

Patterns of hydroid (Cnidaria, Hydrozoa) species richness and distribution in an Arctic glaciated fjord

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Abstract The consequences of global warming are particularly evident in high polar areas. Deglaciation phenomenon—negative mass balance of Svalbard glaciers and recession of tidal glaciers—results in landscape and shoreline change. These areas of very dynamic conditions are now open for primary colonists, among them hydroids, typical early colonists of the vacant substratum. This study aims to explore the patterns of Hydrozoan diversity and distribution in Hornsund (west Spitsbergen). Hydroids associated with shallow water kelp beds as well as those occurring on deeper subtidal soft bottom were collected at sites located along gradients of glacial disturbance (i.e., high mineral sedimentation, ice-berg scouring). Samples were collected by scuba diving (three sites of different distance to active tidal glaciers), van Veen grabs (two sites located in the inner and outer fjord basin), and dredges taken from along a fjord transect. Hydroid diversity differed significantly between sites located in the vicinity of glacier fronts in glaciated bays and sites comparatively free from glacier disturbance. Glacial disturbance results in low frequencies of occurrence and high levels of rarity of hydroids at sites located close to glacier fronts. The species richness of hydroids colonizing the hard substrate elements present in deeper subtidal decreases along the fjord axis (i.e., along the glacial sedimentation gradient).

Keywords Arctic · Hydroids · Glacier disturbance · Climate change · Sedimentation

Introduction

Arctic fjord ecosystems are strongly affected by glacier-derived disturbances mainly derived from the outflow of meltwaters produced by active tidewater glaciers. Factors that affect marine biota include large fresh-water inputs, high levels of concentrations of mineral suspensions in waters, high rates of inorganic sedimentation, and iceberg bottom-scouring (Węsławski et al. 1995; Hop et al. 2002; Włodarska-Kowalczyk and Pearson 2004).

Increased tidewater glacier activity is predicted to be one of the consequences of global warming (Lefauconnier et al. 1994; Svendsen et al. 1996; Włodarska-Kowalczyk and Węsławski 2001). High loads of inorganic material increase water turbidity which influences light conditions and reduces primary production. Furthermore, high levels of inorganic particle sedimentation in the vicinity of glacier outlets “dilute” the organic matter available to benthic consumers (Görlich et al. 1987). The presence of sediment in the water column is regarded as a severe stress agent for hard-bottom macroorganisms, especially suspension feeders (Moore 1977; Görlich et al. 1987; Kukliński 2002; Airoldi 2003). Suspension-feeding organisms in sediment-stressed environments are observed to experience reduced survival and mortality as a consequence of burial, scouring, and clogging of their filtering apparatus by sediment (Moore 1977). This can cause changes in species composition and diversity in communities. Moreover, the distribution patterns of sessile invertebrates are formed by substrate selection processes occurring during larval settlement (Wilson 1968; Hayward 1980). In a sediment-impacted

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environment, the loss of suitable hard substrates can inhibit larval recruitment (Genzano et al. 2002; Irving and Connel 2002; Airoidi 2003).

To study the effect of glacier-derived impact in a glaciated fjord, we chose benthic hydroids as a model group. Hydroids are a poorly known group in Svalbard waters and species new to science and to the region are still being described (Ronowicz 2007; Ronowicz and Schuchert 2007; Voronkov et al. 2010). Despite their small size and delicate forms, hydrozoans play a significant role in the environment (e.g., bioconstructing, energy transfer) and can be useful for monitoring purposes. Their sessile mode of life and phenotypic variations within species make them good indicators of their environmental surroundings (Gili and Hughes 1995). It has been recognized that hydroids are an important component of epibiotic communities in Arctic fjords (Włodarska-Kowalczyk et al. 2009). Hydrozoa represent the third most species-rich group (after Polychaeta and Bryozoa) and together with bryozoans constitute about half of the species present within the kelp forest assemblage in a Svalbard fjord (Włodarska-Kowalczyk et al. 2009). Hydroids are typical early colonists of vacant substrates (Hughes et al. 1991) and play an important role in pelagic-benthic coupling (Gili et al. 1998). They transfer energy from the pelagic to benthic systems (Gili et al. 1998; Bouillon et al. 2004) and viceversa (Orejas et al. 2000). It is documented that presence of hydroids increases the complexity of habitats and enriches benthic communities in relation to the diversity and abundance of benthic fauna (Bradshaw et al. 2003). Hydroid erect colonies can serve as a shelter from predators, nursery grounds, as a substrate for egg deposition or as a physical support for suspension feeders (e.g., encrusting bryozoans, juvenile bivalves) which are lifted up above the sea bottom where current conditions are more favorable and where they are less exposed to sedimentation.

The present study explores the effects of glacial disturbance on the patterns of hydrozoan distribution and diversity in two habitats of an Arctic glacial fjord, the kelp beds, and deeper subtidal region.

Study area

The study was performed in a high Arctic fjord—Hornsund (76°56′–77°03′N; 15°28′–16°45′E), the southernmost fjord in Spitsbergen (Svalbard Archipelago) (Fig. 1).

The area of the fjord is 1,232 km². Its wide entrance (12 km) is oriented toward the west and its broad connection with the open shelf and the lack of a sill enable the penetration of oceanic waters into the central basin of the fjord. The hydrological regime in Hornsund is complex and is formed by the interplay of warm waters transported by the

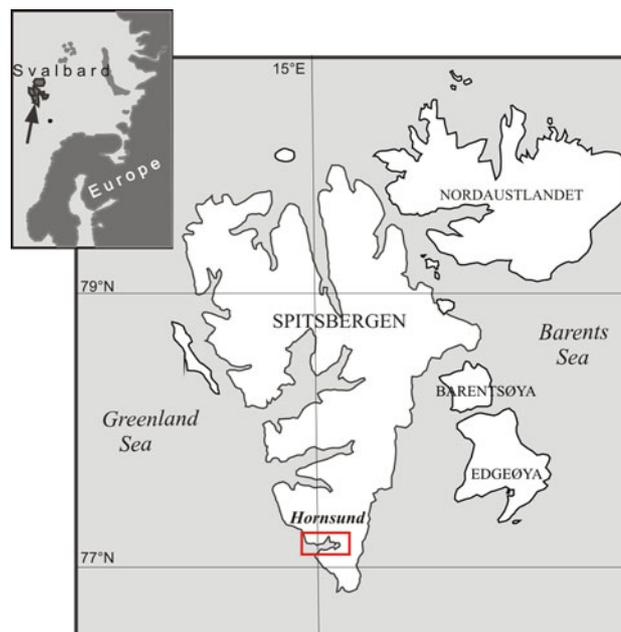


Fig. 1 A map of the study area

West Spitsbergen Current, cold waters transported by the Sørkapp Current, and coastal waters that develop locally and seasonally (Swerpel 1985).

Hornsund is a typical glacial fjord, where ice cliffs constitute 24% of the coastline. Thirteen tidewater glaciers terminate in Hornsund waters (Głowacki 2007). These glaciers strongly modify the physical environment of the fjord by discharging high loads of fresh water and inorganic suspensions. The fjord expanded continually due to the recession of all tidal glaciers. One of the best studied glaciers, Hornbreen, retreated by an average of 140 m annually from 1900 to 1990 (Ziaja 2001). Hansbreen, a glacier located in the vicinity of the Polish Polar Station, has gradually lost 0.5 m of its thickness annually for the last few years because of calving from ice front and evaporation (Głowacki 2007). Active tidewater glaciers discharge icebergs in summer. The commonly used in this article term “glaciated bay” refers to a bay that is located in a vicinity of a tidal glacier and remains under the strong influence of tidal glacier activity.

Methods

Sampling

Hydroids of kelp beds

Hydrozoans inhabiting kelp beds were collected by SCUBA divers at three sites located at different distances to active glacier outflows in July 2003 in Hornsund fjord (Table 1; Fig. 2):

Table 1 Sampling effort and sampling methods used at the studied locations

Site	Coordinates	Depth	Gear	Number of samples
Isbjørnhamna	76°59'46"N; 15°33'27"E	5–10	Diving	133
Gåshamna	76°56'50"N; 15°45'15"E	5–10	Diving	113
Hyrneodden	77°01'20"N; 16°03'27"E	5–10	Diving	94
Inner	77°09'57"N; 16°30'26"E	100–120	Van Veen grab	19
Outer	76°55'15"N; 15°33'25"E	100–115	Van Veen grab	24
A	76°34'57"N; 15°16'08"E	147	Dredge	1
B	76°35'11"N; 15°25'55"E	79	Dredge	1
D	77°00'07"N; 16°12'25"E	99	Dredge	1
E	76°35'18"N; 16°07'20"E	111	Dredge	1
F	76°35'11"N; 16°11'36"E	119	Dredge	1
G	77°01'43"N; 16°18'38"E	123	Dredge	1

**Fig. 2** Sampling sites in Hornsund fjord; diving sites (Isbjørnhamna, Hyrneodden, Gåshamna), dredge sites (A, B, D, E, F, G), and grab samples (Inner and Outer). Glaciers are indicated by white areas

Isbjørnhamna (I)—situated close to the fjord entrance but close to the Hansbreen glacier outflow, with very high inorganic particle sedimentation;

Hyrneodden (H)—situated in the inner part of the fjord, close to several active tidewater glacier outflows, with an intermediate level of inorganic particle sedimentation;

Gåshamna (G)—situated close to the fjord entrance, far from the glacier outflows, with very low inorganic particle sedimentation.

Altogether 340 samples of the three most common macroalgae *Laminaria digitata* (Hudson) Lamouroux, 1813, *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druel & G.W. Saunders, 2006, and *Alaria esculenta* (Linnaeus) Greville, 1830 with associated fauna were collected: 133 samples in Isbjørnhamna, 113 samples in Gåshamna, and 94 samples in Hyrneodden. Samples were collected at each site from depths of 5 and 10 m. Each algal sample was carefully cut from the substrate with a knife and placed in a separate bag of 1 mm mesh size.

Sedimentation rates at all three sites were determined using sediment traps made of PVC cylinders (height—50 cm,

diameter—8 cm) exposed for 24 h (3 replicates at each site). After 24 h, they were recovered from the sea bed and taken to the laboratory and left for another 24 h until the sediments had settled. Then, the supernatant was decanted, and the remaining mixture of water and sediment was filtered through Whatman GF/C 47 mm filters. These were dried at 60°C for 24 h and weighed. The weighed filters loaded with sediment were placed in an oven (450°C) for 24 h and afterward weighed again to determine the mineral matter weight and organic matter loss.

Hydroids of deeper subtidal

The material collected in deeper subtidal zones included samples taken with van Veen grabs and dredges (Table 1; Fig. 2). Samples were collected from aboard the *r/v Oceania*. Grab sampling was performed in Hornsund in July 2005 at two sites: the fjord inner basin, Brepollen, and at the outer part on the southern bank of the fjord entrance (Fig. 2). Six stations were arranged at 200-m intervals along 1-km transects at both locations. Four replicates were collected at each station using a van Veen grab (0.1 m²). Station depths varied from 100 to 120 m on the inner transect and from 100 to 115 m on the outer transect.

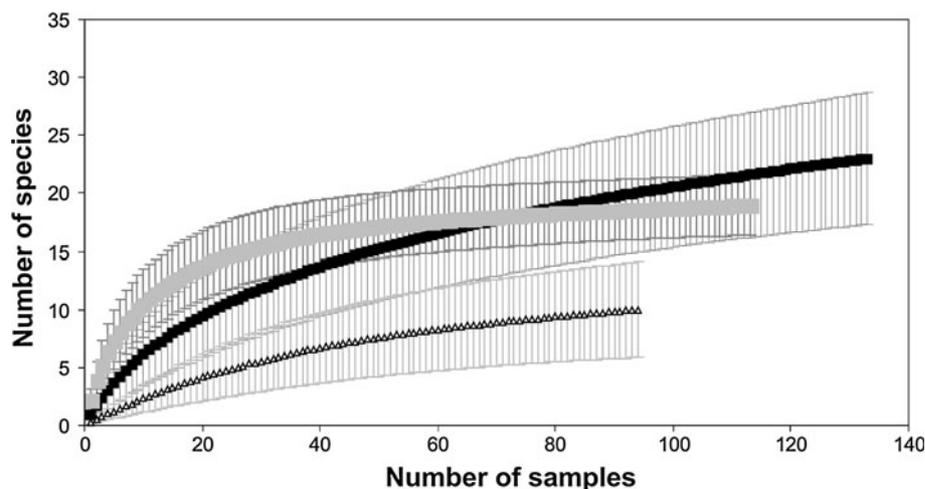
Six samples were collected by dredging along the fjord axis in July 2002 (Fig. 2).

All samples were sieved gently through a sieve of 0.5 mm mesh size and fixed in a 4% formaldehyde solution aboard the ship. Material was sorted and all the hydroid specimens were identified in the laboratory to the lowest possible taxonomic level.

Data analyses

To assess and compare, the species richness of the three kelp beds sites species accumulation curves with 95%

Fig. 3 Species accumulation curves plotted with 0.95 confidence intervals for observed number of species; *black*—Isbjørnhamna, *grey*—Gåshamna, *grey with black dots*—Hyrneodden



confidence intervals were computed using formulae by Colwell et al. (2004). The computation of confidence intervals allows for the direct statistical comparison of the species richness of two data sets, i.e., differences are not significant at $P < 0.05$ if the 95% confidence intervals overlap (Colwell et al. 2004).

The number of species per sample was used as the measure of sample species richness. The differences between sample species richness among sites (for diving sites and grab samples estimated separately) were tested using the nonparametric Kruskal–Wallis test. The pair-wise Mann–Whitney U -test was used for post-hoc multiple comparisons (STATISTICA v. 6, Statsoft).

The number of rare species (uniques—occurring in one sample and duplicates—occurring in two samples) for each site was calculated, and the percentage of rare species in the total number of species was assessed for each site. The frequency of species occurrence at sites was estimated as the percentage of samples at particular sites in which the species occurred to the number of samples at the sites. Then the mean frequency of hydroid occurrence was determined for each site as the mean value of frequencies calculated for all species occurring at a site. Multivariate analysis was performed to identify patterns of hydroid species distribution. The similarity among samples was calculated with the Bray–Curtis index. The differences in species composition among the three sites were tested with the one-way ANOSIM pair-wise test performed with the Primer package v. 6 (Clarke and Warwick 2001).

The frequency of species occurrences in samples collected with the use of diving and grabs was estimated as the percentage of samples in which the species occurred to the total number of samples at the site.

Results

Hydroids of kelp beds

Three sites were located at different distances to active tidal glaciers and differed with respect to glacier disturbance levels. There were clear differences in sedimentation rates of mineral particles. Both mineral and organic sedimentation rates were highest in Isbjørnhamna—the most affected by the tidal glacier ($146.53 \text{ mg dm}^{-3} \text{ day}^{-1} \pm \text{SD } 103.68 \text{ mg dm}^{-3} \text{ day}^{-1}$ and $20.36 \text{ mg dm}^{-3} \text{ day}^{-1} \pm \text{SD } 12.24 \text{ mg dm}^{-3} \text{ day}^{-1}$, respectively) and reached the lowest value in Gåshamna—the site free from direct impact from glaciers ($12.73 \text{ mg dm}^{-3} \text{ day}^{-1} \pm \text{SD } 4.75 \text{ mg dm}^{-3} \text{ day}^{-1}$, and $5.27 \text{ mg dm}^{-3} \text{ day}^{-1} \pm \text{SD } 2.59 \text{ mg dm}^{-3} \text{ day}^{-1}$, respectively). Numerous icebergs (including large grounded ones) were observed at Hyrneodden during the entire sampling period (5 weeks), while at Isbjørnhamna, the icebergs were observed in lower numbers and only occasionally. No icebergs were observed at Gåshamna.

Hydroids were present on collected macroalgal thalli occurring with a frequency of 79% in samples at Gåshamna, 63% at Isbjørnhamna, and 28% at Hyrneodden.

The species accumulation curves plotted against the sampling effort for the three sites did not stabilize toward asymptotic values (Fig. 3). The 95% confidence intervals for the observed number of taxa at Isbjørnhamna and Gåshamna overlap indicating no significant difference in the total species richness between the two sites. The total number of species was the lowest in Hyrneodden and differed significantly from the other two sites.

The maximum total species richness was noted at Isbjørnhamna (23 species) (Fig. 4). However, there were 12 species occurring at low numbers (uniques and duplicates).

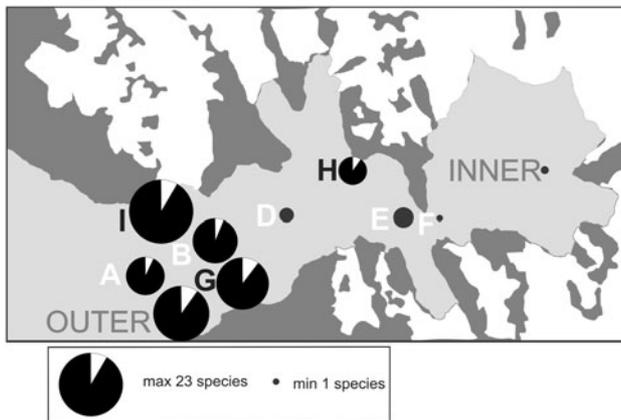


Fig. 4 Total number of hydroid species at the Outer and Inner site, and dredge samples A, B, D, E, F; black—Leptothecata, white—Anthoathecata

Table 2 Comparison of species richness and species rarity at three sites

Site	Total number of species	Number of uniques and duplicates	Percentage of rare species
Gåshamna	19	3	16
Isbjørnhamna	23	12	52
Hyrneodden	10	5	50

A total of 19 species were observed at Gåshamna (with three species at low number of records), while only ten species were recorded at Hyrneodden (with half of them being uniques or duplicates—see “Methods”) (Table 2).

There were significant differences in hydroid sample species richness among the studied sites (Kruskal–Wallis test: $H = 83.85$, $P < 0.05$). The post-hoc pair-wise tests revealed significant differences in sample species numbers between two pairs of sites: Gåshamna—Isbjørnhamna and Gåshamna—Hyrneodden (Mann–Whitney U -test, $P < 0.05$), whereas hydroid sample species richness at Isbjørnhamna and Hyrneodden did not differ significantly (Mann–Whitney U -test: $P > 0.05$).

The highest mean sample species richness was found at Gåshamna (Fig. 5).

The highest mean frequency of hydroid species occurrences was also noted at Gåshamna (10.52%), while at Isbjørnhamna and Hyrneodden values were lower (3.79 and 2.55%, respectively). The most common species occurred with the frequencies exceeding 20% at Gåshamna and Isbjørnhamna, while no species were recorded with frequency over 10% at Hyrneodden (Table 3).

Hydroids in deeper subtidal

Hydroids were present in 79% of grab samples taken at the Outer stations and in 7% of samples taken at the Inner

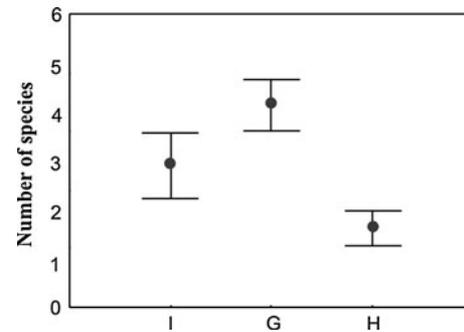


Fig. 5 Number of species per sample (mean \pm 0.95 confidence intervals) at the three sites: I—Isbjørnhamna, G—Gåshamna, H—Hyrneodden

stations. The total number of observed hydroids taxa was 20. All of them were recorded at the Outer site (fjord entrance), while at the Inner site (glaciated bay) only two species were noted (Fig. 4). Most of the species (18 species) belonged to the order Leptothecata. Anthoathecata was represented by only two species (*E. annulatum* and *Sarsia* sp.) present only at the Outer site.

Sample species richness varied significantly between the two sites (Kruskal–Wallis test: $H = 23.58$, $P < 0.05$) and reached on average 5.5 species per sample at the Outer transect and 0.1 species per sample at the Inner transect (Fig. 6).

Hydroid species composition varied between samples of the Inner and Outer sites. *Symplectoscyphus tricuspoidatus* was the most common species at the Outer site (frequency 67%) (Table 3). *Abietinaria pulchra*, *Eudendrium annulatum*, *Sertularia schmidtii*, and *Sertularia cupressoides* occurred at frequencies over 50%. At the Inner site, both *Gonothyrea loveni* and *Lafoeina maxima* occurred with 7% frequency.

Most of the specimens collected were not attached to any substrate. Due to the sampling methods delicate colonies of hydroids are often broken off, although if the coenosarc and hydrant are present the specimen was treated as live-collected. Among the few that were found with substrata, they attached to rocks, bryozoans, two species of other hydrozoans, shells of bivalves and barnacles.

In dredge samples, species richness changed according to the location within the fjord transect. It was lowest (one and zero species per sample) for stations (F and G respectively) in the glaciated bay and sharply rising with increasing distance from the inner fjord. The highest values were at stations A and B (14 and 15 species per sample correspondingly) at the fjord entrance (Fig. 4). The only species collected in the inner fjord was *S. argentea*. Only one representative of the order Anthoathecata, *E. annulatum*, occurred exclusively at the outer stations.

The differences in species composition among the sites under the influence of glacial impact (Inner, F and G) and

Table 3 Frequency of occurrence of hydroid species at sites

Species	I	G	H	Inner	Outer
Leptothecata					
Campanulinidae					
<i>Calycella syringa</i> (Linnaeus, 1758)	**	**			
<i>Campanulina pumila</i> (G.O. Sars, 1874)	*	*	*		
<i>Cuspidella</i> sp.	*	*	*		
<i>Lafoeina maxima</i> Levinsen, 1893				*	**
Haleciidae					
<i>Halecium arcticum</i> Ronowicz and Schuchert 2007	*	**	*		
<i>Halecium curvicaule</i> Lorenz, 1886		*			
<i>Halecium mirabile</i> Schydlofsky, 1902	*	*	*		
<i>Halecium muricatum</i> (Ellis & Solander, 1786)					*
Lafoeidae					
<i>Filellum serpens</i> (Hassall, 1848)	*	*			
<i>Grammaria abietina</i> (M. Sars, 1850)					*
<i>Lafoea dumosa</i> (Fleming, 1820)	*	*	*		*
Sertulariidae					
<i>Abietinaria pulchra</i> (Nutting, 1904)					****
<i>Sertularia albimaris</i> Mereschowsky, 1878					*
<i>Sertularia argentea</i> Linnaeus, 1758	*	*	*		**
<i>Sertularia cupressoides</i> Clark, 1876					***
<i>Sertularia fabricii</i> Levinsen, 1893					*
<i>Sertularia mirabilis</i> (Verrill, 1873)					*
<i>Sertularia schmidtii</i> Kudelin, 1914					****
<i>Sertularia similis</i> Clark, 1877					*
<i>Sertularella rugosa</i> (Linnaeus, 1758)	*	*			*
<i>Symplectoscyphus tricuspoidatus</i> (Alder, 1856)	**	**			****
Campanulariidae					
<i>Orthopyxis integra</i> (MacGillivray, 1842)	*	*			*
<i>Campanularia volubilis</i> (Linnaeus, 1758)	**	**	*		*
<i>Gonothyrea loveni</i> (Allman, 1859)	*	*	*	*	**
<i>Rhizocaulus verticillatus</i> (Linnaeus, 1758)					*
Anthoathecata					
Corynidae					
<i>Sarsia</i> sp.					*
Eudendriidae					
<i>Eudendrium annulatum</i> Nutting, 1898	*	*			****

Frequency: * 1–20%, ** 21–40%, *** 41–60%, **** >60%; I Isbjørnhamna, G Gåshamna, H Hyrneodden

those located in the outer part of the fjord, not affected by the glacial impact (Outer, A, B, D, and E), were significant and high (one-way ANOSIM pair-wise test: $R = 0.58$, $P = 0.01$).

Discussion

Arctic fjord ecosystems are strongly affected by glacier-derived disturbances, mainly by the outflow of meltwater

produced by active tidewater glaciers. Tidewater glaciers are often situated in the innermost parts of the fjords (in Hornsund the majority of glaciers), and they have a strong effect on the physical regimes of whole basins and can impact hard and soft-bottom benthic communities (Farrow et al. 1983; Syvitski et al. 1989; Węśławski et al. 1995; Kukliński 2002; Włodarska-Kowalczyk and Pearson 2004). Species richness decreases along the fjord from the outer part to the inner,

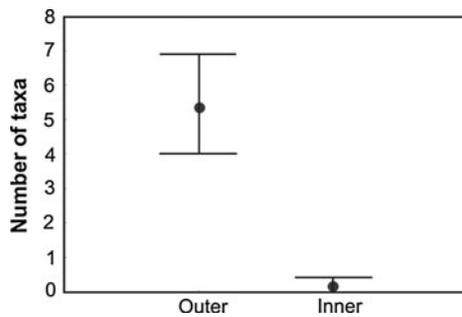


Fig. 6 Mean (± 0.95 confidence intervals) number of species in samples collected at the Outer and Inner stations

indicating that hydroids are vulnerable to environmental stress glacier-derived.

Hydroids in kelp beds

The three sites studied (Isbjørnhamna, Hyrneodden, Gåshamna) differ with regard to hydroid species richness; however, the patterns are different for richness assessed on the scale of single samples (alpha diversity) and on that of whole sites (gamma diversity). The comparison of hydroid sample species richness reveals significant differences between the sites influenced by the glaciers (Isbjørnhamna and Hyrneodden) and the Gåshamna site that is free of glacial impact.

Sample species richness is lower at the two sites situated in the vicinity of glaciers (Isbjørnhamna and Hyrneodden) than at the site located far from glacial inflows (Gåshamna). The impact of sedimentation is the most likely reason for the differences in alpha species richness among the sites studied. A similar decrease in macrobenthic species richness and diversity caused by sedimentation has been observed in soft bottom (Włodarska-Kowalczyk et al. 2005) and rocky bottom (Airoidi 2003) communities. The distribution of hydroid species was significantly related to the amount of silt on the surface of substrate (Voronkov et al. 2010). Magurran (2004) reports that sample species richness is a very sensitive indicator of community perturbation and recommends using sample species richness measures in environmental assessment studies.

Surprisingly, the total number of species per site (gamma diversity) is only lower at Hyrneodden in the inner fjord adjacent to glaciers. There are no significant differences between the other two sites (Isbjørnhamna and Gåshamna) that have different sedimentary regimes, but they are similar in that they are located in the outer part of the fjord. Differences in gamma diversity at different locations in the fjord can be explained by the distance to the fjord entrances and to the local hydroid species pool. According to Buhl-Mortensen and Høisæter (1993), the species pools of fjordic communities are formed by

“...the faunal assemblage outside the fjords, from which the hypothetical fjord colonizers might be recruited.” Since there is no sill at the entrance to the fjord, larvae can enter Hornsund. The outer part of the fjord is more accessible to new hydroid recruits. The distance from Hyrneodden (inner fjord site) to the species pool outside the fjord might be too far for some larvae to cover since hydroid planula larvae typically remain in the water column only a few hours to a few days (Cornelius 1992). Additionally, the gradient of physical conditions from offshore to the inner fjords (oceanic waters modified by glacial melt waters) may represent a “habitat barrier” for the larvae. Klitgaard-Kristensen and Buhl-Mortensen (1999) report that decreases in amphipod and mollusk diversity observed in Norwegian fjords along fjord transects is a result of progressively less favorable environmental conditions towards the fjord head. Environmental conditions such as sediment type, bottom currents, ice scouring, and the quantities and availability of organic carbon change along fjord axes in a way that allows fewer species to thrive in inner basins.

Differing patterns of hydroid frequencies are observed at the three study sites. Half of the species occurring at Isbjørnhamna (52%) and Hyrneodden (50%) are recorded only once or twice, while at Gåshamna rare species comprise only 16% of the species present. The mean hydroid species frequency is higher at Gåshamna in comparison with other sites indicating that species occur more often in the samples collected at this unimpacted site. High sedimentation rates and iceberg scouring at sites situated close to the glacial front presumably restrict hydroid colonization which, in turn, resulted in the low frequencies of occurrence and high levels of rarity there. Thus, species rarity occurs because environmental factors constrain their ranges to small areas and do not permit them to establish wider distributions (Hill and Keddy 1992; Gaston 1994; Greulich et al. 2000). Reasons for rare occurrence may include the following: (1) lack of available habitats corresponding to species requirements; (2) lack of the chances for successful settlement that depend on larval dispersal capacity and establishment ability; (3) lack of the ability of developing into mature stages, and withstanding given physical conditions and biological interactions; (4) lack of reproductive success (Greulich et al. 2000). Since there is no direct glacier impact at Gåshamna, sedimentation rates are low and no iceberg scouring occurs. Thus, the hydroid community here is undisturbed and is older because of the low frequency of physical disturbances.

Hydroids of deeper subtidal

The total species richness and sample species richness of Hydrozoa collected with grabs and dredges in the deeper sublittoral zone decreases from the outer to the inner parts

of the fjord. Studies of hydroids on hard bottom substrate from Kongsfjorden (Spitsbergen) seem to confirm the finding as reduced diversity and biomass in the inner part of the fjord compared to the outer part was observed (Voronkov et al. 2010). Only three species (*S. argentea*, *G. loveni*, *L. maxima*) are present within the innermost glaciated bay, where their occurrence is limited to single records. These three species are characterized by an erect colony morphology that allows them to rise above the sediments and avoid being buried. Their presence in such unfavorable conditions is most likely accidental. Suspended silt is probably a detrimental for hydroids (Round et al. 1961). Withers and Thorpe (1977) suggest that sediment blanketing surfaces might inhibit larval settling or metamorphosis in most species. Another factor limiting hydroid colonization in inner fjordic basins is the lack of hard substrates. The only hard substrates available in the inner parts of fjords are mollusk shells or drop stones, which are likely to be covered by sediment. Soft bottoms and glacial influence can limit hydroid colonization potential and persistence in specific habitats of glaciated bays.

The phenomenon of decreasing species richness and/or occurrence from the outer to the inner parts of fjords is observed throughout the macrobenthic community (Włodarska-Kowalczyk et al. 2005; Renaud et al. 2007) and for many different macrofaunal groups, including bryozoans (Kukliński et al. 2005), sipunculans (Kędra and Włodarska-Kowalczyk 2008), and crustaceans (Legeżyńska, personal communication). Nevertheless, glaciated bays are not deprived of life. The characteristic species for the soft bottom glacial community include bivalves from the families Nuculanidae and Thyasiridae, which are very efficient detritus feeders, and the polychaete *Chone paucibranchiata* (Krøyer 1856) which feeds both on organic particles suspended in waters and on sediment surfaces (Włodarska-Kowalczyk and Pearson 2004). High inorganic sedimentation is not a limiting factor for the suspension-feeding bryozoan *Alcyonidium disciforme* Smitt 1871, a common inhabitant of glaciated bays. The sand particles from its immediate surroundings are sequestered and bound in an external cuticle (Kukliński and Porter 2004) that is likely an adaptation, but one that is not yet fully understood.

Conclusions

Our results indicate that the species richness of hydroids decreases along the fjord axis (i.e., along the glacial sedimentation gradient). The lack of hard substrate together with a very high environmental stress are the major limiting forces for the occurrence of hydroids in the deeper sublittoral zone of the inner fjord. Severe disturbance (high sedimentation rates and frequent iceberg

scouring) results in the low frequencies of occurrence and high levels of rarity of hydroids at sites located close to glacier fronts.

Changes in the marine environment in Arctic fjords (increased tidal glacier activity and increased load of mineral particles) induced by climate change may result in the decrease of hydroid diversity.

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