



Structure of intertidal and subtidal assemblages in Arctic vs temperate boulder shores

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Abstract: Several studies suggest that assemblages in intertidal zones that experience frequent physical extremes (*e.g.* wave-impacts) should be highly dependent on the regional input of propagules. Therefore with higher disturbance in the intertidal zone, higher dependence on the species pool from nearby assemblages (*e.g.* subtidal) should be observed. Here we examine adult community structure to investigate levels of similarity among marine assemblages of Arctic intertidal zones compared with those in adjacent subtidal areas. Additionally we compare Arctic results with similar data from a temperate area. We selected boulder fields as a model habitat and we predicted that subtidal and intertidal diversity would change differently under varying disturbance regimes. Multivariate analysis of data from Arctic and temperate North Atlantic indicates that in the Arctic, intertidal and subtidal assemblages were more similar to each other than were temperate intertidal and subtidal assemblages. We suggest this is not because of species differences but that the temperate areas are less disturbed. The wave and ice battered, highly disturbed intertidal assemblages of the Arctic were composed of a subset of nearby subtidal assemblages with similar dominance structure. Intertidal specialist species were not found in the Arctic samples. In contrast, temperate intertidal boulder-field assemblages had a completely different dominance structure to the adjacent subtidal. Furthermore, temperate intertidal assemblages were composed of different (specialist) species often not found in the subtidal zone. We conclude that more disturbed environments, such as our Arctic study sites, are more dependent on outside sources of recruitment.

Key words: Arctic, North Atlantic, boulder-fields, biodiversity, assemblages similarity.

Introduction

Abiotic disturbance may decrease the influence of biological interactions on realised assemblage structure (Karlson and Cornell 2002). Even low rates of disturbance can obscure the effect of strong competitive interactions in the local

species pool, leading to linear relations between local and regional species pools (Caswell and Cohen 1993). Theory predicts that if regional-scale processes are important, local species richness will increase as a function of the size of the regional species pool (Ricklefs 1987; Cornell and Karlson 1996; Witman *et al.* 2004; Russell *et al.* 2006). On the other hand if local species richness approaches asymptote with increased regional richness, factors (*e.g.* competition or predation) other than the size of the regional species pool constrain local richness (Ricklefs 1987; Cornell and Lawton 1992; Russell *et al.* 2006). Palmer *et al.* (1996) suggested that assemblages in intertidal zones that experience frequent physical extremes (*e.g.* wave-impacts) should be highly dependent on the regional input of propagules. Therefore with higher disturbance in the intertidal zone, higher dependence on the species pool from nearby assemblages (*e.g.* subtidal) should be observed. In this study we investigate how intertidal and nearby subtidal diversity interacts under varying disturbance regime using boulder-fields as a model habitat.

Boulder-fields are very common and ubiquitous coastal habitats worldwide. Although at scales of meters they sometimes appear chaotic and heterogeneous, at others (scales of kilometres) they could be considered fairly uniform and well suited as model substrata for testing ecological hypotheses. Disturbances of substrata such as boulders by storms, waves, scouring by sand or ice are known to affect richness, diversity, abundance and patterns of recruitment (*e.g.* Osman 1977; Shanks and Wright 1986; Sousa 1979; McGuinness 1987a, b; Kukliński and Barnes 2005). Through extreme events, disturbance can occasionally be severe at any shallow locality but there are geographic patterns in disturbance and this shapes organism assemblages. Intensity of disturbance typically increases towards the poles due to summer ice scour (the grounding of icebergs, scraping the sea-bed), intense wave action and fresh water runoff, coupled with freezing temperatures and ice foot during winter (see Gutt *et al.* 1996; Barnes 1999; Barnes and Conlan 2007). Aspects of competition for space in boulder-fields vary in distinct clines from the poles to the tropics, notably becoming more hierarchical towards polar regions (Barnes 2002; Barnes and Kukliński 2003). As with some recent literature investigating marine disturbance and competition, we use Arctic and temperate fjords as model systems.

Some temperate investigations found that high frequencies of disturbance of smaller boulders effectively results in benthic communities remaining in the early stages of colonization (Osman 1977). There is lots of evidence that highly disturbed intertidal boulder assemblages are composed entirely of a subset of local subtidal species or that they mirror current or recent occurrence of meroplankton in the water column (*e.g.* Osman 1977; Sousa 1979). Such assemblages tends to be dominated by species that happen to settle in the highest abundance after the most recent disturbance event or at the time of sampling. However temperate locations exhibit strong habitat patchiness and lack of certain types of disturbance (*e.g.* ice

scour) these patterns are only observed over small scales (only small rocks, highly disturbed areas) or not at all. Therefore substrata from permanently disturbed habitats like the Arctic intertidal zone are expected to exhibit seasonal species dominance over large areas.

In the current study we investigate the structure of subtidal and intertidal boulder-field assemblages from the Arctic and compare them with temperate sites in the north Atlantic. We suggest that if disturbance is high the intertidal richness/diversity will likely be determined by (and recruit from) that in the nearby subtidal zone and that there should be greater similarity between them. If disturbance is low to moderate, intertidal diversity will be not so shaped by the nearby subtidal species pool and there should be low similarity between them. We predict that subtidal and intertidal diversity will interact differently under varying disturbance regimes. We hypothesise that Arctic intertidal assemblages will have more similarity to their adjacent subtidal assemblages due to a higher level of dependence on nearby subtidal species pool than in a less disturbed (temperate) location. Temperate intertidal assemblages are likely to be composed of both species that occur in the subtidal as well as intertidal specialist species due to lower disturbance.

Study area

Six boulder-fields in Arctic fjords and six in temperate North Atlantic fjords were selected as sample sites (Fig. 1). Within the Arctic, two study localities were selected: Kongsfjorden (79°N) and Hornsund (77°N) on the west coast of Spitsbergen (Svalbard Archipelago). Trondheimsfjord (63°N) on the west coast of Norway was chosen as the area for the temperate sites. In each site, samples were collected from the intertidal and nearby subtidal (6 m depth). Samples were collected in summer 2002 (Arctic) and autumn 2003 (Temperate). The substrata at the study sites were characterised by similar size ranges, mixed boulders and cobbles. The study sites also had similar profiles but differed in mean annual seawater and air temperature, tidal amplitude, wave strength and prevalence of ice. At all sites the cobbles and boulders comprised hard, firmly-cemented rocks that did not easily crumble. The high Arctic sites at Svalbard were typically scoured by floating ice during summer months and overlain by fast ice during the winter. In addition the salinity regime of the Svalbard sites fluctuated seasonally, being as low as 25–32 psu in June. The sea temperature at the time of material collection was 3°C, but varies annually from approximately -1.8 to 7°C. Tidal amplitude at Svalbard is typically ~1 m whereas the mean tidal amplitude may range from approx. 1.2 (neap tide) to 2.5 m (spring tide) in the Trondheimsfjord. During the study period, the mean summer coastal sea-water temperatures of the temperate sites were (12–14°C) with salinity varying from 33 to 34 psu.

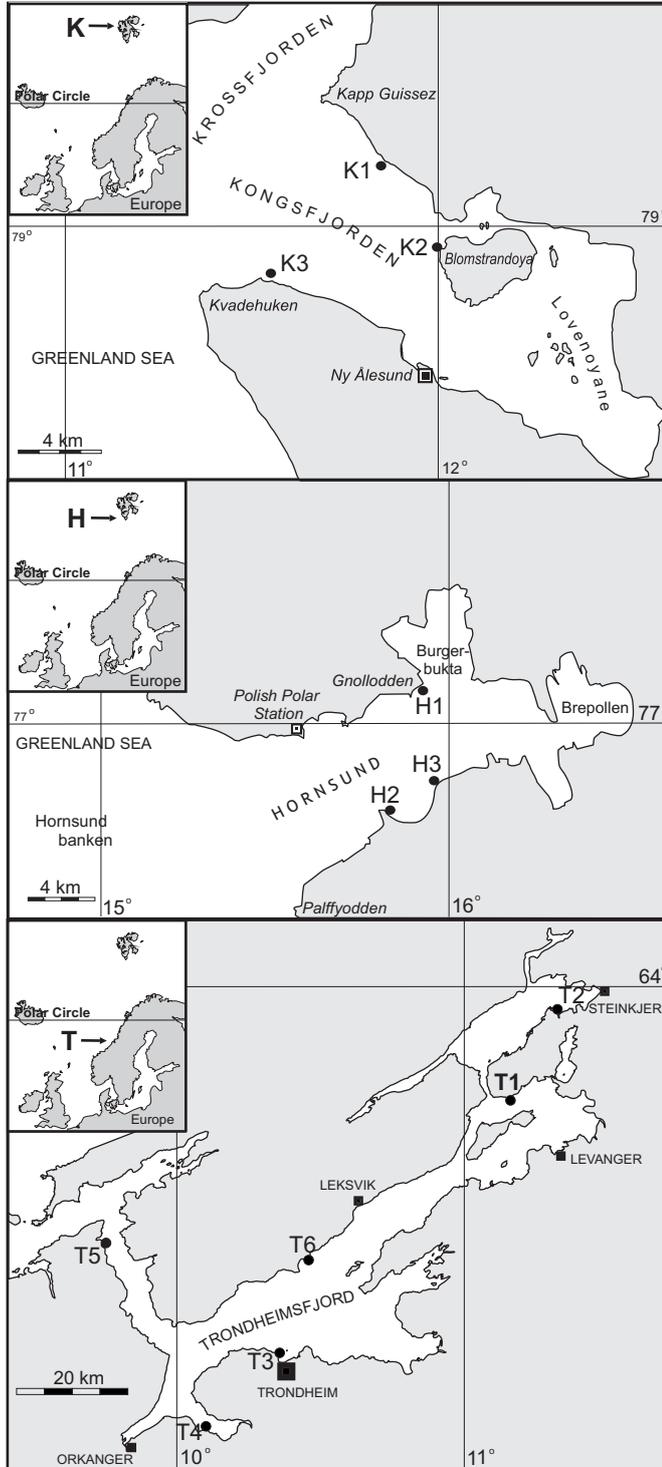


Fig. 1. Northern Atlantic and Svalbard study area showing the sampling locations. The abbreviations are K – Kongsfjorden, H – Hornsund, and T – Trondheimsfjord.

Material and methods

From each of the sites 50 boulder/cobbles were haphazardly collected. In all cases samples were collected from around Extreme Low Water Spring (ELWS) tide level and at 6 m depth (below ELWS). The surface area of the sample substrata was estimated using an inelastic net marked in a grid of cm². The number and identities of all colonisers were recorded to the lowest taxonomic level possible, typically species. For the purpose of this study each colony of a colonial species was considered as one individual. In order to determine whether collected samples were saturated with respect to species pools present in the area for all sites, species accumulation curves were plotted.

Abundance data were subjected to ANOVA with depth as a spatial factor. Data were log transformed prior to analyses to improve homogeneity and normality.

In order to investigate the environmental dynamics and its influence on rock biota we used the probability of faunal occurrence as a proxy. We assumed that a lower probability of an organism's presence indicates higher dynamics of the given environment in contrast to areas where this probability is higher. Therefore rocks from both intertidal and subtidal were divided into size classes (1, 10, 50, 100, 250, 500, 1000 cm²) and the probability of fauna occurrence on them was calculated for each region. Data were plotted as mean \pm standard error against rocks size classes. Comparison between temperate and Arctic intertidal data as well as subtidal was done with use of covariance test ANCOVA. Data were log transformed prior to analyses to improve homogeneity and normality.

To compare the faunal composition and sample similarities, the PRIMER software package was used (Clarke and Gorley 2001). Quantitative data were square-root transformed and the Bray-Curtis similarity measures were calculated (Bray and Curtis 1957). The similarity between samples was mapped using the ordination technique, non-metric multidimensional scaling (nMDS). The SIMPER (similarity percentage) analysis was used to identify the discriminating taxa between observed sample clusters. Taxa were listed in decreasing order by their average contribution to the total average dissimilarity.

Results

The 1200 cobbles collected were colonized by 81637 recruits belonging to 117 taxa. Species accumulation curves were found to approach an asymptote in the assemblages at all the sites (plots not shown). Thus the sampling appears to have been representative in the study areas.

In general the subtidal samples showed a much higher probability of fauna occurring in all size classes compared to those in the intertidal, in both the temperate and Arctic regions (Fig. 2). The probability of fauna occurring on different rock

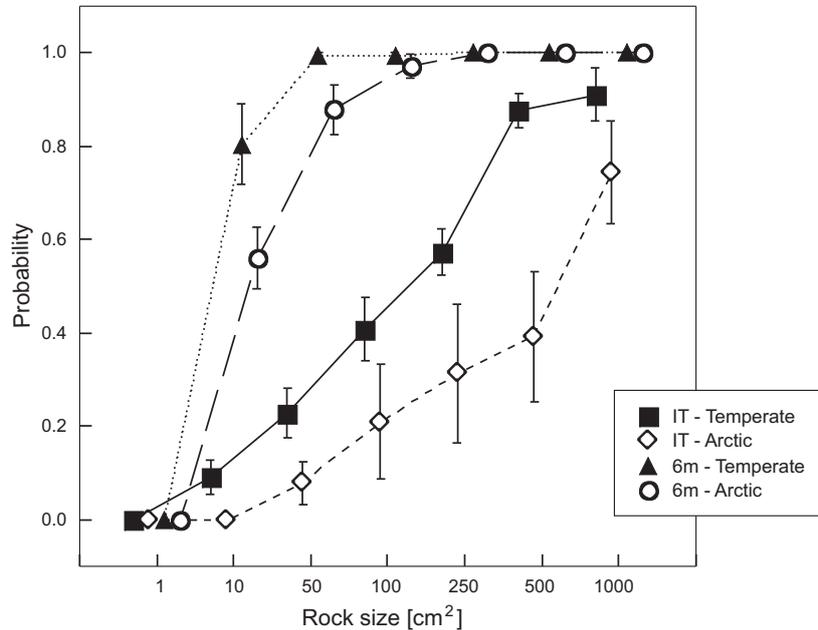


Fig. 2. Probability (mean values \pm standard error) of faunal occurrence with surface area on temperate and Arctic rocks. The abbreviation is IT – Intertidal.

sizes in the intertidal of temperate Trondheimsfjord and Arctic locations was significantly different (ANCOVA; $F_{(1, 80)} = 16.13$, $p < 0.001$, Fig. 2). There was no overlap in any of the investigated size classes of fauna in the intertidal at both areas. Subtidal temperate rocks in the majority of samples had a higher probability of fauna occurring in comparison to those in the Arctic subtidal. However on the >250 cm² size class of rocks, the probability of fauna occurrence was similar at both subtidal locations (Fig. 2). There was no statistical difference between subtidal for these two localities (ANCOVA; $F_{(1, 78)} = 0.33$, $p = 0.565$).

Multivariate analysis (nMDS) showed a greater similarity between the intertidal and subtidal samples in the Arctic fjords than at the temperate fjord (Fig. 3). Thus multivariate analysis supported our interpretation that dynamic Arctic intertidal assemblages have greater similarity to nearby subtidal assemblages than assemblages from a similar habitat (in terms of substrata) from a temperate area.

Intertidal assemblages from Trondheimsfjord were significantly different in species composition and dominance structure to assemblages in the subtidal zone (Table 1). There were only a few species that occurred in the intertidal zone but were not found in samples from the subtidal boulder fields (e.g. bryozoan *Electra crustulenta* Pallas – see Table 1). Macrofaunal abundance in intertidal assemblages (mean 312.8 indiv/m² per site) was significantly (ANOVA, $F_{(1, 10)} = 39.97$, $p < 0.001$) lower than in the subtidal zone (mean 6529.1 indiv/m² per site). The dominant species across the temperate intertidal study locations was the cirriped

Table 1
Values of densities of the most abundant species in the given site in intertidal and subtidal boulder-fields from temperate North Atlantic (individuals number/m²) – all station signs according with Fig. 1 (B – Bryozoa, C – Cirripedia, P – Polychaeta, H – Hydrozoa)

	INTERTIDAL						SUBTIDAL					
	T1	T2	T3	T4	T5	T6	T1	T2	T3	T4	T5	T6
<i>Balanus crenatus</i> Brugičre, 1789 (C)								61.2				
Bryozoa ancestrula					1.6							
<i>Callopora craticula</i> (Alder, 1857) (B)							9.2			132.0	35.2	44.5
<i>Callopora dumerilii</i> (Audouin, 1826)							53.4			4.9	2.5	5.6
<i>Clytia hemisphaerica</i> (Linnaeus, 1767) (H)	3.5		31.6	6.0	1.6	144.1						
<i>Cribrilina cryptoecium</i> Norman, 1903 (B)								71.8		1.2		8.5
<i>Cribrilina punctata</i> (Hassall, 1841) (B)								45.2		148.2	1.3	2.8
<i>Electra crustulenta</i> (Pallas, 1776) (B)				12.0								
<i>Electra pilosa</i> (Linnaeus, 1767) (B)			8.5			4.6			1.5	2.5		
<i>Escharella immersa</i> (Fleming, 1828) (B)							66.2		1.5	371.3	25.2	548.2
Foraminifera indet.							542.8	396.3	369.6	1914.4	118.6	1681.9
<i>Dynamena pumila</i> (Linnaeus, 1758) (H)			1.9			16.9						
<i>Parasmittina trispinosa</i> (Johnston, 1838) (B)											21.4	148.0
<i>Pomatoceros triqueter</i> (Linnaeus, 1758) (P)							5475.6	5859.8	4390.0	1979.8	1284.0	2912.9
Sabelidae indet. (P)				6.0			4.5			13.6		2.8
<i>Semibalanus balanoides</i> (Linnaeus, 1767) (C)	443.3	12.3	86.2	16.5	67.7	3.7	1.8					11.1
<i>Spirorbis tridentatus</i> Levinsen 1883 (P)	3.5		3.6			1.5	425.2	9.4	366.5	482.5	422.5	1833.2
Tubuliporidae indet. (B)							23.9			188.7	99.3	16.9
<i>Verruca stroemia</i> (Müller, 1776) (C)								9.4	1.5	271.4	5.3	98.5

Semibalanus balanoides L. (mean 104.9 indiv/m² per site). In contrast, in the subtidal samples *S. balanoides* was only present at two locations in lower density (mean 2.1 indiv/m² per site) (Table 1). The dominant species at all temperate subtidal locations was the polychaete *Pomatoceros triqueter* L. (mean 3650.3 indiv/m² per site) (Table 1). However, *P. triqueter* did not occur in any intertidal samples. As nMDS showed (Fig. 3), there was considerable dissimilarity between intertidal and subtidal samples of the temperate Trondheimsfjord location. SIMPER analysis indicated that observed dissimilarities between clusters were con-

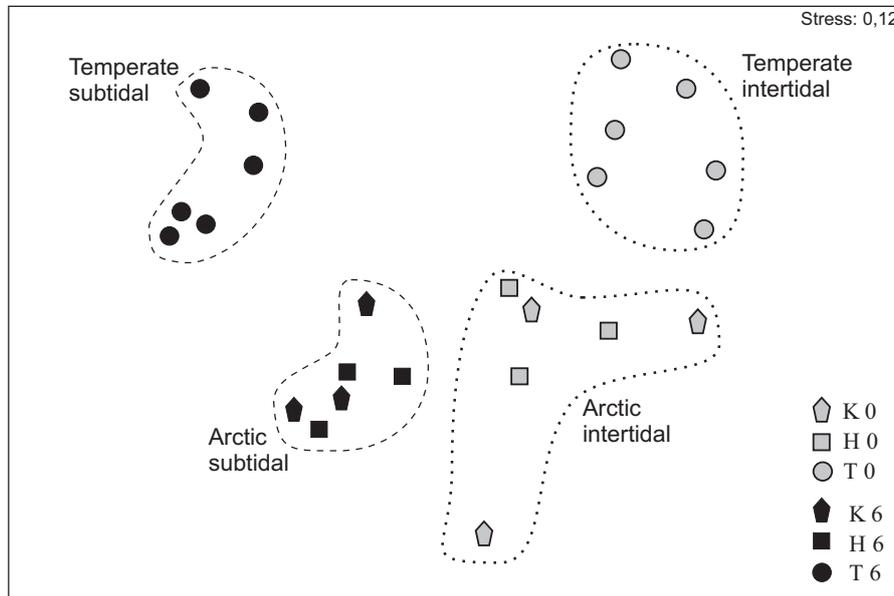


Fig. 3. Multidimensional scaling (nMDS) based on Bray – Curtis similarities calculated from square – rooted transformed species abundance data. The abbreviations are K0 – Kongsfjorden intertidal, H0 – Hornsund intertidal, T0 – Trondheimsfjord intertidal, K6 – Kongsfjorden subtidal 6 m depth, H6 – Hornsund subtidal 6 m depth, and T6 – Trondheimsfjord subtidal 6 m depth.

tributed both by species present in intertidal and subtidal (Table 2). The dominant species from the intertidal (e.g. *S. balanoides*) and subtidal (e.g. *P. triqueter*) were among the most contributing species to observed dissimilarities between intertidal and subtidal assemblages (Table 2).

Table 2
Results of SIMPER analysis with 10 most contributing species to dissimilarities between intertidal and subtidal boulder-fields from temperate North Atlantic (average abundance: individuals number/m²) (B – Bryozoa, C – Cirripedia, P – Polychaeta, H – Hydrozoa)

Species	INTERTIDAL Average abundance	SUBTIDAL Average abundance	Average dissimi- larity	Contri- bution %	Cumu- lative %
Foraminifera indet.	0	987.2	5.51	6.23	6.23
<i>Verruca stroemia</i> (Müller, 1776) (C)	0	64.3	4.7	5.31	11.54
<i>Pomatoceros triqueter</i> (Linnaeus, 1758) (P)	0	3650.3	4.62	5.22	16.76
<i>Clytia hemisphaerica</i> (Linnaeus, 1767) (H)	31.1	0	4.39	4.97	21.73
<i>Escharella immersa</i> (Fleming, 1828) (B)	0	168.7	4.27	4.83	26.56
<i>Semibalanus balanoides</i> (Linnaeus, 1767) (C)	269.8	2.1	4.19	4.73	31.29
Bryozoa ancestrula	0	1.1	3.14	3.55	34.84
<i>Spirorbis tridentatus</i> Levinsen, 1883 (P)	1.4	1312.8	2.95	3.34	38.18
<i>Cribrilina punctata</i> (Hassall, 1841) (B)	0	32.8	2.93	3.31	41.49
<i>Electra pilosa</i> (Linnaeus, 1767) (B)	2.1	0.6	2.64	2.99	44.48

Table 3
Values of densities of the most abundant species in the given site in intertidal and subtidal boulder-fields from Arctic (individuals number/m²) – all station signs according with Fig. 1 (B – Bryozoa, F – Foraminifera, C – Cirripedia, P – Polychaeta)

	INTERTIDAL						SUBTIDAL					
	K1	K2	K3	H1	H2	H3	K1	K2	K3	H1	H2	H3
Bryozoa indet.		1.3					8.5	31.1	2.2		1.5	92.8
“ <i>Callopora lineata</i> ” (Linnaeus, 1767) (B)						1.5	12.8	11.8				1.0
<i>Callopora</i> sp. (B)	1.5	0.7		1.4	1.4		336.6	14.8	5.6	114.0	13.3	4.5
<i>Cauloramphus intermedius</i> Kluge, 1962 (B)							43.3	78.3		5.5	4.4	485.7
<i>Celleporella hyalina</i> (Linnaeus, 1767) (B)						4.6	57.5	4.4		11.2	6.0	5.9
<i>Cibicides lobatulus</i> (Walker and Jacob, 1798) (F)	4.2			2.7			22.4	36.9	24.8	379.4	6.0	164.9
<i>Cribilina annulata</i> (Fabricius, 1780) (B)			1.3	1.4		1.5	596.6	326.3	2.2	218.7	65.9	33.0
Crisidae indet. (B)	1.5						526.2	35.7		1.9	15.0	56.4
<i>Eucratea loricata</i> (Linnaeus, 1758) (B)				4.7			42.7	19.2		1.0	6.0	29.7
<i>Harmeria scutulata</i> (Busk, 1855) (B)	4.2	11.4		2.7	22.2	1.5	2411.6	2771.8	1.1	351.8	324.4	454.5
Hydroid indet.		0.7			1.4			1.0		5.7	1.5	
<i>Microporella arctica</i> Norman, 1903 (B)							374.9	8.9	47.2			1.5
<i>Semibalanus balanoides</i> (Linnaeus, 1767) (C)		4.7	1.3	1871.7	9.1	21.7	98.0	447.4	29.2	457.9	516.9	716.0
<i>Spirorbis</i> sp. (P)		1.8			19.6		6489.1	1885.8	2524.8	86.0	37.5	5.5
<i>Stomachetosella cruenta</i> (Busk, 1854) (B)							93.7	34.0	13.5	78.5	4.5	112.9
<i>Tegella arctica</i> (d’Orbigny 1850) (B)			1.3				147.0	63.5	5.6	65.5	127.3	3.1
<i>Tegella retroversa</i> Kluge, 1952 (B)							16.5	7.4		61.7	4.4	357.9
<i>Tricellaria ternata</i> (Ellis and Solander, 1786) (B)	1.5	0.7		4.7	1.4		34.9	88.6		1.0	1.0	37.1

The abundance of macrobiota in Arctic intertidal assemblages (mean 496.5 indiv/m² per site) was an order of magnitude lower than in the subtidal zone (mean 6267.6 indiv/m² per site) (ANOVA, $F_{(1,10)} = 15.43$, $p = 0.002$). The dominant species at the Arctic intertidal study locations was the cirriped *Semibalanus balanoides* L. (mean 318.1 indiv/m² per site) and the cheilostome bryozoan *Harmeria scutulata* Busk (mean 7.0 indiv/m² per site). In the subtidal samples the polychaete *Spirorbis* sp. (mean 1838.0 indiv/m² per site) and *H. scutulata* Busk (mean 1052.5 indiv/m² per site) were the most abundant species.

Intertidal assemblages at the Spitsbergen study sites were entirely composed of a subset of species found in the adjacent subtidal assemblages (Table 3). There was

Table 4
Results of SIMPER analysis with 10 most contributing species to dissimilarities between intertidal and subtidal boulder-fields from Arctic (average abundance: individuals number/m²) (B – Bryozoa)

Species	INTERTIDAL Average abundance	SUBTIDAL Average abundance	Average dissimilarity	Contribution %	Cumulative %
<i>Stomachetosella cruenta</i> (Busk, 1854) (B)	0	56.1	2.73	3.64	3.64
<i>Tegella armifera</i> (Hincks, 1880) (B)	0	28.0	2.73	3.64	7.27
<i>Lichenopora</i> sp. (B)	0	4.7	2.73	3.64	10.91
<i>Dendrobeatia murrayana</i> (Johnston, 1847) (B)	0	9.4	2.73	3.64	14.54
<i>Tegella arctica</i> (d'Orbigny, 1850) (B)	0.2	118.1	2.24	2.98	17.52
<i>Tegella retroversa</i> Kluge, 1952 (B)	0	95.6	2.18	2.91	20.43
<i>Cauloramphus intermedius</i> Kluge, 1962 (B)	0	180.8	2.18	2.91	23.34
<i>Raymondia rigida</i> (Lorenz, 1886) (B)	0	22.4	2.12	2.83	26.16
<i>Cylindroporella tubulosa</i> (Norman, 1868) (B)	0	68.1	2.12	2.83	28.99
<i>Electra arctica</i> Borg, 1931 (B)	0	77.4	2.12	2.83	31.81

strong overlap between the intertidal and subtidal assemblages. nMDS showed (Fig. 3) that there was high degree of similarity between Arctic intertidal and subtidal samples. SIMPER analysis indicated that subtidal species were contributing the most to the observed pattern (Table 4). The dominant species in the intertidal (*S. balanoides*, *H. scutulata*) and subtidal (*Spirorbis* sp., *H. scutulata*) were not among the most contributing species to observed level of dissimilarities between intertidal and subtidal assemblages (Table 4).

Discussion

It is thought that local diversity typically reflects the richness of the regional species pool (Cornell and Karlson 1996; Witman *et al.* 2004). Sites with high levels of unpredictable disturbance (*e.g.* ice scour) are usually under stronger regional species pool control than those which are less disturbed (Menge and Sutherland 1987; Palmer *et al.* 1996). Theory and most observations suggest that frequently disturbed habitats have community structures which are highly variable, have a high turnover rate, and are determined largely by chance (*e.g.* Osman 1977; Kukliński and Barnes 2005). Palmer *et al.* (1996) and others have termed this the “lottery” effects of arrival and establishment. If conditions are so extreme that the

species pool is restricted to only a small number of tolerant forms, the community should be predictable, with frequent turnover of individual populations (Palmer *et al.* 1996). Moderate disturbance frequency and low-to moderate dispersal may enable superior competitors and slower growers to maintain populations over time (Menge and Sutherland 1987; Barnes and Kukliński 2003). In this study we hypothesised that the diversity of the highly disturbed Arctic intertidal zone would be almost entirely determined by the nearby subtidal species pool. Thus with high disturbance the species composition in the intertidal zone would be expected to be largely a subset of the subtidal species pool. Alternatively if disturbance was just moderate, intertidal diversity would not be so shaped by nearby subtidal species richness, and there would be low similarity between them. Our prediction that subtidal and intertidal diversity would interact differently under varying disturbance regimes was confirmed by our results. The probability of faunal occurrence on Arctic rocks in both the subtidal and intertidal zones was lower than in the temperate area (Fig. 2). This is a clear sign that Arctic assemblages, especially in the intertidal zone, are much more disturbed in comparison to their counterparts from lower latitudes. And indeed there is increase with latitude of, for example, winds strength, and amounts of ice present in near-shore areas (*e.g.* Bentamy *et al.* 1996; Dayton 1990; Conlan *et al.* 1998; Gutt *et al.* 1996).

Multivariate analysis of the assemblage data (Fig. 3) showed that Arctic intertidal and subtidal animal groupings were much more similar to each other than equivalent intertidal and subtidal assemblages were at temperate sites. Highly disturbed intertidal assemblages in the Arctic were a subset of nearby subtidal assemblages with similar dominance structures in both (Tables 1, 3). Intertidal assemblages from temperate less disturbed habitats were composed in many cases of different species (which did not occur subtidally) and assemblages had a different dominance structure to subtidal ones (Tables 1, 3). There is no reason to suspect that our model temperate area, Trondheimsfjord, is unusual with respect to having species in the intertidal that are not found or are rare in the subtidal zone. Species that are intertidal specialists are well known from most of the global coastline, except the polar regions (see Kukliński and Barnes 2005; Waller *et al.* 2006). It could be argued that the intertidal zones of the polar regions have not yet had time for intertidal specialists there to evolve if life was 'bulldozed' out by the last glacial maximum and repeatedly during previous ice ages. However, to a lesser extent this would probably have also happened further south than Trondheimsfjord.

The discriminating taxa driving the observed sample differences between intertidal and subtidal from both areas were contributed by different species (see the SIMPER analysis – Tables 2, 4). In our temperate study area the organisms that contributed the most to these dissimilarities were the dominating species in both assemblages (*e.g.* intertidal: *Semibalanus balanoides*, subtidal: *Pomatoceros triqueter*) (Table 2). In the Arctic the dominant species were similar both in the intertidal and subtidal therefore their contribution to dissimilarities were very low (*e.g.* abundant

Harmeria scutulata) (Table 4). This result also supports our prediction that Arctic intertidal assemblages exhibit a greater degree of similarity to their nearby subtidal and thus intertidal biodiversity is driven by the subtidal biodiversity to greater extent in the Arctic than in less disturbed temperate locations.

We suggest that our study sites, and maybe Arctic intertidal zones in general, do not have self-sustaining, independent, assemblages/communities. New studies in the Antarctic have shown intertidal assemblages are much more developed than thought and probably form proper, though cryptic, communities (Waller *et al.* 2006). There is, however, no evidence that in the Antarctic such communities are self-sustaining or independent and they also seem to be almost entirely a subset of nearby subtidal species. In contrary, distinct independent assemblages have long been known and described on rocky intertidal temperate shores just a few meters apart from subtidal species pools, as found in this study. It seems that Arctic intertidal assemblages are an open subunit within a network of habitat patches linked by dispersal and modified by its timing and level of disturbance. By comparison, temperate intertidal assemblages are more closed, modified both by biological interactions and abiotic factors (though with subtidal predators and competitors increasingly entering with increased immersion time).

Only a few species from the subtidal species pool were present in the Arctic intertidal assemblages (Table 3). This indicates that species pools of intertidal assemblages are influenced by other factors beside subtidal supply of recruits. Many subtidal species may not be able to survive the 'harsher' conditions of the shore such as prolonged aerial exposure, greater absolute and variability in temperature or salinity range. When abiotic disturbance becomes frequent it is capable of preventing competitive exclusion and local extinction occurs for all the species except the most opportunistic and most resistant (Menge and Sutherland 1987; Karlson and Cornell 2002). And indeed intertidal Arctic assemblages are dominated by short-lived species with opportunistic life histories (e.g. *Harmeria scutulata*) (Kukliński and Taylor 2006). Site differences in species diversity and numerical abundance can be driven by many other factors. These include variability in local near-shore oceanography and thus food supply, productivity (Hillebrand and Blenckner 2002) and organic detritus influencing opportunities for growth (Duggins *et al.* 1989). Bustamante *et al.* (1985) found nutrients, microalgal productivity and shore invertebrate abundance to be positively correlated. We consider that biotic factors are probably less relevant as explanations of patterns observed at the Arctic study sites. Assemblage differences at Arctic locations are likely to be strongly modified by shore – associated physical processes (e.g. current patterns, wave forces) (Menge *et al.* 1997). This can be easily seen and was semi-quantified by surveys of the shore environment around west Spitsbergen (Węśławski *et al.* 1988; 1993). In both temperate and Arctic intertidal sites organisms can be protected from biotic sources of mortality (e.g. space is not limiting, reducing mortality associated with competition). In severe conditions physical factors may regulate assemblages more directly as representatives

of upper trophic levels are rare or absent. In more-moderate environments, physical factors are less prevalent in regulating assemblages and as the abundance of consumers increases with environmental moderation, competition tends to increase in importance as a structuring force (Menge and Sutherland 1987).

Several studies have suggested or demonstrated that recruitment can be localized within a site or in the proximity of parental populations and that population and community can be viewed essentially as a closed system (Osman and Whitlatch 1998; Cowen *et al.* 2006). There is evidence that this process is supported by limited dispersal of larvae or asexual recruitment (Osman and Whitlatch 1998 and references therein). The current study suggests that persistence of intertidal temperate boulder-field assemblages is a consequence of local control (within site) of recruit generation. Low to moderate disturbance frequencies offer the greatest opportunity for local control to be highly influential and thus the regional component (subtidal species pool) is likely to be the least influence. It seems that as the time between disturbance events increase (Arctic – temperate), the opportunity for greater local control exists (*e.g.* predator – prey effects may impact community structure until the next abiotic disturbance event). Temperate subtidal boulders were dominated by tubes of the serpulid polychaete *Pomatoceros triqueter* L., which often created three-dimensional structures on substrata due to the multiple layering of tubes. This strong spatial competitor often occupied most available space on boulders. *Semibalanus balanoides* L., although present in very low numbers on subtidal boulders where it was out-competed by *P. triqueter* L. (Kukliński unpublished data), was able to persist in high numbers only on intertidal boulders. Levels of disturbance in many temperate intertidal zones reduce the average resource utilization by the superior competitors, allowing inferior competitors to invade and persist.

Our results give many indications (*e.g.* species composition) that in highly disturbed habitats intertidal and subtidal biodiversity are strongly linked. However more detailed studies, including for example genetic surveys of both intertidal and subtidal populations to reveal similarities between them, are needed to demonstrate total reliance of Arctic intertidal assemblages on subtidal species pools.

Conclusions

This study suggests that Arctic intertidal boulder-field habitats serve as sinks while the adjacent subtidal are their sources. The exchange of recruits between these two zones is high but probably in only one direction, from the subtidal to the intertidal. The presence of a particular set of individuals in the Arctic intertidal is probably very brief. Arctic intertidal zone turnover rates must be high, even within a single year and depend on current water-column inputs. Evolutionary youth, climatic extremes and other factors in the Arctic has resulted in typically impoverished levels of species richness (*e.g.* see Roy *et al.* 1996; Boschi 2000; Crame 2000), illus-

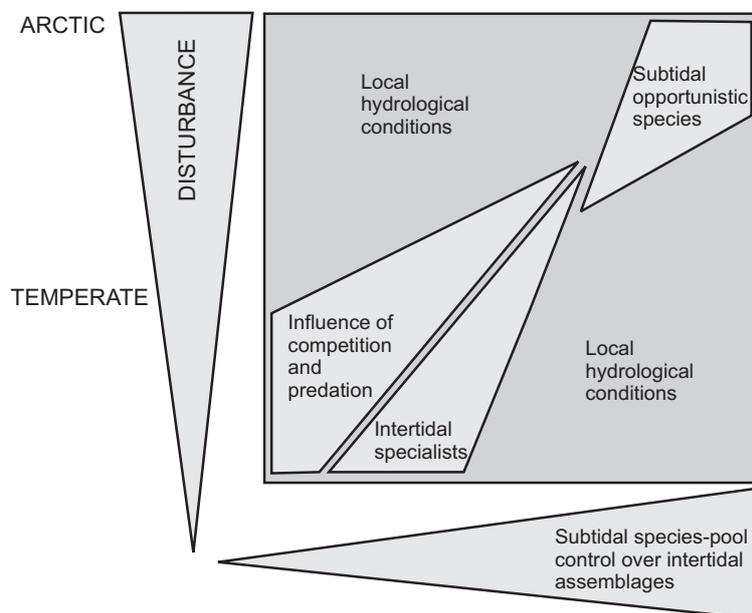


Fig. 4. A suggested model of intertidal boulder-fields assemblage regulation. The model shows the importance of disturbance level on subtidal-intertidal connectivity and its impact on species assemblage composition. Towards higher latitude disturbance level is increasing along with connectivity of subtidal-intertidal communities which is to some extent modified by local hydrological conditions. With increased disturbance predation and competition pressure is lower as well as habitat specialist vanish and are replaced by subtidal opportunistic species.

trated in our study sites by a lack of potential specialists on ephemeral substrata such as boulders. Severe disturbance holds species abundance so low that competition for space is rare (Barnes and Kukliński 2005) and predators can have little effect because of rarity. In striking contrast, temperate intertidal boulder-fields support assemblages independent of subtidal species-pools. The intertidal zone at lower latitudes can act as a refuge, which enable inferior competitors to persist in high abundance despite being not in optimal conditions (Connell 1961; Pain 1974). The main aspects of modification of animal species-richness and numerical abundance in Arctic and temperate intertidal zones by shore – associated physical processes (*e.g.* current patterns, wave forces) can be represented in a schematic model (Fig. 4).

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References

- BARNES D.K.A. 1999. The influence of ice on polar nearshore benthos. *Journal of the Marine Biological Association of the United Kingdom* 79: 401–407.
- BARNES D.K.A. 2002. Polarization of competition increases with latitude. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 269: 2061–2069.
- BARNES D.K.A. and CONLAN K. 2007. Disturbance, colonization and development of Antarctic benthic communities. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 362: 11–38.
- BARNES D.K.A. and KUKLIŃSKI P. 2003. High polar spatial competition: extreme hierarchies at extreme latitude. *Marine Ecology Progress Series* 259: 17–28.
- BARNES D.K.A. and KUKLIŃSKI P. 2005. Bipolar patterns of intraspecific competition in bryozoans. *Marine Ecology Progress Series* 285: 75–87.
- BENTAMY A., GRIMA N., QUILFEN Y., HARSCOAT V., MARONI C. and POULIQUEN S. 1996. An atlas of surface wind from ERS-1 Scatterometer measurements, *IFREMER publication*, IFREMER, DRO/OS, BP 70, 29280 Plouzane, France: 229 pp.
- BOSCHI E.E. 2000. Species of decapod crustaceans and their distributions in the American marine zoogeographic provinces. *Revista de Investigacion y Desarrollo Pesquero* 13: 1–136.
- BRAY J.R. and CURTIS J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325–349.
- BUSTAMANTE R.H., BRANCH G.M. and EEKHOUT S. 1985. Maintenance of an exceptional intertidal grazer biomass in South-Africa – subsidy by subtidal kelps. *Ecology* 76: 2314–2329.
- CASWELL H. and COHEN J.E. 1993. Local and regional regulation of species-area relations: a patch-occupancy model. In: R.E. Ricklefs and D. Schluter (eds) *Species diversity in ecological communities*. University of Chicago Press, Chicago: 99–107.
- CLARKE K.R. and GORLEY R.N. 2001. *PRIMER v5: User Manual/Tutorial*, Plymouth: PRIMER – E
- CONLAN K.E., LENIHAN H.S., KVITEK R.G. and OLIVER J.S. 1998. Ice scour disturbance to benthic communities in the Canadian high Arctic. *Marine Ecology Progress Series* 166: 1–16.
- CONNELL J.H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs* 31: 61–104.
- CORNELL H.V. and KARLSON R.H. 1996. Species richness of reef-building corals determined by local and regional processes. *Journal of Animal Ecology* 65: 233–241.
- CORNELL H.V. and LAWTON J.H. 1992. Species interaction, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* 61: 1–12.
- COWEN R.K., PARIS C.B. and SRINIVASAN A. 2006. Scaling of connectivity in marine populations. *Science* 311: 522–527.
- CRAME J.A. 2000. Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of recent bivalve fauna. *Paleobiology* 26: 188–214.
- DAYTON P.K. 1990. Polar benthos. In: W.O. Smith (ed.) *Polar Oceanography*. Academic Press, London: 631–685.
- DUGGINS D.O., SIMENSTAD C.A. and ESTES J.A. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245: 170–173.
- GUTT J., STARMANS A. and DIECKMANN G. 1996. Impact of iceberg scouring on polar benthic habitats. *Marine Ecology Progress Series* 137: 311–316.
- HILLEBRAND H. and BLECKNER T. 2002. Regional and local impact on species diversity – from pattern to processes. *Oecologia* 132: 479–491.
- KARLSON R.H. and CORNELL H.V. 2002. Species richness of coral assemblages: detecting regional influences at local spatial scales. *Ecology* 83: 452–463.

- KUKLIŃSKI P. and BARNES D.K.A. 2005. Bryodiversity on coastal boulders at Spitsbergen. In: J. Moyano, J. Cancino and P.N. Wase-Jackson (eds) *Bryozoan Studies 2004*. Balkema, Abingdon: 161–172.
- KUKLIŃSKI P. and TAYLOR P.D. 2006. Unique life-history strategy in a successful Arctic bryozoan, *Harmeria scutulata*. *Journal of the Marine Biological Association of the United Kingdom* 86: 1305–1314.
- MCGUINNES K.A. 1987a. Disturbance and organisms on boulder. I. Patterns in the environment and the community. *Oecologia* 71: 409–419.
- MCGUINNES K.A. 1987b. Disturbance and organisms on boulder. II. Causes of patterns in diversity and abundance. *Oecologia* 71: 420–430.
- MENGE B.A. and SUTHERLAND J.P. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* 130: 730–757.
- MENGE B.A., DALEY B.A., WHEELER P.A., DAHLHOFF E., SANFORD E. and STRUB P.T. 1997. Benthic – pelagic links and rocky intertidal communities: bottom – up effects on top – down control? *Proceedings of National Academy of Sciences of United States of America* 94: 14530–14535.
- OSMAN R.W. 1977. The establishment and development of a marine epifaunal community. *Ecological Monographs* 47: 37–63.
- OSMAN R.W. and WHITLATCH R.B. 1998. Local control of recruitment in an epifaunal community and the consequences to colonization processes. *Hydrobiologia* 375/376: 113–123.
- PAINE R.T. 1974. Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15: 93–120.
- PALMER M.A., ALLAN J.D. and BUTMAN C.A. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends in Ecology and Evolution* 11: 322–325.
- RICKLEFS R.E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235: 167–171.
- ROY K., JABŁOŃSKI D. and VALENTINE J.W. 1996. Higher taxa in biodiversity studies: Patterns from eastern Pacific marine molluscs. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 351: 1605–1613.
- RUSSEL R., WOOD S.A., ALLISON G. and MENGE B.A. 2006. Scale, Environment, and trophic status: the context dependency of community saturation in rocky intertidal communities. *American Naturalist* 167: 158–170.
- SHANKS A.L. and WRIGHT W.G. 1986. Adding teeth to wave action: the destructive affects of wave-born rocks on intertidal organisms. *Oecologia* 69: 420–428.
- SOUSA W.P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60: 1225–1239.
- WALLER C., BARNES D.K.A. and CONVEY P. 2006. Ecological contrasts across an Antarctic land-sea interface. *Austral Ecology* 31: 656–666.
- WĘSŁAWSKI J.M., WIKTOR J., ZAJĄCZKOWSKI M. and SWERPEL S. 1993. Intertidal zone of Svalbard 1. Macroorganism distribution and biomass. *Polar Biology* 13: 73–79.
- WĘSŁAWSKI J.M., ZAJĄCZKOWSKI M., KWAŚNIEWSKI S., JEZERSKI J. and MOSKAL W. 1988. Seasonality in an Arctic fjord ecosystem: Horsund, Spitsbergen. *Polar Research* 6: 185–189.
- WITMAN J.D., ETTER R.J. and SMITH F. 2004. The relationship between regional and local species diversities in marine benthic communities: A global perspective. *Proceedings of National Academy of Sciences of United States of America* 101: 15644–15669.

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