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Hydroid epifaunal communities in Arctic coastal waters (Svalbard): effects of substrate characteristics

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Abstract The knowledge of cryptic epifaunal groups in the Arctic is far from complete mostly due to logistic difficulties. Only recently, advances in sample collection using SCUBA diving techniques have enabled to explore delicate hydroid fauna from shallow waters. This study is the first attempt to examine the relationship between substrate property (such as size of rock, morphological characteristics of algal or bryozoan host) and hydroid community composition and diversity in the Arctic. Samples of substrates for hydroid attachment including rocks, algae, bryozoans and other hydrozoans were collected around the Svalbard. Examination revealed no substrate-specific species. The substrate property did not have a strong influence on hydroid community. Both species composition and richness were not related to colonized rock surface area and to morphological characteristic of algal host. Therefore, results indicate the opportunistic nature of hydroid fauna in terms of substrate preference. However, the presence or absence of hydroids depended on the surface area of rocky substrate. Hydroids were more often present on rocks of larger surface area. Erect hydroids and bryozoans were important attachment surface for stolonal hydroids.

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Introduction

Hydroids (sessile stage of Hydrozoa) may grow on a variety of hard substrates (rocks, plastics, glass, wood) as well as on living or dead organisms (Gili and Hughes 1995). They are known as common components of fouling communities. Owing to their rapid growth rates and opportunistic nature, hydroids are successful pioneer organisms that are often among the first colonists of unoccupied surface (Boero 1984; Hughes et al. 1991). In frequently disturbed environments, they are capable of establishing the first stage of epibiotic succession (Dean and Hurd 1980; Orlov 1997). Their dominance is usually only temporary and limited to the first phases of succession (Boero 1984). In next stages of succession, they are frequently replaced by superior competitors such as algae, ascidians, sponges, barnacles, bryozoans and polychaetes (Boero 1984; Barnes and Kuklinki 2004). However, there is also an example indicating a different settlement strategy of hydroid. Experimental panel assemblage dominated by *Hydractinia echinata* (Fleming 1828) was very persistent and did not change throughout several recruitment seasons (Sutherland 1981). This means that this species is long lived and resistant to larval recruitment of other species (Sutherland and Karlson 1977; Sutherland 1981).

Both ecological papers and taxonomical revisions frequently report the type of substrate to which hydroids are attached (Naumov 1969; Zamponi et al. 1998; Schuchert 2001; Genzano et al. 2009). However, detailed analyses of the relationships between substrate characteristics and hydroid diversity or community structure in the Arctic are lacking. Some efforts have been recently undertaken to examine the substrate type and its hydrozoan fouling assemblage in the Arctic (Ronowicz et al. 2008, 2013; Voronkov et al. 2010). In other regions, this topic is much

better recognized. A rich literature is dedicated to examine both the epiphytic (Coma et al. 1992; Watson 1992; Faucci and Boero 2000) and the epizootic (Boero and Hewitt 1992; Cerrano et al. 2001; Puce et al. 2008) interactions of hydroids with their host organisms. Rocky substrate was much less investigated. There are a few published surveys in which rocks and cobbles are mentioned to serve as substrates for hydroid settlements, but with no reference to substrate characteristics (e.g., Nishihira 1965; Genzano and Rodriguez 1998; Henry et al. 2008).

In this paper, we describe patterns of distribution and diversity of hydroids colonizing four substrates: rocks, algae, Bryozoa and Hydrozoa in the Arctic waters of Svalbard archipelago. We explore the effects of substrate characteristics on hydroid community composition and diversity.

Study area

The sampling area was located around the Svalbard archipelago (Fig. 1), a group of islands between 74°–81°N and 10°–35°E. The largest island is Spitsbergen. The archipelago features an Arctic climate, with significantly higher temperatures on the west coast than on the east one. This is caused by the influence of warm Atlantic waters flowing northward along the west coast with the West Spitsbergen Current ($T > 2$ °C, $S > 34.7$ PSU) (Svendsen et al. 2002). Cold water masses from the north ($T < 0$ °C, $S = 34.3$–34.8 PSU) flows southward as the East Spitsbergen Current and mostly affects the eastern part of the

Svalbard Archipelago (Loeng 1991). The southern extension of this cold water masses, the Sørkapp Current, turns to the north beyond South Cape, and then, runs north parallel to the West Spitsbergen Current.

The most characteristic attributes of the Svalbard landscape are glaciers covering over 60 % of its land mass and deep and narrow fjords of glacial origin indenting main islands. The fjords are filled with soft sediment delivered with glacier outflows. Hard bottom prevails in shallow areas exposed to strong currents (Gulliksen and Svensen 2004).

Methods

Material used in this study comes from several scientific expeditions to Svalbard aboard the r/v *Oceania* (July 2002, 2004, 2005, 2006, 2007), the r/v *Jan Mayen* (September 2001), and the r/v *Lance* (October 2007), as well as during expeditions based at the Polish Polar Station in Hornsund in July 2003 and July 2006 (Table 1). Supplementary samples, provided by Akvaplan-niva, were collected off the east coast of Svalbard in 1996. The majority of the sampling stations were located off the west coast of Spitsbergen, especially in Hornsund fjord. Altogether 557 samples were collected from around the entire archipelago with use of different types of gears (SCUBA divers, dredging, van Veen grab with a catch area of 0.1 m^2), from intertidal down to 329 m depth. The samples were fixed in a 4 % buffered formalin solution. Substrates with attached fauna were carefully examined in the laboratory. Hydroid

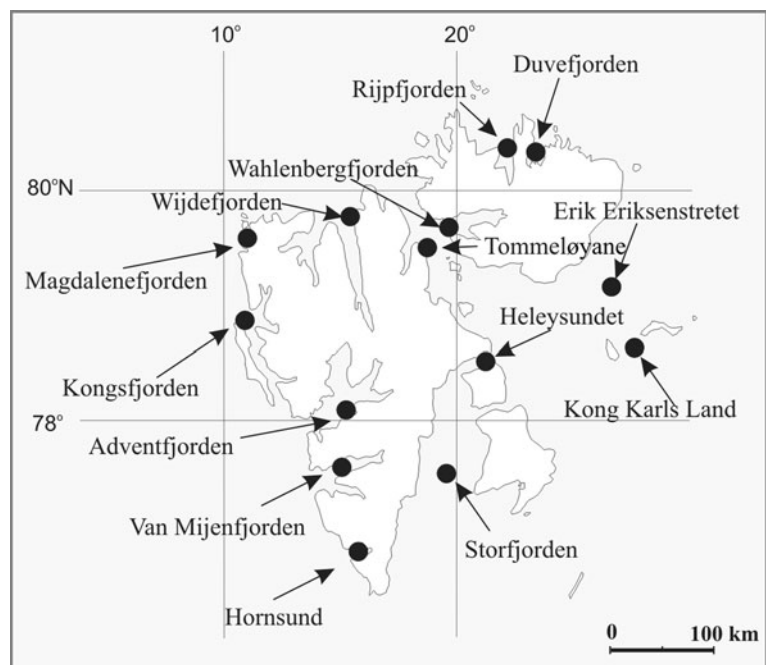**Fig. 1** Svalbard archipelago with sampling sites marked with *circles*

Table 1 Station sampling information

Station	Coordinates	Depth (m)	Years	Type of gear	Number of samples
Adventfjorden	78°15′15″; 15°29′47″	20–80	2004	Van Veen grab	12
Duvefjorden	80°08′32″; 23°07′32″	119–183	2001	Van Veen grab	3
Erik Eriksenstretet	–	219	1996	Van Veen grab	1
Heleysundet	78°25′50″; 21°18′46″	13	2001	Diving-frame	1
Hornsund	76°59′46″; 15°33′27″	5–10	2003	Diving-algae	340
	76°55′13″; 15°33′06″	5–26	2003	Diving-qualitative	73
	77°01′16″; 16°05′50″	0–20	2006	Diving-frame	41
	76°35′18″; 16°07′20″	79–147	2002	Dredge	6
	76°55′17″; 15°33′57″	100–210	2005	Van Veen grab	48
Kong Karls Land	–	117	1996	Van Veen grab	3
Kongsfjorden	78°35′02″; 11°35′02″	10–20	2001	Diving-qualitative	4
	78°35′; 10°35′	103–329	2007	Triangle sledge	3
	79°00′28″; 10°00′28″	145–320	2004	Van Veen grab	5
Magdalenefjorden	79°33′59″; 11°05′07″	51–100	2007	Van Veen grab	2
Rijpfjorden	–	5–30	2007	Diving-qualitative	2
	80°27′; 22°34′	140	2007	Triangle sledge	1
Storfjorden	–	109	1996	Van Veen grab	3
Tommeløyane	79°19′46″; 18°28′01″	23	2001	Diving-frame	2
Wahlenbergfjorden	79°23′41″; 19°29′49″	10–30	2001	Diving-qualitative	1
Wijdefjorden	71°04′32″; 16°02′41″	10–20	2001	Diving-qualitative	1
Van Mijenfjorden	77°31′14″; 16°22′14″	25–107	2007	Van Veen grab	5

species were identified to the lowest level possible under a stereomicroscope and microscope whenever needed. Then, each substrate was treated as a separate sample, for example, each rock collected in the whole studied area was treated as a separate sample in the analysis of hydroid fauna associated with rocks. The species occurrence on substrate was noted, but the numbers of colonies were not assessed. It is often impossible with modular and clonal organisms to determine the size and extent of particular colonies throughout epifaunal communities (Gili and Hughes 1995). We use a term *species record* to articulate the species' presence and *number of records* to count the species occurrences on particular substrate.

Rocks

Rock samples were separated a priori according to depth of collection into shallow and deep with the boundary at 40 m depth. Such division was supported by the distribution of another colonial epifaunal taxon—Bryozoa in Arctic fjords (Kukliński et al. 2005) and in western Norway (Ryland 1963). The rationale behind this division was substrate and light limitation below 40 m depth, larval response to light during dispersal, and temperature and salinity fluctuations in the upper water column.

The surface area of each rock was measured using a plastic net marked with a cm^2 grid. Additionally, the

diameter of each rock was measured so they could be sorted by size category. The classification followed the Wentworth scale (Wentworth 1922) in which the size of particles determines the rock class name: fine gravel (4–8 mm), medium gravel (8–16 mm), coarse gravel (16–32 mm), very coarse gravel (32–64 mm) and cobble (64–245 mm). The correlations between the number of species per sample and rock size and the number of species per sample and depth were calculated with use of Spearman's rank correlation coefficient. Logistic regression was used to predict the probability of hydroid presence or absence on rocks. The model describes the relationship between independent variables (depth classes: shallow ≤40 m and deep >40 m and rock surface area) to the binary dependent variable (presence or absence of hydroids). Rosenbrock and quasi-Newton methods of estimation were performed while building the logistic models. The t statistic was used to test the significance of individual logistic regression coefficients for each independent variable (i.e., to test the null hypothesis in logistic regression that a particular logit (effect) coefficient was zero). The Wald test was used to check whether the model was improved significantly after entering each variable (STATISTICA v. 6, Statsoft). Pearson's chi-square test of independence was used to test whether hydroid occurrence on rocks differed between different rock size classes and in different depth classes.

Relationships between species distributions and depth and rock size were examined using the BIO-ENV procedure. The similarity matrices were based on Bray–Curtis index for biotic species data and on Euclidean distance for environmental variables (analysis performed with use of PRIMER package v. 6, Clarke and Warwick 2001).

Algae

The collected algae were divided into groups of species related to their taxonomic affinities or morphological characteristics. Three groups of species representing divisions were identified: Chlorophyta, Phaeophyta and Rhodophyta. The algal species were classified according to morphological types (modified after Lippert et al. 2001) as follows: (1) foliose to membranous—*Phycodrys rubens, Alaria esculenta, Callophyllis cristata;* (2) filamentous—*Odonthalia dentata, Acrosiphonia sonderi, Chorda tomentosa, Dumontia contorta, Dictiosiphon foeniculaceus, Desmarestia aculeata, Sphacelaria arctica;* and (3) leathery—*Saccharina latissima, Laminaria digitata, Laminaria solidungula, Laminaria hyperborea, Fucus distichus.*

One-way ANOSIM pair-wise statistic was used to test dissimilarities between hydroid assemblages colonizing Phaeophyta and Rhodophyta division and between different algal morphological types (PRIMER package v. 6, Clarke and Warwick 2001). Non-metric multidimensional scaling (nMDS) of Bray–Curtis similarities of hydroid species occurrence on algae was conducted for all samples (PRIMER package v. 6, Clarke and Warwick 2001).

Bryozoa and Hydrozoa

All hydroid–bryozoan and hydroid–hydroid associations which are defined as the number of hydroid records on bryozoan or other hydroid host were noted.

The morphological forms of bryozoan and hydrozoan host species were recorded. Bryozoans were classified as erect (upright shoots) or encrusting (flat, runner-like colonies), hydroids—as erect (upright shoots) or stolonal (horizontal, runner-like colonies). One-way analyses of similarities ANOSIM were used to test dissimilarities in hydroid composition among different bryozoan host species and among different hydrozoan host species (PRIMER package v. 6, Clarke and Warwick 2001). The frequency of hydroid occurrence on particular substrate was calculated as the percentage of substrate samples colonized by species in the total number of colonized substrate. The mean sample species richness on the colonized substrates was determined. The nonparametric Kruskal–Wallis test was used to check for significant differences in the species richness among: (1) rock samples from different depth zones and of different size classes, (2) algal samples of

Phaeophyta and Rhodophyta (Chlorophyta was excluded from the analysis because of the small number of records) and representing different algal morphological types (STATISTICA v.6, Statsoft).

Results

Several substrates collected during present study were colonized by hydroids: rocks, 14 taxa of algae, other hydroids, bryozoans, bivalve shells, gastropods, *Balanus* sp., shells of *Buccinum* sp. inhabited by hermit crabs, crab exoskeletons, polychaete tubes, ascidians, poriferans, soft corals and foraminiferans. For the detailed analyses, we have chosen the most frequently colonized substrate types, that is, rocks, algae, bryozoans and other hydroids. As many as 34 % of algae and 31 % of rocks were colonized by hydroids. Bryozoa and Hydrozoa were colonized less frequently (9 and 3 % of substrate samples, respectively). In total, 43 species of hydroids were noted on selected substrates in Svalbard waters (Table 2). Fifteen species inhabited only one type of substrate but all of them were rare.

Rocks

There were 384 rock samples examined in the study area. Thirty-one percent of rocks were colonized by hydroids. There were 25 species recorded on this type of substrate and five of them were present exclusively on rocky substrates (*Abietinaria pulchra, Eudendrium* cf. *rameum, Lafoeina maxima, Sertularia schmidti, Sarsia loveni*). However, their total number of records was very low (<10). The mean rock sample species richness was 1.5 (±0.7 SD) and varied between 1 and 6 species per rock.

The samples included rocks of surface area ranging from 0.5 to 836 cm^2 and were collected at depths from 5 to 329 m. The frequency of occurrence of hydroids on rocky substrate was higher in shallow samples (≤40 m) and reached 41 % comparing to 19 % in samples collected at depths >40 m. Differences between the two depth zones were significant as was shown by χ^2 test statistic (test $\chi^2 = 20.45$, $p < 0.001$). The occurrence of hydroids varied significantly between different rock size classes (test $\chi^2 = 35.5$, $p < 0.001$) and increased with the increasing rock size.

The logistic regression model was significant (test $\chi^2 = 47.69$, $p < 0.001$). Both surface area and depth class of studied rocks had a significant influence on hydroids presence ($p < 0.05$ for both factors). Hydroids were recorded more often in shallow waters (Estimate value of logistic regression = −1.281) and on rocks of larger surface area (Estimate value of logistic regression = 0.005). The depth was much more important than surface area in shaping the hydroids' occurrence on rocky substrates.

Table 2 Hydroid occurrence on different substrate types

| Species	Rocks	Algae	Bryozoa	Hydrozoa
Leptothecata				
Campanulariidae				
Campanularia volubilis (Linnaeus, 1758)	+	+	+	+
Gonothyraea loveni (Allman, 1859)	+	+	+	+
Obelia longissima (Pallas, 1766)	+	+	+	+
Orthopyxis integra (MacGillivray, 1842)	+	+	+	+
Rhizocaulus verticillatus (Linnaeus, 1758)	+		+	
Campanulinidae				
Calycella syringa (Linnaeus, 1758)	+	+	+	+
Campanulina pumila (G.O. Sars, 1874)	+	+	+	
*Cuspidella procumbens (*Kramp, 1911)	+	+	+	+
Cuspidella sp.	+	+	+	
Lafoeina maxima (Levinsen, 1893)	+			
Opercularella lacerata (Johnston, 1847)	+	+		
Haleciidae				
*Halecium arcticum (*Ronowicz & Schuchert, 2007)	+	+	+	+
Halecium curvicaule (Lorenz, 1886)	+	+	+	+
Halecium mirabile (Schydlowsky, 1902)	+	+	+	+
Halecium muricatum (Ellis & Solander, 1786)		+	+	
Halecium cf. speciosum (Nutting, 1901)		+		
Halecium textum (Kramp, 1911)		+		
Lafoeidae				
Filellum serpens (Hassall, 1848)		+	+	
Lafoea dumosa (Fleming, 1820)	+	+	+	+
Sertulariidae				
Abietinaria pulchra (Nutting, 1904)	+			
Sertularella polyzonias(Linnaeus, 1758)			+	
Sertularella rugosa (Linnaeus, 1758)		+	+	
Sertularella tenella (Alder, 1856)		+		+
Sertularia argentea (Linnaeus, 1758)	+	+		
Sertularia schmidti (Kudelin, 1914)	+			
Symplectoscyphus tricuspidatus (Alder, 1856)	+	+	+	+
Tiarannidae				
Stegopoma plicatile (M. Sars, 1863)	+		+	+
Anthoathecata				
Bougainvilliidae				
Bougainvillia cf. *superciliaris* (L. Agassiz, 1849)	+	+	+	+
Rhizorhagium roseum (Sars, 1874)	+		+	+
Eudendriidae				
Eudendrium annulatum (Norman, 1864)	+	+		
Eudendrium arbuscula (Wright, 1859)		+		
Eudendrium cf. *capillare (*Alder, 1856)	+	+		
Eudendrium cf. *rameum* (Pallas, 1766)	+			
*Eudendrium unispirum (*Schuchert, 2008)			+	
Eudendrium sp.1			+	
Corynidae				
Coryne sp.		+		+
Sarsia loveni (M. Sars, 1846)	+			
Sarsia sp.	+	+		
Hydractiniidae				
Clava multicornis (Forskal, 1775)		+		
Hydractinia cf. *monoon* (Hirohito, 1988)		+		
*Hydractinia serrata (*Kramp, 1943)				+
Oceaniidae				
Similomerona nematophora (Antsulevich, 1986)		+	+	
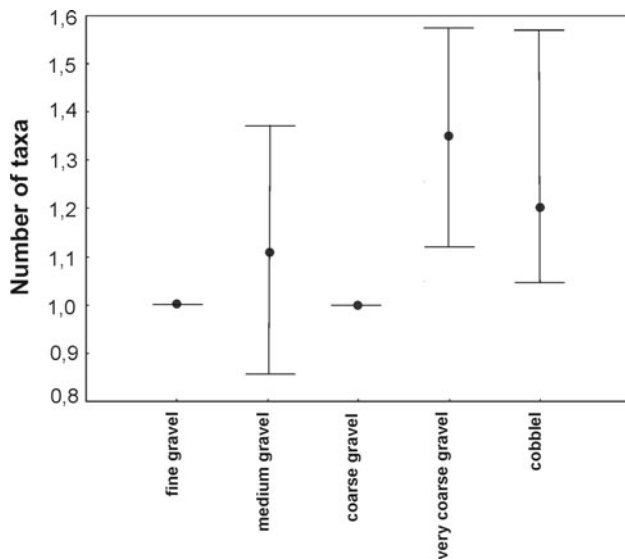
Fig. 2 Number of hydroid taxa (mean ± 0.95 confidence intervals) on rocks in different size classes

There was no significant relationship between sample species richness and depth (Spearman's rank correlation: $R = -0.02$, $p > 0.05$).

Mean number of species per sample (on colonized rocks) did not differ between classes of rock size (Kruskal–Wallis test: $H = 7.03$, $p > 0.05$) (Fig. 2). However, the correlation between number of species and rock size

(treated as continuous variable) was significant but low (Spearman's rank correlation: $R = 0.21$, $p < 0.05$). The species composition on rocks was not related to either rocks' surface area (Spearman's rank correlation: $R = -0.017$, $p > 0.05$) or depth (Spearman's rank correlation: $R = 0.109$, $p < 0.05$) that was confirmed by RELATE procedure.

Stolonal species (*Bougainvillia* cf. *superciliaris*, *Cuspidella procumbens*) more commonly occupied smaller-sized rocks with the exception of *Campanularia volubilis* which occurred more frequently on larger rocks, while erect forms (e.g., *Lafoea dumosa* and *Sarsia* sp.) were most often recorded on coarse, very coarse gravel and cobbles.

Algae

A total of 391 specimens of algae were examined. Among 17 investigated algal species, one belonged to the division Chlorophyta, 11 to Phaeophyta and five to Rhodophyta (Table 3). Fourteen species out of 17 collected algal species and 34 % of collected algal specimens were epiphitized by hydroids. Collected algal species represented three morphological types: foliose to membranous, filamentous and leathery.
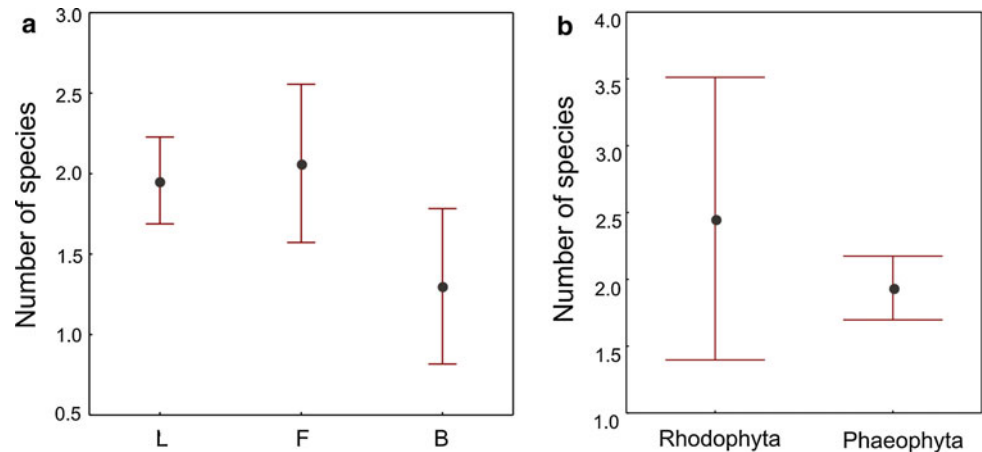
Altogether 27 hydrozoan species were found on algae. The highest number of hydroid species (21) and hydroid records (209) were found on Phaeophyta, which were also

Table 3 List of collected species of macroalgae

Algae	N_T	N_A	N_{AH}	$N{sp}$
Chlorophyta	2	2	2	1
Acrosiphonia sonderi (Kützing) Kornmann, 1962	2	2	2	1
Phaeophyta	344	209	101	21
Alaria esculenta (Linnaeus) Greville, 1830	155	53	33	15
Chorda tomentosa Lyngbye, 1819	1	1	1	1
Desmarestia aculeata (Linnaeus) Lamouroux, 1813	1	1	1	1
Dictiosiphon foeniculaceus (Hudson) Greville, 1830	1	3	1	3
Fucus distichus Linnaeus, 1765	1	2	1	2
Laminaria digitata (Hudson) Lamouroux, 1813	62	50	21	15
Laminaria hyperborea (Gunnerus) Foslie, 188	1	1	1	1
Laminaria solidungula J. Agardh, 1868	19	8	5	7
Saccharina latissima (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders, 2006	100	72	37	20
Saccorhiza dermatodea (De La Pylaie) J. Agardh, 1868	2	0	0	0
Sphacelaria arctica Harvey, 1857	1	1	1	1
Laminaria sp.	6	157	6	12
Rhodophyta	27	54	26	18
Callophyllis cristata (Agardh) Kutzing, 1849	2	2	2	
Dumontia contorta (S.G. Gmelin) Ruprecht, 1850	4	3	4	2
Odonthalia dentata (Linnaeus) Lyngbye, 1819	3	3	3	2
Phycodrys rubens (Linnaeus) Batters, 1902	17	46	17	17
Ptilota plumosa (Linnaeus) Agardh, 1817	1	0	0	0

N_T—total number of collected algae, N_A—number of hydroid records on algal substrate, N_{AH}—number of algal specimens colonized by hydroids, N_{sp}—number of hydroid species associated

most intensively sampled (Table 3). Eighteen species and
54 records were noted on Rhodophyta. Chlorophyta served
as substrate for hydroid settlement only twice. The only
species colonizing Chlorophyta was *C. volubilis*. Frequency of hydroid occurrence was higher on Rhodophyta
(96 %) comparing to Phaeophyta (29 %).

Halecium cf. *speciosum*, *Halecium textum*, *Eudendrium
arbuscula*, *Hydractinia* cf. *monoon* were noted exclusively
on algae but were all very rare species (number of records
<3).

The mean sample species richness on colonized algae
was 1.4 ranging from a minimum of 1 species to a
maximum of 10 species per algae (maximum species
richness found on *P. rubens*). No significant differences in
mean sample species richness among the three morphological types of algae (foliose to membranous, filamentous and leathery) (Kruskal–Wallis test: $H = 5.35$,
$p > 0.05$) (Fig. 3a) or between Phaeophyta and Rhodophyta (Kruskal–Wallis test: $H = 0.22$, $p > 0.05$) (Fig. 3b)
were noted.

There were also no significant dissimilarities in species
composition between either Rhodophyta and Phaeophyta
(one-way ANOSIM: Global $R = 0.032$, $p > 0.05$) or
among three algal morphological types (one-way ANOSIM:
Global $R = 0.027$, $p > 0.05$). No separation of samples
between different morphological forms and between Phaeophyta and Rhodophyta could be detected on the nMDS
plots (Fig. 4a, b). Even if multivariate analysis did not
indicate significant effects of taxonomic or morphological
algal categories on hydroid species composition, some
patterns of distribution of hydroid morphological forms
could be observed among the dominant four algal host
species. Hydroid species with erect colony form (*Halecium
arcticum*, *Halecium curvicaule* and *Symplectoscyphus tricuspidatus*) were more common on brown algae (*L. digitata*, *S. latissima* and *A. esculenta*), while stolonal hydroid
colonies (*C. volubilis*, *Orthopyxis integra* and *Calycella
syringa*) most frequently colonized red algae (*P. rubens*).
One exception was erect *Halecium muricatum* noted on *P.
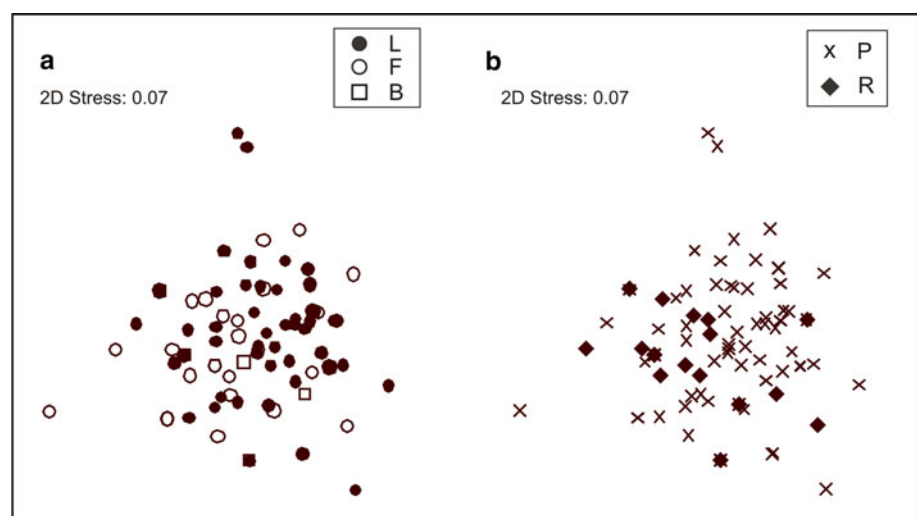rubens*.

Table 4 List of bryozoan host species and their morphological forms (*E* erect, *En* encrusting) colonized by hydroids (uniques and duplicates are excluded)

Host species	Morpological form	Number of records	Number of hydroid species	Most frequent colonist species
Cheilostomata				
Celleporella hyalina (Linnaeus, 1767)	En	1	1	*C. volubilis*
Dendrobeania sp.	E	8	12	*C. volubilis*
Eucratea loricata (Linnaeus, 1758)	E	43	12	*C. volubilis*
		28		*C. syringa*
		6		*C. pumila*
		3		*H. mirabile*
Cystisella saccata (Busk, 1856)	E	1	1	*G. loveni*
Tricellaria ternata (Ellis & Solander, 1786)	E	29	12	*C. volubilis*
		22		*C. syringa*
		3		*C. pumila*
		3		*H. mirabile*
Ctenostomata				
Alcyonidium sp.	E	3	5	*C. procumbens*
Bowerbankia composita (Kluge, 1955)	E	4	3	*C. volubilis*
		3		*C. syringa*
Cyclostomata				
Crisia eburnea (Linnaeus, 1758)	E	2	1	*C. volubilis*
Bryozoa indet		15		*C. syringa*
		10		*C. volubilis*
		2		*O. integra*
		7		*H. arcticum*
		6		*L.. dumosa*
		5		*C. pumila*
		5		*S. tricuspidatus*
		4		*F. serpens*
		4		*H. mirabile*
		3		*H. curvicaule*
		3		*H. muricatum*

Bryozoa as substrate

Twenty-four hydroid species were found on eight bryozoan species (Table 4). The most often colonized bryozoans were *Eucratea loricata* with 90 hydroid records observed on bryozoan host and *Tricellaria ternata* with the number of 69 noted specimens. Majority of colonized bryozoan species were of erect colony form. Only one bryozoan host *Celleporella hyalina* was an encrusting species.

The highest number of hydroid records was noted on bryozoans of the order Cheilostomata (90 % of all records). Nine percent of hydroid records were on bryozoan species of Ctenostomata and only 1 % on Cyclostomata. *C. volubilis* was found attached to the highest number of bryozoan species (6 species) and also the most frequently (51 %). Other hydrozoan species that were most often found on Bryozoa included *C. syringa* (36 %), *L. dumosa* (8 %) and *Campanulina pumila* (8 %).

There was a significant but low dissimilarity in hydroid species composition among different bryozoan host species (one-way ANOSIM, global $R = 0.095$, $p < 0.05$).

Hydroids as substrate

Fifteen hydroid species served as a substrate for 16 hydroid colonists (Table 5). The highest total number of hydroid colonists' species was found on *S. tricuspidatus* (8 species). The highest sample species richness was recorded on specimens of *Obelia longissima* (5 species), *Sertularella polyzonias* and *S. tricuspidatus* (each 4 species). Among the most frequent ($F > 10$ %) species colonizing other hydroids were *C. volubilis* (36 %), *C. syringa* (28 %) and *O. integra* (13 %). There were significant but low differences in hydroid colonists' composition among different hydroid substrate species (one-way ANOSIM: Global $R = 0.152$, $p < 0.05$).

Table 5 The list of hydroid substrate and hydroid colonists and their morphological forms (*E* erect, *S* stolonal): N sp. all—number of all specimens examined in the present study, N sp. col.—number of specimens that were colonized by other hydroids

Substrate	Morphological form of substrate	N sp. all	N sp. col.	Most frequent colonist species	Morphological form of colonist species
Anthoathecata					
E. cf. *capillare*	E	5	1	*B.* cf. *superciliaris*	S
E. annulatum	E	29	3	*C. volubilis*	S
				C. syringa	S
				H. arcticum	E
Leptothecata					
F. serpens	S	19	1	*C. volubilis*	S
G. loveni	E	49	4	*S. plicatile*	E
				E. sp.	E
H. arcticum	E	78	4	*R. roseum*	S
				C. syringa	S
				C. procumbens	S
H. muricatum	E	28	5	*C. volubilis*	S
				O. integra	S
				C. syringa	S
				L. dumosa	E
				S. tricuspidatus	E
H. textum	E	8	2	*C. syringa*	S
				C. procumbens	S
L. dumosa	E	107	3	*C. volubilis*	S
				O. integra	S
				O. longissima	E
L. maxima	E	16	1	*G. loveni*	E
O. longissima	E	15	5	*B.* cf. *superciliaris*	S
				C. syringa	S
				Coryne sp.	S
				O. integra	S
				H. serrata	S
R. verticillatus	E	10	1	*L. dumosa*	E
S. cupressoides	E	18	3	*C. volubilis*	S
S. rugosa	E	27	2	*H. mirabile*	S
				S. tenella	E
S. tricuspidatus	E	146	19	*C. volubilis*	S
			4	*C. syringa*	S

Hydroids predominantly occupied hydroids of the order Leptothecata (Fig. 5). Species of the family Sertulariidae were most often colonized by other hydroids both in case of number of species (4 species of Sertulariidae, which made up 27 % of all hydroid substrates) (Fig. 5a) and number of records (48 %) (Fig. 5b). Regarding antoathecates, merely two species of the family Eudendriidae provided a substrate for colonizing hydroids.

Hydroid species living on other hydroids belonged to nine families (Fig. 6). Species of the order Anthoathecata were in the minority comparing to Leptothecata. Campanulariidae were observed attached to other hydroids with the highest number of records (41 %) (Fig. 6b) and with the highest richness (4 species which made up 23 % of all hydroid colonist species) (Fig. 6a).

Discussion

The most common substrates colonized by hydroids in the study area include rocks, macroalgae, bryozoans and other hydrozoans. Despite the fact that some hydroid species were observed attached to only one type of substrate, we cannot draw conclusions about substrate specificity. These species were particularly rare in the study area; thus, more material is needed to confirm their substrate preferences.

Fig. 5 Distribution of hydroid substrate among different families in terms of number of species (a), number of hydroid records as hydroid host (b)
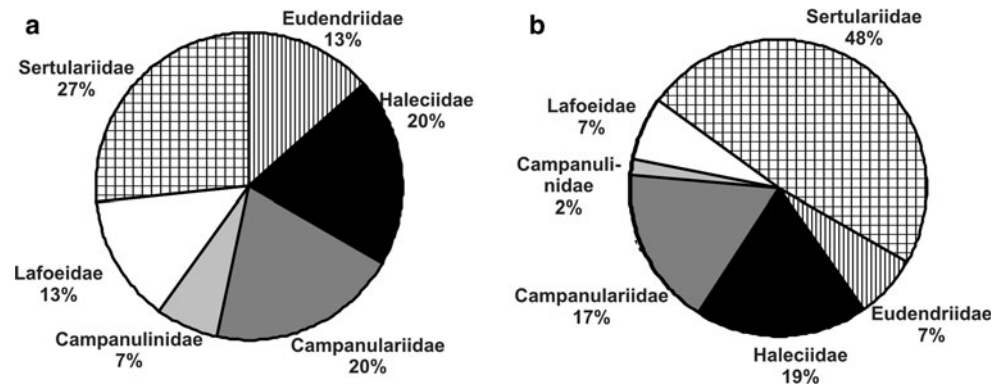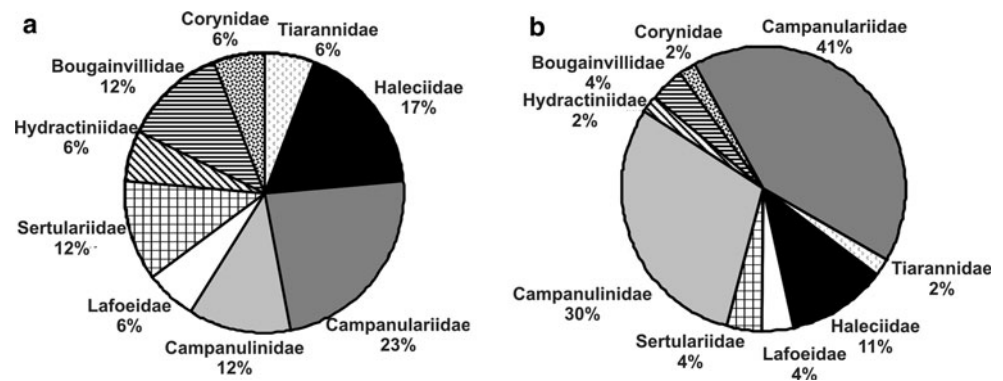

Fig. 6 Distribution of colonists among different families in terms of species number (a), number of records (b)

Rocks

As pioneer organisms, hydroids are present even on the smallest rocks that are prone to frequent mechanical disturbances. The surface of the smallest rock colonized by hydroid (*B.* cf. *superciliaris*) was 0.5 cm². No distinct correlation between species richness and rock size was observed in the present study. However, hydroids occurred more often on rocks of larger size. A marked trend of increasing numbers of species with increasing rock surface is observed for lithophyllic bryozoan communities in the Arctic and Antarctic waters (Barnes et al. 1996; Kukliński et al. 2006). Such patterns are explained by the higher frequency of disturbance caused by wave forces affecting smaller rocks (rolling over and overturning by storms and currents) (Osman 1977). Small rocks are regularly subjected to mechanical scratching, which means the associated biota is only maintained in the early stages of succession. Conversely, the larger rocks remain stable and undisturbed for longer time, and thus, the succession stage of the assemblages is likely to be more advanced. According to the intermediate disturbance hypothesis, (Connell 1978) local species diversity is maximized when ecological disturbance is neither too rare nor too frequent. The largest rocks and boulders that do not turn over do not necessarily support the highest diversity. Owing to the absence of disturbance, species number falls as a result of

competitive elimination of inferior competitors by one or a few dominant species (Osman 1977). Medium-sized rocks should have the highest diversity as they are old enough to accumulate number of species and become disturbed before dominance can occur (Osman 1977).

Factors related to depth are significant in determining hydroid occurrence and species richness on rocky substrates. Although the disturbing impact of many physical factors decreases with depth (e.g., wave action, strong currents, iceberg scouring), rocks occurring in shallow waters are colonized by hydroids more frequently, and hydroid species richness is slightly higher on rocks in shallow waters. The shallow water zone (0–40 m depth) is more diverse in terms of habitat availability, especially in the Arctic. In the deeper part of fjords and continental shelf around Svalbrd, the soft homogenous bottom predominates. Shallow waters are also more favorable for suspension-feeding organisms because of better food availability and water flow conditions (Faucci and Boero 2000).

The hydroid species composition on rocky substrates is relatively homogenous and generally not related to rock surface area or sampling depth. However, some patterns of distribution among the most common species are noted. Stolonal *B.* cf. *superciliaris*, *C. volubilis* and *C. procumbens* are found more often on small rocks. Species with erect growth (e.g., *L. dumosa* and *Sarsia* sp.) forms are more common on larger, stable substrates. This tendency

concurs with Bishop's concept of spatial refuge (Bishop 1989). This author contends that peripheral habitats, often small and ephemeral and/or associated with unstable conditions (e.g., small rocks), can provide refuge from competition and can be favorable for poor space competitors.

Algae

The total number of hydroid species recorded is comparable on Phaeophyta (21 species) and Rhodophyta (18 species). Single species was noted on Chlorophyta. The differences, however, in sample species richness and species composition between red and brown algae are not significant (green algae was excluded from the statistical analysis because of the small number of records). Very similar results were obtained in the study of macrofauna associated with macroalgae in Spitsbergen fjord (Kongsfjorden). The same number of hydroid species was noted on red and brown algae, while there were none on green algae (Lippert et al. 2001). Different trends of hydroid preference for algal substrates are reported from various regions. A tendency for hydroids to favor algae from the Phaeophyta division over Rhodophyta and Chlorophyta is observed near Asamushi, Japan (Nishihira 1965, 1966), and in the mangrove ecosystem at Twin Cays, Belize (Calder 1991). Shepherd and Watson (1970) and Genzano and Rodriguez (1998) report opposite hydroid preferences with Rhodophyta favored over Phaeophyta in south Australia and the coastal waters of Argentina, respectively.

The selection of particular algae by larvae depends on many factors. Green algae are scarcely ever inhabited by epifauna. Nishihira (1965) designated some characteristic features of Chlorophyta, such as their morphological appearance, short life span, and position in the mid-littoral zone, as being disadvantageous for epifaunal settlement. Epibiont larval preferences for specific algal groups might be driven by inhibiting or attracting mechanisms connected with secretions produced by algal tissues (Nishihira 1968; Shepherd and Watson 1970; Oswald and Seed 1986). Larval settlement might be deterred by tannic substances secreted by many brown algae or the mucus excreted by some brown and red algal tissues (Shepherd and Watson 1970). Conversely, positive chemotaxis induced by some fucoid exudates attracts the larvae of the athecate hydroid *Coryne uchidai* Stechow 1931 to inhabit *Sargassum* sp. (Nishihira 1968).

Despite pronounced variation in the morphology of algal substrates (foliose to membranous, filamentous or leathery), there are no significant differences in associated hydroid diversity or composition. In study of the fauna associated with macroalgae in Kongsfjorden, Lippert et al. (2001) demonstrated that faunal composition was unrelated to the morphological form of algae. Nishihira (1966, 1967, 1968) stated that the physical appearance of the algal thallus (shape, texture, rugosity, hardiness) played an important role in the selection of algae by hydrozoan larvae. In the present material, the effect of thallus morphology on the composition of hydroid epiphytes is only detected when differences in the frequency of occurrence of the most common colonist species are compared. Stolonal *C. volubilis* was the only species that occasionally colonized filamentous, delicate algae like *A. sonderi*, *C. tomentosa* or *D. contorta*. The lack of sedentary animals on narrow filamentous thalli is a consequence of their smaller diameter size when compared to the size of hydrozoan larvae and stolons (Nishihira 1967). The thick growth of "hairs" on *C. tomentosa* prevents epiphytes from attaching to them. Some species that form erect colonies (*H. arcticum*, *H. curvicaule*, *S. tricuspidatus*) are the most common on the rhizoids of brown algae (*L. digitata*, *S. latissima* and *A. esculenta*). The rhizoids of these kelp species are highly structured, three-dimensional substrates with a number of crevices in the center. Some hydrozoan larvae display positive rugotaxis. They select rugose surfaces, crevices and depressions along the thalli as their attachment sites (Nishihira 1967; Shepherd and Watson 1970). Large colonies of erect forms are probably more adapted to live on stable substrates provided by kelp holdfasts. Smaller colonies of stolonal *C. volubilis*, *O. integra* and *C. syringa* most frequently colonized the fronds of foliose *P. rubens*, which offer much more delicate and flexible surface.

Bryozoa

Bryozoans are an important substrate source for hydroid settlement. About one-third of all hydroid records and 40 % (23 species) of hydroid species are noted on this type of substrate. Bryozoans have often been noted as a substrate colonized by hydroids (e.g., Genzano and Rodriguez 1998; Genzano and Zamponi 2003; Henry et al. 2008; Genzano et al. 2009); however, no detailed descriptions (such as bryozoan host taxonomic composition) on the epizoic type of associations between hydrozoans and bryozoans are included in these studies. Piraino et al. (1992) described the parasitic relationship between the hydroid *Halocoryne epizoica* Hadzi, 1917, and the bryozoan *Schizobrachiella sanguinea* (Norman 1868), in which the hydroid lived in obligate association and feeds on the lophophoral tentacles of its bryozoan host. Osman and Haugsness (1981) reported a mutualistic relationship between the hydroid *Zanclea* sp. and the bryozoans *Schizoporella errata* (Waters 1878) and *Celleporaria brunnea* (Hincks 1884). Colonies of both associates were highly integrated, with the skeletons of the bryozoan covering the hydroid hydrorhiza, and both partners take advantage of increased survival and competitive ability.

In the current study, the hydroids most often settle on bryozoans of the order Cheilostomata. This is certainly linked to bryozoan distribution patterns in Svalbard waters. Kukliński ([2004](#)) reported that species representing the order Cheilostomata constituted about 80 % of the taxa occurring in Spitsbergen coastal waters. However, the hydroid preference to colonize Cheilostomata bryozoans can also result from morphological characteristics of species representing this order. Many species of Cheilostomata are larger in size and have complex, erect form what is in opposite to majority of Ctenostomata and Cyclostomata, which are mostly characterized by small size and encrusting colony type (Kukliński, unpublished observation). In the present study, almost all host species are of erect colony forms. Large bryozoan colonies are supposed to be a favorable substrate for suspension-feeding colonists since upright shoots can raise the hydroids into the water column where better water flow and food conditions are coupled with protection from burial by mineral particles. They also provide fast growing, three-dimensional structures beneficial for early colonists. Bryozoans are one of the stronger space competitors in the Arctic that yield only to ascidians and demosponges during encounters, but they are more common (Barnes and Kukliński [2004](#)). The strategy of colonizing the surface of winners instead of competing with them for primary space can be an efficient strategy for relatively weak hydrozoan competitors (Orlov [1997](#)). This strategy is employed by variety of other macroinvertebrates. Many bryozoans are obligate epiphytes that take advantage of competitor-free algal substratum (Seed and O'Connor [1981](#); Bishop [1989](#)). Upright sessile epifauna serves as shelter and nursery ground for juvenile scallops (Bradshaw et al. [2003](#)).

Hydroids as substrate

Few studies focus on the phenomenon of either vagile or sessile epizoism on hydroids (Millard [1973](#); Hughes [1975](#); Orlov [1997](#); Bavestrello et al. [1996](#)). Hydroid–hydroid associations are most often noted only briefly in taxonomic and/or ecological studies (e.g., Schuchert [2001](#); Genzano and Rodriguez [1998](#); Zamponi et al. [1998](#); Henry et al. [2008](#); Genzano et al. [2009](#)). Large colonies of hydroids are known to offer refuge and food supply for deposit feeders and carnivores (Hughes [1975](#)). As substrates, hydroids can increase both the diversity and the abundance of benthic fauna in coastal waters (Bradshaw et al. [2003](#)), and they constitute the major substrate for epizoic hydrozoan fauna, for example, on the Argentinian continental shelf (Genzano and Zamponi [2003](#)). The advantage of colonizing asexually reproducing substrates such as Hydrozoa is the unlimited and permanent growth of new hydrocauli (i.e., the new substrate) and the better access to seston they provide to

suspension-feeding animals. A continuously growing substrate can be colonized quickly by epizoic hydroids from neighboring hydrocauli through stoloniferous growth (Genzano et al. [2009](#)). Orlov ([1997](#)) examined the hydroid–hydroid associations closely and identified the morphological plasticity of colonists as an adaptation of hydroids to an epizoic mode of life. In a study of multilevel epizoic hydroid complexes, Orlov ([1997](#)) observed that the colony structure of some species established on other hydroids differed substantially from those described for other substrates. The size of the host hydranths and epizoic hydrozoan colonies differed, with the latter usually being smaller (Orlov [1997](#)). Such differentiation can reduce competition between the epibiont and the host for food items of the same size.

Hydrozoan colonies are an important substrate for hydroid colonization. As many as 15 species of hydroids (26 % of all the species recorded in this study area) support other associated hydroid species (18 species). About 6 % of all the hydroid records are noted on other hydroids. The host species belong mainly to the order Lepthothecata and the family Sertulariidae. Hydroid colonies that carry other organisms must be quite large and stiff enough to resist additional ballast. The study material includes hydroid specimens colonized by a number of other species; these include those of a large colony size such as *O. longissima* (colonized by five epizoic hydroids) and rigid forms like *S. polyzonias* and *S. tricuspidatus* (each hosting four epizoic species). In contrast, hydroid colonists are mostly characterized by stolonal morphology forms and/or minute sizes. The most common hydroid colonists belong to the families Campanulariidae (41 %) and Campanulinidae (30 %). The majority of Campanulariidae records (*C. volubilis* and *O. integra*) and all Campanulinidae consist of stolonal species. Only two records of erect Campanulariidae (*G. loveni* and *O. longissima*) are noted on other hydroids; however, these colonies did not reach a substantial size (Ronowicz, personal observation).

Conclusions

This study provides information about the effect of substrate characteristics on hydroid epibionthic communities in Svalbard region. Hydroids are successful pioneer organisms that can rapidly colonize available rocky, algal or animal surfaces. The opportunistic nature of hydroids is reflected in the lack of substrate specificity of hydroid species and in the fact that the species composition is similar regardless of substrate type. Also, substrate characteristics such as rock surface area, morphological types of algae and different divisions of algal host do not have a large influence on hydroid species composition. The presence of hydroids is related to the surface area of rocky

substrate. Significant but low dissimilarities characterized hydroid assemblages dwelling on different hydrozoan and bryozoan hosts. Erect colonies of bryozoans and hydroids constitute important substrates for hydroid settlement (mainly stolonal forms). Colonization of the available upright surface (algae, erect bryozoans or hydroids) is a strategy that enables to settle on indeterminately growing substrate that provides a spatial refuges from highly competitive primary space.

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