

Factors affecting biodiversity on hermit crab shells

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Abstract This study explores the abundance, diversity and assemblage structure of epifauna on the shells used by two hermit crab species (*Pagurus bernhardus* and *P. pubescens*) in the Arctic (Svalbard and Northern Norway) and investigates the biotic and physical drivers of such patterns. Contrary to our expectations, we found that location (which reflects the variability in environmental conditions and the local species pool of potential colonizers) is a key determinant not only in the cold, ice-scoured, glacier-dominated Arctic shallows of Svalbard but also in boreal Norwegian fjords, where other factors were hypothesized to be more important. Depending on region, shell area and identity were of lesser magnitude, with larger and more irregular shells containing more diverse assemblages. Crab host species also

played a role (*P. pubescens*-inhabited shells supported larger number of individuals and higher diversity than those of *P. bernhardus*) but this effect might be species or region specific. In this study, no effect of crab gender could be detected. The study indicated that epifaunal assemblages of hermit crab shells are influenced by complex set of factors that interact together to different degree at various locations.

Keywords Mobile hard substrate · Epifaunal assemblages · Hermit crabs · Biodiversity · Arctic · SCUBA

Introduction

In many marine environments, hard surfaces are a limiting resource (Jackson, 1977; Kuklinski et al., 2008; Wahl, 2009), but some organisms have hard externa which provide a surface for colonization. Such epibiosis is common and widespread across many groups of sessile taxa. Numerous living organisms, called basibionts, thus become the substrate for settlement and development of others (Wahl, 1989; Harder, 2009). An example of potential basibionts is decapod crustaceans, which are a species-rich and abundant group with a broad geographical distribution (Hayward & Ryland, 1999). They are long-lived, slow-moving and large enough to provide considerable substrate for other invertebrates. On soft substrata

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they are often one of the few providers of hard substrates (Gili et al., 1993; Di Camillo et al., 2008; Balazy & Kuklinski, 2013). Their calcified exoskeletons are physiologically inactive with respect to filtration or osmoregulation (Fernandez-Leborans, 2010). Not surprisingly therefore, decapods are one of the most frequently used substrates for epibionts which is reflected in the literature as focus for ecologists studying epibiosis (Connell & Keough, 1985; Dick et al., 1998; Hayward & Ryland, 1999; McGaw, 2006; Dvoretzky & Dvoretzky, 2008, 2009, 2010).

Among Decapoda, the superfamily Paguroidea (hermit crabs) is a classic example of hard mobile substrate providers (Sandberg & McLaughlin, 1988; Balazy & Kuklinski, 2013). Their naked abdomens are not calcified, and to protect themselves hermit crabs must find and occupy empty gastropod shells or other materials such as bivalve and scaphopod shells, polychaete tubes, sponge, corals, wood or even hollowed-out fragments of stones (Lancaster, 1988; Williams & McDermot, 2004 and references therein). Thus, in the case of hermit crabs not only the body surfaces but also other non-living resources used by these animals can serve as a new substrate for colonization. Williams & McDermot (2004) and McDermott et al. (2010) found >550 invertebrate species associated with over 180 species of hermit crab species worldwide. The most abundant epifaunal groups include arthropods, polychaetes and cnidarians. Epibiont assemblages of the common hermit crab *Pagurus bernhardus* (Linnaeus, 1758) include nearly 120 epifaunal species in the North Sea (Skagerrak-Kattegat area, Jensen & Bender, 1973; Reiss et al., 2003).

Even if some hermit crab species together with their associates are well known and often host higher biodiversity compared to other surrounding hard substrates (Balazy & Kuklinski, 2013), factors affecting the composition and diversity of these assemblages remain poorly understood (Williams & McDermot, 2004). This is also true for epibiosis of other crustaceans (Fernandez-Leborans, 2010) and hard mobile substrates in general. The recognition of the factors correlating with diversity of these rich assemblages could be important to aid understanding biodiversity drivers in coastal systems. Even though some factors affecting biodiversity on hard mobile substrates have been already recognized by

manipulative experiments, they have largely been performed in isolated, homogeneous environments that have not incorporated various environmental parameters. Thus, the extent to which such factors dominate what happens in real environments is unknown. Typically, a wide range of abiotic factors, biological processes and their interplay can influence epifaunal assemblages (Dayton, 1984; Menge & Sutherland, 1987; Smith & Witman, 1999). Among them, substrate size (Barnes & Clarke, 1995; McGaw, 2006; Kuklinski et al., 2008), host and shell species identity (Conover, 1979), its condition (documented in the case of decapods other than hermit crabs, Dvoretzky & Dvoretzky, 2010) seem to play important roles. Secondary factors reported to date include host gender or depth of occurrence, although these have been rarely investigated (Fernandez-Leborans, 2010; Dvoretzky & Dvoretzky, 2010). To our knowledge, the most comprehensive work concerning various factors has been on two sympatric hermit crab species: *Pagurus pollicaris* Say, 1817 and *Pagurus longicarpus* Say, 1817, from Tampa Bay, Florida (Conover, 1979). This showed that epifaunal species richness increased with shell size but without altering their density. The identity of the host crab also strongly influenced the epibiota, whilst the identity of gastropod shell was of little importance.

Our study aims to describe factors affecting epifaunal species composition and abundance (i.e. epifaunal assemblage structure), diversity (S , H') and total abundance (N) on gastropod shells used by hermit crabs from Northern Norway, across Barents Sea's shallow bank (Svalbard Bank) to Spitsbergen Island (Svalbard Archipelago). This is the northern latitudinal extreme of hermit crab ranges, where the ecologies of host and epifauna remain poorly understood (Barnes et al., 2007). Besides investigating the potential impacts of substrate size, crab and shell identity, we additionally include factors that have been rarely investigated before, such as crab gender and location. In the cold, ice-scoured, glacier-dominated Arctic shallows, environmental conditions are severe—so we hypothesize that on Svalbard, location (that reflects the variability in environmental conditions and the local species pool of potential colonizers) is a key determinant, while factors like crab species and gender, shell area or its identity become more important in boreal Norwegian fjords.

Materials and methods

Study area

Study sites were three coastal locations (Isfjord, Kongsfjord, Smeerenburg) in the west of Spitsbergen Island, the largest one of the Svalbard Archipelago, one offshore location to the south on Svalbard Bank and two coastal locations in Northern Norway (Mjosund and Kvalsund, Fig. 1). All locations are within the warm and saline ($T > 3^{\circ}\text{C}$, $S > 35$, Loeng, 1991) North Atlantic Current which, through its extension—the West Spitsbergen Current (WSC)—influences west Atlantic latitudes as high as $76\text{--}80^{\circ}\text{N}$, giving them a mild ‘sub-Arctic’ character (Hop et al. 2002; Svendsen et al., 2002). However, Svalbard waters are also strongly influenced by cold freshened Arctic water ($T < 0^{\circ}\text{C}$, S 34.3–34.8) transported by the East Spitsbergen Current (ESC), and glacial and riverine inflow (Loeng, 1991; Cottier et al., 2010).

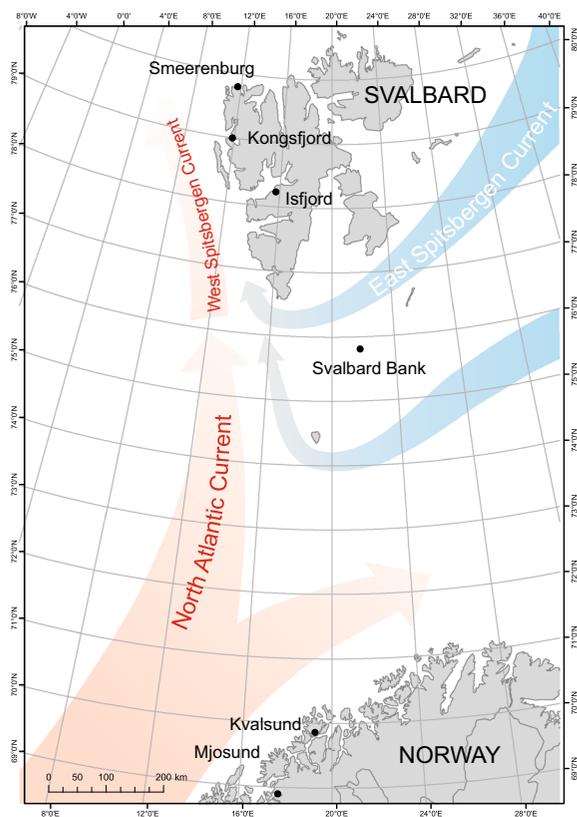


Fig. 1 Study area with marked sampling sites and important currents

Hydrographic conditions inside the Spitsbergen fjords remain in dynamic balance between these two large water masses and local water, and can vary considerably between locations depending on fjord shape, bathymetry at the mouth (sill presence), tidal currents and wind directions (Svendsen et al., 2002; Basedow et al., 2004). Iceberg scouring, sedimentation and fresh water runoff form steep environmental gradients visible along the fjord’s axis from the innermost, glacier-influenced part of the fjords towards its mouth (Włodarska-Kowalczyk & Pearson, 2004). Fjordic seabeds of Svalbard are typically covered with soft sediments and drop stones. The macrobenthic assemblages there are mostly dominated by infaunal bivalves and polychaetes (Włodarska-Kowalczyk, 2007). Wherever hard bedrock is present, dense kelp forest (*Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druhl & G.W. Saunders, 2006; *Laminaria* spp. J.V. Lamouroux, 1813) and rich epibenthic assemblages of echinoids, cnidarians, ascidians, sponges, barnacles, bryozoans and sedentary polychaetes are abundant (Barnes & Kuklinski, 2005; Barnes et al., 2007). Spider (*Hyas* spp. Leach, 1814) and hermit crabs (*Pagurus* spp. Fabricius, 1775) are commonly found across these areas in large numbers (Kaczmarek et al., 2005; Berge et al., 2009; Balazy et al., 2015). *Pagurus* spp. occurs also ~ 50 nm southeast of Spitsbergen—at Svalbard Bank. This rise in the seabed that peaks at just 30–40 m depth is covered mostly by a thick layer of barnacle and mollusk shell fragments overlying coarse sand and gravel. In a front between North Atlantic and Arctic water masses, with strong tidal currents and vertical mixing, Svalbard Bank is considered to be a very productive area (Elverhoi & Solheim, 1983; Sakshaug et al., 2009).

The study sites in Northern Norway were located in Mjosund and Kvalsund. These narrow, shallow sounds connect the open sea with fjords that cut deep into the land. Without significant influence of glaciers, rivers and creeks are the main source of freshwater input (Wassmann et al., 1996). Water masses are, however, well mixed vertically due to strong tidal currents (Holte & Oug, 1996). Sea temperature varies from ~ 3.5 to 8°C ; thus, water rarely freezes and salinity ranges from 31 to 34 (Loeng, 1991; Oug, 1998). The seabed is characterized, similarly to Spitsbergen, by a mix of cobbles and boulders overlying mud and silt. On patches of mud/silt polychaetes, bivalves and

gastropods dominate (Holte & Oug, 1996). Hard bedrock is typically overgrown by leaf-shaped red, green and coralline algae and serpulid polychaete reefs (Haines & Maurer, 1980; Oug, 2001). Barnacles, ascidians, bryozoans and sponges are also common and abundant epifaunal taxa. Among decapods, along with the edible crab *Cancer pagurus* Linnaeus, 1758 and two species of *Hyas*, three pagurid species occur [*Pagurus pubescens* Krøyer, 1838; *P. bernhardus*; *Anapagurus chiroacanthus* (Lilljeborg, 1856); Bahr & Gulliksen, 2001; Barnes et al., 2007].

Protocol

Hermit crabs were collected in August 2009 in two ways: haphazardly picked by SCUBA divers (Mjosund, Kvalsund, Isfjord, Kongsfjord, Smeerenburg) and by triangular dredge (1 m each side, Svalbard Bank). Samples were preserved in 4% formaldehyde buffered with seawater, and transported to the laboratory. Crab identity, gender and gastropod shell identity were determined for each individual. The external surface area (SA) of a shell was estimated following the technique of Bergey & Getty (2006). A shell was carefully wrapped in a thin layer of stock aluminium foil and all overlapping or excess areas were trimmed off. The foil was then weighed (B) and the SA was calculated from the equation $SA = 0.0495 + 413.59 * B$, $R^2 = 0.948$ (this equation was obtained after weighing pieces of foil of known surface area). All fauna larger than 1 mm found on the shell surface, including the shell aperture, were identified to the lowest possible taxonomic level, typically to species. Determination of polychaete species was made according to Jirkov (2001) using tube morphology (Kupriyanova & Jirkov, 1997). However, identification of Spirorbinae generally requires inspection of morphological characteristic of soft body parts and some of the spirorbids were classified into morpho-groups: *Spirorbis* sp./*Bushiella* sp./*Pilleolaria* sp., Spirorbinae juvenile, Spirorbinae undetermined. The number of individuals in each group/species was counted, with each colonial organism considered as one 'individual'.

Statistical analysis

Epifaunal assemblages colonizing hermit crab-inhabited shells were analysed separately at Svalbard

(fjords and the offshore location, Fig. 1.) and separately in Northern Norway due to strong differences between those regions (the two hermit crab species were recorded together only in Northern Norway). Non-parametric PERMANOVA procedures were used to test for differences in both multivariate (species composition and abundance) and univariate (species number, total abundance and Shannon–Wiener diversity) characteristics of the epifauna in groups of samples defined by 3 or 4 factors. For material collected at Svalbard, three fixed factors were included: (1) location, (2) crab gender and (3) shell identity (i.e. family). For Northern Norway, four fixed factors were considered: (1) location, (2) crab species, (3) crab gender and (4) shell identity (i.e. family). Because epifaunal diversity and abundance can be strongly related to the area of the substrate (Conover, 1979; McGaw, 2006; Kuklinski et al., 2008), gastropod shell area was included as a covariable in all analyses. The statistical significances of each of the multivariate and univariate variance components were tested using 9999 permutations of residuals under a reduced model (Anderson & ter Braak, 2003).

Prior to the multivariate analysis for epifaunal species composition and abundance (i.e. epifaunal assemblage structure), data were square-root transformed to assure a more balanced view of the assemblage structure as this transformation reduced the influence of the most numerous taxa (Clarke & Gorley, 2001). The analyses were conducted on a zero-adjusted Bray–Curtis dissimilarity matrix. To visualize and compare the importance of each factor, their Sqrt values of PERMANOVA, given in Table 1, were plotted. Sqrt values are the square-root transformed sizes of the variance components, expressed as a percentage of the total variation. Variance components were obtained using mean squares (MS, Table 1) from PERMANOVA (Anderson et al., 2008). Significant effects of factors documented by PERMANOVA main tests were further examined with the use of post hoc, pair-wise tests. When both a significant effect of a factor and significant interaction between two factors were detected, pair-wise tests for differences between different levels of a factor were performed separately within each level of the other factor, as recommended by Anderson et al. (2008). However, at Svalbard, due to limited number of samples, the effects of the factor location were

Table 1 Results of PERMANOVA tests for differences in hermit crab epifaunal assemblages

Region	Factor	df	Epifauna structure			Pair-wise comparisons		
			MS	F	P	Sqrt		
Svalbard	Shell area	1	92905.0	60.626	0.000	17.4		
	Location	3	36888.0	24.072	0.000	23.0	Is ≠ Sm Is ≠ Ko Is ≠ SB Sm ≠ K Sm ≠ SB Ko ≠ SB *	
	Crab gender	1	1910.4	1.247	0.253	1.6		
	Shell identity	4	11866.0	7.744	0.000	18.3	B ≠ N B ≠ T B ≠ O/M ≠ N M ≠ T/N ≠ T N ≠ O **	
	Location × shell identity	9	3898.9	2.544	0.000	15.8		
	Location × crab gender	3	1989.5	1.298	0.121	3.7		
	Shell identity × crab gender	4	1599.3	1.044	0.397	2.0		
	Shell identity × crab gender × location	5	1225.5	0.799	0.823	-6.8		
	Residual	271	1532.4			39.1		
	Total	301						
Northern Norway	Shell area	1	18497.0	9.740	0.000	11.0		
	Location	1	35151.0	18.510	0.000	23.8	Pp: Kv ≠ Mj/Pb: Kv ≠ Mj ***	
	Crab sp.	1	13711.0	7.220	0.000	16.8	Kv : Pp ≠ Pb/Mj: Pp ≠ Pb *****	
	Crab gender	1	2395.2	1.261	0.252	2.8		
	Shell identity	5	3480.5	1.833	0.001	10.0	L ≠ M L ≠ B	
	Location × crab sp.	1	3762.0	1.981	0.033	8.6		
	Location × crab gender	1	1982.2	1.044	0.412	1.7		
	Location × shell identity	4	2424.5	1.278	0.138	8.3		
	Crab sp. × crab gender	1	2085.4	1.098	0.358	2.7		
	Crab sp. × shell identity	2	1487.1	0.783	0.740	-6.4		
	Crab gender × shell identity	3	1040.3	0.548	0.971	-8.8		
	Location × crab sp. × crab gender	1	1254.2	0.661	0.754	-7.6		
	Location × crab sp. × shell identity	1	2421.9	1.275	0.244	8.9		
	Location × crab gender × shell identity	3	1304.0	0.687	0.873	-12.2		
	Crab sp. × crab gender × shell identity	2	1952.0	1.028	0.426	3.3		
	Location × crab sp. × crab gender × shell identity	1	2199.2	1.158	0.320	9.9		
Residual	107	1899.0			43.6			
Total	136							

For pair-wise comparisons only results with significance level $P < 0.05$ are shown (* only on Buccinidae shells, ** only in Isfjord, *** on both hermit crab species, ***** in the two Northern Norway locations)
 Locations: Is Isfjord, Sm Smeerenburgfjord, Ko Kongsfjord, SB Svalbard Bank, Kv Kvalsund, Mj Mjosund, Shell identity: B Buccinidae, N Naticidae, T Trochidae, M Muricidae, L Littorinidae, O Others. Crab sp.: Pp *P. pubescens*, Pb *P. bernhardus*

analysed only for Buccinidae shells (they were most abundant and distributed in all the investigated fjords), while the effects of Shell identity were examined for samples collected in Isfjord (the largest fjord with all shell groups present). SIMPER routine (similarity percentages—species contributions) was used to reveal which species were responsible for the differences among epifaunal assemblages. Only species with contributions >10% were reported. In order to remove the confounding effect of different gastropod shell areas for SIMPER analyses, abundance data for each epifaunal species were averaged by shells total abundance prior to the analyses.

As univariate descriptors of the epifaunal assemblages, species number (S), total abundance (N) and Shannon–Wiener diversity index (H') were calculated. PERMANOVA main and pair-wise tests in this case were conducted on Euclidean-distance similarity matrices (untransformed data, Clarke et al., 2006; Anderson et al., 2008). Spearman's rank correlations (Sokal & Rohlf, 1981) were used to determine relationship between the gastropod shell area and S , N , H' .

The epifauna abundance data in SIMPER analysis and graphical visualizations of number of individuals (N) were expressed as the number of individuals per cm^2 of surface area, but in all other analyses (S , H'), as the number of individuals per shell.

PERMANOVA main and pair-wise test, calculation of diversity measures (S , H') were performed in PRIMER v6 with the PERMANOVA+ add-on (Clarke & Gorley, 2001; Anderson et al., 2008). Spearman's rank correlations analyses were done in STATISTICA v. 10 (StatSoft Inc.). Significance level for all statistical tests used was $P = 0.05$.

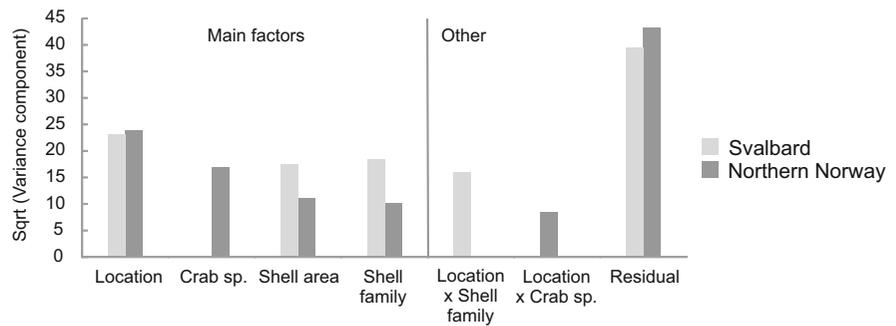
Results

The 439 gastropod shells collected across both areas (Svalbard—302, Northern Norway—137) were inhabited by two hermit crab species (*Pagurus pubescens* and *P. bernhardus*). At Svalbard, only *P. pubescens* was found. In Northern Norway, it was dominant (*P. pubescens* 62%, *P. bernhardus* 38%). In total, 36,736 epifauna individuals from 102 taxa were recorded (31,851 individuals from 92 taxa at Svalbard, and 4885 individuals and 55 taxa in Northern Norway). Shells used by *P. pubescens* in Northern Norway

hosted in total 3263 individuals from 48 taxa, whereas those of *P. bernhardus* hosted 1622 individuals and 41 taxa. Shells collected at Svalbard were colonized by 1665 individuals (1–24 species), whilst in Northern Norway 1223 individuals (1–14 species) colonized the shells. Although gastropod shells collected at Svalbard were significantly larger than those from Northern Norway (1.4–87.7 cm^2 at Svalbard vs. 0.9–40.2 cm^2 in Northern Norway), the range of Shannon–Wiener diversity index for epifauna for both areas was the same (0–2.3). Among all epifaunal taxa, Bryozoa and Polychaeta were represented by the highest numbers of species (67 and 15, respectively). Epifaunal assemblages at Svalbard were dominated by the barnacle *Semibalanus balanoides* (Linnaeus, 1767) and sedentary polychaetes [*Circeis armoricana* Saint-Joseph, 1894; *Spirorbis* sp./*Bushiella* sp./*Pilleolaria* sp.; *Bushiella evoluta* (Bush, 1905) and *Paradexiospira* sp. Caullery & Mesnil, 1897]. The next most abundant species were bryozoans [*Myrzoella plana* (Dawson, 1859); *Celleporella hyalina* (Linnaeus, 1767); *Alcyonidium mamillatum* Alder, 1857; *Patinella* sp. Gray, 1848; *Cauloramphus intermedius* Kluge, 1962; *Tegella arctica* (d'Orbigny, 1853); *Callopora* sp. Gray, 1848] and the foraminifer *Lobatula lobatula* (Walker & Jacob, 1798). In Northern Norway's assemblages, sedentary polychaetes [juvenile forms of Serpulidae; *Spirobranchus triqueter* (Linnaeus, 1758); *C. armoricana*; *Spirorbis* sp./*Bushiella* sp./*Pilleolaria* sp.] and two foraminiferan species [*Discorbis rosacea* (d'Orbigny, 1826) and *L. lobatula*] prevailed.

Multivariate analysis showed that hermit crab epifaunal community structure differed significantly between locations, crab species and shell identity, and that there were significant interactions between factors (Table 1). The structure of these assemblages also showed a highly significant relationship with shell area. Multivariate variations indicated by Sqrt values (see M&M), in both study areas, were greatest from one shell replicate to the other (residual), followed by investigated factors in order of decreasing contribution to the total variability: location, crab sp. (only Northern Norway), shell identity and shell area. Interactions between location and shell identity (only Svalbard) as well as location and crab sp. (Northern Norway) were also a significant sources of variation in hermit crab epifaunal assemblages, but were less important (Table 1; Fig. 2).

Fig. 2 Scale of variance in hermit crab epifaunal assemblages explained by different factors. Only factors with significant effects ($P < 0.05$) are shown. Crab sp. is not a factor at Svalbard as only one species (i.e. *Pagurus pubescens*) was found there (see “Results” section)



Location

Pair-wise tests indicated differences in epifaunal assemblage structure among all the four Svalbard locations (Table 1). Dissimilarity revealed by SIMPER analysis, ranged from 55.9% (Svalbard Bank vs. Isfjord) to 86.7% (Svalbard Bank vs. Kongsfjord). For each pair of locations, species that contributed the most to the observed differences were the barnacle *Semibalanus balanoides* and the sedentary polychaetes: *Paradexiospira* sp. or *Circeis armoricana*, or both of these species (Table 2; Fig. 3a). Significant differences in species number, abundance and diversity index were also found among Svalbard’s locations (Fig. 4). Pair-wise analyses indicated that the most diverse hermit crab epifaunal assemblages were found on the shells from Kongsfjord and Smeerenburgfjord, yet these shells hosted the lowest number of individual epibionts (Fig. 4b, c). Svalbard Bank was the location with the highest number of epifaunal individuals but the lowest diversity index (Fig. 4b, c).

Differences in epifaunal assemblage structure between the two Northern Norway locations were present considering both *Pagurus pubescens* and *P. bernhardus* (Table 1; Fig. 3b). Dissimilarity between Kvalsund and Mjosund revealed by SIMPER analyses reached 81.9% (*P. pubescens*) and 84.9% (*P. bernhardus*). The differences observed were due to higher relative abundances of sedentary polychaetes (*Circeis armoricana*, juvenile forms of Serpulidae) in Kvalsund and foraminiferans (*Lobatula lobatula*, *Discorbis rosacea*) in Mjosund (Table 2; Fig. 3b). The number of species and individuals were higher in Mjosund than in waters of Kvalsund, but each time these differences were found only for one crab species—*S* for *P. bernhardus* and *N* for *P. pubescens* (Fig. 4a, b). Values of Shannon–Wiener diversity indices were

similar in both locations, regardless of the crab species (Fig. 4c).

Hermit crab species

Two hermit crab species (*P. pubescens* and *P. bernhardus*) occurred only in Northern Norway. SIMPER analyses performed separately for two Northern Norway locations showed 73.9% (Kvalsund) and 68.4% (Mjosund) dissimilarity between the assemblages overgrowing shells of the two hermit crabs. In Kvalsund, SIMPER identified sedentary polychaetes (juvenile forms of Serpulidae and *C. armoricana*) as taxa responsible for differences in epifauna, although differences in their relative abundance between the two hermit crabs were small (Table 2; Fig. 3b). In Mjosund, juvenile forms of Serpulidae and *Spirobranchus triqueter* prevailed on shells used by *P. bernhardus*, while foraminiferans (*Discorbis rosacea*, *Lobatula lobatula*) dominated on *P. pubescens*-inhabited shells. Shells carried by *P. pubescens* supported larger number of epifaunal species and individuals and a higher diversity than *P. bernhardus* (PERMANOVA $P < 0.05$, individual test values not shown, Fig. 4).

Shell identity

There were significant differences in the structure of epifaunal assemblages among gastropod shell families (Table 1). Pair-wise tests showed significant effects in seven out of ten, pair-wise comparisons of gastropod shell families (Table 1). Dissimilarity revealed by SIMPER analysis ranged from 57.6% (Buccinidae vs. Naticidae) to 84.5% (Naticidae vs. Trochidae). Species with the largest contributions to observed differences were *Semibalanus balanoides* (prevailing

Table 2 Results of SIMPER analyses identifying taxa with highest contributions to differences between hermit crab epifaunal assemblages

Region	Factor	Taxa	Relative abundance (%)		Average dissimilarity	Contribution (%)	Cumulative contribution (%)	
Svalbard	Location		Isfjord	Smeerenburg				
		<i>Semibalanus balanoides</i>	41	25	16.63	24.17	24.17	
		<i>Circeis armoricana</i>	14	16	7.87	11.44	35.61	
			Isfjord	Kongsfjord				
		<i>Semibalanus balanoides</i>	41	8	18.61	24.61	24.61	
		<i>Paradexiospira</i> sp.	3	32	14.88	19.68	44.28	
		<i>Circeis armoricana</i>	14	21	8.76	11.59	55.87	
			Isfjord	Svalbard Bank				
		<i>Semibalanus balanoides</i>	41	78	21.14	37.81	37.81	
		<i>Circeis armoricana</i>	14	2	6.60	11.81	49.63	
			Smeerenburg	Kongsfjord				
		<i>Paradexiospira</i> sp.	7	32	13.85	19.26	19.26	
		<i>Semibalanus balanoides</i>	25	8	11.93	16.59	35.84	
		<i>Circeis armoricana</i>	16	21	8.48	11.79	47.63	
			Smeerenburg	Svalbard Bank				
		<i>Semibalanus balanoides</i>	25	78	27.94	39.64	39.64	
		<i>Circeis armoricana</i>	16	2	7.56	10.73	50.36	
			Kongsfjord	Svalbard Bank				
		<i>Semibalanus balanoides</i>	8	78	35.40	40.81	40.81	
		<i>Paradexiospira</i> sp.	32	0	15.75	18.16	58.97	
	<i>Circeis armoricana</i>	21	2	9.83	11.33	70.31		
		Shell identity		Buccinidae	Naticidae			
	<i>Semibalanus balanoides</i>		41	71	20.85	36.18	36.18	
	<i>Circeis armoricana</i>		14	3	7.40	12.84	49.02	
			Buccinidae	Trochidae				
	<i>Celleporella hyalina</i>		5	38	18.07	22.27	22.27	
	<i>Semibalanus balanoides</i>		41	16	18.02	22.21	44.49	
			Buccinidae	Others				
	<i>Lobatula lobatula</i>		6	43	20.62	26.42	26.42	
	<i>Semibalanus balanoides</i>		41	16	16.55	21.19	47.61	
			Muricidae	Naticidae				
	<i>Semibalanus balanoides</i>		11	71	30.94	37.51	37.51	
	<i>Circeis armoricana</i>		23	3	11.91	14.44	51.95	
	<i>Bushiella evoluta</i>		16	8	8.75	10.61	62.56	
			Muricidae	Trochidae				
	<i>Celleporella hyalina</i>		9	38	18.00	21.32	21.32	
	<i>Circeis armoricana</i>		23	5	12.10	14.33	35.65	
	<i>Lobatula lobatula</i>		16	13	11.11	13.16	48.81	
	<i>Semibalanus balanoides</i>		11	16	9.10	10.78	59.59	
			Naticidae	Trochidae				
	<i>Semibalanus balanoides</i>		71	16	29.50	34.90	34.90	
	<i>Celleporella hyalina</i>	1	38	18.91	22.37	57.27		
	Naticidae	Others						
<i>Semibalanus balanoides</i>	71	16	29.20	35.33	35.33			
<i>Lobatula lobatula</i>	1	43	21.42	25.91	61.25			

Table 2 continued

Region	Factor	Taxa	Relative abundance (%)		Average dissimilarity	Contribution (%)	Cumulative contribution (%)	
Northern Norway	Location		<i>P. Pubescens</i>					
			Kvalsund	Mjosund				
			<i>Discorbis rosacea</i>	6	41	18.77	22.93	22.93
			Serpulidae juv.	36	5	16.89	20.63	43.56
			<i>Lobatula lobatula</i>	11	27	12.32	15.05	58.61
			<i>Circeis armoricana</i>	17	1	8.37	10.22	68.83
				<i>P. bernhardus</i>				
				Kvalsund	Mjosund			
			Serpulidae juv.	31	17	16.97	19.99	19.99
			<i>Discorbis rosacea</i>	2	23	11.72	13.81	33.80
			<i>Lobatula lobatula</i>	5	22	10.82	12.75	46.55
			<i>Circeis armoricana</i>	20	3	10.00	11.78	58.33
		Crab sp.		Kvalsund				
				<i>P. pubescens</i>	<i>P. bernhardus</i>			
			Serpulidae juv.	36	31	18.43	24.95	24.95
			<i>Circeis armoricana</i>	17	20	12.37	16.75	41.70
				Mjosund				
				<i>P. pubescens</i>	<i>P. bernhardus</i>			
			<i>Discorbis rosacea</i>	41	23	17.90	26.16	26.16
			<i>Lobatula lobatula</i>	27	22	14.60	21.34	47.50
			Serpulidae juv.	5	17	9.38	13.71	61.21
			<i>Spirobranchus triqueter</i>	7	15	7.13	10.42	71.63
			Shell identity		Littorinidae			
		Muricidae						
	Serpulidae juv.	13		38	17.86	22.69	22.69	
	<i>Circeis armoricana</i>	16		13	10.64	13.52	36.21	
	<i>Discorbis rosacea</i>	17		7	9.44	12.00	48.21	
	<i>Lobatula lobatula</i>	15		12	8.86	11.26	59.47	
		Littorinidae						
		Buccinidae						
	Serpulidae juv.	13		39	18.39	23.22	23.22	
	<i>Discorbis rosacea</i>	17		11	10.52	13.28	36.50	
	<i>Circeis armoricana</i>	16		10	9.75	12.31	48.81	
	<i>Lobatula lobatula</i>	15		9	8.27	10.43	59.25	
	<i>Lobatula lobatula</i>	15	9	8.27	10.43	59.25		

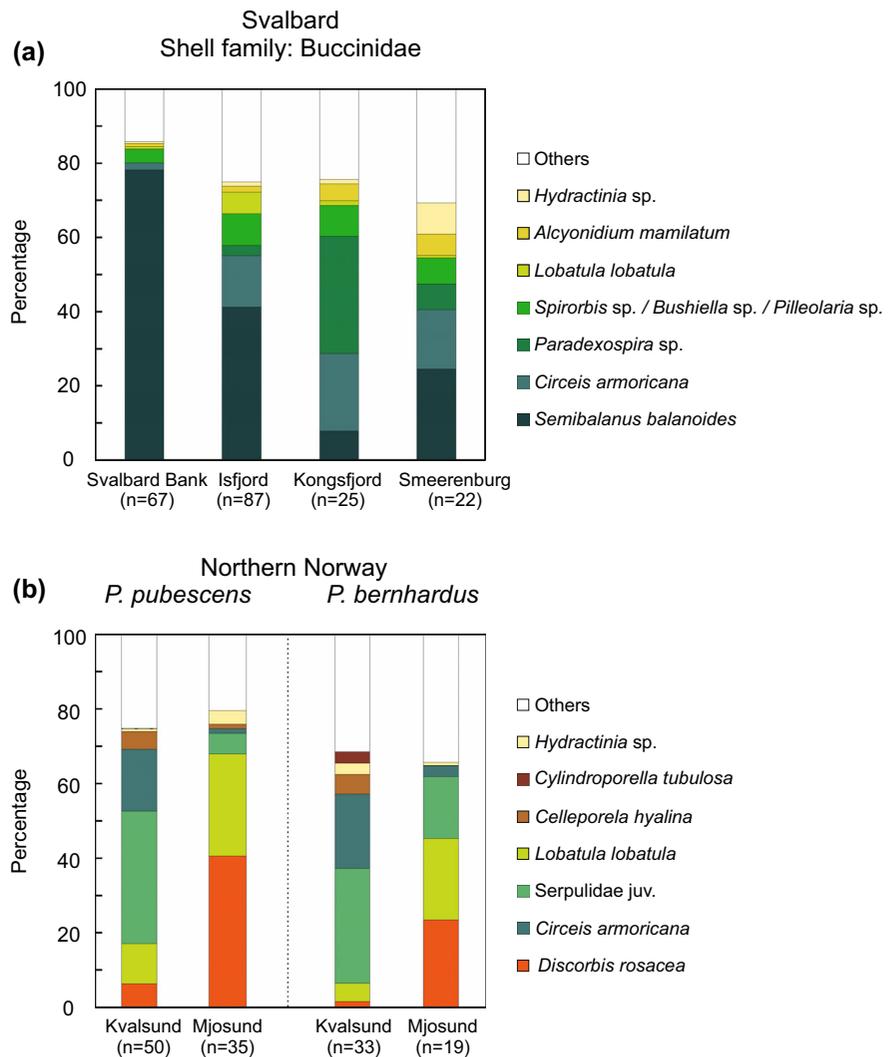
Only taxa with contributions higher than 10% are shown

on Naticidae shells), *C. armoricana* (prevailing on Muricidae shells), *Celleporella hyalina* (predominating on Trochidea shells) and *Bushiella evoluta* (on Muricidae, Table 2; Fig. 5a). More epifaunal species were found on Buccinidae and Muricidae than on Trochidae shells (Fig. 6a). Buccinids supported higher diversity than Trochidae and Naticidae (Fig. 6b).

In Northern Norway, irrespective of hermit crab identity, pair-wise tests indicated significant differences between the epifaunal communities on shells

from Littorinidae and Muricidae, Littorinidae and Buccinidae (Table 1). SIMPER analyses showed 78.7% dissimilarity between Littorinidae and Muricidae, and 79.2% between Littorinidae and Buccinidae. Species that played the greatest role in discriminating these groups of samples were juvenile forms of Serpulidae, prevailing on Muricidae and Buccinidae shells, and *C. armoricana* and foraminiferans (*Discorbis rosacea*, *Lobatula lobatula*), dominant on Littorinidae shells (Table 2; Fig. 5b). In Northern

Fig. 3 Proportion of epifauna by taxon and locations at Svalbard (a) and Northern Norway (b)



Norway, Shell identity had no influence on the number of species, individuals nor biodiversity (PERMANOVA $P > 0.05$).

Shell area

All assemblage parameters studied varied significantly (PERMANOVA $P < 0.05$) with gastropod shell area in both study areas, except for biodiversity at Svalbard (Table 1, individual test values for S , N and H' not shown). There were more epifaunal species with increasing shell size in Northern Norway ($r_s = 0.31$, $t = 3.84$, $P < 0.001$), more individuals ($r_s = 0.18$, $t = 2.09$, $P = 0.039$) and the diversity index was higher ($r_s = 0.25$, $t = 3.06$, $P = 0.003$). Similar patterns were observed at Svalbard where the number of

epifaunal species ($r_s = 0.68$, $t = 16.32$, $P < 0.001$) and number of individuals increased with shell size ($r_s = 0.78$, $t = 21.28$, $P < 0.001$). In Northern Norway the average shell had a surface area of 14.5 cm^2 and diversity of 1.1 and was the substrate for 35.7 epifaunal individuals belonging to 5.9 species. The average shell found at Svalbard was larger (23.7 cm^2), and hosted more epibiont individuals (mean 105.5)

Fig. 4 Mean number (with 95% confidence intervals) of epifaunal species (a) individuals (b) and Shannon–Wiener diversity (H' , c) of gastropod shells found in four Svalbard (only on Buccinidae shells, Table 1) and two Northern Norway locations (for both hermit crab species). Significant differences ($P < 0.05$) revealed by PERMANOVA were present whenever the test values are shown. Pair-wise analyses with $P < 0.05$ are marked with arrows

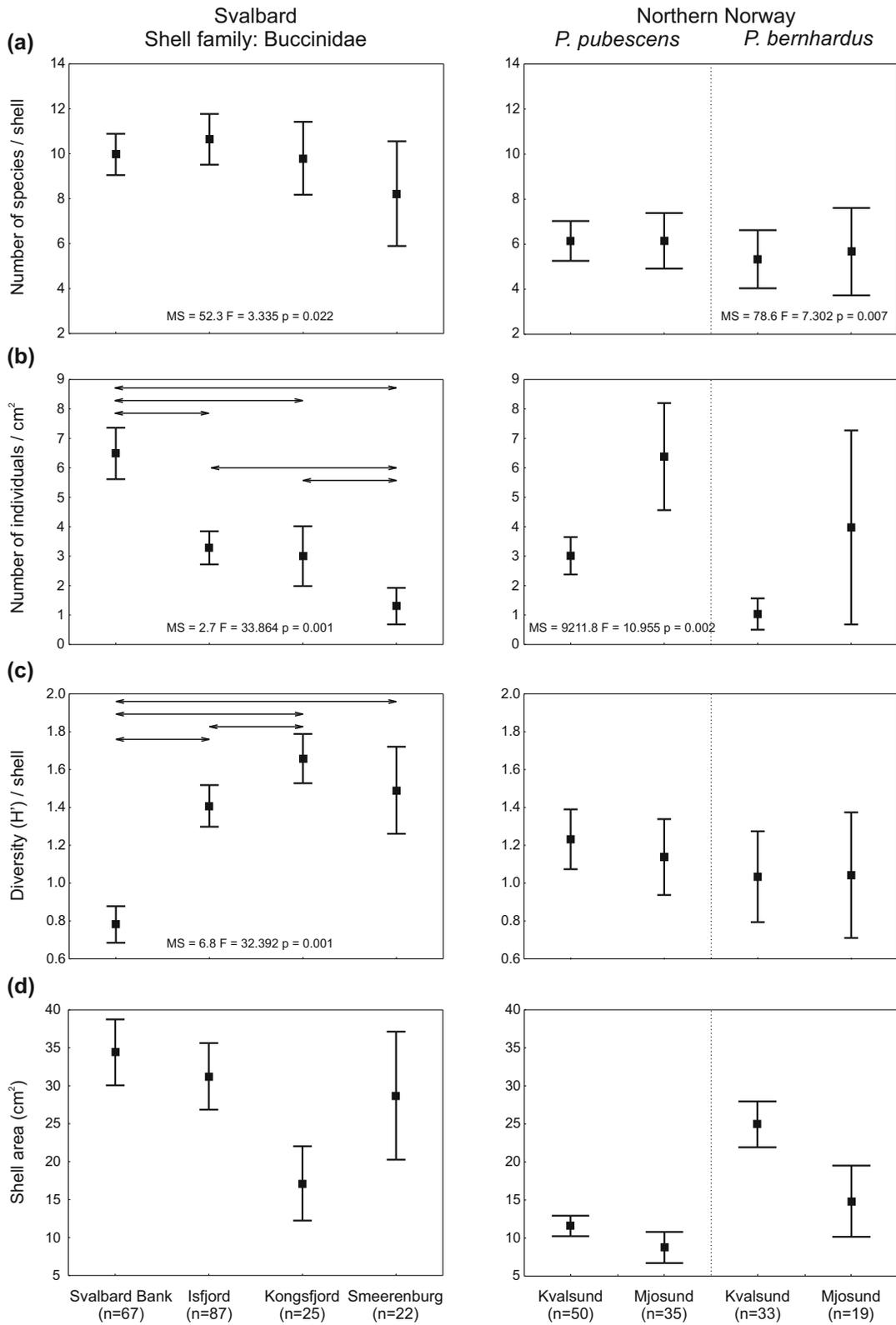
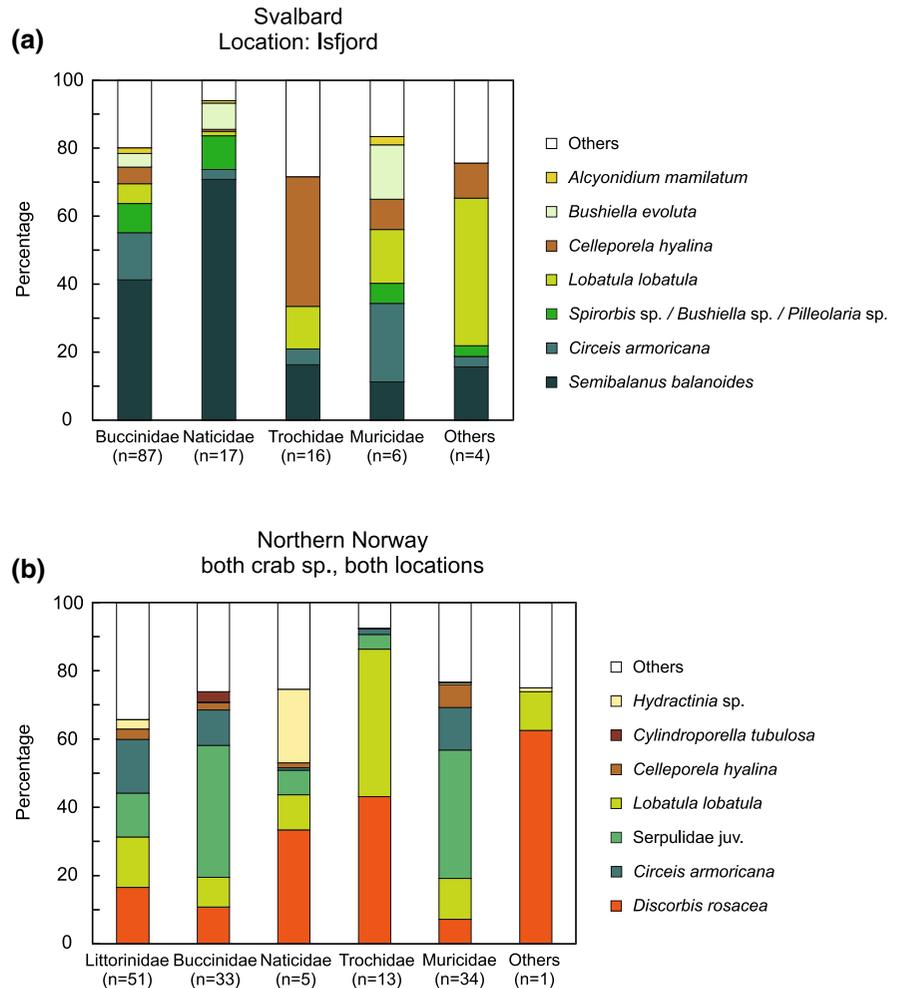


Fig. 5 Most abundant epifaunal taxa and their percentages in epibiont communities on shells representing various gastropod shell families at Svalbard (a) and Northern Norway (b)



and species (8.4), whilst the diversity of epibionts was the same (1.1). When numbers were converted to values per cm^2 of shell surface area, the number of species was equal (0.4 sp. cm^{-2}), but the number of individual epibionts was higher at Svalbard (4.5 ind. cm^{-2}) than in Northern Norway (2.5 ind. cm^{-2}).

Discussion

Despite the common pattern of autocorrelation in marine ecological samples (i.e. tendency of samples collected closer to each other to be more similar than those farther apart, e.g. Underwood & Chapman 1996), the greatest multivariate variations in hermit crab epifaunal assemblages from the two regions in the current study occurred between their replicates (i.e. from sample to sample). This has been found in other

studies of benthic invertebrates (Underwood & Chapman, 1996; Anderson et al., 2005; Włodarska-Kowalczyk & Wesławski, 2008). In hermit crab assemblages, where on a small surface the first colonist is able to occupy the majority of available space and dominate, outcompete or prevent recruitment of other species (McLean, 1983), priority effects (Sutherland, 1974) may serve as a potential mechanism for the observed pattern. Large overall number of species that occurred across all gastropod shells sampled might be also responsible for this. Although during this study we did not record as many epifaunal species as listed in the literature (e.g. Jensen & Bender 1973, p. 120 taxa), we still found 92 taxa at Svalbard and 55 in Northern Norway. Taking into account that typical gastropod shell was the substrate for 8.4 (Svalbard) or 5.9 (Northern Norway) species, and assuming the random selection of first colonizers and

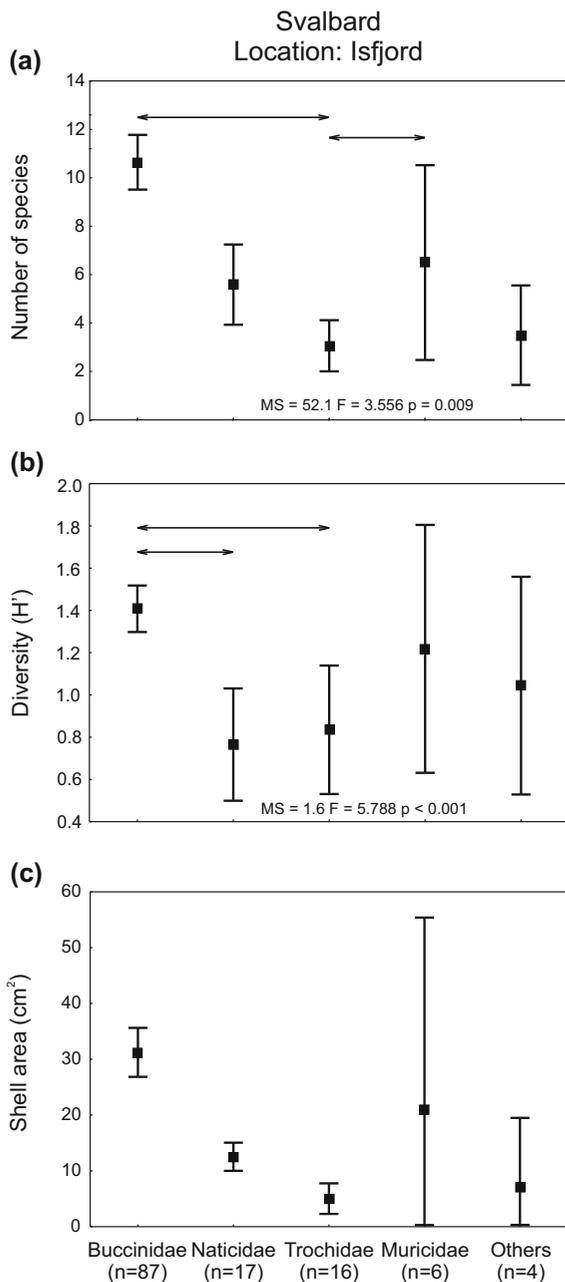


Fig. 6 Mean number (with 95% confidence intervals) of epifaunal species (**a**) and Shannon–Wiener diversity (H' , **b**) between gastropod shell families found at Svalbard (only in Isfjord). Significant differences ($P < 0.05$) revealed by PERMANOVA where present whenever the test values are shown. Pair-wise analyses with $P < 0.05$ are marked with arrows

in consequence—the dominant epibiont species, the probability that on the next shell there will be different species set is large.

Regardless of large environmental differences between Northern Norway and Svalbard, variations observed in epifaunal assemblages were the greatest between locations (i.e. fjords) not as hypothesized only on Svalbard but in both of these regions. Local species diversity draws from regional species pools, but has been found by some studies to be driven by small scale, local environmental settings (Witman et al., 2004; Renaud et al., 2009). The Svalbard locations used in the current study differed largely in their physical (e.g. hydrology, bathymetry, ice action, distance from land and glaciers, influence of terrigenous material input, sediment or freshwater discharge and bottom substratum), and thus biological settings (Jorgensen & Gulliksen, 2001; Włodarska-Kowalczyk & Pearson, 2004; Kuklinski & Porter, 2004). This was clearly reflected in the samples collected. Svalbard Bank, for example, mainly comprises barnacle and mollusc shell fragments (Elverhoi & Solheim, 1983). Epifaunal assemblages there had the highest number of individuals and the lowest Shannon–Wiener diversity index (Fig. 4b, c) due to mass occurrence of barnacles [mostly *S. balanoides*, but also *Balanus balanus* (Linnaeus, 1758) and *Balanus crenatus* Bruguière, 1789; Fig. 3a] overgrowing each other and forming dense clusters. The highest richness of epibiont species and amongst the highest epifaunal diversity occurred at Kongsfjord probably due to the intermediate oceanographic conditions there, supporting an Arctic and boreal species mix (Hop et al., 2002; Svendsen et al., 2002). Northern Norway, also subjected to the North Atlantic Current, is a more homogenous environment, yet in its Kvalsund waters serpulid polychaete reefs dominate the macrobenthos (Haines & Maurer, 1980) and were also apparent on hermit crab shells (Fig. 3b). Known for their gregarious behaviour (Scheltema et al., 1981) and strong spatial competition (Kuklinski & Barnes, 2008), they are able to monopolize a small surface such as a hermit crab shell in a short time, probably hindering other epibionts from colonization. This might explain the smaller number of species recorded in Kvalsund. In Mjosund, foraminiferans (*Lobatula lobatula* and *Discorbis rosacea*) contributed to the larger number of epifaunal individuals observed there. Species like *L. lobatula* prefer hard substrates and strong currents that ensure well mixed water and reduced sedimentation (Klitgaard Kristensen & Sejrup, 1996). In general, such conditions prevail in both the Northern Norway

study locations (Holte & Oug, 1996), so perhaps local variations in sedimentation rates, as at Tanafjord (Corner et al., 1996), could be responsible for the differences observed.

The differences in epifaunal assemblages between the hermit crab species (*Pagurus pubescens* and *P. bernhardus*) documented in this study contrast with reports from the North Sea (Reiss et al., 2003), where, except several cases, no major difference in the mean number of species or abundance of epifauna between these two hermit crab hosts was found. On the other hand Conover (1979), studying *Pagurus pollicaris* and *P. longicarpus* from Florida, observed such differences and attributed them to a rate at which hermit crabs change their shells. Species which abandon shells less frequently offer more stable and predictable habitat for epibionts. In our study, shells inhabited by *P. pubescens* were covered by a larger number of species and individuals and had higher diversities than those used by *P. bernhardus*. The ecology (e.g. habitat, breeding and behaviour) of the two hermit crab species seems similar (Samuelsen, 1970; Hazlett, 1981; Lancaster, 1988, 1990), and there were no detectable influences of gastropod shell type (interaction of crab sp. \times shell identity was not significant), so these differences could be caused by the fact that the two hermit crabs change shells in a different manner. This is possible as majority of hermit crab populations are shell limited (Kellogg, 1976; Barnes et al., 2007) and frequency of moulting/ changing shells can vary even between specimens of the same kind kept in similar conditions (Pike & Williamson, 1958). Differences in epifaunal assemblages between hermit crab hosts may be finally region specific (Norwegian Sea vs. North Sea) and future studies are needed to assess this.

Although host gender influence on epifaunal communities seems unlikely, such effects have been documented in the literature. Most of them are related to true crabs (Brachyura) and attributed to differences between the sexes in migratory habits, growth rate, length of intermoult period, shell use or abrasion during mating (Abelló, 1986; Abrams, 1988; Lancaster, 1990; Ingle, 1996; Key et al., 1997; Gherardi, 2004; Fernandez-Leborans, 2010). Genders may also exhibit specific preferences concerning epibionts (e.g. female preference of shells without *Hydractinia* sp. Van Beneden, 1844; Damiani, 2003). In our study, both hermit crab species genders occurred in the same

habitats. We did not find any major differences in the frequency of occurrence in *Hydractinia*-covered shells between males and females of either crab species in Northern Norway or Svalbard. Shell use (number of shell types and their percentage) also did not differ. Consequently, there were no significant variation caused by gender of *P. pubescens* or *P. bernhardus* in these areas (Table 1). These findings correspond with previous studies on anomuran decapods belonging to the family Lithodidae (e.g. red king crab *Paralithodes camtschaticus* (Tilesius, 1815) from the Barents Sea, Dvoretzky & Dvoretzky, 2010; but this may also vary, see Klitin, 2003).

Epifaunal assemblages in the waters of Tampa Bay, Florida varied little between the different shell species, suggesting that shell identity may not be an important factor directly influencing epifauna (Conover, 1979). Our results corroborate these findings—shell identity was indicated by PERMANOVA as one of the least influential factors, but still significant. Many of the epibiotic species larvae driven by specific preferences (e.g. substrate texture and contour, biomineralogy, presence of biofilms) do not randomly attach to exposed surfaces but instead actively seek suitable places for settlement (Crisp & Barnes, 1954; Wahl, 1989; Bavestrello et al., 2000; Berntsson et al., 2000). One of the spatial dominants from Svalbard, for example, *Semibalanus balanoides*, exhibits so-called “rugophilic” tendency, i.e. the tendency for settlement in grooves and concavities (Crisp & Barnes, 1954). In the present study, however, this species was characteristic both for irregular Buccinidae shells (*Buccinum glaciale* Linnaeus, 1761; *Buccinum undatum* Linnaeus, 1758; *Buccinum polare* Gray, 1839; *Buccinum scalariforme* Kiener, 1834) and for smooth shells of Naticidae [*Cryptonatica affinis* (Gmelin, 1791); *Euspira pallida* (Broderip & Sowerby, 1829)]. Other species indicated by SIMPER analysis to be those contributing most to observed differences between the shell types were not specific to any shells and were recorded also on other substrates (e.g. polychaete *C. armoricana* and bryozoan *Celleporella hyalina* were found on stones and pebbles, carapaces of various crustaceans, or algae; Hayward & Ryland, 1999; Jirkov, 2001; Włodarska-Kowalczyk et al., 2009). In the case of other species, reports in the literature suggest broad occurrences without substrate-specific fidelity (Keough & Downes, 1982). In general however, for the majority of epibionts, rough surfaces

seem to be more attractive than smooth (Crisp & Ryland, 1960; Teitelbaum, 1966; Crisp, 1974; Mills, 1976; Köhler et al., 1999; Herbert & Hawkins, 2006). Pits and grooves of irregular shells ensure larger number of refuges, lowered probability of destruction by physical disturbance (e.g. overturning) and higher adhesion (Barry & Dayton, 1991; Pech et al., 2002). This was also the case in our study where large, irregular Buccinidae shells supported higher diversities than smooth Naticidae.

Previous studies have shown that for most epifaunal species, the most important single factor influencing their presence or abundance is availability of suitable substrata (Kuklinski et al., 2006, 2008; Dvoretzky & Dvoretzky, 2009). Here shell area was not the most important factor but still had a significant influence on almost all investigated parameters (S , N , H in Northern Norway; S , N at Svalbard; Table 1). Larger shells provide a larger target area for settling larvae, but are also inhabited by older hermit crabs which change their shells less frequently because they grow more slowly (Tendal & Dinesen, 2005). Prolonged, undisturbed time for growth and development is advantageous for colonization of epifauna. Therefore, unsurprisingly, the number of epifaunal species and individuals increased with shell size.

Summing up, regardless of the study region (Svalbard vs. Northern Norway), local environmental settings, that is the hydrology, physical conditions and local species pools, had the greatest influence on epifaunal assemblages occurring on hard mobile substrate. Obviously, the relative importance of different factors depends on the spatial scale of the investigation, and one might expect that when the conditions are similar (e.g. study sites are located close to each other), other factors, such as shell area and its identity, or crab species, might gain in importance.

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References

- Abelló, P., 1986. Anàlisi de les poblacions de crustacis decàpodes demersals al litoral català: aspectes biològics del braquiur *Liocarcinus depurator*. Dissertation, Universitat de Barcelona.
- Abrams, P. A., 1988. Sexual difference in resource use in hermit crabs: consequences and causes. In Chelazzi, G. & M. Vannini (eds), Behavioral Adaptation to Intertidal Life. Plenum, New York: 283–296.
- Anderson, M. J. & C. J. F. Ter Braak, 2003. Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* 73: 85–113.
- Anderson, M., C. Diebel, W. Blom & T. Landers, 2005. Consistency and variation in kelp holdfast assemblages: spatial patterns of biodiversity for the major phyla at different taxonomic resolutions. *Journal of Experimental Marine Biology and Ecology* 320: 35–56.
- Anderson, M. J., R. N. Gorley & K. R. Clarke, 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth.
- Bahr, G. & B. Gulliksen, 2001. Variation of the epifauna on pier-pilings between 1980 and 1992 near the city of Tromsø, Northern Norway. *Polar Biology* 24: 282–291.
- Balazy, P. & P. Kuklinski, 2013. Mobile hard substrata—An additional biodiversity source in a high latitude shallow subtidal system. *Estuarine Coastal and Shelf Science* 119: 153–161.
- Balazy, P., P. Kuklinski, M. Włodarska-Kowalczyk, D. K. A. Barnes, M. Kedra, J. Legezynska & J. M. Weslawski, 2015. *Pagurus* spp. at its northernmost range – distribution, abundance and shell use of Arctic hermit crabs. *Polar Research* 34: 21412.
- Barnes, D. K. A. & A. Clarke, 1995. Epibiotic communities on sublittoral macroinvertebrates at Signy Island, Antarctica. *Journal of the Marine Biological Association of the United Kingdom* 75: 689–703.
- Barnes, D. K. A. & P. Kukliński, 2005. Low colonisation on artificial substrata in arctic Spitsbergen. *Polar Biology* 29: 65–69.
- Barnes, D. K. A., P. Kukliński & M. Włodarska-Kowalczyk, 2007. Richness, abundance and shell use of subarctic and arctic hermit crabs. *Marine Biology* 152: 1133–1142.
- Barry, J. P. & P. K. Dayton, 1991. Physical heterogeneity and the organization of marine communities. In Kolasa, J. & S. T. A. Pickett (eds), Ecological Heterogeneity. Springer, New York: 270–320.
- Basedow, S. L., K. Eiane, V. Tverberg & M. Spindler, 2004. Advection of zooplankton in an Arctic fjord (Kongsfjorden, Svalbard). *Estuarine, Coastal and Shelf Science* 60: 113–124.
- Bavestrello, G., C. Bianchi, B. Calcinai, R. Cattaneo-Vietti, C. Cerrano, C. Morri, S. Puce & M. Sara, 2000. Bio-minerology as a structuring factor for marine epibenthic communities. *Marine Ecology Progress Series* 193: 241–249.

- Berge, J., P. Renaud, K. Eiane, B. Gulliksen, F. Cottier, O. Varpe & T. Brattegard, 2009. Changes in the decapod fauna of an Arctic fjord during the last 100 years (1908–2007). *Polar Biology* 32: 953–961.
- Bergey, E. & G. M. Getty, 2006. A review of methods for measuring the surface area of stream substrates. *Hydrobiologia* 556: 7–16.
- Berntsson, K., P. Jonsson, M. Lejhall & P. Gatenholm, 2000. Analysis of behavioural rejection of micro-textured surfaces and implications for recruitment by the barnacle *Balanus improvisus*. *Journal of Experimental Marine Biology and Ecology* 251: 59–83.
- Clarke, K., P. Somerfield & M. Chapman, 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology* 330: 55–80.
- Clarke, K. R. & R. N. Gorley, 2001. PRIMER v. 6: User Manual/Tutorial. PRIMER-E, Plymouth.
- Connell, J. H. & M. J. Keough, 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. In Pickett, S. T. A. & P. S. White (eds), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando.
- Conover, M. R., 1979. Effect of gastropod shell characteristics and hermit crabs on shell epifauna. *Journal of Experimental Marine Biology and Ecology* 40: 81–94.
- Corner, G. D., P. I. Steinsund & R. Aspeli, 1996. Distribution of recent benthic foraminifera in a subarctic fjord-delta: Tana, Norway. *Marine Geology* 134: 113–125.
- Cottier, F., F. Nilsen, R. Skogseth, V. Tverberg, J. Skardhamar & H. Svendsen, 2010. Arctic fjords: a review of the oceanographic environment and dominant physical processes. *Geological Society Special Publication* 344: 35–50.
- Crisp, D. J., 1974. Factors influencing the settlement of marine invertebrate larvae. In Grant, P. T. & M. A. Mackie (eds), *Chemoreception in marine organisms*. Academic Press, London: 177–267.
- Crisp, D. J. & H. Barnes, 1954. The orientation and distribution of barnacles at settlement. *Journal of Experimental Marine Biology and Ecology* 38: 429–446.
- Crisp, D. J. & J. S. Ryland, 1960. Influence of filming and of surface texture on the settlement of marine organisms. *Nature* 185: 119.
- Damiani, C. C., 2003. Reproductive costs of the symbiotic hydroid *Hydractinia symbiolongicarpus* (Buss and Yund) to its host hermit crab *Pagurus longicarpus* (Say). *Journal of Experimental Marine Biology and Ecology* 288: 203–222.
- Dayton, P. K., 1984. Processes structuring some marine communities: are they general? In Strong, D. R., D. Simberloff, G. A. Lawrence & A. B. Thistle (eds), *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton: 181–197.
- Di Camillo, C., M. Bo, S. Puce, S. Tazioli, C. Frogliã & G. Bavestrello, 2008. The epibiotic assemblage of *Geryon longipes* (Crustacea: Decapoda: Geryonidae) from the Southern Adriatic Sea. *Italian Journal of Zoology* 75: 29–35.
- Dick, M. H., W. E. I. Donaldson & W. Vining, 1998. Epibionts of the tanner crab *Chionoecetes bairdi* in the region of Kodiak Island, Alaska. *Journal of Crustacean Biology* 18: 519–528.
- Dvoretzky, A. G. & V. G. Dvoretzky, 2008. Epifauna associated with the northern stone crab *Lithodes maia* in the Barents Sea. *Polar Biology* 31: 1149–1152.
- Dvoretzky, A. G. & V. G. Dvoretzky, 2009. Fouling community of the red king crab, *Paralithodes camtschaticus* (Tilesius 1815), in a subarctic fjord of the Barents sea. *Polar Biology* 32: 1047–1054.
- Dvoretzky, A. G. & V. G. Dvoretzky, 2010. Epifauna associated with an introduced crab in the Barents Sea: a 5-year study. *ICES Journal of Marine Science* 67: 204–214.
- Elverhoi, A. & A. Solheim, 1983. *The Physical Environment – Western Barents Sea, 1:1500000, Sheet A: Surface Sediment Distribution*. Norsk Polarinstitutt Skrifter 179A. Norwegian Polar Institute, Tromsø.
- Fernandez-Leborans, G., 2010. Epibiosis in Crustacea: an overview. *Crustaceana* 83: 549–640.
- Gherardi, F., 2004. Resource partitioning between sexes in the “unconventional” hermit crab, *Calcinus tubularis*. *Behavioral Ecology* 15: 742–747.
- Gili, J. M., P. Abello & R. Villanueva, 1993. Epibionts and intermolt duration in the crab *Bathynectes piperitus*. *Marine Ecology Progress Series* 98: 107–113.
- Haines, J. L. & D. Maurer, 1980. Benthic invertebrates associated with a serpulid polychaete assemblage in a temperate estuary. *Internationale Revue der Gesamten Hydrobiologie* 65: 643–656.
- Harder, T., 2009. Marine epibiosis: concepts, ecological consequences and host defence. In Flemming, H. C., P. S. Murthy, R. Venkatesan & K. Cooksey (eds), *Marine and Industrial Biofouling, Vol. 4. Springer Series on Biofilms*, Berlin, Heidelberg: 219–231.
- Hayward, P. J. & J. S. Ryland (eds), 1999. *The Marine Fauna of the British Isles and North-West Europe: Volume 1: Introduction; Protozoans – Arthropods*. Oxford University Press, Oxford.
- Hazlett, B. A., 1981. The behavioural ecology of hermit crabs. *Annual Review of Ecology, Evolution and Systematics* 12: 1–22.
- Herbert, R. J. H. & S. J. Hawkins, 2006. Effect of rock type on the recruitment and early mortality of the barnacle *Chthamalus montagui*. *Journal of Experimental Marine Biology and Ecology* 334: 96–108.
- Holte, B. & E. Oug, 1996. Soft-bottom macrofauna and responses to organic enrichment in the subarctic waters of Tromsø, Northern Norway. *Journal of Sea Research* 36: 227–237.
- Hop, H., T. Pearson, E. N. Hegseth, K. M. Kovacs, C. Wiencke, S. Kwaśniewski, K. Eiane, et al., 2002. The marine ecosystem of Kongsfjord, Svalbard. *Polar Research* 21: 208.
- Ingle, R. W., 1996. Shallow-water crabs: keys and notes for identification of the species. 2nd edition. In Barnes, R. S. K. & J. H. Crothers (eds) *Synopses of the British Fauna. Field Studies Council, Shrewsbury*. 25: 1–243.
- Jackson, J., 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *American Naturalist* 111: 743–767.
- Jensen, K. & K. Bender, 1973. Invertebrates associated with snail shells inhabited by *Pagurus bernhardus* (L.) (Decapoda). *Ophelia* 10: 185–192.
- Jirkov, I. A., 2001. Polychaeta of the Arctic Ocean. Yanus-K, Moscow.

- Jorgensen, L. L. & B. Gulliksen, 2001. Rocky bottom fauna in arctic Kongsfjord (Svalbard) studied by means of suction sampling and photography. *Polar Biology* 24: 113–121.
- Kaczmarek, H., M. Włodarska-Kowalczyk, J. Legeżyńska & M. Zajaczkowski, 2005. Shallow sublittoral macrozoobenthos in Kongsfjord, West Spitsbergen, Svalbard. *Polish Polar Research* 26: 137–155.
- Kellogg, C. W., 1976. Gastropod shells: a potentially limiting resource for hermit crabs. *Journal of Experimental Marine Biology and Ecology* 22: 101–111.
- Keough, M. J. & B. J. Downes, 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia* 54: 348–352.
- Key Jr, M. M., J. W. Volpe, W. B. Jeffries & H. K. Voris, 1997. Barnacle Fouling of the Blue Crab *Callinectes sapidus* at Beaufort, North Carolina. *Journal of Crustacean Biology* 17: 424–439.
- Klitgaard Kristensen, D. & H. P. Sejrup, 1996. Modern benthic foraminiferal biofacies across the northern North Sea. *Sarsia* 8: 97–106.
- Klitin, A. K., 2003. The Red King Crab along the Shores of Sakhalin and the Kuril Islands: Biology, Distribution, and Functional Structure of the Area. *Natsrybresursy*, Moscow: 253 (in Russian).
- Köhler, J., P. Hansen & M. Wahl, 1999. Colonization patterns at the substratum-water interface: how does surface microtopography influence recruitment patterns of sessile organisms? *Biofouling* 14: 237–248.
- Kuklinski, P. & D. K. A. Barnes, 2008. Structure of intertidal and subtidal assemblages in Arctic vs temperate boulder shores. *Polish Polar Research* 29: 203–218.
- Kuklinski, P. & J. Porter, 2004. *Alcyonidium disciforme* Smitt, 1871: an exceptional Arctic bryozoan. *Journal of the Marine Biological Association of the United Kingdom* 84: 267–275.
- Kuklinski, P., B. Gulliksen, O. J. Lonne & J. M. Węśławski, 2006. Substratum as a structuring influence on assemblages of Arctic bryozoans. *Polar Biology* 29: 652–661.
- Kuklinski, P., D. K. A. Barnes & M. Włodarska-Kowalczyk, 2008. Gastropod shells, hermit crabs and Arctic bryozoan richness. In Hageman, S. J., M. M. Key Jr. & J. E. Winston (eds), *Bryozoan Studies 2007. Proceedings 14th International Bryozoology Association Conference*. Virginia Museum of Natural History Special Publication No. 15, Martinsville: 93–100.
- Kupriyanova, E. K. & I. A. Jirkov, 1997. Serpulidae (annelida, polychaeta) of the Arctic Ocean. *Sarsia* 82: 203–236.
- Lancaster, I., 1988. *Pagurus bernhardus* (L.) - an introduction to the natural history of hermit crabs. *Field Studies* 7: 189–238.
- Lancaster, I., 1990. Reproduction and life history strategy of the hermit crab *Pagurus bernhardus*. *Journal of the Marine Biological Association of the United Kingdom* 70: 129–142.
- Loeng, H., 1991. Features of the physical oceanographic conditions of the Barents Sea. *Polar Research* 10: 5–18.
- McDermott, J. J., J. D. Williams & C. B. Boyko, 2010. The unwanted guests of hermits: a global review of the diversity and natural history of hermit crab parasites. *Journal of Experimental Marine Biology and Ecology* 394: 2–44.
- McGaw, I. J., 2006. Epibionts of sympatric species of Cancer crabs in Barkley sound, British Columbia. *Journal of Crustacean Biology* 26: 85–93.
- McLean, R., 1983. Gastropod shells: a dynamic resource that helps shape benthic community structure. *Journal of Experimental Marine Biology and Ecology* 69: 151–174.
- Menge, B. A. & J. P. Sutherland, 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* 130: 730–757.
- Mils, C. E., 1976. The Association of hydractiniid hydroids and hermit crabs, with new observations from North Florida. In Mackie, G. O. (ed), *Coelenterate ecology and behavior*. Plenum Press, London: 467–476.
- Oug, E., 1998. Relating species patterns and environmental variables by canonical ordination: an analysis of soft-bottom macrofauna in the region of Tromsø, northern Norway. *Marine Environmental Research* 45: 29–45.
- Oug, E., 2001. Polychaetes in intertidal rocky and sedimentary habitats in the region of Tromsø, northern Norway. *Sarsia* 86: 75–83.
- Pech, D., P. L. Ardisson & E. Bourget, 2002. Settlement of a tropical marine epibenthic assemblage on artificial panels: influence of substratum heterogeneity and complexity scales. *Estuarine, Coastal and Shelf Science* 55: 743–750.
- Pike, R. B. & D. I. Williamson, 1958. Observations on the distribution and breeding of british hermit crabs and the stone crab (Crustacea: Diogenidae, Paguridae and Lithodidae). *Proceedings of the Zoological Society of London* 132: 551–567.
- Reiss, H., S. Knauper & I. Kroncke, 2003. Invertebrate associations with gastropod shells inhabited by *Pagurus bernhardus* (Paguridae) secondary hard substrate increasing biodiversity in North Sea soft-bottom communities. *Sarsia* 88: 404–415.
- Renaud, P. E., T. J. Webb, A. Bjoergesaeter, I. Karakassis, M. Kedra, M. A. Kendall, C. Labruno, N. Lampadariou, P. J. Somerfield, M. Włodarska-Kowalczyk, E. Vanden Berghe, S. Claus, I. F. Aleffi, J. M. Amouroux, K. H. Bryne, S. J. Cochrane, S. Dahle, S. Degraer, S. G. Denisenko, T. Depez, C. Dounas, D. Fleischer, J. Gil, A. Gremare, U. Janas, A. S. Y. Mackie, R. Palerud, H. Rumohr, R. Sarda, J. Speybroeck, S. Taboada, G. van Hoey, J. M. Weslawski, P. Whomersley & M. L. Zettler, 2009. Continental-scale patterns in benthic invertebrate diversity: insights from the MacroBen database. *Marine Ecology Progress Series* 382: 239–252.
- Sakshaug, E., G. Johnsen, S. Kristiansen, C. von Quillfeldt, F. Rey, D. Slagstad & F. Thingstad, 2009. Phytoplankton and primary production. Chapter 7. In Sakshaug, E., G. Johnsen & K. Kovacs (eds), *Ecosystem Barents Sea*. Tapir Academic Press, Trondheim: 167–208.
- Samuelsen, T. J., 1970. The biology of six species of Anomura (Crustacea, Decapoda) from Raunefjorden, western Norway. *Sarsia* 45: 25–52.
- Sandberg, L. & P. A. McLaughlin, 1988. Crustacea, Decapoda, Paguridae. *Marine invertebrates of Scandinavia* No. 10. Scandinavian University Press, Oslo: 113.
- Scheltema, R. S., I. P. Williams & C. Loudon, 1981. Gregarious settlement by the larvae of Hydroides. *Marine Ecology Progress Series* 5: 69–74.
- Smith, F. & J. D. Witman, 1999. Species diversity in subtidal landscapes: maintenance by physical processes and larval recruitment. *Ecology* 80: 51–69.

- Sokal, R. R. & F. J. Rohlf, 1981. Biometry, 2nd ed. WH Freeman and Company, New York.
- Svendsen, H., M. Beszczyńska, J. O. Hagen, B. Lefauconnier, V. Tverberg, S. Gerland, J. B. Orbeak, et al., 2002. The physical environment of Kongsfjorden-Krossfjorden, and Arctic fjord system in Svalbard. *Polar Research* 21: 133–166.
- Teitelbaum, M., 1966. Behavior and settling mechanism of planulae of *Hydractinia echinata*. *Biological Bulletin, Marine Biological Laboratory, Woods Hole* 131: 410–411.
- Tendal, O. S. & G. E. Dinesen, 2005. Biogenic sediments, substrates and habitats of the Faroese shelf and slope. *BIOFAR Proceedings 2005*: 224–242.
- Underwood, A. & M. Chapman, 1996. Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107: 212–224.
- Wahl, M., 1989. Marine epibiosis. 1. Fouling and antifouling—some basic aspects. *Marine Ecology Progress Series* 58: 175–189.
- Wahl, M. (ed.), 2009. *Marine Hard Bottom Communities – Patterns, Dynamics, Diversity, and Change*, Ecological Studies, Vol. 206. Springer, New York.
- Wassmann, P., H. Svendsen, A. Keck & M. Reigstad, 1996. Selected aspects of the physical oceanography and particle fluxes in fjords of northern Norway. *Journal of Marine Systems* 8: 53–71.
- Williams, J. D. & J. J. McDermot, 2004. Hermit crab biocoenoses: a worldwide review of the diversity and natural history of hermit crab associates. *Journal of Experimental Marine Biology and Ecology* 305: 1–128.
- Witman, J. D., R. J. Etter, F. Smith & R. T. Paine, 2004. The Relationship between regional and local species diversity in marine benthic communities: a global perspective. *Proceedings of the National Academy of Sciences of the United States of America* 101: 15664–15669.
- Włodarska-Kowalczyk, M., 2007. Molluscs in Kongsfjorden (Spitsbergen, Svalbard): a species list and patterns of distribution and diversity. *Polar Research* 26: 48–63.
- Włodarska-Kowalczyk, M. & T. Pearson, 2004. Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen). *Polar Biology* 27: 155–167.
- Włodarska-Kowalczyk, M. & J. M. Weslawski, 2008. Mesoscale spatial structures of soft-bottom macrozoobenthos: physically controlled/impooverished versus biologically accommodated/diverse communities. *Marine Ecology Progress Series* 356: 215–224.
- Włodarska-Kowalczyk, M., M. Szymelfenig & M. Zajackowski, 2007. Dynamic sedimentary environments of an Arctic glacier-fed river estuary (Adventfjorden, Svalbard). II. Meio- and macrobenthic fauna. *Estuarine Coastal and Shelf Science* 74: 274–284.
- Włodarska-Kowalczyk, M., P. Kukliński, M. Ronowicz, J. Legeżyńska & S. Gromisz, 2009. Assessing species richness of macrofauna associated with macroalgae in Arctic kelp forests (Hornsund, Svalbard). *Polar Biology* 32: 897–905.