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Variability of competition at scales of 10^1 , 10^3 , 10^5 , and 10^6 m: encrusting arctic community patterns

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Abstract Variability in interference competition was studied in benthic marine communities of the arctic and subarctic Atlantic intertidal and shallow subtidal zones. We sampled multiple square-metre quadrats at distances of 10^1 , 10^3 , and 10^5 m apart around the high polar island of Spitsbergen (Svalbard Archipelago). We also took some similar samples in Iceland and in the Faeroe Islands (10^6 m apart from Spitsbergen samples). Encrusting fauna were present on high arctic intertidal rocks but we only found competitive interactions on subtidal substrata. On subarctic Icelandic and Faeroese shores, in contrast, spatial competition was common even in the intertidal zone. Analysis of variance of competition intensity data (numbers of interactions per area) revealed multiple factors to be significant influences explaining variability. Amongst the 10^1 -, 10^3 -, and 10^5 -m spatial scales, only the largest emerged as a significant term. Whether intra- or interspecific competition dominated the types of interactions varied greatly between sites: 21–97% of competition was intraspecific. The proportion of competitive encounters resulting in a decided outcome (i.e. a win for one competitor and a loss for the other, rather than a tie or standoff between them) showed little variability at any scale. All the values of competition transitivity (how hierarchical a pecking order is) were very high compared to values reported in the literature from any other (polar or non-polar) locality. Variability in this measure was generally < 10% across scales. We conclude from our data that great care must be taken in interpreting patterns of competition

between similar taxa in large-scale space or time. Not only did most aspects of competition in our study communities vary significantly at the 10^5 -m scale but different aspects of competition varied at different scales and by hugely different amounts.

Introduction

Darwin (1859) regarded competition for resources as a major force shaping both the ecology and evolution of species. There is an increasing appreciation of the roles of other influences, particularly stochastic events, but competition is regarded to be of no less importance to communities today. Competition, even direct contests, need not always reduce relative contribution to the next generation of all participants (Wall and Begon 1985), but it is probable that this is frequently the case. In the high polar environment the consequences of marine benthic competition are severe; nearly all encounters result in a loser, which is overgrown and smothered (Barnes 2002). In small-scale experiments competition can reduce species populations to extinction (Gause 1935; Connell 1961; Brown and Davidson 1977; Hairston 1980; Tilman et al. 1981). Whether competition explains major evolutionary declines or disappearance of taxa remains debatable (Thayer 1985; Rhodes and Vermeij 1993; McKinney et al. 1998). In ecology, perception of pattern or process often depends on what aspect is measured (Underwood and Fairweather 1986; Barnes and Dick 2000; McKinney et al. 2001). Measuring change in competition at multiple scales was our purpose in this study, and evaluation of appropriateness of measures was paramount. We consider the intensity of competition to be an important aspect of change in competition along spatial gradients, one that seems to generate many paradigms but few data-backed conclusions (McGuinness 1990). As well as measuring intensity, we also quantified relative frequencies of

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intra- versus interspecific competition. In mobile land animals few direct encounters are symmetric (Wagnon et al. 1966; Clutton-Brock et al. 1979), but amongst marine benthos, ties can be common (Jackson 1979; Schmidt and Warner 1986). Only in a tied outcome can both competitors be assured of surviving. Losers may be completely overgrown, though some may survive total smothering for limited periods (Todd and Turner 1988). At a community level, measuring how hierarchical the structure of community is indicates successional and climactic states (Rubin 1982; Tanaka and Nandakumar 1994) though this does vary with latitude (Barnes 2002).

Importance is increasingly being attached to wide-scale studies rather than to spot observations/experiments in time, space, or relatedness. In the cases of change in competition over time, space, or relatedness there is now data in the literature for the far ends of the spectrum but paucity of multiple-scale data (but see McKinney 1995). It remains difficult, therefore, to be able to assess at what scale any effect is critical. Over the last four decades marine benthic taxa have proved to be cornerstones in ecology, particularly for interpreting underlying influences of competition (e.g. Connell 1961; Dayton 1971; Paine 1974; Jackson 1979; Gould and Calloway 1980; Sebens 1986; Tanaka and Nandakumar 1994). Using encrusting benthic taxa has many advantages, including (1) temporal: there is a long interaction duration (a record is preserved of the identities of interacting competitors and the result, even in fossils, thus enabling studies at large time scales); (2) spatial: most such animals are small (so large data sets can be collected in small spaces, which increases study resolution and creates access to study change over smaller spatial scales); and (3) taxonomic: there is ease of identification, even long after death or as fossils, and a variety of organisms from conspecifics to those from different kingdoms commonly compete for space, creating access to virtually all relatedness scales.

In this study we investigated how variability in interference competition amongst the shallow marine encrusting assemblages in Arctic and subarctic localities alters with scale. To do so, we sampled multiple square-metre quadrats at distances of 10^1 , 10^3 , 10^5 , and 10^6 m apart in the high Arctic (Spitsbergen, Svalbard Archipelago). The aspects of competition we chose to focus on are those we believe to be primary in shaping community patterns: intensity (encounters per unit area), transitivity (how hierarchical the 'pecking order' is), the proportion of interspecific relative to intraspecific encounters, and the proportion of encounters that result in decided outcomes (where one competitor loses and the other wins, rather than a tie). As many of these change across large-scale (latitudinal) gradients (Barnes 2000, 2002), our principal hypothesis is that change in competition structure at the community level is predictable: greater differences in competition structure occur at larger spatial scales. Disturbance is one of the principal processes shaping community structure, and

therefore competition within the community. Ice scour, a major agent of polar disturbance, though likely to create patchiness, decreases with depth (Dayton 1990; Gutt et al. 1996; Gutt 2001). Our second hypothesis was that competition intensity would increase with depth due to reduced frequency of ice scour. Finally we hypothesised that density-dependant factors (crowding) would emerge as important influences on interaction intensity, including percent cover of substrata and colonist density or, in Lewontin and Levins' (1989) terms, 'organism-weighted density'.

Materials and methods

Study area and species

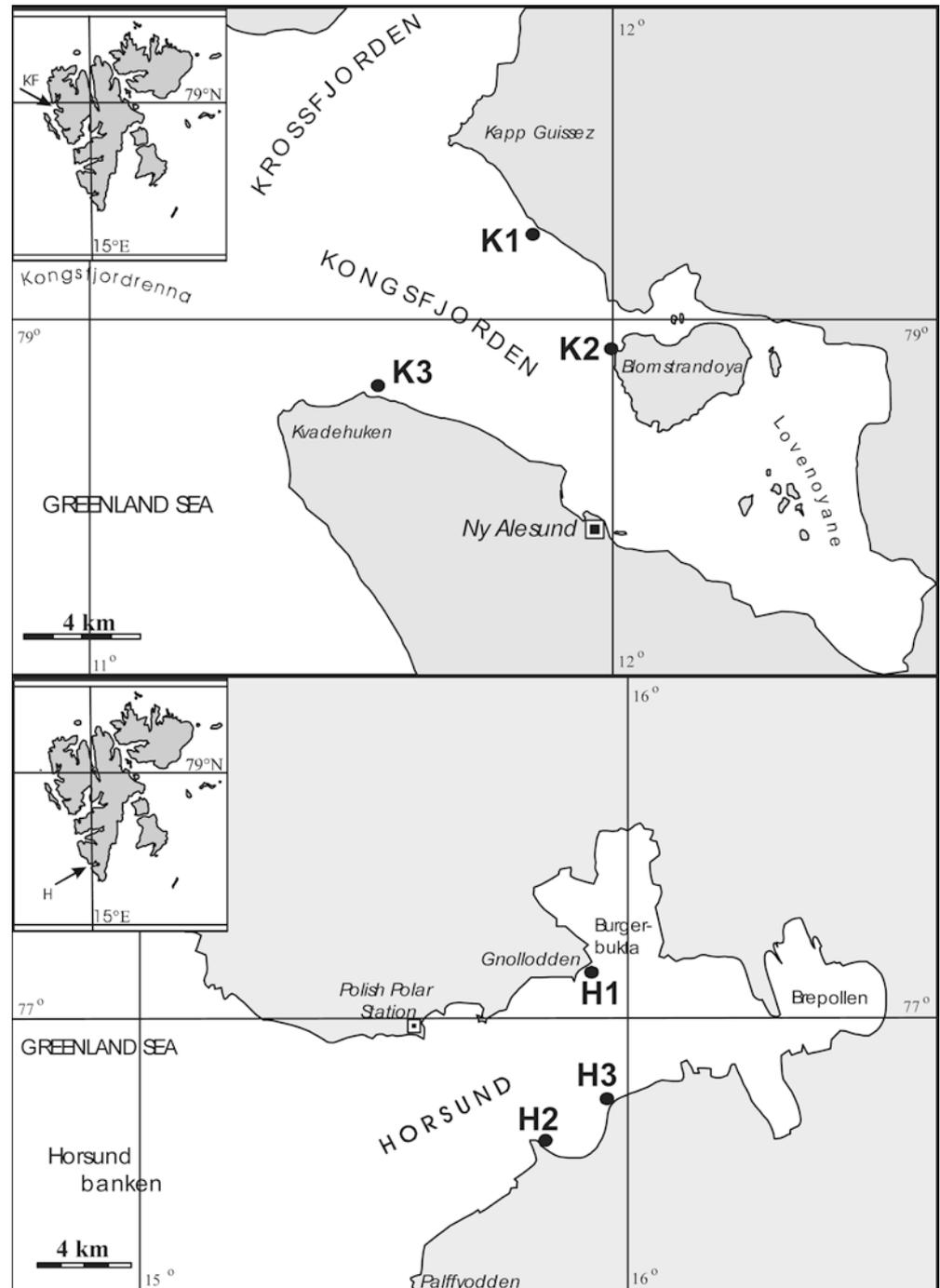
The main study region was Spitsbergen Island (part of the Svalbard Archipelago) in the Arctic. Within this region two study localities were selected that were ≥ 100 km apart: Kongsfjord (79°N) and Horsund (77°N). Within these localities three sites were chosen, each ≥ 1 km apart. At each site ≥ 25 boulder samples were taken (≥ 10 cm apart) at two spots, which were ≥ 10 m apart. We denote these as simply K1 ($79^\circ 01.8'\text{N}$, $11^\circ 49.8'\text{E}$), K2 ($78^\circ 59.5'\text{N}$, $11^\circ 58.9'\text{E}$), and K3 ($78^\circ 58.5'\text{N}$, $11^\circ 29.8'\text{E}$) at Kongsfjord and H1 ($77^\circ 00.8'\text{N}$, $15^\circ 33.3'\text{E}$), H2 ($76^\circ 56.8'\text{N}$, $15^\circ 48.4'\text{E}$), and H3 ($76^\circ 57.4'\text{N}$, $15^\circ 55.6'\text{E}$) at Horsund (Fig. 1). In each case samples were collected from the intertidal, 6-m, and 12-m depth. Thus samples were collected at four scales of distance apart, each of which was approximately two orders of magnitude different in proximity from the next. Samples taken within quadrats (the lowest scale) did not, however, contain enough data to be used individually so were pooled to provide more robust data. In addition to the sampling at Svalbard, samples were collected at two subarctic sites in each of two localities (Iceland and Faeroe Islands) to enable comparisons at the 10^6 -m scale with material collected at a similar time (August 2002), with a similar protocol. Only intertidal samples were collected in Iceland, whereas intertidal, 6-m, and 12-m samples were collected in the Faeroe Islands.

Despite the widely varying proximities of samples, all experienced broadly similar environmental conditions. The boulder samples were collected during summer (July) 2002. Sea temperature at the time of material collection was approximately 3°C at all sites (annual variation approximately -1.8 to $+4^\circ\text{C}$). Waters throughout Svalbard are subjected to ice scour from floating ice during summer months. Inner fjord areas are characteristically covered by winter fast ice, which occurs less often and extensively in the central and outer parts of the fjord (Wesawski et al. 1988). Like temperature, the salinity regime of near bottom waters is stable, varying from just 33 to 34 psu. Only at the surface and intertidal does salinity change rapidly around June (32–25 psu; see Swerpel 1985; Wesawski et al. 1988). The potential suite of competitors, and their biomass, on intertidal and subtidal boulders has been reported by Wesawski et al. (1993) and Kuklinski (2001), respectively. Potential major competitors for space on boulders in both regions included balanomorph barnacles, cheilostome and cyclostome bryozoans, colonial ascidians, tubicolous polychaetes, and occasional *Calcarea* and demosponge Porifera (sponges).

Protocol

At least 25 (randomly selected) boulders, together with a surface area totalling $6,900\text{ cm}^2$ (± 244.7 SE) were collected from each site at each of the three depths; intertidal (extreme low water, spring tide level), 6 m, and 12 m. The total- and animal-colonised surface areas of each boulder were estimated using an inelastic net marked in a grid of square centimetres. The number of all colonists and

Fig. 1 The position of localities and sites in Spitsbergen, Svalbard. Kongsfjord locality (upper map) and the three sites K1, K2, and K3 are illustrated in relation to the settlement of Ny Alesund. Horsund locality (lower map) and the sites H1, H2, and H3 are shown in relation to the Polish polar research station



interactions (aggressive encounters) between them were counted. Contact between two or more recruits was designated as an interaction if both were live and 5% or more of the organism periphery was affected. Interactions were defined and scored as overgrowth (i.e. a win for one of the competitors), following the established criteria (Sebens 1986; Tanaka and Nandakumar 1994; Barnes 2002), if the loser's feeding apparatus was obscured (thus activity prevented). Encounters were termed as tied when mutual (equal) overgrowth took place or skeletal build-up but no overgrowth (frequently referred to as a standoff) occurred. From the raw data the density of interspecific, intraspecific, and (by combination of these) total competitive encounters was calculated. Secondly the density of competitive encounters with decided (rather than tied) outcomes was calculated.

Data analysis

Competition-intensity data was first tested for normality and where necessary was arc-sine transformed to meet the assumptions for analysis of variance (ANOVA). The variable we used as our response term (competition intensity) was the number of encounters per unit area. We included in the ANOVA 'organism-weighted density' biological factors: (1) percent cover and (2) recruit number. We also included the spatial factors locality, site, and quadrat, as well as depth. Although the inclusion of many factors makes interpretation more complex we had a priori reasons for believing any of those included could be important. We then plotted the strongest emergent factor against competition intensity to probe it in more detail. In this plot we also included the Iceland and Faeroe

Island data. The reduced nature of the Iceland and Faeroe Island data sets (in contrast to the multi-scale polar data) precluded them from inclusion in the ANOVA but enabled limited comparisons of mean values. We used detrended correspondence analysis (DCA) to visualise relative similarity between community competition and spatial factors by using frequency of occurrence of species interaction pairs rather than the more conventional approach (in biodiversity studies) of using simply species occurrence. Ordinations, useful for visualising data with gradient rather than divisive underlying structure, arrange data into multi-dimensional space such that points with close proximity correspond to similar suites of competitive interactions. DCA has advantages over standard CA in correcting for axis termini compression (relative to axis middle) and in that the second axis has no systematic relation with the first axis (canonical correspondence analysis, CCA, the remaining technique for examining gradient structure, is direct and more complex—being used in conjunction with various simultaneously collected environmental data). We tabulate the eigenvalues associated with the two axes extracted. Finally comparative data were also taken from the literature including Alaska (Dick and Ross 1988; Barnes and Dick 2000). We analysed underlying structure of interference competition at the community level by using an index formulated to measure how hierarchical (i.e. transitive) a given set of interactions between competitors is. We used Tanaka and Nandakumar's (1994) transitivity index because of comparative advantages such as its independence of competitor or observation number. Of the indices formulated by Tanaka and Nandakumar (1994) we used the win index, WI, in which $P_{ij}[W]$ is the probability of each species winning any encounter:

$$WI = \sqrt{\frac{\sum_{i=1}^n \sum_{j=1}^n P_{ij}[W]^2}{\frac{n(n-1)}{2}}}$$

Finally we compared how different some aspects of competition are between communities at varying distances apart. So, for example, to compare how dissimilar the level of hierarchical structure within communities was with varying distance apart, we compared the output of Tanaka and Nandakumar's (1994) index between each pair of quadrats within depths—at each scale. So at the scale of 10^1 (within site) there were six possible comparisons at each depth (e.g. K1: Q1 vs Q2, K2: Q1 vs Q2, and so on to H3: Q1 vs Q2). At higher scales there are more possible comparisons so six were randomly chosen (for example K1 Q1 vs K2 Q1, H2 Q2 vs H3

Q1, etc.) to standardise n . Plots were then constructed showing the six dissimilarity values for each scale. These percentage data were arcsine transformed and then tested for normality using the Anderson–Darling test. Regressions were then fitted as lines of best fit to data shown to be non-significantly different from normal. The whole process was repeated for other aspects of competition such as the probability of individual organisms experiencing interference competition.

Results

Intensity of competition

Competitive interactions between encrusting animals occurred at all sites (though not on every sample) and not in the intertidal zone on any sample (Table 1). Although there were fauna present at each intertidal site, the absence of interference competition essentially means that the analyses of Spitsbergen data were conducted on data from the subtidal zone only. Polychaete (annelid) worms formed more than half the individuals colonising boulders sampled but most were of small size and so were involved in proportionally few interactions. Nearly all interactions involved cheilostomatid bryozoans (Table 1) and most of these were in competition with other cheilostomatids. ANOVA on all interference competition (inter- and intraspecific) showed that of the six factors included, three were significant, validating a multivariate approach. Of the three factors that the analysis showed to significantly explain some of the competition data variability, percent cover had the highest F ratio and lowest P values (Table 2). Of the three spatial scales considered here, only at the highest (10^5 m) did the intensity of competition differ geographically. There was also a significant influence of depth but the presence of a significant interaction term between depth and site suggests the strength of the influence of depth varied between sites. To investigate

Fig. 2 Intensity of competition (encounters per square centimetre) with percent faunistic cover of substratum. Data is pooled by locality and depth (as the only factors to be significant in models in Tables 1, 2, and 3). The regression line shown has significance as illustrated on the plot

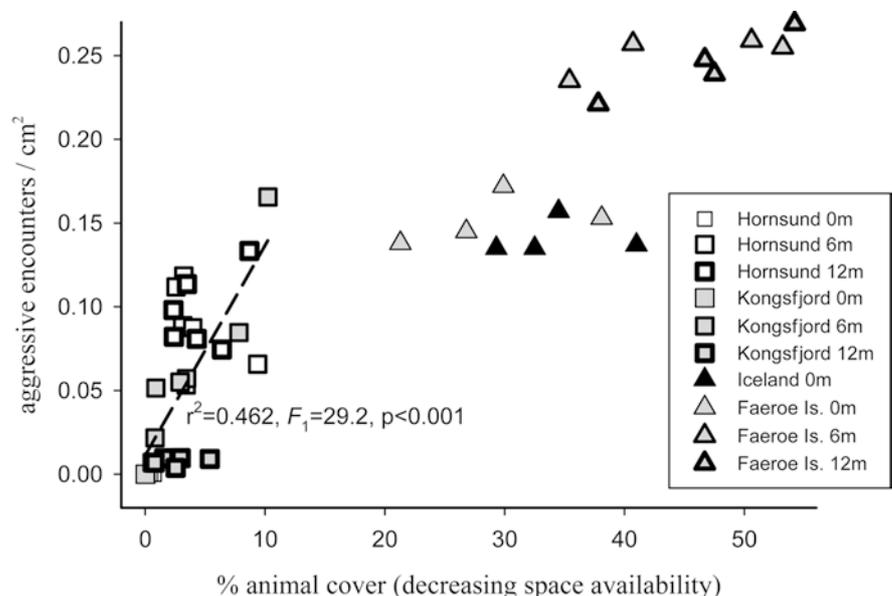
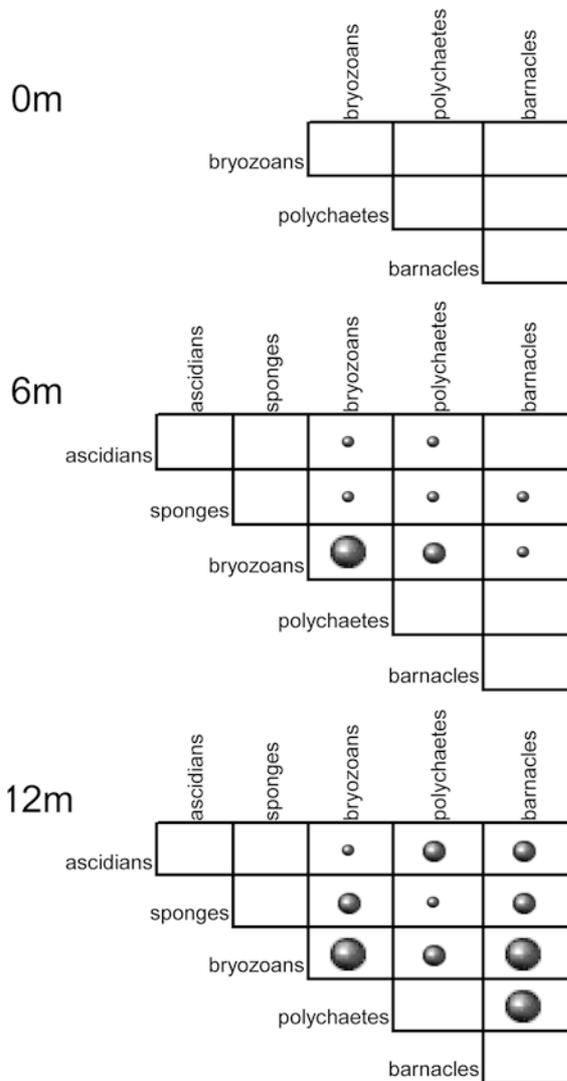
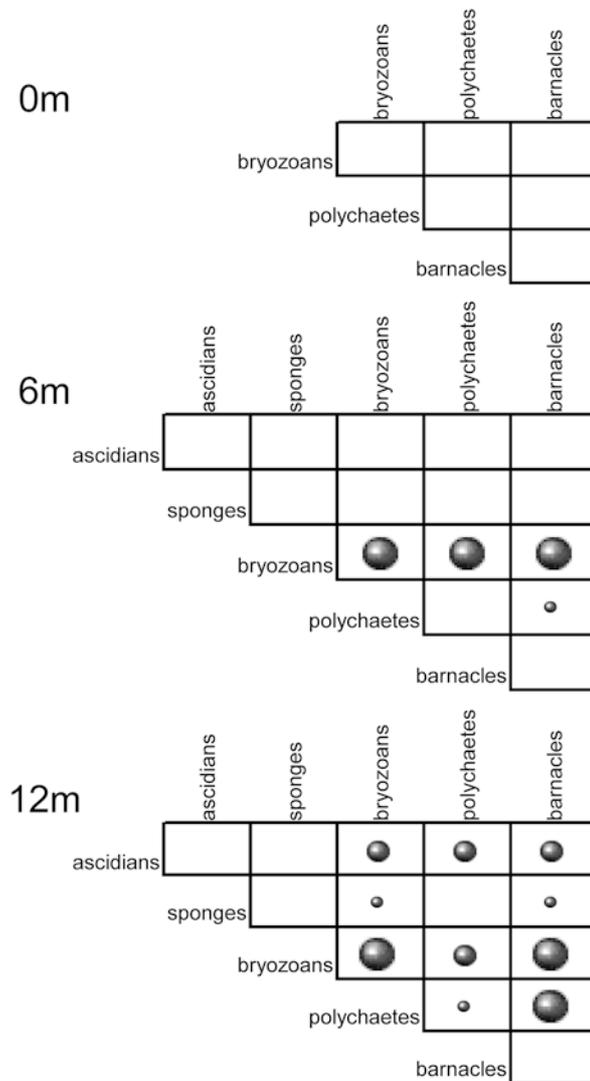


Table 1 Occurrence of and competition between encrusting fauna with depth in the West Spitsbergen localities Kongsfjord and Horsund. Taxa found at each depth and at each site are listed on

Kongsfjord



Horsund



the trend between proportional (percent) cover of rocks and density of interference competition these were plotted together with equivalent data from the Iceland and Faeroese samples (Fig. 2). The intensity of competition increased steeply with the level of animal cover but although the relationship was highly significant (ANOVA indicated on plot), the regression line only explained 46% of data variability. It is clear that the subarctic data do not fit the same relationship as those from Spitsbergen. The data range in the subarctic plot barely overlaps with the high arctic data in either competition intensity or the animal coverage of rocks. Although the absolute values of competition intensity are higher in the subarctic, those for a given level of animal coverage are higher in the arctic. Furthermore this can be stated with an appreciation that the data is robust to site and quadrat patchiness (but that significance within region variability occurs on a scale of 10^5 m). This difference

pairwise matrices. *Dots* indicate competitive encounters between each pair; at one site (*small dots*), at two sites (*medium dots*), and at all three sites (*large dots*)

between localities indicated in the ANOVA (Table 2) was not, however, apparent from the plot.

ANOVA of intensity of competition between different competitors (interspecific) as in the analysis of total competition (interspecific and intraspecific) showed three significant factors explaining variability (Table 3). Furthermore, the three factors were the same in both analyses. As with total competition, animal coverage of substratum was highly significant, as was depth. Likewise of the three spatial scales examined, only the largest significantly explained data. The third ANOVA, of intraspecific interactions, also showed substratum cover and locality to be significant, but not depth (Table 4). So the models indicated that explanatory variables of intra-, inter- or total competition were not very different and that small-scale effects were not important. A major difference in intra- and interspecific competition was revealed by DCA of species pair interactions partitioned

Table 2 ANOVA results on influences on intensity of *all* interference competition in subarctic encrusting marine animal communities

Source	<i>df</i>	Seq SS	Adj SS	Adj MS	<i>F</i>	<i>P</i>
Percent cover	1	0.97092	0.28137	0.28137	6.77	0.010
Recruit number	1	0.08487	0.02641	0.02641	0.64	0.426
Locality	1	0.23846	0.20260	0.20260	4.87	0.028
Site	2	0.02110	0.03448	0.01724	0.41	0.661
Quadrat	1	0.04230	0.04618	0.04618	1.11	0.293
Depth	2	0.59781	0.36699	0.18350	4.41	0.013
Locality×Site	2	0.04923	0.06960	0.03480	0.84	0.434
Locality×Quadrat	1	0.02472	0.03153	0.03153	0.76	0.384
Locality×Depth	2	0.11942	0.12129	0.06064	1.46	0.234
Site×Quadrat	2	0.15274	0.15019	0.07509	1.81	0.166
Site×Depth	4	0.45405	0.45848	0.11462	2.76	0.028
Quadrat×Depth	2	0.21450	0.21188	0.10594	2.55	0.080
Locality×Site×Quadrat	2	0.00905	0.00925	0.00463	0.11	0.895
Locality×Site×Depth	4	0.08700	0.07958	0.01990	0.48	0.751
Locality×Quadrat×Depth	2	0.09507	0.09439	0.04719	1.14	0.323
Site×Quadrat×Depth	4	0.21157	0.21223	0.05306	1.28	0.279
Locality×Site×Quadrat×Depth	4	0.02918	0.02918	0.00730	0.18	0.951
Error	322	13.38437	13.38437	0.04157		
Total	359	16.78636				

by quadrat, site, locality, and depth (Fig. 3). In both cases the two axes extracted had high eigenvalues (Table 5) and extraction of further axes would have contributed little further explanation of data trends. Patterns of intraspecific competition did not convincingly separate depths or spatial scales in DCA 1 but merely demonstrated greater variability in the Kongsfjord data than that in Hornsund. In contrast, the interspecific competition data (DCA 2) separated the data clearly by locality and depth. Although the axes do not necessarily code for a variable in the DCA procedure, the data do split along geographic and bathymetric gradients as indicated on the plot.

The probability of an individual animal experiencing competition in the high arctic study site varied by more than an order of magnitude between localities and depths from 0.01 to 0.18 (Table 6). Thus the range of the number of competitive encounters per individual is similar to the number of competitive encounters per square centimetre (Fig. 2). The probabilities of competition all multiply about threefold if the tiny spirorbid polychaetes (which are numerically dominant but involved in few interactions) are not included. The variability in the chance of organisms experiencing competition (which was double within three sites, that is, just 10 m apart), clearly demonstrates the level of patchiness within the ecosystem. The level of variability between samples significantly increases with distance between them (Fig. 4). So is the variability between our arctic and subarctic samples what might be expected given the distance between them? In both cases the answer seems to be yes. At 12 m depth the variability between arctic and subarctic samples was not significantly different from that between arctic samples 100 km apart (Student's $T = -1.69$, $P = 0.13$). In contrast at 6 m the equivalent comparison showed variability between arctic samples 100 km apart was significantly different from

that between arctic and subarctic samples (Student's $T = 2.49$, $P = 0.034$).

Competition structure

The overall structure of interference competition in the high arctic communities studied was highly hierarchical (transitive). Tanaka and Nandakumar's (1994) index, which is used to measure how hierarchical/transitive a community is, has potential output from 0 to 1. Low values indicate networks (intransitivity) whilst high values show hierarchies. The values obtained from our sample communities were all high, ranging from 0.77 to 0.93 (Table 6). Competition transitivity varied very little at any scale: the maximum dissimilarity between any pair of communities was just 13%. Variability in transitivity was lowest between samples 10¹ m apart and there was a significant trend of increasing dissimilarity with distance (Fig. 5). The associated r^2 value did, however, reveal that the trend explained relatively little of the variability and at 12 m there was no significant trend. Communities were uniformly highly hierarchical across spatial scales, thus major patchiness was not apparent.

The proportion of interspecific competition varied from 20.8 to 97.2% (Table 6) or from communities with almost no intraspecific encounters to those heavily dominated by them. In striking contrast to patterns of transitivity with spatial scale considered, dissimilarity between communities in terms of the proportion of interspecific competition (compared to intraspecific) varied to a huge degree (Fig. 6). The maximum was 56% dissimilarity and more than half the values were above the maximum dissimilarity for transitivity. Furthermore there was high variability at all spatial scales and no significant trend. This indicates major patchi-

Table 3 ANOVA results on influences on intensity of *interspecific* interference competition in high arctic encrusting marine animal communities

Source	<i>df</i>	Seq SS	Adj SS	Adj MS	<i>F</i>	<i>P</i>
Percent cover	1	0.402324	0.073826	0.073826	9.14	0.003
Recruit number	1	0.051964	0.001785	0.001785	0.22	0.639
Locality	1	0.070184	0.096191	0.048096	3.95	0.030
Site	2	0.027597	0.018756	0.018756	2.32	0.129
Quadrat	1	0.006736	0.007193	0.007193	0.89	0.346
Depth	2	0.103503	0.098545	0.049273	6.10	0.003
Locality×Site	2	0.010675	0.008017	0.004008	0.50	0.609
Locality×Quadrat	1	0.003839	0.002599	0.002599	0.32	0.571
Locality×Depth	2	0.021769	0.020300	0.010150	1.26	0.286
Site×Quadrat	2	0.044847	0.042418	0.021209	2.62	0.074
Site×Depth	4	0.079773	0.078960	0.019740	2.44	0.047
Quadrat×Depth	2	0.040484	0.039746	0.019873	2.46	0.087
Locality×Site×Quadrat	2	0.001437	0.001106	0.000553	0.07	0.934
Locality×Site×Depth	4	0.038191	0.039266	0.009816	1.21	0.304
Locality×Quadrat×Depth	2	0.002197	0.002083	0.001042	0.13	0.879
Site×Quadrat×Depth	4	0.051774	0.051847	0.012962	1.60	0.173
Locality×Site×Quadrat×Depth	4	0.005895	0.005895	0.001474	0.18	0.947
Error	322	2.602148	2.602148	0.008081		
Total	359	3.565336				

Table 4 ANOVA results on influences on intensity of *intraspecific* interference competition in high arctic encrusting marine animal communities

Source	<i>df</i>	Seq SS	Adj SS	Adj MS	<i>F</i>	<i>P</i>
Percent cover	1	0.12723	0.07287	0.07287	4.41	0.036
Recruit number	1	0.00174	0.01165	0.01165	0.71	0.402
Locality	1	0.08247	0.08079	0.08079	4.89	0.028
Site	2	0.02718	0.03014	0.01507	0.91	0.403
Quadrat	1	0.00925	0.01092	0.01092	0.66	0.417
Depth	2	0.21947	0.09194	0.04597	2.78	0.063
Locality×Site	2	0.02537	0.04423	0.02211	1.34	0.263
Locality×Quadrat	1	0.01485	0.02320	0.02320	1.40	0.237
Locality×Depth	2	0.04144	0.04805	0.02402	1.45	0.235
Site×Quadrat	2	0.03949	0.04009	0.02004	1.21	0.298
Site×Depth	4	0.30307	0.31894	0.07974	4.83	0.001
Quadrat×Depth	2	0.08310	0.08220	0.04110	2.49	0.085
Locality×Site×Quadrat	2	0.00688	0.00674	0.00337	0.20	0.815
Locality×Site×Depth	4	0.14174	0.13346	0.03337	2.02	0.091
Locality×Quadrat×Depth	2	0.06139	0.06095	0.03047	1.85	0.160
Site×Quadrat×Depth	4	0.05319	0.05358	0.01340	0.81	0.519
Locality×Site×Quadrat×Depth	4	0.01953	0.01953	0.00488	0.30	0.881
Error	322	5.31667	5.31667	0.01651		
Total	359	6.57407				

ness in the proportion of competition that is interspecific at all scales. Therefore even with a very large number of samples, this measure is unlikely to be useful in critical comparisons of competition or assemblage structure (other than by degree of patchiness).

Most interspecific encounters in all communities ended in decided outcomes, and in three communities (e.g. K3, Q2 at 6 m) they all did (Table 6). Difference in communities with respect to proportion of competitive encounters resulting in decided outcomes (Fig. 7) was about half as variable as that for the proportion of interspecific interactions. Nevertheless it was still twice as variable as that for transitivity. No significant trend was found and patchiness was evident at all spatial scales. So despite the mostly high values of decided outcomes, the variability of dissimilarity across scales in our data suggests that for meaningful ecological

comparisons, nothing but very large numbers of observations are likely to be useful.

Discussion

Competition has been demonstrated to be a major force in shaping organism distribution, abundance, and survival in the short term (Gause 1935; Connell 1961, 1983; Brown and Davidson 1977; Clutton-Brock et al. 1979; Hairston 1980; Karlson 1999). The long-standing viewpoint pioneered by Darwin (1859) is that it probably has had fundamental importance at most scales in time in the evolution of our current fauna, as it does in space now. Yet demonstration of the process, or even aspects of it, has remained decidedly small scale. There have been protracted discussions of whether competition, predation, and ecological harshness are really different

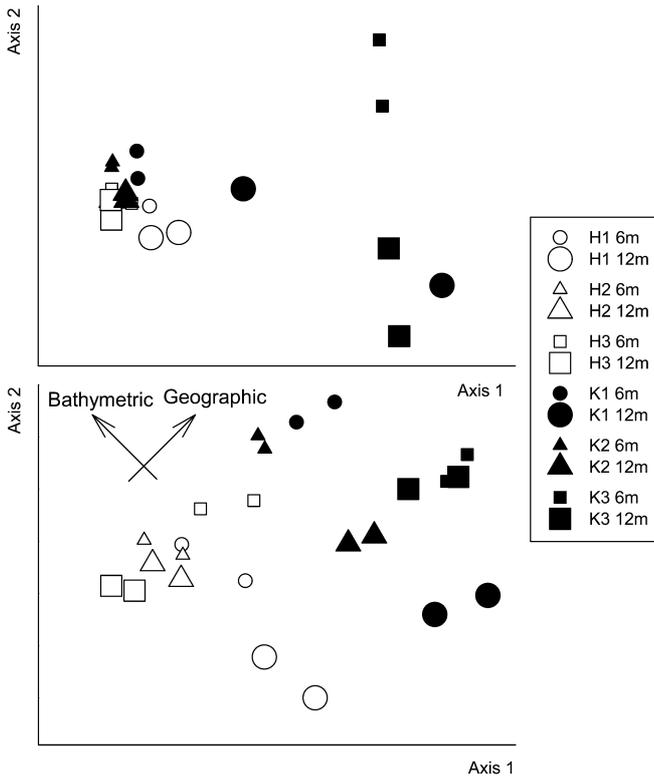


Fig. 3 Detrended correspondence analysis (DCA) of intraspecific competition (*upper*) and interspecific competition (*lower*) similarity between spatial scales and depths. The axes do not code for a specific variable in DCA; proximity of points relates to similarity. Approximate trends of depth and distance are illustrated by *arrows*

Table 5 Eigen values for detrended correspondence analysis (DCA) (Fig. 3)

	Axis 1	Axis 2	Axis 3	Axis 4
DCA 1 eigenvalue	0.87	0.14	0.06	0.05
DCA 2 eigenvalue	0.66	0.40	0.24	0.11

between regions of the world, such as between temperate zones and the tropics (Vermeij 1976; McGuinness 1990). Even species richness along latitudinal, longitudinal, or

bathymetric gradients, perhaps the most intensively studied ecological variable, is still hotly debated, largely due to a paucity of meaningful data (Stehli et al. 1967; Stehli and Wells 1971; Clarke 1992; Roy et al. 1998; Clarke and Lidgard 2000; Crame 2000; Gray 2001). With most studies of competition, observation and collection of the data is so consuming of time and effort that reported studies are almost all restricted to one example of one community whether they be plants (Sousa 1979; Tilman et al. 1981) or animals: terrestrial (Wagnon et al. 1966; Brown and Davidson 1977; Clutton-Brock et al. 1979; Hairston 1980) or marine (Connell 1961; Dayton 1971; Paine 1974; Jackson 1979; Sebens 1986; Tanaka and Nandakumar 1994). Considerable debate and effort has been generated by ecologists on how best to interpret this meagre data and formulae for analysing contact matrices of paired interactions (e.g. De Vries 1995; Tufto et al. 1998), indices of transitivity (e.g. Rubin 1982; Tanaka and Nandakumar 1994), and the importance of tied versus decided interactions (Schmidt and Warner 1986) or reversals of dominance (Chornesky 1989; Karlson 1999), amongst other ideas. Only by massive studies or compiling literature with similar experimental protocols, however, have large-scale patterns in time (McKinney 1995), space (Barnes 2002), or relatedness (Diamond 1987; Barnes 2003) become meaningful.

The data we present here shows that competition is rare in the high arctic intertidal but common in subtidal zones (Table 1). Indeed interspecific competition is abundant (and different) enough from place to place to be able to separate sample localities, sites, and depths by interaction type alone (Fig. 3). Our first hypothesis concerned whether change in competition with scale was predictable—that is, are samples taken further apart more dissimilar? Our analyses showed that this depended on what aspect of competition was considered (Figs. 4, 5, 6, 7) and thus distance between samples does not necessarily reflect similarity. So small-scale spot studies (the majority of the ecological literature) cannot simply be taken as representative samples of the wider community around them. A single sample of competi-

Table 6 Variability in aspects of interference competition between encrusting fauna at the study quadrats, sites and localities

	Kongsfjord						Horsund					
	K1		K2		K3		H1		H2		H3	
	Q1	Q2	Q1	Q2	Q1	Q2	Q1	Q2	Q1	Q2	Q1	Q2
6 m												
Probability of competition	0.13	0.06	0.10	0.12	0.03	0.04	0.18	0.15	0.12	0.10	0.13	0.12
Transitivity	0.77	0.85	0.83	0.80	0.93	0.91	0.90	0.88	0.86	0.87	0.80	0.85
Percent interspecific	65.4	76.6	32.4	28.5	87.7	91.3	37.2	66.1	20.8	32.0	73.0	40.1
Percent decided outcomes	90.0	92.8	64.0	83.5	91.2	100	97.7	98.7	96.9	95.8	86.3	91.4
No. competitor species	13	14	8	8	7	9	10	11	7	8	11	9
12 m												
Probability of competition	0.04	0.03	0.01	0.02	0.02	0.04	0.09	0.11	0.13	0.12	0.10	0.09
Transitivity	0.93	0.93	0.88	0.87	0.82	0.80	0.92	0.91	0.89	0.88	0.92	0.91
Percent interspecific	85.7	64.2	82.9	45.1	97.2	87.3	89.2	87.4	26.8	32.8	25.0	25.9
Percent decided outcomes	98.7	100	86.2	75.0	97.1	100	97.8	98.7	95.6	92.3	87.7	87.6
No. competitor species	12	9	7	5	6	9			7	8	8	9

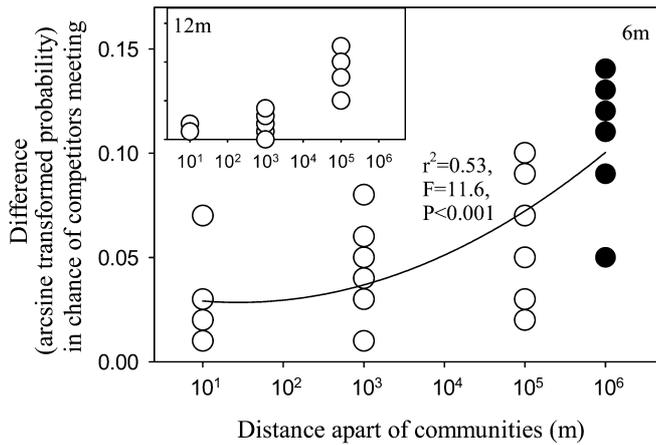


Fig. 4 Community difference with spatial scale in the probability of individual animals experiencing competition. *Open symbols* are Spitsbergen data and *filled symbols* are subarctic data. *Main plots* are 6-m data and *inserts* (with *y*-axes scaled as main plots) are 12-m data; $n = 6$ for all scales

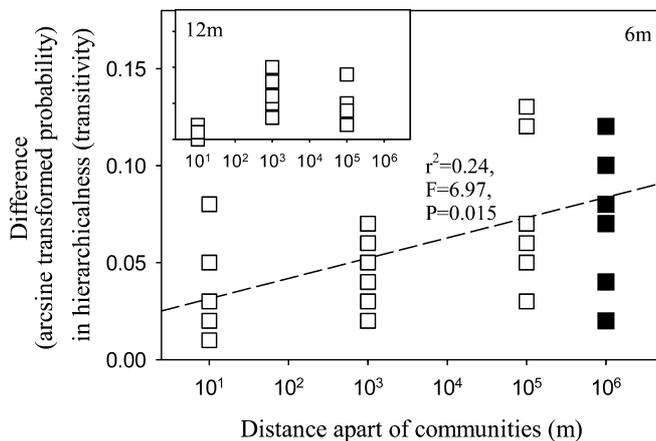


Fig. 5 Community difference with spatial scale in transitivity (how hierarchical a pecking order is). *Symbols and plots* are otherwise as in Fig. 4

tion in a high Arctic community at Spitsbergen can show that it is clearly organised along a very hierarchical structure. In the same way a similar sample in a different region, such as the Caribbean, can show that it is organised quite differently (Buss and Jackson 1979; Jackson 1979). Information is missing, though, that enables evaluation of how different they really are, and why. Answering the how requires an appreciation of variability at multiple scales (Karlson and Cornell 1998; Gutt and Piepenburg 2003). Of course this has been appreciated for decades in ecological sampling and forms the mainstay of modern methods. Because, however, sampling competition within a community requires taking many replicate observations of different competitor pairings, it has been assumed that replication is there and that a species contact matrix shows how species in that given locality interact. The variability in our data at the community level suggests otherwise (Table 6). Most problematical is the finding that

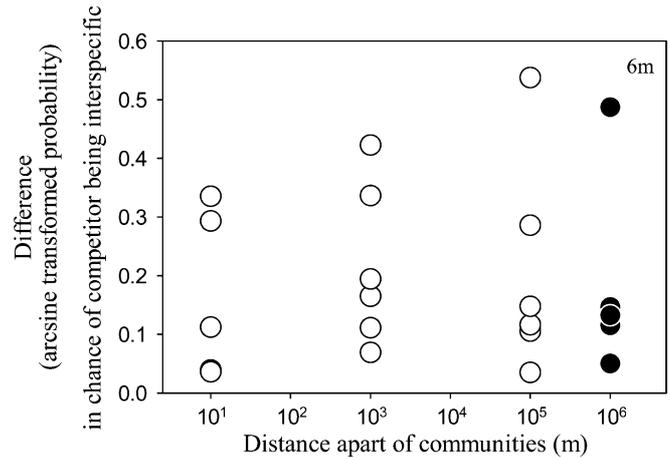


Fig. 6 Community difference with spatial scale in proportion of competitive encounters that were interspecific. *Symbols* are as in Fig. 4

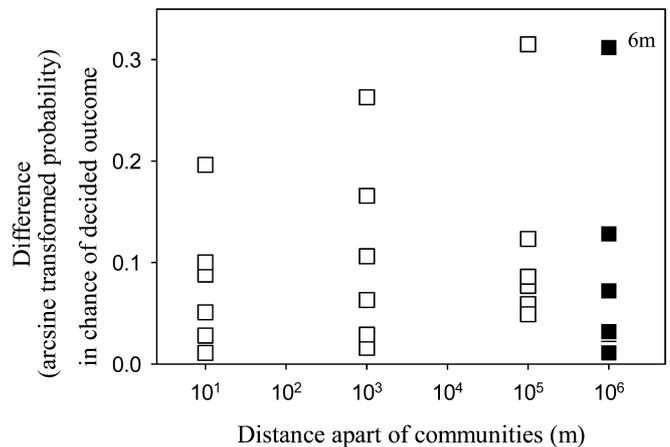


Fig. 7 Community difference with spatial scale in proportion of competitive encounters that had a decided outcome (win/loss compared to a tie). *Symbols* are as in Fig. 4

different aspects of competition alter with different magnitudes of variability and do so at different scales. So can we explain why different aspects of competition vary along different spatial scales and by different amounts (at the location of our study)?

In high polar environments (such as Spitsbergen) ice has a major role in sculpting the structure of benthic communities either in the form of ice scour (Dayton 1990; Gutt et al. 1996; McCook and Chapman 1997; Conlan et al. 1998; Gutt 2001) or anchor ice (Dayton et al. 1974; Dayton 1989). Most pieces of ice are small, so very shallow benthos is most frequently scraped. This scour decreases with depth although some areas at any depth may be sheltered by topography. Thus there is a wide range of disturbance and habitat ages, which should be patchy due to the essentially random nature of scour for a given depth. Although suggested at large scale, the intermediate disturbance hypothesis (Connell 1978; Huston 1979) should logically be applicable at

other scales. Thus at points of very high environmental stress and disturbance, species and populations may be reduced but they may also be similarly depleted at very low levels by competition or predation (Menge and Sutherland 1987). At points where combined stresses are lowest, maximal diversity might be intuitively expected to occur. Maughan and Barnes (2000) termed this point a 'minimum stress inflexion'.

In the polar intertidal, ice-mediated disturbance is so high that communities are depauperate of species (Dayton 1990; Arntz et al. 1994) and as shown here, void of competition for space (0 m in Table 1). At 6 m depth, limited communities exist and animals are abundant and big enough for spatial encounters to occur regularly. Our second hypothesis was that competition would be more severe with depth. Although we found none in the intertidal zone, competition at 12 m was no more severe than at 6 m (Table 6, Fig. 2). We suspect that investigation of just three depths was simply insufficient to test this hypothesis. Typically areas in which scouring is most frequent may comprise just a few common species involved in intraspecific competition with conspecific neighbours (Barnes and Clarke 1998). Areas that are more ice sheltered are likely to have a wider range of species, as communities have longer periods to develop. Completely sheltered areas, in contrast, could be dominated by competitively dominant species (Barnes 2002). In tropical environments, (which generally experience much less wave action than those at higher latitudes, see Barnes 2002), major storms or other disturbance can likewise thin the normal community, allowing opportunistic r-strategists to achieve levels of high abundance temporarily (Wulff 1995; Karlson 1999). Our finding of patchiness of interspecific competition and proportion of decided outcomes (in interspecific competition) at all spatial scales investigated (Table 6 and Figs. 6,7) suggests that iceberg scouring is random at such scales. This seems reasonable given that all our sites were on an open shelf without protection either from unusual bathymetry or geography.

So why is transitivity or likelihood of experiencing competition (Figs. 4,5) less variable (cf. other aspects, Figs. 6, 7)? Transitivity is ultimately a measure of how strict a pecking order is. Ties, reversals in competition (where in competition between A and B, A wins some interactions and B others), or competitive loops (in which A dominates over B, despite being of lower average competitive rank than B) all serve to reduce transitivity (see Russ 1982; Tanaka and Nandakumar 1994). Competitions between certain taxa, such as ascidians (data in Grosberg 1981; Schmidt and Warner 1986), tend to result in intransitive networks, whereas others, such as bryozoans, are usually much more hierarchical. Our finding that the level of transitivity in communities varied little (relative to other aspects of competition) and was not sensitive to patchiness seems likely to be explained by an independence of the number or abundance of competitors. Hypothetically if one area (X) is scoured by ice more regularly than another (Y)

then at place X there will probably be less interspecific competition and fewer competitor meetings and fewer competitors. For example, if on the few occasions when A does meet B, at place X, it still dominates as proportionally often as at place Y, then places X and Y are similarly hierarchical. Similarly, if at place X, competitor A beats B and C 90% of the time and B beats C 90% of the time—it will have an identical value of transitivity as place Y in which A beats B, C, D, and E 90% of the time, B beats C, D, and E 90% of the time, C beats D and E 90% of the time, and D beats E 90% of the time. Intensity of competition (interactions per unit area) only varied significantly at the 10^5 m scale (Tables 2, 3, 4) and the probability of competition (interactions per individual animal) increased with increasing scale (Fig. 4). This was probably due to depression of many of the Kongsfjord values but we do not know why this should be, other than suggesting the area is uniformly more disturbed than our other study locality (Horsund).

Our third and final hypothesis concerned whether density-dependent factors were important. Crowding clearly emerged as having a strong link to intensity of competition (Fig. 2), but the importance of crowding is already well known for shellfish rearing (see Orensanz et al. 1998) and even encrusting organisms elsewhere (Barnes and Clarke 1998). What we have shown is that competition intensity was only significantly different with changing percent cover, not density of individuals (Tables 2, 3, 4). Lewontin and Levins (1989) tried to separate the effect of mean density and actual crowding by using the terms 'resource-weighted density' and 'organism-weighted density'. We, however, used two different measures of 'organism-weighted density' to further try to separate density from actual crowding. It seems clear that lots of small individuals in an area represents much less crowding than lots of larger ones, hence our finding that animal density did not emerge as a significant influence on competition, whereas proportional space occupied by animals did (Table 2). The only scale to emerge as significant was that at 10^5 —this should be encouraging to ecologists: we interpret this (in the context of trying to address large-scale issues) that if this scale can be taken into account by appropriate experimental design, major sampling at smaller scales may be unnecessary, at least in communities similar to those studied here. Clearly, though, the effect of scale does alter with the aspect of even a specific area (competition) within ecology.

In conclusion, our hypothesis that competition would increasingly change with scale and that all aspects would change similarly was firmly rejected. We feel that we have insufficiently tested our second hypothesis that competition intensity would increase with depth, though we found a major difference between the intertidal and subtidal zones. Finally, density-dependent factors were important as hypothesised in our last test but we found no effect of density of individuals—only availability of space was crucial. Now that we have quantified the behaviour of certain aspects of competition in a partic-

ular type of community, the most obvious course of action is to investigate the largest scale left: 10^7 m (between regions) using this type of community.

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