Boeck, 1861) | A | B | x | | x | x | | x | x | 1, 2 | x | x | 1 | | 11 | | | 11 | 1 | 1 | 11 | 11 |
| *Metopa* spp. | Boeck, 1871 | A | B | | | | | 7 | | x | | x | x | 7 | | 11 | | | | | | | 11 |
| *Metopa boeckii* | Sars, 1892 | A | B | x | x | x | x | | x | x | | x | x | | 11 | 11 | | | | | | 11 | 11 |
| *Metopa bruzelii* | (Goës, 1866) | A | B | x | | x | x | | | | 1, 2 | | x | 1 | 1 | 1 | 1 | 1 | 1 | | 1 | | 1 |
| *Metopa glacialis* | (Krøyer, 1842) | A | B | | | x | x | 9, 2 | | x | 2 | | x | 9 | | | | | | | | | 9 |
| *Metopa pusilla* | Sars, 1892 | A | B | x | | x | x | 9 | | x | | | | 9 | | | | | | 9 | | | 9 |
| *Metopa robusta* | Sars, 1892 | A | B | x | x | x | | | x | x | | | | | | | 11 | | 11 | | | | 11 |
| *Metopa sinuata* | Sars, 1892 | A | B | x | | x | x | 9 | | x | | | | 9 | | | | | | 9 | | | 9 |
| *Monoculodes latimanus* | (Goës, 1866) | A | B | x | x | x | x | 9, 2 | x | x | | x | x | 9, 11 | 11 | 11 | | | 9 | 9 | | 9 | 9, 11 |
| *Monoculodes packardi* | Boeck, 1871 | A | B | x | x | x | x | 2 | x | x | 1, 2 | x | x | 11 | 1, 11 | 1, 11 | 11 | 11 | 1 | | | 11 | 11 |
| *Monoculodes* sp. | Stimpson, 1853 | A | B | | | | | 8 | x | x | | x | x | 7, 8 | | | | | 8 | | 7 | | 7, 8 |
| *Munna* sp. 1 | Krøyer, 1839 | A | B | | | | | | x | x | | | | | | | 11 | 11 | 11 | | 7 | | 11 |
| *Munna* sp. 2 | Krøyer, 1839 | A | B | | | | | 7 | | x | | | | 7 | | | | | 7 | | 7 | | |
| *Neohela monstrosa* | (Boeck, 1861) | A | B | x | | x | x | | | | 1, 2 | x | x | | 1, 11 | 1, 11 | 11 | | 1 | | | | 1, 11 |
| *Neopleustes pulchellus* | (Krøyer, 1846) | A | B | x | | x | x | | | | 1, 2 | | x | 1 | | | | | 1 | | | | |
| *Odius carinatus* | (Bate, 1862) | A | B | x | | x | x | 9 | | x | 2 | | x | 9 | | | | | | 9 | | | 9 |
| *Onisimus brevicaudatus* | Hansen, 1887 | A | B | | | x | x | | | | 1, 3 | x | x | | 11 | | | | 1 | | | | 11 |
| *Onisimus caricus* | Hansen, 1887 | A | B | | | x | x | 7, 6 | | x | 1, 2, 3 | | x | 1, 3, 7, 6 | 1, 3 | | | | 1, 3, 7, 6 | | | 1, 3, 6 | |
| *Onisimus edwardsi* | Krøyer, 1846 | A | B | x | | x | x | 7, 8, 6, 9 | x | x | 1, 2, 3 | x | x | 3, 7, 8, 6, 9 | 3, 11 | | | | 8, 6, 11 | | 1, 3, 7, 6, 9 | 1, 9, 11 | 1, 3, 7, 8, 6, 9, 11 |
| *Onisimus glacialis* | (Sars, 1900) | A | B | | | x | x | | | | | x | x | | | | * | | | | | | 11 |
| *Onisimus litoralis* | (Krøyer, 1845) | A | B | x | | x | x | 6, 9 | | x | 1, 2, 3 | x | x | 1, 3, 6, 9 | | | | | 1, 3, 6 | 9 | 1, 3 | 1, 3, 9, 11 | 1, 3, 6, 9, 11 |
| *Onisimus plautus* | Krøyer, 1845 | A | B | x | | x | x | 6 | | x | 1, 2 | x | x | 1, 6, 11 | | | | | 6 | | | 6, 11 | |
| *Onisimus* spp. | Boeck, 1871 | A | B | | | | | | x | x | | x | x | | 11 | 11 | 11 | | | | | 11 | 11 |
| *Orchomene serratus* | (Boeck, 1861) | A | B | x | | x | | | x | x | | | | | | | 11 | | | | | | 11 |
| *Orchomenella minuta* | (Krøyer, 1846) | A | B | x | | x | x | 7, 6 | x | x | 1, 2, 3 | x | x | 1, 3, 7, 6, 11 | 3, 11 | 11 | 11 | 11 | 1, 3, 7, 6, 11 | 7 | 3, 7, 6 | 3, 11 | 1, 3, 6, 11 |
| *Parapleustes assimilis* | (Sars, 1882) | A | B | x | x | x | x | 7, 5, 9 | | x | | | | 7, 5, 9 | | | | | | | 7, 9 | 9 | 5, 9 |
| *Parapleustes bicuspis* | (Krøyer, 1838) | A | B | x | | x | x | 7, 5, 9 | | x | 1, 2 | x | x | 1, 7, 5, 9 | 11 | | | | 7, 9, 11 | 1 | 1, 7, 5, 9 | 9 | 1, 5, 9, 11 |
| *Parapleustes gracilis* | (Buchholz, 1874) | A | B | x | | x | x | 9 | | x | | | | 9 | | | | | 9 | 9 | 9 | 9 | |
| *Parapleustes monocuspis* | (Sars, 1893) | A | B | | | x | | 7 | x | x | | | | 7, 1 | | | | | | | 7 | | 11 |
| *Pardalisca cuspidata* | Krøyer, 1842 | A | B | x | x | x | x | | x | x | | | | 11 | 11 | 11 | 11 | | | | | | 11 |
| *Pardalisca tenuipes* | Sars, 1893 | A | B | x | x | x | x | | x | x | | | | | 11 | 11 | | | | | | | 11 |
| *Paroediceros lynceus* | (Sars, 1858) | A | B | x | x | x | x | 7, 8, 6, 9 | x | x | 1, 2, 3 | x | x | 1, 7, 8, 6, 9, 11 | 11 | 11 | 11 | | 1, 7, 8, 9 | 9 | 7 | 7, 9, 11 | 7, 8, 11 |

**Table 4** (*Continued*)

| Taxon | | Order | Group | Distribution | | | | | | | | | | Habitat of occurrence | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Large scale distribution | | | | Kongsfjorden and Hornsund records | | | | | | Depth [m] | | | | | Bottom type | | | Fjord basins | |
| | | | | I | II | III | IV | K_L | K_C | K_T | H_L | H_C | H_T | <50 | 50–100 | 100–200 | 200–300 | >300 | Soft | Hard | Algae | In | Out |
| *Photis reinhardi* | Krøyer, 1842 | A | B | x | | x | x | | | | | x | x | | | 11 | | 11 | | | | | 11 |
| *Phoxocephalus holbolli* | (Krøyer, 1842) | A | B | x | | x | x | | x | x | | x | x | | | 11 | 11 | | 11 | | | | 11 |
| *Pleustes (Pleustes) panoplus* | (Krøyer, 1838) | A | B | x | | x | x | 7, 9, 2 | x | x | 1, 2 | | x | 1, 7, 9, 11 | | | | | 1, 7, 9 | 1 | 1, 7, 9 | 9 | 1, 9, 11 |
| *Pleustomesus medius* | (Goës, 1866) | A | B | | | x | x | | | | 1, 2 | x | x | 1 | 1 | 1, 11 | | | | | 11 | | 1, 11 |
| *Pleusymtes glaber* | (Boeck, 1861) | A | B | x | | x | x | 5, 9 | | x | | | | 5, 9 | | | | | 9 | 9 | | 9 | 5, 9 |
| *Pleusymtes glabroides* | (Dunbar, 1954) | A | B | | | x | x | 7, 9 | | x | 1, 2 | | x | 1, 7, 9 | | | | | | 7, 9 | 1 | | 1, 7 |
| *Pleusymtes pulchella* | (Sars, 1876) | A | B | x | | x | x | 9, 2 | | x | | | | 9 | | | | | | 9 | | | 9 |
| *Pontoporeia femorata* | Krøyer, 1842 | A | B | x | x | x | x | 7 | x | x | 1, 2 | x | x | 1, 7, 11 | 1, 11 | 1, 11 | 1 | | 1, 11 | | | | 1, 11 |
| *Priscillina armata* | (Boeck, 1861) | A | B | | | x | | 8 | | x | | | | 8 | | | | | 8 | | | | 8 |
| *Protomedeia* sp. | Krøyer, 1842 | A | B | | | | | 8 | | x | | x | x | 8 | | 11 | | | | | | | 8, 11 |
| *Protomedeia fasciata* | Krøyer, 1842 | A | B | x | | x | x | 9 | x | x | | x | x | 9 | 11 | | | | | 9 | | | 9, 11 |
| *Protomedeia grandimana* | Brüggen, 1906 | A | B | x | | x | x | | x | x | 1, 2 | | x | 1 | 1, 11 | 1 | | | 1, 11 | | | | 1, 11 |
| *Quasimelita formosa* | (Murdoch, 1885) | A | B | x | | x | x | 7, 2 | x | x | 1, 2 | x | x | 1, 7, 11 | 11 | 1, 11 | | | 1, 7 | | 7 | 11 | 1, 11 |
| *Quasimelita quadrispinosa* | (Vosseler, 1889) | A | B | | x | x | x | | x | x | | x | x | 11 | 11 | 11 | 11 | 11 | 11 | | | | 11 |
| *Rhachotropis aculeata* | (Lepechin, 1780) | A | B | x | x | x | x | 9 | x | x | 1, 2 | x | x | 1, 11 | 11 | 11 | 11 | 11 | | 1 | 1 | | 1, 11 |
| *Rhachotropis helleri* | (Boeck, 1871) | A | B | x | x | x | x | 2 | x | x | | | | | | | 11 | 11 | | | | | 11 |
| *Rhachotropis inflata* | (Sars, 1883) | A | B | x | x | x | x | 7, 9 | x | x | | | | 7, 9, 11 | 11 | 11 | | | | 7, 9 | | | 9, 1 |
| *Rhachotropis macropus* | Sars, 1893 | A | B | x | x | x | x | 2 | x | x | | | | | | | | 11 | | | | | 11 |
| *Rostroculodes borealis* | (Boeck, 1871) | A | B | x | x | x | x | 7 | x | x | 1, 2 | | x | 1, 7, 11 | 11 | 11 | 11 | 11 | 1, 7, 11 | | 1, 9, 7 | 9 | 9, 11 |
| *Rostroculodes longirostris* | (Goës, 1866) | A | B | | x | x | x | 7 | x | x | 1, 2 | x | x | 1, 7 | 11 | 11 | | | 1, 7 | | | | 11 |
| *Rozinante fragilis* | (Goës, 1866) | A | B | | | x | x | 9 | | x | 1 | x | x | 1, 9 | | 11 | | | | 9 | | 9 | 1, 11 |
| *Schisturella pulchra* | (Hansen, 1887) | A | B | x | x | x | x | | x | x | | | | | | | 11 | | 11 | | | | 11 |
| *Socarnes bidenticulatus* | (Bate, 1858) | A | B | x | | x | x | | | | 1, 2 | | x | 1 | 1 | 1 | 1 | | 1 | | | | 1 |
| *Socarnes vahlii* | (Krøyer, 1838) | A | B | x | | x | x | 9 | x | x | | | | 9, 11 | | | | | | | | 9 | 9, 1 |
| *Stegocephalus inflatus* | Krøyer, 1842 | A | B | x | x | x | x | | x | x | 1, 2 | x | x | 1 | 1, 11 | 11 | 11 | 11 | 1, 11 | | | 11 | 11 |
| *Stenopleustes latipes* | (Sars, 1858) | A | B | x | x | x | x | | x | x | | x | x | | 11 | | | | | | | | 11 |
| *Stenothoidae* indet. | Boeck, 1871 | A | B | | | | | | x | x | | x | x | 11 | 11 | 11 | 11 | | | | | | 11 |
| *Syrrhoe crenulata* | Goës, 1866 | A | B | x | x | x | x | 7, 9, 2 | x | x | 1, 2 | x | x | 7, 9, 11 | 1, 11 | 1, 11 | 11 | 11 | 1, 11 | 7, 9, 11 | 7, 9 | | 1, 9, 11 |
| *Themisto abyssorum* | Boeck, 1870 | A | P | x | x | x | x | 2, 12 | x | x | 1, 2 | x | x | 11 | 11 | 11 | 11 | | | | | 11 | 11 |
| *Themisto libellula* | Goës, 1865 | A | P | x | | x | x | 2, 12 | x | x | 1, 2 | x | x | | 11 | 11 | 11 | | | | | 11 | 11 |
| *Tiron spiniferus* | (Stimpson, 1853) | A | B | x | | x | x | | | | | x | x | | | 11 | | | 11 | | | | 11 |
| Tryphosinae indet. | Lowry & Stoddart, 1997 | A | B | | | | | | | | | x | x | | | | 11 | | | | | | 11 |
| *Tryphosella horingi* | (Boeck, 1871) | A | B | x | | x | x | | | | 2 | | x | | | | | | | | | | |
| *Tryphosella schneideri* | (Stephensen, 1921) | A | B | x | | x | x | 9 | | x | | x | x | 9 | | 11 | | | 11 | 9 | | | 9, 11 |
| *Tryphosella spitzbergensis* | (Chevreux, 1926) | A | B | x | | x | x | | | | | x | x | | 11 | | 11 | | | | | | 11 |
| *Unciola leucopis* | (Krøyer, 1845) | A | B | x | | x | x | 7 | x | x | 1, 2 | x | x | 7 | 1, 11 | 1, 11 | 11 | 11 | 1, 7, 11 | | | | 1, 11 |
| *Westwoodilla caecula* | (Bate, 1857) | A | B | x | x | x | x | 9, 2 | x | x | | x | x | 9, 11 | 11 | 11 | | | | | | | 9, 11 |
| *Weyprechtia pinguis* | Krøyer, 1838 | A | B | | | x | x | 7, 5, 9, 2 | x | x | 1, 2 | | x | 1, 7, 5, 9, 11 | 11 | | | | 7, 9 | | 1, 7, 9 | 9, 11 | 1, 5, 9, 11 |
| *Brachydiastylis resima* | (Krøyer, 1846) | C | B | x | x | x | x | 1 | x | x | | x | x | 7 | 11 | | | | 7 | | | | 11 |
| *Campylaspis rubicunda* | (Liljeborg, 1855) | C | B | x | x | x | x | 2 | x | x | 1 | x | x | 1 | 1, 11 | 1, 11 | 1, 11 | 1, 11 | 1, 11 | | | 1, 11 | 1, 11 |
| *Diastylis edwardsii* | (Krøyer, 1841) | C | B | x | | x | x | 2 | | x | | | | | | | | | | | | | |
| *Diastylis goodsiri* | (Bell, 1855) | C | B | x | x | x | x | 7, 2 | x | x | 1 | x | x | 1, 7, 11 | 1, 11 | 1, 11 | 1, 11 | 1, 11 | 1, 7, 11 | | | 1, 11 | 1, 11 |
| *Diastylis lucifera* | (Krøyer, 1837) | C | B | x | x | | x | 7 | x | x | 1 | x | x | 1, 7, 11 | 1, 11 | 1 | 1 | 1, 11 | 1, 7, 11 | | | 11 | 1, 11 |
| *Diastylis rathkei* | (Krøyer, 1841) | C | B | x | x | x | x | 7 | x | x | 1, 2 | x | x | 1, 7, 11 | 1, 11 | 1, 11 | 1, 11 | | 1, 7, 11 | 7 | | 1, 11 | 1, 11 |
| *Diastylis scorpioides* | (Lepechin, 1780) | C | B | x | x | x | x | | x | x | 1, 2 | x | x | 1 | 1, 11 | 1, 11 | 1, 11 | 11 | 11 | 11 | | 11 | 1, 11 |
| *Diastylis spinulosa* | Heller, 1875 | C | B | x | x | x | x | | | | 1 | | x | 1 | 1 | 1 | | | 1 | | | 1 | 1 |
| *Diastylis sulcata* | Calman, 1912 | C | B | | | x | | | | | | x | x | | | 11 | | | | | | | 11 |
| *Ektonodiastylis nimia* | (Hansen, 1920) | C | B | | x | x | | | | | | x | x | | 11 | | | | | | | | 11 |
| *Eudorella emarginata* | (Krøyer, 1846) | C | B | x | x | x | x | 2 | x | x | 1 | x | x | 1, 11 | 1, 11 | 1, 11 | 1, 11 | 1, 11 | 1, 11 | | | 1, 11 | 1, 11 |
| *Hemilamprops cristatus* | (Krøyer, 1846) | C | B | x | | x | x | | | | | x | x | | 11 | 11 | | | | | | | 11 |
| *Lamprops fuscatus* | (Sabine, 1824) | C | B | x | | x | x | 7, 9 | x | x | | | | 7, 9, 11 | 11 | | | | 7, 9 | 9 | 7 | 9 | 9, 1 |

**Table 4** (*Continued*)

| Taxon | | Order | Group | Distribution | | | | | | | | | | Habitat of occurrence | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Large scale distribution | | | | Kongsfjorden and Hornsund records | | | | | | Depth [m] | | | | | Bottom type | | | Fjord basins | |
| | | | | I | II | III | IV | K_L | K_C | K_T | H_L | H_C | H_T | <50 | 50–100 | 100–200 | 200–300 | >300 | Soft | Hard | Algae | In | Out |
| *Leptostylis villosa* | (Krøyer, 1841) | C | B | x | x | x | x | | x | x | | x | x | | | 11 | 11 | | | | | | 11 |
| *Leucon* spp. | Krøyer, 1846 | C | B | | | | | 2, 9 | x | x | | x | x | 9, 11 | 11 | 11 | 11 | 11 | 11 | 9 | | | 9, 1 |
| *Caridion gordoni* | (Spence Bate, 1858) | D | P | x | | x | | | | | | x | x | | | | | | | | | | |
| *Eualus gaimardii gaimardii* | (H. Milne Edwards, 1837) | D | B/P_l | x | | x | x | 7, 6, 9 | x | x | 1, 3 | x | x | 1, 7, 5, 6, 9, 11 | 1, 11 | 11 | 11 | | 1, 6, 11 | 1, 7, 6, 9, 11 | 7, 5, 11 | 1, 6 | 1, 5, 6, 9, 11 |
| *Hyas araneus* | Leach, 1816 | D | B/P_l | x | | x | x | 7, 6, 9, 2 | x | x | 1, 2, 3 | x | x | 1, 7, 5, 6, 9, 11 | 1, 3, 11 | 1, 11 | 1, 11 | 1 | 3, 7, 6, 9, 11 | 7, 9, 11 | 7, 5 | 1, 9 | 1, 3, 5, 6, 9, 11 |
| *Hyas coarctatus* | (Montagu, 1815) | D | B | x | | x | x | 2 | | x | | | | | | | | | | | | | |
| *Lebbeus polaris* | (Goës, 1866) | D | B/P_l | x | | x | x | 9, 2 | x | x | 1, 2 | | x | 1, 7, 9, 11 | 1, 11 | 1, 11 | 1, 11 | 1, 11 | 7, 9, 11 | 1, 7, 9 | 1, 7 | 9, 11 | 1, 9, 11 |
| *Pagurus pubescens* | Krøyer, 1838 | D | B/P_l | x | | x | x | 7, 6, 9, 2 | x | x | 1, 2, 3 | x | x | 1, 7, 6, 9, 11 | 1, 3, 11 | 1, 11 | 1, 11 | 1 | 1, 3, 6, 11 | 1, 7, 6, 9 | 7 | 1, 9 | 1, 3, 6, 9, 11 |
| *Pandalus borealis* | Krøyer, 1838 | D | B | x | | x | x | 7, 2 | x | x | 1, 2 | x | x | 7 | 1, 11 | 1, 11 | 1, 11 | 1, 11 | 1 | 7 | | 11 | 1, 11 |
| *Sabinea septemcarinata* | (Sabine, 1824) | D | B/P_l | x | | x | x | 2 | x | x | 1, 2 | x | x | 1, 5, 11 | 1, 11 | 1, 11 | 1, 11 | 1, 11 | 1, 11 | | 5 | 1, 11 | 1, 5, 11 |
| *Sclerocrangon boreas* | (Phipps, 1774) | D | B/P_l | x | | x | x | 7, 8, 9, 2 | x | x | 1, 2 | | x | 1, 7, 8, 9, 11 | 1, 11 | 1 | 1 | 1 | 1, 8, 11 | 1, 7, 9 | 1, 7 | | 1, 8, 9, 11 |
| *Sclerocrangon ferox* | (Sars G.O., 1877) | D | B | x | | x | x | | | | 1 | | x | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | |
| *Spirontocaris phippsii* | (Krøyer, 1841) | D | B | x | | x | x | 9 | | x | | | | 9 | | | | | | 9 | | | 9 |
| *Spirontocaris spinus* | (Sowerby, 1805) | D | B/P_l | x | | x | x | 7, 2 | x | x | 1 | x | x | 1, 7, 5, 11 | 1, 11 | 1, 11 | 1, 11 | 1, 11 | 7 | 1, 7 | 1, 7, 5 | 11 | 1, 5, 11 |
| *Meganyctiphanes norvegica* | (M. Sars, 1857) | E | P | | | x | x | 4, 12 | x | x | | x | x | | | | | | | | | | |
| *Nematoscelis megalops* | G.O. Sars, 1883 | E | P | | | | | 4, 12 | | x | | | | | | | | | | | | | |
| *Thysanoessa inermis* | (Krøyer, 1846) | E | P | x | | x | x | 4, 2, 12 | x | x | 1, 2, 4 | x | x | 1, 12 | 1, 11, 12 | 1, 4, 11, 12 | 1, 11, 12 | 1 | | | | 1, 4, 11 | 1, 4, 4, 11 |
| *Thysanoessa longicaudata* | (Krøyer, 1846) | E | P | x | | x | x | 4, 12 | x | x | 1, 4 | x | x | 1 | 1 | 1, 4 | 1, 11 | 1 | | | | | 1, 4 |
| *Thysanoessa raschii* | (M. Sars, 1864) | E | B | x | | x | x | 4, 12 | x | x | 1, 4 | x | x | 1 | 1 | 1, 4 | | | | | | 1, 4 | 1, 4 |
| *Eugerda* sp. | Meinert, 1890 | I | B | | | | | | x | x | | x | x | 11 | 11 | 11 | 11 | 11 | 11 | | | 11 | 11 |
| *Eurycope cornuta* | Sars, 1864 | I | B | x | | x | x | 2 | x | x | | x | x | 11 | 11 | 11 | 11 | 11 | 11 | | | 11 | 11 |
| *Gnathia* sp. | Leach, 1814 | I | B | | | | | | x | x | | | | | | | 11 | | | | | | 11 |
| *Ilyarachna hirticeps* | Krøyer, 1838 | I | B | x | x | x | x | | | | 1 | | x | 1 | 1 | 1 | | | 1 | | | | 1 |
| *Janira maculosa* | (Krøyer, 1847) | I | B | x | | x | x | 7 | x | x | | | | | 11 | | 11 | | | | | 11 | 11 |
| *Janiralata tricornis* | Sars, 1865 | I | B | | | x | x | 9 | | x | | | | 9 | | | | | | 9 | | 9 | 9 |
| *Munna fabricii* | Krøyer, 1846 | I | B | x | | x | x | 9 | x | x | 1 | | x | 1, 9, 11 | 1 | 1 | 1 | 1 | 1 | 9 | 11 | 1, 9 | 1, 9, 11 |
| *Munna groenlandica* | Hansen, 1916 | I | B | | x | | | 9 | | x | | | | | | | | | | | | | |
| *Munna kroyeri* | Goodsir, 1842 | I | B | x | | | | 9 | | x | | | | | | | | | | | | | |
| *Munna pellucida* | Gurjanova, 1930 | I | B | | | x | | 9 | | x | | | | | | | | | | | | | |
| *Munna spitzbergensis* | Gurjanova, 1930 | I | B | | | x | x | 5, 9 | | x | | | | 5, 9 | | | | | | 9 | 5 | | 5, 9 |
| *Munnopsis typica* | M. Sars, 1861 | I | B | x | x | x | x | 7, 2 | x | x | 1 | x | x | 1, 7 | 1, 11 | 1, 11 | 1, 11 | 1, 11 | 1, 7, 11 | | 11 | 1, 11 | 1, 11 |
| *Pleurogonium spinosissimum* | (Sars G.O., 1866) | I | B | x | | x | | | x | x | | x | x | | | 11 | | | | | | | 11 |
| *Synidotea nodulosa* | (Krøyer, 1846) | I | B | | | x | x | 8 | | x | 1, 2 | | x | 1, 8 | 1 | 1 | 1 | 1 | 1, 8 | | 1 | | 1 |
| *Boreomysis arctica* | (Krøyer, 1861) | M | P | x | x | x | x | 2 | x | x | | | | | | | | | | | | | |
| *Erythrops erythrophthalma* | (Goës, 1864) | M | P | x | x | x | x | 7 | x | x | 1 | x | x | 1, 7 | 1, 11 | 1, 11 | 1, 11 | 1 | 11 | | | | 1, 11 |
| *Mysis mixta* | Liljeborg, 1853 | M | P | x | | x | x | | | | 1, 3 | | x | 1 | | | | | | | | | 1 |
| *Mysis oculata* | (Fabricius, 1780) | M | P | x | x | x | x | 7, 9 | x | x | 1, 2 | x | x | 1, 7, 5, 9, 11 | 11 | 11 | | | 7, 9 | 9 | 7, 5 | 1, 11 | 1, 5, 9, 11 |
| *Parerythrops obesa* | (Sars G.O., 1864) | M | P | x | | x | x | 2 | | x | | | | | | | | | | | | | |
| *Pseudomma truncatum* | S.I. Smith, 1879 | M | P | x | x | x | x | 2 | x | x | 1 | x | x | 1 | 1, 11 | 1, 11 | 1, 11 | 1, 11 | | | | 11 | 1, 11 |
| *Stilomysis grandis* | (Goës, 1864) | M | P | x | | x | x | 7 | x | x | 1 | x | x | 7 | 11 | 11 | | | 7 | | | 11 | 11 |
| Tanaidacea indet. | Dana, 1849 | T | B | x | x | x | x | 7 | x | x | 2 | x | x | 7, 10, 11 | 10, 11 | 10, 11 | 10, 11 | 10, 11 | 10, 7 | | | 10.11 | 10.11 |

*Order:* A — Amphipoda, C — Cumacea, D — Decapoda, E — Euphausiacea, I — Isopoda, M — Mysida, T — Tanaidacea. *Group:* B — benthic, P — pelagic, C — cryopelagic, P_l — planktonic larvae. *Distribution:* I — Norwegian coast (Brattegard and Holthe, 2001), II — deep Greenland Sea (Brandt, 1997), III — Barents Sea (Sirenko, 2001), IV — Svalbard Archipelago (Palerud et al., 2004), K_L — literature records for Kongsfjorden, K_C — current study record for Kongsfjorden, K_T — all records for Kongsfjorden, H_L — literature records for Hornsund, H_C — current study record for Hornsund, H_T — all records for Hornsund. *Habitat of occurrence:* depth ranges, bottom types and fjord basins. References in superscripts: 1, Węsławski (1990); 2, Gulliksen et al. (1999); 3, Legeżyńska et al. (2000); 4, Buchholz et al. (2010); 5, Lippert et al. (2001); 6, Legeżyńska (2001); 7, Kaczmarek et al. (2005); 8, Laudien et al. (2007); 9, Voronkov et al. (2013); 10, Błażewicz-Paszkowycz and Sekulska-Nalewajko; 11, current study; 12, Dalpadado et al. (2016).

fjord, $S_{obs}$ reached 89 (with 0.95 CI intervals from 81 to 97) in Hornsund and 96 (with 0.95 CI intervals from 89 to 103) in Kongsfjorden. *Chao2* gave very similar results for Hornsund (109 species, with 0.95 CI intervals from 96 to 141) and Kongsfjorden (110 species, with 0.95 CI intervals from 100 to 136).

Overall, Amphipoda followed by Cumacea were the most abundant and represented by the highest numbers of species in the benthic samples (Fig. 2). In Hornsund, they constituted 86% of specimens in the VV samples and 73% in the RD samples; in Kongsfjorden the respective values were 61% and 52%. Decapoda were abundant only in the RD samples (24% in Hornsund and 22% in Kongsfjorden). Tanaidacea and Isopoda contributed more to the total number of specimens collected in Kongsfjorden (VV samples: 38%, RD samples: 14%) than in Hornsund (12% and 1.2%, respectively). Mysids were frequent and numerically important only in the RD samples from Kongsfjorden ($F$ = 65.4%, $D$ = 12.1%) (Fig. 2). Among the 44 families, Oedicerotidae (Amphipoda) comprised the highest number of species (13) followed by Lysianassidae (Amphipoda, 9 species), Uristidae (Amphipoda, 8 species), Calliopidae (Amphipoda, 8 species) and Diastylidae (Cumacea, 8 species). As regards abundance, the 10 most dominant species made up between 69% and 89% of the total number of individuals collected in each fjord, depending on the sampling gear. Across the entire data set, there was a high proportion of rare taxa. Thirty species occurred in just one sample and only 16 species were noted with a frequency of >10%. The cumacean *Eudorella emarginata* was the most frequent ($F$ = 69%) and most abundant species ($D$ = 11%) in the benthic material.

### 4.2.1. Grab samples (VV)

Hornsund and Kongsfjorden shared several frequent and numerically important species, but the results of the PERMANOVA tests showed differences in species composition between the two fjords, between the glacial bays and outer basins within the fjords, and between the respective basins of the both fjords (Table 5). The separation of infauna between fjords and basins is illustrated in the fjord-basin oriented CAP ordination (Fig. 5). The 10 most dominant species respectively made up 81% and 89% of the total number of individuals collected in Hornsund and Kongsfjorden. In both fjords, the glacial basins were dominated by small-bodied tanaids and the cumacean *E. emarginata*, which, however, were much more abundant in Kongsfjorden (Fig. 6). Melitid amphipods, despite their moderate frequency, exhibited a substantial dominance in the outer parts of the fjords, reaching the highest densities noted in the whole material (*Quasimelita formosa* up to 166 ind. 0.1 $m^{-2}$; *Quasimelita quadrispinosa* up to 225 ind. 0.1 $m^{-2}$). A number of rare taxa were recorded in all the basins. In Brepollen 12 taxa (67% of all the taxa recorded) were found in just one sample and 9 (50% of all the taxa recorded) were represented by just one specimen, while in the inner Kongsfjorden 3 species among 13 taxa (27% of all the taxa recorded) were noted as individual specimens and in just one sample. Singletons made up 26% (out of 51 species recorded) and 18% (out of 62 species recorded) and unique specimens 31% and 26% in the outer Kongsfjorden and Hornsund, respectively. Species richness, diversity and variation in taxonomic distinctness did not differ significantly between Hornsund and Kongsfjorden. The average taxonomic distinctness and numbers of individuals per sample were significantly higher in Kongsfjorden than in Hornsund. In Hornsund, species richness, density and diversity were significantly higher in the fjord's main basin than in the glacial bays. In Kongsfjorden, the central basin and glacial bay did not differ with regard to density or the diversity of crustacean fauna, but species richness, Hurlbert index and variance of taxonomic distinctness were lower in the inner bay. Comparison of the main basins of the two fjords showed the average species richness, Shannon—Wiener and Hurlbert diversity indices and variances of taxonomic distinctness to be higher in Hornsund than in Kongsfjorden, whereas density and average taxonomic distinctness did not differ significantly. The glacial bay of Kongsfjorden had

**Table 5** Results of two-way PERMANOVA comparisons of density and diversity indices (VV samples) and one-way PERMANOVA (RD, MPS, TT samples).

| Gear | Source | *N* | *S* | *H* | ES(50) | avTD | varTD | TAX | SIZE | FUN |
|---|---|---|---|---|---|---|---|---|---|---|
| VV | F | 5.96$^{*}$ | 0.00 | 0.00 | 0.18 | 16.1$^{***}$ | 2.15 | 8.26$^{***}$ | 12.29$^{***}$ | 14.14$^{***}$ |
| | B | 3.50 | 35.05$^{***}$ | 29.69$^{***}$ | 0.22 | 24.2$^{***}$ | 37.50$^{***}$ | 11.76$^{***}$ | 18.45$^{***}$ | 24.71$^{***}$ |
| | F × B | 6.12$^{*}$ | 4.9$^{*}$ | 7.8$^{**}$ | 21.32$^{***}$ | 28.6$^{***}$ | 11.73$^{***}$ | 3.82$^{***}$ | 3.54$^{**}$ | 9.51$^{***}$ |
| | Post hoc pairwise tests for F × B | Hi < Ki$^{**}$<br>Hi < Ho$^{**}$ | Hi < Ki$^{**}$<br>Ki < Ko$^{**}$<br>Hi < Ho$^{***}$ | Ho > Ko$^{**}$<br>Hi < Ho$^{***}$ | Hi < Ki$^{**}$<br>Ho > Ko$^{***}$<br>Hi < Ho$^{**}$<br>Ki < Ko$^{***}$ | Hi < Ki$^{***}$<br>Hi < Ho$^{***}$ | Ho > Ko$^{***}$<br>Hi < Ho$^{***}$<br>Ki < Ko$^{*}$ | Hi < Ki$^{***}$<br>Ho > Ko$^{***}$<br>Hi < Ho$^{***}$<br>Ki < Ko$^{***}$ | Hi > Ki$^{***}$<br>Ho > Ko$^{***}$<br>Hi < Ho$^{***}$<br>Ki < Ko$^{***}$ | Hi < Ki$^{***}$<br>Ho > Ko$^{***}$<br>Hi < Ho$^{***}$<br>Ki < Ko$^{***}$ |

| Gear | Source | *N* | *S* | *H* | ES(50) | TAX | SIZE | FUN |
|---|---|---|---|---|---|---|---|---|
| RD | F | 6.68$^{**}$ | 0.36 | 1.09 | 2.57 | 2.63$^{**}$ | 0.43 | 1.63 |
| MPS | F | 2.2 | 0.47 | 5.52$^{*}$ | 5.00$^{*}$ | | | |
| TT | F | 0.46 | 6.74$^{*}$ | 7.18$^{**}$ | 4.27 | | | |

*N*, number of specimens per sample; *S*, number of taxa per sample; *H*, Shannon—Wiener index; ES(50), Hurlbert index; avTD, average taxonomic distinctness; varTD, variance of taxonomic distinctness; TAX, taxonomic composition; SIZE, size structure; FUN, functional traits.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

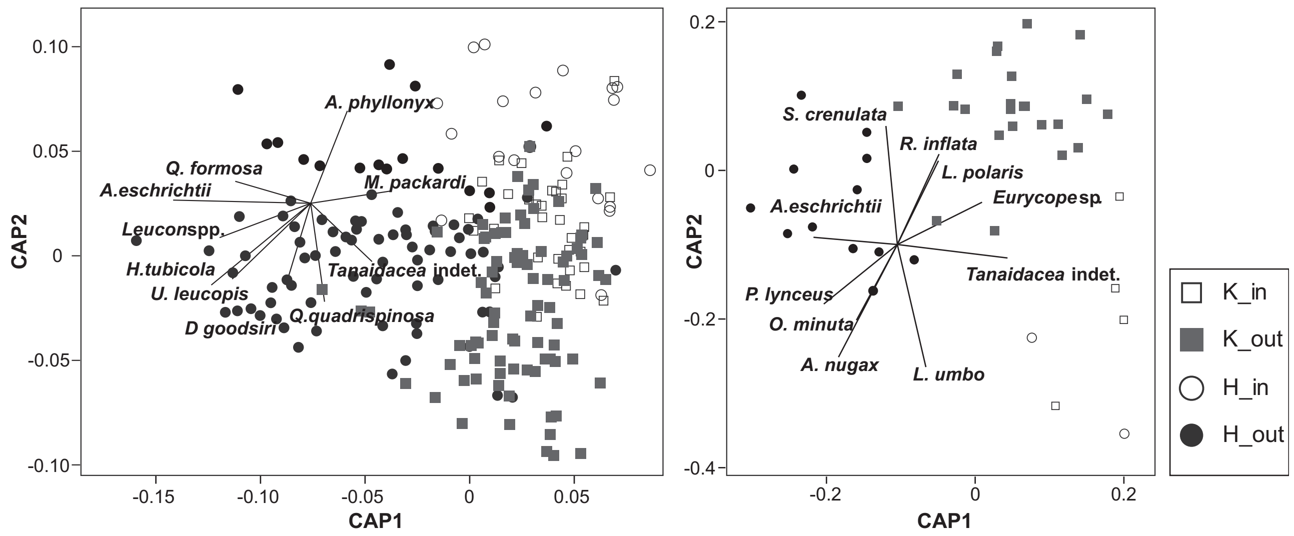

**Figure 5** Results of CAP analysis based on the Bray—Curtis similarity of species composition in the benthic samples from Kongsfjorden (K) and Hornsund (H), and their inner glacial bays (in) and outer basins (out); square root transformed VV data (left-hand panel); presence/absence RD data (right-hand panel). Taxa with Spearman rank correlations with CAP axes >0.35 for VV samples and >0.45 in RD samples are shown. Full species names can be found in Table 4.

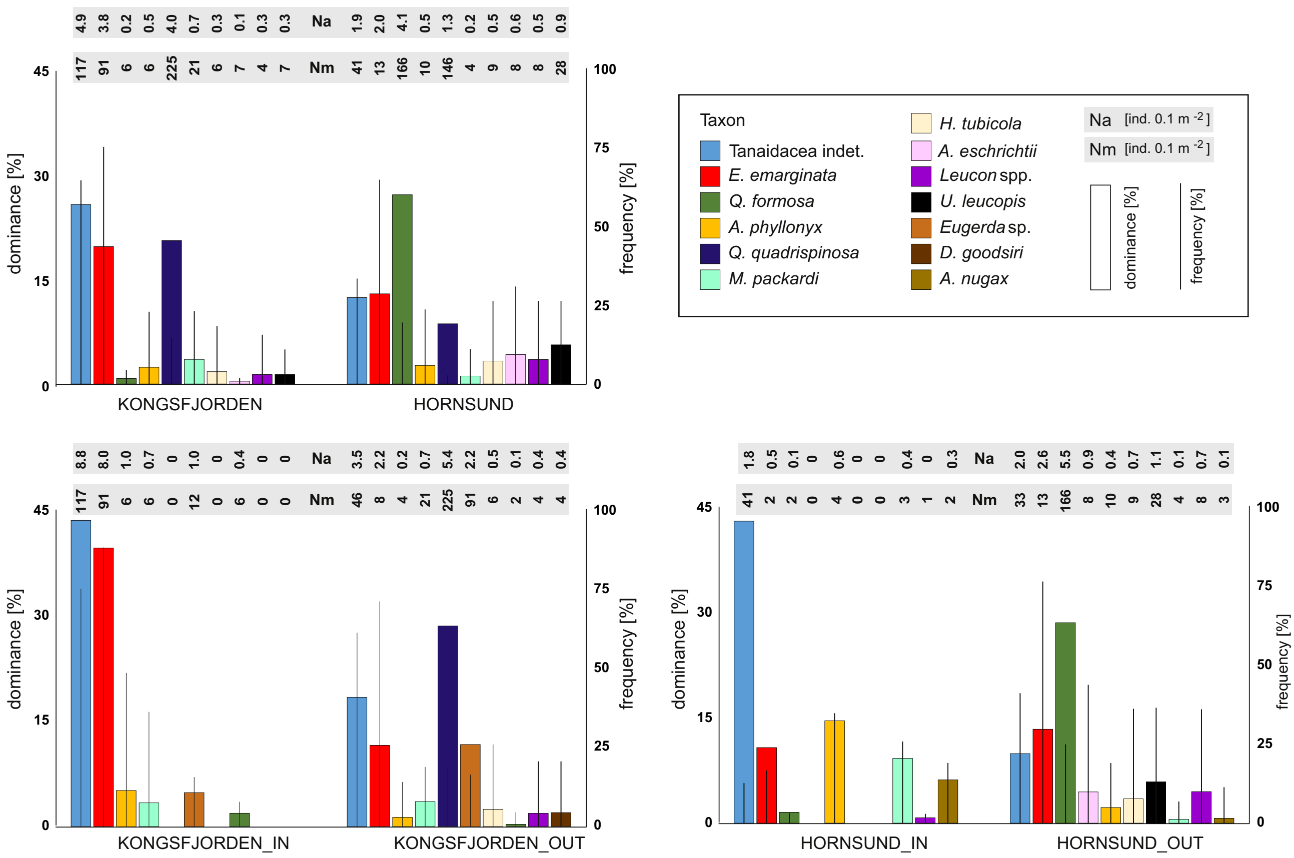

**Figure 6** Dominance, frequency and density of the species that contributed most to the dissimilarity between the malacostracan communities of Kongsfjorden and Hornsund and their inner glacial bays (in) and outer basins (out) based on SIMPER analysis of VV samples. Ten species with the highest contribution to the overall dissimilarity are shown for each comparison. The average density (Na; ind. 0.1 $m^{-2}$) and maximum density (Nm; ind. 0.1 $m^{-2}$) are shown for each taxon above the dominance/frequency graphs. Full species names can be found in Table 4.

higher densities, species richness, Shannon–Wiener and Hurlbert diversity indices and the average taxonomic distinctness than the glacial bays of Hornsund (Fig. 7, Table 5).

The results of PERMANOVA indicated that the functional structure and size composition of the infaunal communities (explored with VV sampling) differed among the two fjords, the inner and outer basins within each fjord and the respective basins of both fjords (Table 5). Eleven functional groups were recorded, detritus-feeders being predominant. Discretely motile detritus feeders (Kongsfjorden: 51%, Hornsund: 43%) and motile subsurface detritus feeders (Kongsfjorden: 38%, Hornsund: 11%) were dominant in the glacial bays, whereas mobile surface deposit feeders were typical of the outer fjords (Kongsfjorden: 34%, Hornsund: 39%). Numbers of motile and discretely motile suspension feeders increased towards the open sea, comprising 21% of the individuals in outer Hornsund and 10% in outer Kongsfjorden. The proportions of facultative and obligate carnivores ranged from 8 to 40% in the glacial bays of Kongsfjorden and Hornsund, respectively (Fig. 8). The Kongsfjorden fauna was numerically dominated by the smallest species, whereas in Hornsund the size composition was more even. In both fjords organisms belonging to the two smallest size classes (<10 mm) were dominant in the glacial bays (Kongsfjorden: 93%, Hornsund 73%). Crustaceans up to 15 mm comprised 55% and 91% of all individuals collected in the outer parts of Hornsund and Kongsfjorden, respectively. The proportion of species longer than 20 mm was distinctly higher in both the inner (10%) and outer (37%) basins of Hornsund than in Kongsfjorden (3% in each basin) (Fig. 9).

### 4.2.2. Dredge samples (RD)

The species composition in the RD samples differed significantly between the two fjords (Fig. 5). The ten most dominant species made up 69% and 74% of the total number of individuals collected in Hornsund and Kongsfjorden, respectively (Table 6). The number of species in the dredge samples was variable but on average much higher in Kongsfjorden (306.5 ± 342.8 ind. per sample) than in Hornsund (57.5 ± 55.0 ind. per sample) (one-way PERMANOVA, pseudo-*F*

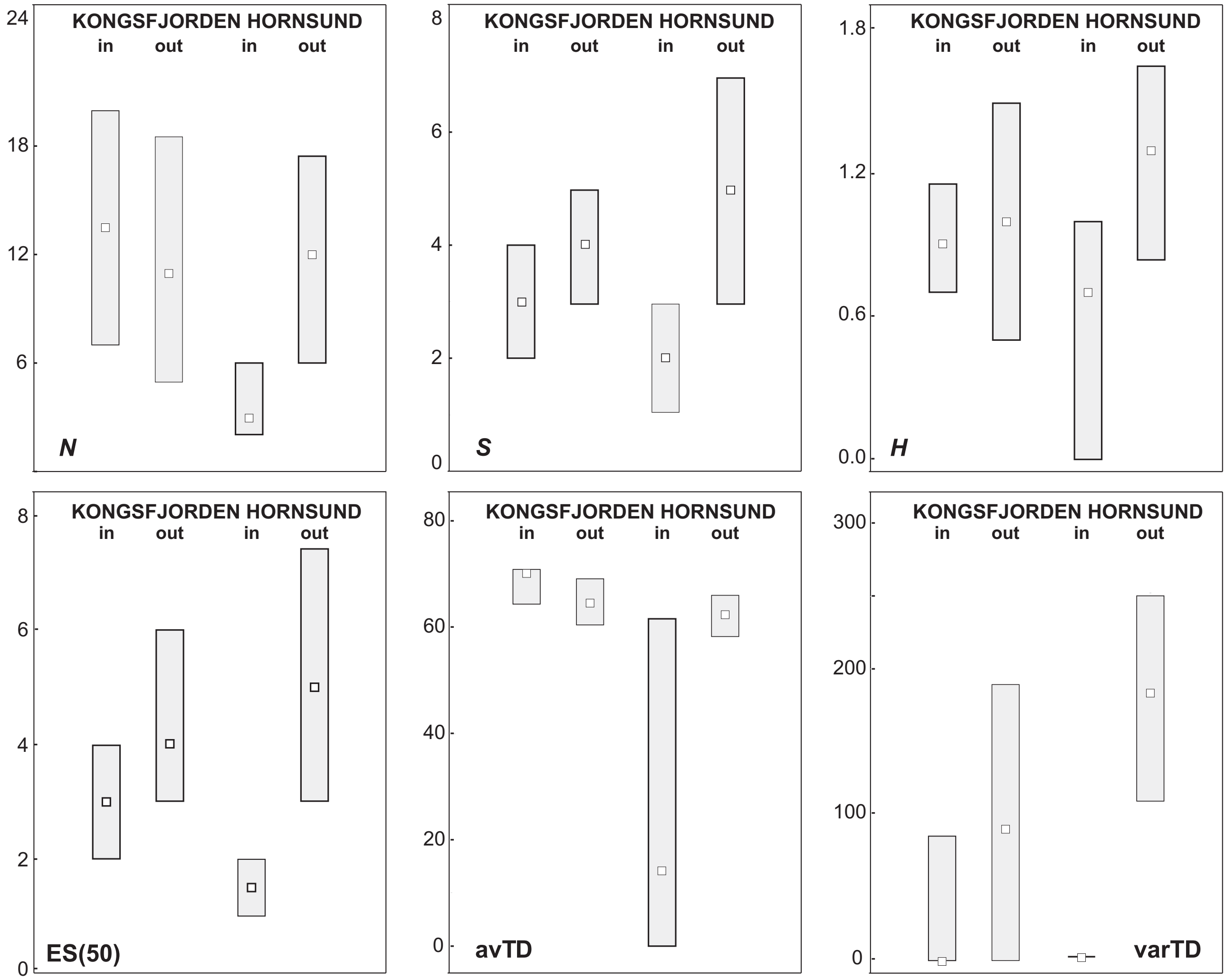

**Figure 7** Density ($N$ — number of specimens per 0.1 m$^{-2}$) and diversity [$S$ — number of species per sample; $H$ — Shannon–Wiener index; ES(50) — Hurlbert index; avTD — average taxonomic distinctness; varTD — variance of taxonomic distinctness] for VV samples. The boxes represent the interquartile range from the 25th to the 75th percentile, while the white squares represent the median value; in — inner glacial bays; out — outer basins.

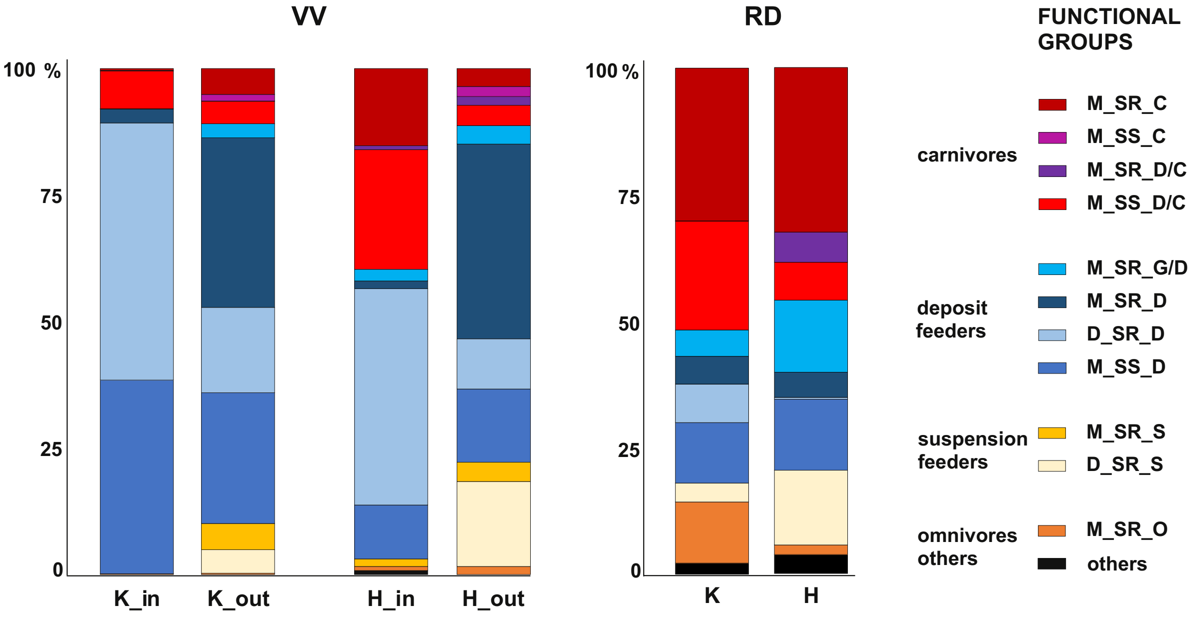

**Figure 8** Percentages of individuals belonging to certain functional groups in the total number of specimens taken with a grab (VV) or a dredge (RD) in Kongsfjorden (K) and Hornsund (H), and their inner glacial bays (in) and outer basins (out). Functional group codes: M — motile; D — discretely mobile; SR — surface feeder; SS — subsurface feeder; C — carnivore; D/C — deposit feeder/facultative carnivore; G/D — microalgae grazer/deposit feeder; D — deposit feeder; S — suspension feeder; O — omnivore.

**Table 6** The ten most dominant species collected with a dredge in Hornsund and Kongsfjorden.

| Kongsfjorden | | | | Hornsund | | | |
|---|---|---|---|---|---|---|---|
| Taxon | D | F | Tn | Taxon | D | F | Tn |
| *Monoculodes packardi* (A) | 14 | 44 | 1116 | *Sabinea septemcarinata* (D) | 16 | 54 | 122 |
| *Lebbeus polaris* (D) | 10 | 48 | 792 | *Diastylis goodsiri* (C) | 9 | 62 | 68 |
| *Eudorella emarginata* (C) | 9 | 70 | 775 | *Eudorella emarginata* (C) | 9 | 54 | 65 |
| Tanaidacea indet. (T) | 8 | 41 | 630 | *Orchomenella minuta* (A) | 6 | 54 | 44 |
| *Arrhis phyllonyx* (A) | 7 | 70 | 616 | *Haploops tubicola* (A) | 5 | 46 | 40 |
| *Spirontocaris spinus* (D) | 5 | 52 | 439 | *Ampelisca eschrichtii* (A) | 4 | 54 | 32 |
| *Pseudomma truncatum* (M) | 5 | 44 | 402 | *Diastylis scorpioides* (C) | 4 | 46 | 31 |
| *Eurycope* sp. (I) | 4 | 52 | 330 | *Arrhis phyllonyx* (A) | 4 | 61 | 31 |
| *Syrrhoe crenulata* (A) | 4 | 56 | 321 | *Eualus gaimardi* (D) | 4 | 46 | 29 |
| *Mysis oculata* (M) | 4 | 11 | 296 | *Unciola leucopis* (A) | 4 | 46 | 28 |
| *Eualus gaimardi* (D) | 4 | 37 | 291 | *Leucon* spp. (C) | 4 | 46 | 27 |

D, dominance; F, frequency of occurrence; Tn, total number of specimens; A, Amphipoda; C, Cumacea; D, Decapoda; T, Tanaidacea.

12.1, $p < 0.001$, PERMDISP: $t = 1.9$, $p > 0.1$). There were no differences between the two fjords in average species richness (Kongsfjorden: 16.3 ± 6.4; Hornsund: 14.8 ± 8.5) and Shannon—Wiener (1.9 ± 0.5 and 2.1 ± 0.9, respectively) or Hurlbert indices (10.5 ± 3.9 and 13.5 ± 8.2, respectively). Fifteen functional groups were found in both fjords. Mobile forms were in the overwhelming majority, accounting for 81—86% of the fauna. In terms of feeding mode, facultative and obligate carnivores were dominant, making up 60% and 52% of the samples from Hornsund and Kongsfjorden, respectively, and there were 19% of deposit feeders in Hornsund and 25% in Kongsfjorden. The relative abundance of suspension-feeding organisms was much higher in Hornsund (19%) than in Kongsfjorden (4%) (Fig. 8). The Kongsfjorden fauna was dominated by individuals smaller than 20 mm (75%), whereas in Hornsund approximately half the specimens were smaller than and half were larger than 20 mm. However, the PERMANOVA results indicated that neither the functional structure nor the size composition differed between two fjords (Fig. 9).

## 5. Discussion

### 5.1. Sampling efficiency

Each type of sampling gear has specific advantages and limitations, and its optimal performance also depends upon the depth and type of substrate. This results in little consistency among datasets obtained using different types of gear, in terms not only of taxonomic composition but also of

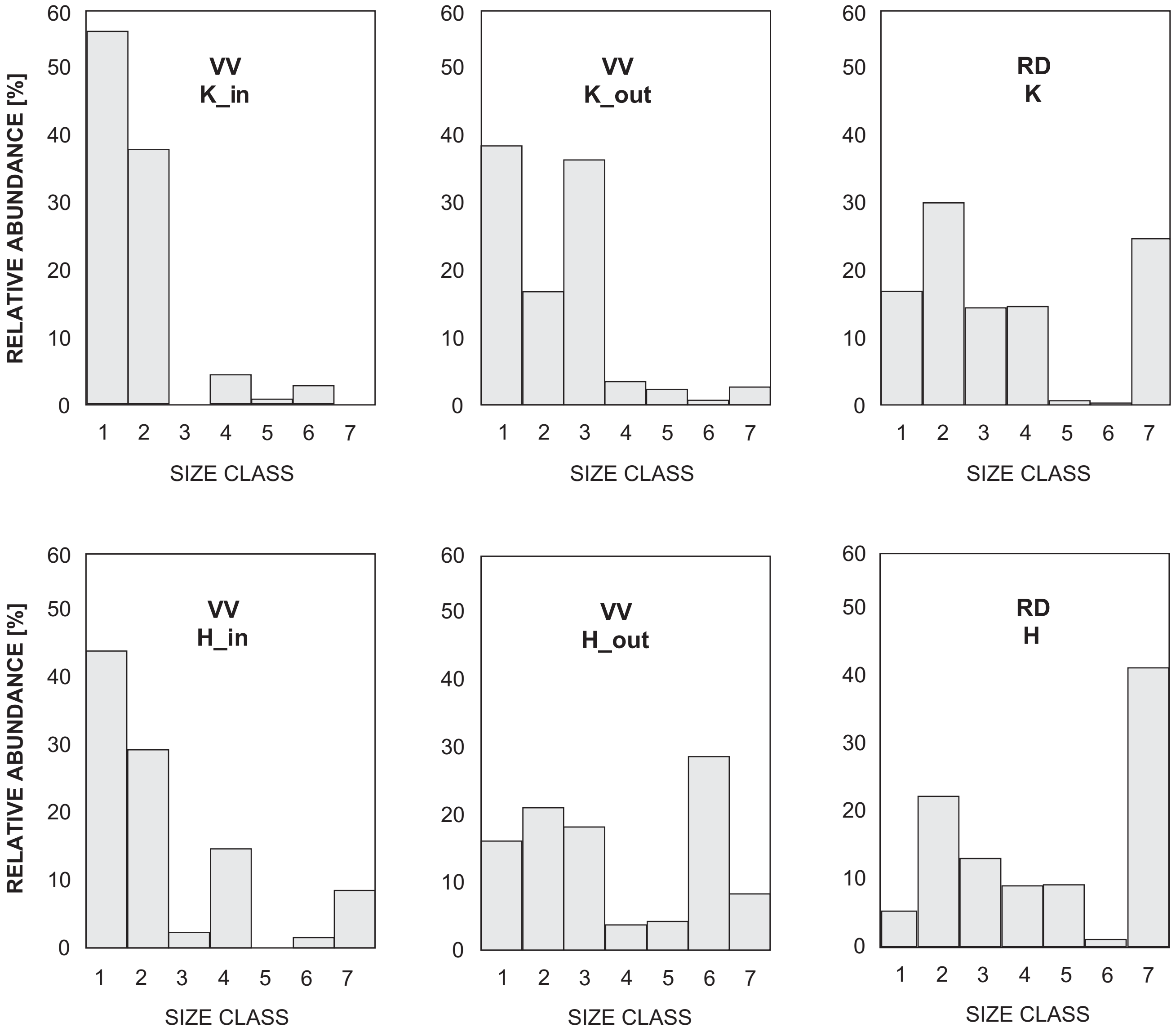

**Figure 9** Percentages of individuals belonging to particular size classes in the total number of specimens taken with a grab (VV) or a dredge (RD) in Kongsfjorden (K) and Hornsund (H), and their inner glacial bays (in) and outer basins (out). Size class codes: 1: 0—5 mm; 2: 6—10 mm; 3: 11—15 mm; 4: 16—20 mm; 5: 21—25 mm; 6: 26—30 mm; 7: >30 mm.

functional groups (Brandt and Schnack, 1999; Flannery and Przeslawski, 2015; Jørgensen et al., 2011; Fig. 8). The application of different samplers is, therefore, essential for obtaining a comprehensive synthesis of the community as a whole (Jørgensen et al., 2011). This is particularly evident in the case of the ecologically diversified Malacostraca, characterized as they are by a patchy distribution and abundance. Moreover, some aspects of crustacean behaviour, such as high mobility, the formation of swarms or aggregations and the active avoidance of sampling gear (Hirche et al., 2015; Sainte-Marie and Brunel, 1985), can severely limit sampling effectiveness. Thus, the van Veen grab with its relatively small catching area (0.1 m$^2$) was less effective (on average 4 species per sample) than a dredge (on average 15—16 species per sample) employed in similar habitats and depth ranges. However, among the gear used the grab was the only type suitable for infauna sampling (Flannery and Przeslawski, 2015), and the large number of samples taken seemed to compensate for this limitation, since the total number of species collected with it (88 species) was comparable to that collected with the dredge (100 species). Dredging accumulates organisms over a long distance and covers mobile as well as scarce forms. Besides epibenthic taxa, the dredged material also contains considerable numbers of infauna that are swirled up in front of the gear (Brandt and Schnack, 1999). However, neither the grab nor the dredge used in this study was able to provide sufficient coverage of the highly mobile hyperbenthos and scavenging Crustacea, known to form aggregations on carcasses (Brandt and Barthel, 1995; Sainte-Marie, 1986). Estimating the composition and densities of such taxa is dependent on specialized equipment, such as sledges with epi- and suprabenthic samplers (Brandt and Barthel, 1995) or baited traps (Legeżyńska, 2001; Nygård, 2011).

The majority of benthic samples in current study came from the subtidal zone (average sampling depth 129 m in Hornsund and 165 m in Kongsfjorden) with a uniformly soft bottom, which is not the type of substrate preferred by most crustacean species. In this habitat, 89 species were recorded in Hornsund and 96 in Kongsfjorden. A similar species richness has been reported for Polychaeta in Hornsund (86 species recorded between 100 and 250 m; Kędra et al., 2013) and for Mollusca in Kongsfjorden (87 species recorded between 5 and 390 m; Włodarska-Kowalczuk, 2007). Shallow (>50 m) bottom areas, which host rich communities of small vagile invertebrates, are still relatively poorly studied because they are not accessible to research vessel operations. A scuba-diving investigation of hard-bottom benthos between 0 and 30 m in Kongsfjorden recorded the occurrence of at least 60 malacostracan species, 37 of which were not found in this study (Voronkov et al., 2013). Dredging in the same fjord on a variety of bottom substrata between 5 and 50 m yielded 49 malacostracan taxa (Kaczmarek et al., 2005). It is, therefore, clear that a broad survey across the entire range of depths and habitats based on the concurrent use of different gear types to cover infauna, epifauna and hyperbenthos is needed in order to obtain a realistic species inventory.

## 5.2. Species richness

Despite the considerable number of samples taken, the species accumulation curves for $S_{obs}$ of benthic taxa in Kongsfjorden and Hornsund were not asymptotic, suggesting that some species remained undetected in both fjords. The *Chao2* estimator indicated that a larger number of species could be present. $S_{obs}$ may be downward biased owing to the large percentages of rare species. The overlapping values of 0.95 CI of both $S_{obs}$ and *Chao2* suggest that a generally similar richness of malacostracan species may be expected in both fjords.

Combining our data with published records of species richness in Kongsfjorden and Hornsund revealed the presence of around 190 malacostracan taxa: this is about 50% of the species known from the whole Svalbard archipelago area within latitudes 74°—81°N and longitudes 10°—35°E (Palerud et al., 2004). This is a surprisingly high percentage, given the limited area and depth range available in the fjords compared with the whole archipelago. Comparison of our data with other published assessments from the European Arctic is problematic, since sampling effort, collecting methods and depth coverage differ among them. Although a substantial drop in Arthropoda species richness with increasing latitude has been recorded along the Norwegian coast (Narayanaswamy et al., 2010), no obvious poleward pattern exists in the Arctic Ocean (Brandt, 1997; Weisshappel and Svavarsson, 1998). The highest diversity of Malacostraca has been reported from the thoroughly studied Barents Sea (68—81°N), east of Svalbard, the highly heterogeneous ecosystem of which hosts a rich mixture of Arctic and North Atlantic taxa (>500 species) (Sirenko, 2001). A diversity of malacostracan fauna is also characteristic of the western part of the Greenland Sea, west of Svalbard: even a small number of samples (31 epibenthic sledge samples) at three localities from the shelf down to deep waters (67—81°N; 45—2681 m) yielded over 200 species of peracarid crustaceans (i.e. amphipods, isopods, cumaceans and tanaidaceans) (Brandt, 1997). Just five short trawls with the same gear along the eastern Greenland shelf revealed 181 peracarid species between 158 and 251 m (Stransky and Brandt, 2010). Even based on these limited data, a huge difference in malacostracan biodiversity between the eastern and western sides of the Greenland Sea can be assumed and is probably related to differences in primary water masses, ice cover and primary productivity in these two areas (Narayanaswamy et al., 2010).

## 5.3. Factors determining the distribution and composition of pelagic and benthic malacostracan communities

While the regional species pool is the upshot primarily of evolutionary history, numerous environmental factors, including the properties and distribution of water masses, sedimentation regime, type of available substrata, quality and quantity of food may determine malacostracan distributions (Brandt, 1993, 1995, 1997; Weisshappel and Svavarsson, 1998). Moreover, certain aspects of their biology (e.g. direct vs. larval development) and ecology (pelagic vs. benthic habitat, sessile vs. vagile lifestyle, food and habitat preferences) (Brandt et al., 2012) may be important in creating distribution patterns.

The data on large-scale distribution, summarized in Table 4, indicate that the majority of malacostracan species hitherto recorded in Kongsfjorden and Hornsund show remarkably wide depth ranges and are widely distributed in the North Atlantic and the Arctic. 72% of all 186 taxa were noted along the north coast of Norway and 87% in the Barents Sea. The current species richness and taxonomic composition clearly reflect the glacial history of the Arctic Ocean. At the last glacial maximum, the entire shelf of the Atlantic Arctic was covered with glacial ice that extended beyond the shelf-break and would have precluded the existence of a shallow-water fauna (Jakobsson et al., 2014). Recolonization of the Spitsbergen fjords by species originating from the North Atlantic and deep Arctic Ocean started only 10 000 years ago, after the ice sheet had retreated. Most benthic taxa do not have a planktonic larval stage; this may limit their potential for dispersal and delay colonization of the fjords (Jażdżewski et al., 1995). As a result, the fjord fauna is impoverished and dominated by widespread boreal-Arctic taxa, with a high faunal affinity to the North Atlantic.

Lying at the boundary between the Barents and Greenland Seas, Svalbard is exposed to a variety of hydrological regimes (Walczowski, 2013). Advection of shelf waters has been considered a major factor shaping the pelagic community in the fjords (Dalpadado et al., 2016; Gluchowska et al., 2016). The list of planktonic taxa obtained in our samples is typical of coastal Svalbard waters and consists of a mixture of boreal-Arctic and boreal-Atlantic elements (Węsławski et al., 2000). Their relative contribution to the total abundance in each fjord mirrors the different influences of Atlantic and Arctic waters (see the next section).

The broad distribution of benthic species across the latitudinal and depth gradients may suggest that hydrological conditions and depth have a negligible influence on their presence in these two fjords. Nonetheless, the small depth range in them may be unfavourable to some taxa. For example, species numbers of tanaids and isopods tend to rise with increasing depth in the Greenland Sea (Brandt, 1997). Similarly, Svavarsson (1997) observed that the species diversity of isopods in the Arctic Ocean peaks in the 320—1100 m depth zone. On the other hand, in contrast to the open sea, fjords contain shallow, structurally complex microhabitats (Kaczmarek et al., 2005; Tatarek et al., 2012; Włodarska-Kowalczuk, 2007; Włodarska-Kowalczuk et al., 2009) that may be species-rich 'hot spots' of benthic crustaceans. Indeed, there is a gradual decrease of species richness with increasing depth in Kongsfjorden and Hornsund: 125 species were reported from waters shallower than 50 m, the number of species fell from 89 to 68 between 50 and 200 m, and only 46 species were found to be living at depths greater than 300 m. A similar depth-related species richness pattern was recorded in gammarid amphipods from the Barents Sea (Bryazgin, 1997). However, the dominant shallow water species in the Spitsbergen fjords are known to be associated with macroalgae vegetation (Kaczmarek et al., 2005; Legeżyńska, 2008; Lippert et al., 2001; Ronowicz et al., 2013), others, such as scavenging lysianassoid amphipods, may benefit from the pelagic and benthic food abundant in this depth zone (Legeżyńska, 2001). Thus, one can assume that substrate heterogeneity rather than depth itself may be responsible for the observed high species richness. This assumption is further supported by the results of soft-bottom studies from shallow Kongsfjorden waters: only 10 species of Crustacea were found between 5 and 30 m on the uniform sand-clay sediment of the outer fjord (Laudien et al., 2007), the same number of species within the same depth zone was collected from the unconsolidated muddy bottom in the Kongsbreen glacial bay (Kaczmarek et al., 2005).

Bottom type is generally considered an important factor structuring entire benthic communities. Jażdżewski et al. (1995) highlighted the low heterogeneity of substrata as one of the main reasons for the poor amphipod diversity in the Arctic. One of the results of glacial activity is the prevalence of fine-grained sediments. Subtidal sediments (>50 m) throughout the fjords are dominated by glacio-marine deposits, which are mostly silt and clay (Drewnik et al., 2016; Włodarska-Kowalczuk and Pearson, 2004). The sediments in the inner and outer basins are similar in their granulometry, but differ in stability (Włodarska-Kowalczuk and Pearson, 2004). A muddy bottom obviously favours the occurrence of burrowing taxa, such as oedicerotid amphipods, cumaceans and tanaids, which are dominant in the inner basins of Kongsfjorden and Hornsund. These taxa can persist on the sediment surface because of their negligible weight (tanaids) or can actively move through or over the soft substratum (*E. emarginata*, oedicerotids). On the other hand, homogeneous fine-grained sediments are regarded as the least favourable habitat for most highly specialized amphipods (Buhl-Mortensen, 1996). For example, relatively large domiculous amphipods, such as *Ampelisca*, *Haploops* and *Unciola*, require a compact bottom and do not colonize the loose sediments in the inner bays (this study). Similarly, Buhl-Mortensen (1996) observed the decreasing dominance of tube-dwelling amphipods from offshore to the inner fjord in southern Norway. As already mentioned, the richest malacostracan community inhabits a diverse shallow water substrata which provide good foraging opportunities and shelter from predators and environmental stressors.

Another factor regulating species distribution may be food availability. Fjords provide benthic fauna with relatively good feeding opportunities; pelagic production is supplemented by other sources, not available in the open sea, such as macro- and microphytobenthos and terrestrial organic matter (Hop et al., 2002; Renaud et al., 2015; Zaborska et al., 2016). Because of their surprisingly variable and flexible feeding behaviours (Dauby et al., 2001; Huenerlage et al., 2015; Legeżyńska et al., 2012), crustaceans can exploit a variety of food sources, adjusting their diet according to local conditions. Fjord morphology, high rates of organic matter fluxes and inorganic sedimentation (Zajaczkowski, 2008) enhance sediment accumulation and inhibit extensive organic matter mineralization (Smith et al., 2015). The surplus of organic matter settled on the bottom in the form of detritus can persist long-buried in the sediments, supporting local benthic communities and releasing them from the dependence on highly seasonal fluctuations of primary production fluxes (Dunton and Schell, 1987; Kędra et al., 2013; McMeans et al., 2013; Renaud et al., 2015). Indeed, detritus has been shown to be an important all-year-round source of food for amphipod communities in the Spitsbergen fjords (Legeżyńska et al., 2012). However, while the food supply seems to be assured in the outer fjord basins, the fauna of the glacial bays may suffer from both a scarcity and the poor quality of food. Typically, organic matter availability diminishes towards the glacial bays (Włodarska-Kowalczuk and Pearson, 2004; Kędra et al., 2010) owing to a number of factors related to glacier activity: decrease in primary production (Piwosz et al., 2009) and dilution of the sedimenting organic matter by the high inorganic sediment load (Görlich et al., 1987).

The pronounced decline of infauna species richness from the outer to the inner basins of Hornsund (62—18 species) and Kongsfjorden (52—15 species) is in accordance with general trends observed in both soft-bottom (Kędra et al., 2013; Włodarska-Kowalczuk et al., 2005, 2012) and hard-bottom benthic communities (Voronkov et al., 2013). Two explanations for the lower faunal diversity in the fjords have usually been put forward: 'the barrier hypothesis', which assumes that geomorphological barriers such as sills or habitat fragmentation may prevent colonization by an offshore species pool, and the 'habitat hypothesis', which attributes the lower diversity of the fjord fauna to the less favourable environmental conditions relative to offshore habitats (Buhl-Mortensen, 1996; Włodarska-Kowalczuk et al., 2012). Both Hornsund and Kongsfjorden lack entrance sills, which should facilitate the penetration of shelf fauna into the fjords. The inner basins, however, are separated from the main fjords by shallow (20—50 m) sills, that may act as a barrier to dispersal. If sills really do act as barriers preventing benthos dispersal, one would expect a different performance of taxa with various dispersal modes in the inner basins (Buhl-Mortensen, 1996). However, a drop in species richness has also been reported in polychaetes with a pelagic larval stage (Kędra et al., 2013; Włodarska-Kowalczuk and Kędra, 2007). Therefore, it can be assumed that the observed trends of diversity are not directly connected with the presence of sills, but rather with the environmental settings characteristic of the outer and inner fjords.

The decline in benthic fauna diversity along the offshore-inner fjord gradient in the Arctic is most commonly attributed to chronic physical disturbances generated by the activity of tidal glaciers (Kędra et al., 2013; Włodarska-Kowalczuk et al., 2005, 2012; Włodarska-Kowalczuk and Węsławski, 2008). Environmental stressors, i.e. high rates of mineral sedimentation, the substantial turbidity of water, unconsolidated muddy sediments and reduced amounts of organic matter, have a detrimental effect on the macrofauna, which may manifest itself in a biodiversity decline, lower abundance and taxonomic distinctness, reduced biomass and simplification of the functional structure (Kędra et al., 2013; Włodarska-Kowalczuk, 2007; Włodarska-Kowalczuk et al., 2005). Nonetheless, major benthic taxa tend to respond differently to glacier-induced disturbances. The diversity and abundance of polychaetes drop considerably with increasing proximity to the glaciers, both in Hornsund (Kędra et al., 2013) and Kongsfjorden (Włodarska-Kowalczuk and Kędra, 2007), while the species richness of molluscs does not change much along the Kongsfjorden axis and their density is significantly higher in the glacial bays than in other basins of the fjord (Włodarska-Kowalczuk, 2007). Crustaceans do not respond to the proximity of glaciers in Kongsfjorden, which is why Włodarska-Kowalczuk and Kędra (2007) stated that other factors must be responsible for their spatial variability. Current results from Kongsfjorden support their conclusion: there has been a decline in the total number of species, but otherwise the malacostracan communities of the inner and outer basins have not varied in average density and diversity. A totally different picture emerged for Hornsund, where the malacostracans of the innermost glacial basin (Brepollen) were clearly less diversified and much poorer in both species and numbers compared to the outer basin community (see the next section). This suggests that the crustaceans' response may be highly variable and difficult to account for. The lack of a clear response to glacier-induced disturbances has also been observed in Antarctic cumaceans (Pabis and Błażewicz-Paszkowycz, 2011).

Environmental conditions in the inner fjord basins may lead to simplification of the functional structure of the faunal associations (Włodarska-Kowalczuk et al., 2005). The benthic communities of the inner fjords are usually dominated numerically by small, mobile, surface detritus feeders represented by several species that cope well with glacial sedimentation disturbances (Włodarska-Kowalczuk, 2007; Włodarska-Kowalczuk et al., 2005, 2012). The same trend holds true in the case of crustaceans. Two taxa that are predominant in the inner bays of both fjords were tanaids and the cumacean *E. emarginata*. Tanaids are elongated crustaceans that are usually less than 2 mm long and most often occur within the surface sediment layer. Their ecology is still poorly known. According to Błażewicz-Paszkowycz and Sekulska-Nalewajko (2004), they prefer sites with unstable sediments. All the species identified by Błażewicz-Paszkowycz and Sekulska-Nalewajko (2004) from the Kongsfjorden samples (included in our material) belong to the suborder Tanaidomorpha, which are assumed to be tubicolous (Błażewicz-Paszkowycz et al., 2012); some species, however, may be free-living inside delicate corridors made of mud particles (Błażewicz-Paszkowycz, 2007). Most tanaids are regarded as non-selective deposit feeders, but the representatives of Pseudotanaidea found in our material may be micropredators feeding on harpacticoida and foraminifera (Prof. M. Błażewicz-Paszkowycz, personal communication). The cumacean *E. emarginata* is a widely distributed eurybathic Arctic-boreal burrowing species. It was the most frequent taxon in our benthic materials, recorded throughout the depth range, but the most abundant in the soft, unconsolidated sediments of inner Kongsfjorden. A similar habitat preference of *Eudorella* spp. was observed in Norwegian (Holte, 1989) and Antarctic fjords (Błażewicz and Jażdżewski, 1995). *Eudorella* has been classified as a phytodetritus feeder (Błażewicz-Paszkowycz and Ligowski, 2002; Legeżyńska et al., 2012). Other important members of the glacial bay communities were the oedicerotids *Arrhis phyllonyx* and *Monoculodes packardi*. Oedicerotidae species are known to dominate soft bottoms and are especially dominant in the fjords (Buhl-Mortensen, 1996). They are highly mobile forms, capable of exploiting both sediment and epibenthic food sources such as detritus and meiofauna (Enequist, 1949; Legeżyńska et al., 2012). In accordance with the general trends observed in macrofauna (e.g. Włodarska-Kowalczuk et al., 2005, 2012), the Malacostraca of the outer fjord basins were functionally more diversified. A more compact bottom and higher primary production (Piwosz et al., 2009) promotes the occurrence of tube-dwelling amphipods such as *Ampelisca eschrichtii*, *Haploops tubicola* and *Unciola leucopis*, which are 'interface feeders', using their antennae to collect particles from both the sediment surface and the water column (Legeżyńska et al., 2012).

## 5.4. Kongsfjorden vs. Hornsund

The results of the PERMANOVA analysis suggest different taxonomic, functional and size compositions of the malacostracan assemblages in the two fjords, but these differences can be regarded as different expressions of the same species pool since they were largely due to the varying dominance patterns of the same set of species. This concurs with the results of the study by Berge et al. (2009) on Decapoda in Isfjorden (Spitsbergen). Although some 30 species were unique to each fjord, none of these taxa was numerous or frequent. It, thus, appears that the 'core set' of species is common to both fjords.

The different performance of the same species pool in the two fjords could be due to several factors. Firstly, Kongsfjorden and Hornsund differ in terms of geomorphology and dominant water masses. The geomorphological features at the mouth of Kongsfjorden permit a twofold faster rate of water exchange with this fjord (Promińska et al., 2017), which receives warm Atlantic water from the West Spitsbergen Current via the deep Kongsfjordrenna. In contrast, the advection of shelf waters is weaker in Hornsund, the mouth area of which is rather shallow (maximum depth about 150 m; Promińska et al., 2017). Furthermore, the strong hydrological front on the adjacent shelf partially blocks the inflow of Atlantic waters which, along with the stronger penetration of Arctic waters carried by the Sørkapp Current from the Barents Sea, results in the more Arctic character of this fjord (Walczowski, 2013). Shelf water advection has a major impact on the pelagic system (Buchholz et al., 2010; Dalpadado et al., 2016; Gluchowska et al., 2016). The absolute predominance of *T. abyssorum* observed in Kongsfjorden is in accordance with the recent study by Dalpadado et al. (2016). The dominance of this species, together with the presence of Atlantic euphausiid species such as *Meganyctiphanes norvegica* and *Nematoscelis megalops* (Buchholz et al., 2010), has been recognized as a clear sign of the "Atlantification" of Kongsfjorden, which is happening as a result of the rising temperatures of the Atlantic waters penetrating into it (Dalpadado et al., 2016). On the other hand, the predominance of a more Arctic species, *T. inermis*, in Hornsund has been attributed to the cold conditions persisting due to the influence of the coastal Sørkapp Current (Buchholz et al., 2010). The input of coastal currents may also explain the high dominance level of Decapoda larvae in Hornsund (this study). The shallow rocky bottom on the shelf south of Hornsund is an important spawning ground for the hermit crab *P. pubescens* (Balazy et al., 2015). The direct influence of different water masses on benthic fauna distribution seems less probable, but benthic communities may be impacted indirectly, e.g. by changes in the planktonic community possibly modifying feeding conditions. We observed higher proportions of suspension-feeding species in Hornsund, which is in accordance with the higher primary production rates reported for this fjord by Piwosz et al. (2009). These species may also be benefitting temporarily from sedimenting ice-algae diatoms, which are associated with pack ice remnants carried by the Sørkapp Current from the Barents Sea.

According to our results the benthic malacostracan community of inner Hornsund is more impoverished than that of the corresponding area of Kongsfjorden. A significant drop in species richness was observed in both fjords, but only in Hornsund was it accompanied by a significant decrease in density and diversity. This seems quite surprising since the organic carbon content is higher in the Hornsund glacial bay than in the inner Kongsfjorden (Drewnik et al., 2016; Kędra et al., 2010; Włodarska-Kowalczuk and Pearson, 2004). However, higher percentages of terrestrial organic carbon are characteristic of the surface sediments in Hornsund (Zaborska et al., 2016). Koziorowska et al. (2016) reported that terrestrial organic carbon makes up to 82% of total carbon pool in the inner Hornsund. Compared to fresh marine organic matter, terrestrial carbon is regarded as a less suitable food source because most marine organisms appear to be unable to digest and assimilate refractory compounds such as cellulose and lignin without their prior microbial breakdown (Antonio et al., 2010).

The poor performance of malacostracans in the inner Hornsund may also be due to its greater isolation. Hornsund contains several distinct basins, and only a very narrow (1.7 km) passage connects the innermost glacial bay (Brepollen) with the main fjord basin (Drewnik et al., 2016; Moskalik et al., 2013). As a result, Brepollen is a truly isolated habitat, with very limited water exchange and a persistent near-bottom layer of cold winter waters. In contrast, Kongsfjorden's central basin takes the form of an elongated deep trough that almost reaches the inner sill. The narrowest cross section (~4 km) is located in the central part of the fjord; closer to the glacier there is a broad connection allowing unhampered penetration of upper water layers into the glacial bay.

Based on observations from Brepollen, where the near-bottom temperature has remained between −1.8°C and −0.6°C during the last 30 years, Węsławski et al. (2011) suggested that the inner fjord basins may be acting as refugia for stenothermic Arctic species. Although the dominance of widely distributed Arcto-boreal taxa in the inner fjords demonstrated in this study does not support this concept, we did observe a clear preference for the inner bay habitats in two typical Arctic species — *Onisimus caricus* and *Lepidepecreum umbo*.

## 6. Conclusions

There is general agreement that the Arctic Ocean is currently in a transition towards a new, warmer state (Narayanaswamy et al., 2010). Oceanographic variability has been proven to have a direct and detectable influence on pelagic (Dalpadado et al., 2016) and benthic fauna (Berge et al., 2005; Beuchel et al., 2006; Kortsch et al., 2012) in Spitsbergen fjords. Owing to the influence of different water masses, 'warm' Kongsfjorden and 'cold' Hornsund could serve respectively as examples of areas in a transition state and true Arctic areas. Our results suggest that the contrasting hydrological regimes have a strong impact on the pelagic malacostracan communities, but govern neither the distribution nor the diversity of benthic taxa, which are influenced more by the interaction of several factors, such as depth, sediment type, microhabitat variety and food availability and quality. The majority of species collected were widely distributed Arctic-boreal forms, capable of surviving over the whole range of temperatures and salinities noted in both fjords. Our results suggest that habitat homogenization resulting from the predicted increase of sediment discharge associated with accelerated glacier melt will severely affect benthic malacostracan communities. A clear decline of species richness was observed on the uniform muddy bottoms of the glacial bays of both fjords, although the patterns of species density and diversity differed in Kongsfjorden and Hornsund. The greater impoverishment of the benthic malacostracan community found in the Hornsund glacial bay was probably due to its greater isolation and poorer quality of sediment organic matter in comparison with the corresponding area of Kongsfjorden. Trends common to the glacial bays of both fjords were the numerical dominance of individuals belonging to the smallest species and the reduced trophic diversity. The variability in the taxonomic, size and functional composition of pelagic and benthic malacostracan communities may be ecologically important, and therefore requires further detailed study. As the heterogeneous habitats of the shallow sublittoral are likely to be diversity and density hot spots for benthic malacostracans, an extensive survey across the entire range of shallow water habitats is needed in order to obtain a realistic inventory of the fjords' species.

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