Polarization of competition increases with latitude

David K. A. Barnes

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road,
Cambridge CB3 0ET, UK (dkab@bas.ac.uk)

Many organisms overlap in their use of resources in space and time. Where and when resources are restricted, species must compete for them. Living space, often a critical resource controlling food and mate availability, is directly contested by organisms in most habitats. The ensuing animal interactions generally result in a winner gaining space and a loser, which may die. Contact matrices from studies of interference competition in encrusting marine Bryozoa (clonal and colonial animals), spanning at least 60° latitude in both hemispheres, were analysed and subjected to a modern transitivity index. Only data for Bryozoa were used because (i) use of a single taxon with restricted ecology simplifies the scope for types of encounters, (and therefore) interpretation; and (ii) ecological bias is reduced because bryozoans are abundant at all latitudes. The analysis shows that assemblage competition is more hierarchical towards both poles. Thus, poorer competitors fail more frequently in interactions with increasing latitude. The cause of this trend is the simplification of overall outcomes between competitors, such as fewer ties, reversals in outcome or competitive loops (where low-ranking competitors beat those of higher ranking). The implication of such a trend is that the maintenance of biological diversity at high latitudes may principally be by physical rather than biological (competition) processes. Certainly, ocean surface energy increases with latitude through wind and wave action (and ice scour in polar regions).

Keywords: interference competition; hierarchies; transitivity; disturbance

1. INTRODUCTION

Darwin believed competition to be a major force behind natural selection, leading to evolution in the characteristics of species. For more than a century since then, ecologists have sought to measure competition between organisms. It has become apparent that competition, particularly for space, may frequently occur not just between individuals of the same or related species, but even between members of different classes, phyla or even kingdoms (Jackson 1979a; Hochberg & Lawton 1990). The outcomes of competitive encounters between organisms may vary with taxon: those between mobile forms typically have determinate win/loss (Wagnon *et al.* 1966; Clutton-Brock *et al.* 1979), whereas tied results (stand-offs, mutual overgrowth and fusion) tend to be restricted to sessile animals (Schmidt & Warner 1986; Tanaka & Nandakumar 1994). Mathematicians and ecologists have, over many decades, developed an array of models and indices (resulting from compiled field observations) to estimate the underlying structure of assemblage competition from contact matrices. One of the most fundamental aspects of competition is the degree to which the overall structure is hierarchical or transitive (Rubin 1982). A strict hierarchy is characterized by the presence of an ultimate competitor, which is dominant over all others, through a spectrum of competitive ability to one submissive to all others. This contrasts with a network or intransitive structure. Such a network has no clear ranking of competitors, and consequently no overall dominant species or individual. Some sessile marine communities have been found to be structured by non-transitive networks mediated either by incomplete dominance of superior competitors (A generally overgrows B, but not always; and B generally overgrows C, but not always) or backloops (A

overgrows B, B overgrows C, but C overgrows A). In other marine communities, a similar state may result from almost entirely tied competitive outcomes (Quinn 1982; Russ 1982; Schmidt & Warner 1986; Sebens 1986; Chornesky 1989; Tanaka & Nandakumar 1994). Alternatively, a network may prevail through more complex interactions, including non-contact stand-offs, rather than outcomes of necessarily aggressive physical interactions (Schoener 1983; Menge & Sutherland 1987).

This study attempted to gauge whether large-scale latitudinal patterns exist in the structure of assemblage organization due to change in the nature or outcomes of interference competition. Major geographic parameters (latitudinal, longitudinal, bathymetric, hemispherical and marine versus terrestrial gradients) have all been considered as principal sources of variability in organism traits. Early theories of simple clines, such as species richness and reproductive gradients with latitude (see Pianka (1966) and Mileikovsky (1971), respectively) have been shown to be more complicated by between site variability (McGuinness 1990) or non-compliance of particular taxa (Pearse *et al.* 1991). In addition, some latitudinal and longitudinal patterns in taxon richness seem to be better explained by time gradients rather than geographical influences (Crame 2000). Nevertheless, strong species-richness gradients have been identified in certain taxa in the northern hemisphere (Roy *et al.* 1998; Clarke & Lidgard 2000). Although there have been extended inconclusive discussions about gradients in some aspects of organism organization structures (e.g. niche diversification; see Connell 1978), latitudinal (or other geographical) trends in competition have not, to the author's knowledge, been suggested before.

In this study, I quantified the hierarchical nature of encrusting marine organism assemblages from Alaska to

Antarctica. The study involved the choice and organization of competitor pair data to form matrices, which complied with the assumptions and requirements of Tanaka & Nandakumar's (1994) transitivity index. Index scores were then organized by latitude of the study assemblage. To avoid complications of between clade (distinct phylogenetic taxa) interactions, the taxon that I used was that best represented in the literature in terms of usable dominance data matrices. Cheilostome bryozoans have proved highly valuable in the investigation of effects of environment constancy (Hughes & Jackson 1990), transoceanic variability (Jackson & Herrera Cubilla 2000) and long-term evolutionary and ecological patterns of persistence (see McKinney *et al.* 1998). They also constitute a particularly suitable group for examining global patterns of competition, in being sessile, abundant and easily accessible on rocky shores at any latitude. More importantly for this study, spatial competition is easily recognizable and the outcome readily identified, although most studies have determined results only at one point in time. Nevertheless, such 'snapshots' seem to give fairly predictable outcomes, at least with bryozoan–bryozoan interactions (Russ 1982; Tanaka & Nandakumar 1994; D. K. A. Barnes, personal observation). The working hypothesis for this study was that the level of assemblage transitivity would not significantly differ with latitude or between hemispheres. Cheilostome bryozoans are modular colonial organisms (formed of repeating units, or zooids) that are exclusively aquatic, mostly marine and have been the subject of 23 studies with appropriate methods for my analyses (Jackson 1979b; Quinn 1982; Russ 1982; Lopez Gappa 1989; Turner & Todd 1994; Nandakumar 1995; Barnes 2000 and references therein; Maughan 2000; Barnes & Arnold 2001). Appropriateness was dictated by the minimum sample size of interactions between competitor pairs, scoring of all three outcomes (win, loss and tie) and taxonomic resolution.

2. MATERIAL AND METHODS

(a) Data assembly

Data that included outcome scores from measurements of interference competition between cheilostome bryozoan species pairs were extracted from 16 published (and seven unpublished) reports. Literature used in this study included studies of competitive encounters at polar, temperate and tropical latitudes in both hemispheres. No relevant studies were found north of 60° N, whilst assemblages are almost unknown south of 70° S owing to ice-sheet cover or lack of marine environment. In many cases, studies reported in the literature described and demonstrated datasets where competition for space was intense despite the fact that total space was not limiting. This is due to confined areas of settlement and recruitment within this space (e.g. only the under-surfaces of boulders are typically crowded). All data matrices involved the outcomes of competitor pairings at species level and used similar definitions of win, loss and tie. Aggressive encounters between colonies, which resulted in either mutual, but equal, overgrowth or skeletal build-up but no overgrowth, were scored as ties. Monitoring of such outcomes has shown that ties are temporally stable and have genuine status equivalent to win or loss (Sebens 1986; Tanaka & Nandakumar 1994; D. K. A. Barnes, personal observation). It is appreciated, however, that the recorded outcomes of interactions are not instantaneous

absolutes, and longer-term survival and reproduction may alter ecological implications of the apparent outcome since bryozoan growth tends to be slow.

(b) Data treatment

All data were arranged into species-pair contact matrices (see table 1). All published interactions involving species not belonging to the cheilostomatid order (grey shading in table 1) were removed to form matrices entirely constituted by cheilostome–cheilostome encounters. Removal of fast-growing taxa, such as stenostomes, can have strong implications for the structure of competition, but this may vary from increasing (Turner & Todd 1994) to unchanging or decreasing the hierarchical nature (Barnes & Dick 2000). In addition, species that did not interact with two or more other competitors were removed (see table 2) because empty cells represent a source of error, effectively decreasing the value of the transitivity index. Thus, each dataset was reduced to a matrix similar to table 2 in which each competitor meets all (or virtually all) other competitors.

Tanaka & Nandakumar's (1994) transitivity index was calculated from the data within each final matrix. The index tends from zero to unity and is independent of the number of competitors or observations. Any of the three indices can be used for comparison of assemblage structure, although only the win index (which gives identical output to the loss index) was used. (Index formulae: WI, win index; LI, loss index; SI, stand-off index.)

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

$$LI = \sqrt{\sum_{i=1}^n \sum_{j=1}^n P_{ij}[L]^2 / (n(n-1)/2)}$$

$$SI = \sqrt{\sum_{i=1}^n \sum_{j=i+1}^n P_{ij}[S]^2 / (n(n-1)/2)}$$

Here, $P_{ij}[W]^2$ for the first row of the matrix (of table 2) is the sum of the squares of the top-right values divided by the bottom-right values in each cell of the matrix. For example, for the first cell (*Tegella aquilostri* versus *T. armifera*), this value is $(5/16)^2$ or 0.098. For each equation, n represents the number of competitors (species) in the matrix (11 in table 2). Within a cell, higher values indicate that the stronger competitor is the more dominant. For the overall matrix, higher indices indicate an increasingly hierarchical interaction scheme.

The interaction data used in this study originated from two substratum types: natural rock and artificial panels. As surface heterogeneity is a potential source of interaction (and therefore index output) variability and panels are designed to reduce heterogeneity, the two surface types were compared. A two-way ANOVA was used (following a Anderson–Darling normality test) on data from the three sites for which both natural and artificial data were available to partition total variation into sums of squares for sites, substrata and the interaction effect. The index was then plotted against latitude and the effects of panel versus natural substrata, geographical isolation and northern versus southern hemisphere contrasts were also considered.

Probability of a win for a higher-ranking competitor was also plotted against the difference in rank between competitors. As this involved the use of some probabilities approaching one, data were angular-transformed ($y = \sin^{-1} \sqrt{p}$) to allow for any eventual curvilinearity. For a binomial proportion based on n trials,

Table 1. Matrix of competitive interactions for Alaskan cheilostomatid, ctenostomatid and cyclostomatid bryozoans (latter two clades are shaded grey). (Data, from Barnes & Dick (2000), are displayed in standard form: see Turner & Todd (1994) and Barnes & Arnold (2001). If rows represent competitor A and columns represent competitor B, for each cell the top left, top right and bottom left the data give, respectively, the number of ties between species A and B, wins by B (losses by A) and wins by A (losses by B). The number in the bottom right of each cell is the total number of observed interactions for that species pair.)

<i>T. armifera</i>	<i>T. aquilirostris</i>	<i>M. plana</i>	<i>L. neosocialis</i>	<i>Cauloramphus</i> sp.	<i>Cyclostomatids</i>	<i>M. californica</i>	<i>T. arctica</i>	<i>Lichenopora</i> sp.	<i>C. decidua</i>	<i>Microporella</i> sp.	<i>C. annulata</i>	<i>P. alba</i>	<i>Alcyonidium</i> sp.	<i>C. tubulosa</i>	<i>Celleporella</i> sp.	<i>C. craticula</i>
<i>Tegella armifera</i>	2 9	5 4 3 10	3 10	2 1	1 4 10 13	2 3 2	0 1 1 4	0 1 1 4	0 0 22	0 2 13	2 17 6	1 4 4	3 8 10	1 0 19	0 7 10	
<i>Tegella aquilirostris</i>		0 11 8 19		0 1	0 2 1 4	1 0 0 1	1 2 6 7	1 2 4 12	0 1 4 12	0 2 0 6	2 0 3 5	2 3 24	2 8 29	1 16	5 24 33	
<i>Myrionoella plana</i>	1 6	0 7	1 0	1 0	2 5 1 7	14 5 6 0	4 0 4	3 0 3	0 0 3	0 9 5	11 11 11	0 5 11	2 5 3	0 8 15	0 41 16	
<i>Lagamocella neosocialis</i>				0 3	0 5 4 13	0 4 1 2	1 0 1 0	1 0 1 0	1 1 0 1	1 5 8		2 2 5	2 15 9		3 16 23	
<i>Cauloramphus</i> sp.					0 2 4 0	0 4 0 4	2 9 2	9 2		9 7 3	2 35 5	2 35 5	20 5	2 2	0 9 11	
<i>other Cyclostomatids</i>					1 3 2 6	6 3 9	1 12	9		9 25 4	9 11 5	2 3	2 3	2 24	1 77 97	
<i>Microporella californica</i>					4 3 1 7	3 1 3 6	1 6 8	1 15		14 14 6	2 6 3	3 3	3 7	0 3	0 8 11	1 2 5
<i>Tegella arctica</i>					3 7 2	2 6 2	4 1 15	1 2 0	0 0 0	0 0 0	2 9 2	2 5	2 5	2 7	2 26 32	
<i>Lichenopora</i> sp.					6 9	6 9	2 1 1	1 1 1	1 2 1	2 5 0	0 5 3	14 0	0 7	0 20	0 5 10	
<i>Callopora arctica</i>									8 5	12 2	2 21	29 6	14 6	1 1	1 16	0 8
<i>Callopora decidua</i>										6 7	1 15	8 3	4 13	0 5	0 21	37 1
<i>Microporella sp.</i>										3 6	4 3	36 17	68	0	1 3	12
<i>Cribrilina annulata</i>										2 11	2 9	15 68	42	6	0 34	51
<i>Porella alba</i>										7	26 27	102	6	27	2 2	89 174
<i>Alcyonidium sp.</i>											9	6	5	3	0 10	9
<i>Cylindroporella tubulosa</i>											5	20	1	9	3 14	33
<i>Callopora craticula</i>																

Table 2. Matrix of competitive interactions for Alaskan cheilostome bryozoans from Barnes & Dick (2000) with non-cheilostomes removed, as were competitors that did not meet two or more competitors. Data otherwise presented as in table 1.

<i>T. armifera</i>		2	5	4	3	2	1	1	0	1	1	0	0	2	2	0	1	4	3	7	10
<i>Tegella armifera</i>		9	16	3	10	1	4	2	3	2	4	22	22	13	17	6	7	44	51	25	42
<i>T. aquilirostris</i>				0	11	0	0	1	0	0	1	1	0	2	0	2	0	3	2	5	4
<i>Tegella aquilirostris</i>				8	19	1	1	1	2	6	7	12	13	6	8	3	5	24	29	24	33
<i>Myrzoella plana</i>						0	0	1	0	1	3	0	0	9	5	0	0	5	2	11	6
<i>Myrzoella plana</i>						3	3	5	6	0	4	3	3	37	51	11	11	8	15	41	58
<i>Cauloramphus sp.</i>								4	0	4	2			9	7	3	2	35	5	9	11
<i>Cauloramphus sp.</i>								2	6	3	9			9	25	4	9	11	51	77	97
<i>Microporella californica</i>										2	1	0	0	0	0	0	2	9	2	2	4
<i>Microporella californica</i>								6	9	1	1	1	1	1	1	0	2	16	27	26	32
<i>Tegella arctica</i>												2	1	2	5	0	0	5	3	5	10
<i>Tegella arctica</i>												5	8	5	12	2	2	21	29	21	36
<i>Callopora arctica</i>														3	6	4	3	36	17	3	12
<i>Callopora arctica</i>														2	11	2	9	15	68	9	24
<i>Microporella sp.</i>																6	13	33	42	34	51
<i>Microporella sp.</i>																7	26	27	102	89	174
<i>Cribritina annulata</i>																		9	6	10	9
<i>Porella alba</i>																		5	20	14	33
<i>Porella alba</i>																			40	36	
<i>Celleporella sp.</i>																			73	149	

Table 3. Results of two-way ANOVAs: (a) on sites, substrata and interaction between sites and substrata and (b) pooling interaction and residual sums of squares. SS, sums of squares; MS, mean squares.

source	d.f.	SS	MS	F	p
(a) including interaction					
site	2	0.048 07	0.024 03	56.55	< 0.001
substratum	1	0.000 68	0.000 68	1.59	0.254
interaction	2	0.001 40	0.000 70	1.65	0.269
error	6	0.002 55	0.000 43		
total	11	0.052 69			
(b) pooling interaction and error sums of squares					
site	2	0.048 07	0.024 03	48.68	< 0.001
substratum	1	0.000 68	0.000 68	1.37	0.276
error	8	0.003 95	0.000 49		
total	11	0.052 69			

the variance of the observed proportion is $p(1-p)/n$, which is a quadratic function with its greatest value at $p = 0.5$ and falling to zero at $p = 0$ and 1. The standard error attached to the proportions indicates that this model is not needed and a plot of y versus rank difference was almost identical to the plot of original data. In cases where proportions approach zero or one, a straight line cannot apply because it allows out-of-range values. A more useful general model is the logistic regression, of which $\text{logit}(p) = \log[p/(1-p)]$ is assumed to be linear in the predictor. In this case, a plot of $\text{logit}(p)$ against rank difference also showed a very similar trend to original data, so transformation was applied to the data.

3. RESULTS

The interactions between most competitor pairs (matrix cells) of assemblages were rarely determinate (i.e. in few cases did one competitor win all encounters). Furthermore, in few cases were all of the interactions between competitor pairs decisively won or lost rather than tied. Competitive reversals (in which a lower-ranking competitor significantly outcompeted a species of higher rank) also were present in most assemblages (e.g. *Microporella* sp. versus *Cribrilina annulata* in table 2). This apparent complexity and variability at competitor-pair level was, however, relatively unimportant to assemblage-level patterns (in transitivity). Both the squaring and square-rooting of Tanaka & Nandakumar's (1994) formulae and the large number of competitor pairings resulting from matrices of just 11 competitors (table 2) make the procedure robust to any particular anomalous competitor-pair output. The win-index output of Tanaka & Nandakumar's (1994) transitivity index varied between 0.56 and 0.88. There was no evidence for differences between the two types of substrata (artificial and natural) or any interaction effect between substrata and sites (table 3). To increase the degrees of freedom for estimating random error (thereby gaining power for effect detection), the interaction sum-of-squares was pooled with the residual sums-of-squares, but the conclusion of the analysis was the same (table 3). The highest values of transitivity were found in assemblages at the northernmost and southernmost extremes studied: Kodiak Island (Alaska) and Adelaide Island

Figure 1. Assemblage (interference competition) transitivity with latitude and isolation in the southern hemisphere. Data are taken from published and unpublished sources, summarized in Barnes (2000). The line of best fit is a significant linear regression with equation (win index = $0.51 + 5.59 \text{ latitude}$, ANOVA d.f. = 1, $F = 219$, $p < 0.001$). Black circles, nearshore; grey circles, offshore; open circle, mainland.

(Antarctica), respectively (figure 1). These high-latitude assemblages show near linear hierarchies in which a few species won most encounters (*Tegella armifera* and *T. aquilostri* in Alaska; see table 2) against all other competitors. Owing to the strength (p -value) and fit (r^2 -value) of the relationship in figure 1, no correction was deemed necessary or appropriate for ecological differences of latitude (the difference between one degree of latitude differs itself with latitude). In addition, a few species lost most spatial interactions (*Porella alba* and *Celleporella* sp. in Alaska), whilst competitors intermediate between these extreme performers were ranked in succession. Overall, therefore, the probability of winning in such a structured assemblage typically increased with the difference between the ranking of competitor species (figure 2).

The win index increased with latitude of assemblage sampled (ANOVA, d.f. = 2, $F = 47.0$, $p = 0.021$), indicating an increase in transitivity of interference competition with latitude. Thus, competition in encrusting assemblages changes from essentially a network structure at low

Figure 2. Probability of a win for higher-ranking competitors with difference in rank between competitors. Data are shown as mean with standard error, calculated from values in table 2.

Figure 3. Assemblage (interference competition) transitivity with latitude for the northern hemisphere. Squares, artificial substrata (recruitment/settlement panels) and circles, natural substrata. Data taken from published and unpublished sources, summarized in Barnes (2000). The overall line of best fit is a quadratic regression ($r^2 = 75.5$) with equation (win index = $0.6272 + 3.265 \times 10^{-4}$ latitude + 4.52×10^{-5} latitude²) and significance given by (ANOVA, d.f. = 2, $F = 13.89$, $p < 0.002$).

latitudes to one of a more hierarchical nature at high latitudes. There was no obvious effect of isolation, although there were insufficient appropriate studies from continental margins (compared with inshore and offshore islands) to test this fully. Transitivity values from northern hemisphere assemblage data were similar to those in the southern hemisphere (figure 3), except for a slightly reduced range. Northern hemisphere values also formed a cline with latitude, though the relationship differed from that of southern-hemisphere data in being nonlinear (figure 3).

4. DISCUSSION

(a) *Competition, coexistence, complexity and trend emergence*

Competition amongst sessile groups of organisms, such as plants or marine benthos, may take many forms, often simultaneously. Competitive interactions may be exploitation, interference or both and may operate in a wide

variety of physical and chemical processes (Schoener 1983; Menge & Sutherland 1987). Jackson (1979a) suggested that assemblage complexity might be maximized when competing taxa were more taxonomically distant (such as phyla or classes) or differed in growth form (unitary versus colonial). Models of species diversity patterns (Menge & Sutherland 1987) have further emphasized this potential complexity of competition in assemblages by predicting the dynamism of results with trophic structure, recruitment, environmental stress levels and predation. Whilst appreciation of the possibilities for complexity is important, some abundant and ubiquitous situations involve simple spatial competition between members of a single taxon, with most of the described factors being approximately static. Analysis of cheilostome bryozoan assemblages, which dominate the habitat of marine boulder under-surfaces across the globe, in the present study has demonstrated strong trends emerging from relatively uncomplex data.

The lowest values of transitivity (0.56–0.7) in the present study are not unusual, even within encrusting sessile benthic animals. Data from Stebbing (1973) on ctenostome and cheilostome bryozoans gave a (win index) value of 0.32 when subjected to Tanaka & Nandakumar's (1994) index. The small size of Stebbing's (1973) dataset, coupled with the fact that only one cheilostome was represented, precluded its inclusion in the present study. Spatial competition in an ascidian assemblage, studied by Schmidt & Warner (1986), produced an even lower value of just 0.26. The lowest possible theoretical values are 0.707 (with no tied outcomes) if every competitor wins exactly half of all encounters with every other, or 0.00 (with tied outcomes) if all competitors have tied outcomes in every encounter. The upper value is 1.0 if the competitors are perfectly ranked, headed by an assemblage dominant winning all encounters and a completely inferior competitor losing all interactions at the base of the hierarchy.

The upper values of assemblage transitivity are among the most hierarchically organized groupings described. The societies of many mammals, such as stags (Clutton-Brock *et al.* 1979), are organized along rather strict hierarchical lines, but competition within such groups is intraspecific. The extent to which social structure is hierarchical clearly varies with species and may even vary within populations of certain species, such as microtine mammals (Krebs 1985). Interspecific competition has even greater potential to vary because of the range of structures or mechanisms possessed by different species. Many of the multispecies bryozoan assemblages reported here were, nevertheless, organized in similar fashion to the intraspecific hierarchies of elephant seals or stags, but only at high latitude. Whilst trends of assemblage organization (figures 1 and 3) seem robust with latitude, some caution is needed when interpreting data from the high southern latitudes as they are from a very restricted longitudinal range: the Antarctic Peninsula region only. This is by necessity since this area represents the only shallows for nearly 10 degrees of latitude and so it is also atypical for its latitude in many ways due to its position relative to features such as the Weddell Sea gyre (which generates cool water). Furthermore, although latitude is given linear scaling, a one-degree change of latitude at the poles or

Figure 4. Assemblage (interference competition) transitivity with latitude and isolation in the Southern Ocean (Antarctic Peninsula and Scotia Arc data only). Data source and presentation as in figure 1. The line of best fit ($r^2 = 92.8$) is a significant linear regression, ANOVA d.f. = 1, $F = 64.1$, $p < 0.001$. Black circles, nearshore; grey circles, offshore.

tropics may be different ecologically from that in temperate regions. This is difficult to correct for and probably has little importance to the relationship presented as the trend seems statistically highly robust.

(b) *Why should polar assemblages be more hierarchical?*

The complex models of Menge & Sutherland (1987) and previous work (e.g. Connell 1985; Roughgarden 1986) suggested competition to be of low level and ecologically unimportant in situations of low recruitment and growth and high availability of free space. Overall, levels of recruitment and growth typically are low in shallow polar benthic communities (Stanwell-Smith & Barnes 1997), but competition has emerged as one of the dominant processes dictating assemblage structure (Barnes & DeGrave 2002). Although in polar bryozoans (and other taxa) gross recruitment (recruits year⁻¹) may be low and individual/colony growth slow, recruit and adult densities can be very high because recruits occur on the restricted space of boulder under-surfaces only. Most recruits experience high levels of interference competition before they are two years old (Barnes & DeGrave 2002). Whilst the simplicity of most polar boulder assemblages was expected and the importance of polar competition was not, given model predictions (Menge & Sutherland 1987), neither explains the here-observed hierarchical structure. An alternative view could be that the level of nearshore polar disturbance is more intermediate on temporal and spatial scales and so fits the model well, but little evidence has been presented of higher levels of disturbance in other equivalent environments. Certainly, by wind speed and wave height (and speed) there is a general trend to increasing energy with latitude (figure 5a,b).

Many of the (competitor) species in the present study have wide latitudinal ranges with the exception of the Antarctic species, which are mainly endemic (see Hayward 1995). This is important because it indicates that differential levels of transitivity are not simply a result of different suites of competitors. In fact, if only Antarctic data (54° S, albeit only from the Antarctic Peninsula region)

Figure 5. Mean surface wind speed and wave height with latitude for ocean basins. (Long dashes, Atlantic ocean; short dashes, Pacific ocean; dotted and dashed line, Indian ocean; solid line, mean global). Windspeed data from Bentamy *et al.* (1996).

are plotted against latitude, the trend still holds (figure 4). Differences in competitor identity are, therefore, unlikely to be important in explaining observed data variability.

There are at least two probable causes and mechanisms behind cheilostomatid dominance becoming more hierarchical towards the poles. First, tied outcomes of interactions become rarer, (Barnes 2000) although the explanation for this remains obscure. Second, the number of competitor pairs in which one species completely dominates the other increases (Barnes 2000). Because Tanaka & Nandakumar's (1994) index involves squaring outcome scores, both of these have a strong influence on raising the output value. The number of competitors also decreases towards the poles as frequent ice scour and other physical conditions associated with polar shores have a stronger influence (Barnes 2000). This in turn changes the frequency of interspecific encounters with respect to those that are intraspecific.

Competition becoming more hierarchical with latitude means that the effect of competition is more severe. With no extrinsic influence, such competition would result in a few species monopolizing all space. Antarctic benthic species richness is, however, high and in some places arguably as high as in tropical coral reefs (Brey *et al.* 1994). Unlike tropical reefs where species richness may be maintained by extensive non-transitive networks with no true dominant (Jackson & Buss 1975; Buss & Jackson 1979; Chornesky 1989), diversity in polar environments must be

maintained by non-biological mechanisms. Disturbance in the polar marine environment is variable and can be very high, mainly through the action of ice scour (Arntz *et al.* 1994). Menge & Sutherland (1987) considered that competition (for space) would be only slight and diversity low in environments receiving frequent abrasion, such as shallow polar seas. The current work indicates that diversity is maintained by this highly frequent and catastrophic nature of disturbance in polar regions, for without it, a few species would outcompete all others and monopolize space. In shelves, crevices or caves, which are protected from ice scour, there is evidence that competitively dominant species do indeed monopolize large areas of space. In addition to increasing the potential establishment of non-native species by invasion and their possibly exceeding thermal tolerance limits of native species, global temperature change and ice melt may, therefore, present another mechanism of diversity reduction: less ice would reduce environmental heterogeneity by lessening disturbance.

While ice scour may explain the trend to increasingly hierarchical organization of assemblages within polar waters, the same process cannot be responsible for the same trend continuing across the ice-free temperate and tropics. Ice scour is just one agent of mechanistic disturbance, however, and in ice-free periods in polar waters and year-round in non-polar waters the main form of energy is wave action. Mean wind speed increases from the equator to polar regions (figure 5a) across all oceans, and mean wave height (and energy) increases correspondingly (figure 5b). This study indicates that the increase in energy from the tropics to the poles drives the organization of the marine assemblages tested to become increasingly hierarchical, principally by wave action but additionally by ice scour at high latitude.

REFERENCES

- Arntz, W. E., Brey, T. & Gallardo, V. A. 1994 Antarctic zoo-benthos. *Oceanogr. Mar. Biol. A. Rev.* **32**, 251–303.
- Barnes, D. K. A. 2000 Diversity, recruitment and competition on island shores at south-polar localities compared with lower latitudes: encrusting community examples. *Hydrobiologia* **440**, 37–44.
- Barnes, D. K. A. & Arnold, R. J. 2001 Competition, sublethal mortality and diversity on Southern Ocean coastal boulder communities. *Polar Biol.* **24**, 447–454.
- Barnes, D. K. A. & DeGrave, S. 2002 Modelling multivariate determinants of growth in Antarctic bryozoans. In *Proc. 12th Int. Bryozoology Association Conf.* (ed. P. Wyse-Jackson, M. Spencer-Jones & C. Butler), pp. 7–17. Dublin: Balkema.
- Barnes, D. K. A. & Dick, M. A. 2000 Overgrowth competition between clades: implications for interpretation of the fossil record and overgrowth indices. *Biol. Bull.* **199**, 85–94.
- Bentamy, A., Grima, N., Quilfen, Y., Harscoat, V., Maroni, C. & Pouliquen, S. 1996 An atlas of surface wind from ERS-1 Scatterometer measurements. IFREMER publication, p. 229, IFREMER, DRO/OS, BP 70, 29280 Plouzane, France.
- Brey, T., Klages, M., Dahm, C., Gorny, M., Gutt, J., Hain, S., Stiller, M., Arntz, W. E., Wägele, J.-W. & Zimmerman, A. 1994 Antarctic benthic diversity. *Nature* **368**, 297.
- Buss, L. W. & Jackson, J. B. C. 1979 Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *Am. Nat.* **113**, 223–234.
- Chornesky, E. A. 1989 Repeated reversals during spatial competition between corals. *Ecology* **70**, 843–855.
- Clarke, A. & Lidgard, S. 2000 Spatial patterns of diversity in the sea: bryozoan species richness in the north Atlantic. *J. Anim. Ecol.* **69**, 799–814.
- Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979 The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav.* **27**, 211–225.
- Connell, J. H. 1978 Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1310.
- Connell, J. H. 1985 Variation and persistence of rocky shore populations. In *The ecology of rocky coasts* (ed. P. G. Moore & R. Seed), pp. 57–69. London: Hodder & Stoughton.
- Crame, J. A. 2000 Evolution of taxonomic gradients in the marine realm: evidence from the composition of recent bivalve faunas. *Palaeobiology* **26**, 188–214.
- Hayward, P. J. 1995 *Antarctic cheilostomatous Bryozoa*. Oxford University Press.
- Hochberg, M. E. & Lawton, J. H. 1990 Competition between kingdoms. *Trends Ecol. Evol.* **5**, 367–370.
- Hughes, D. J. & Jackson, J. B. C. 1990 Do constant environments promote complexity of form? The distribution of bryozoan polymorphism as a test of hypotheses. *Evolution* **44**, 889–905.
- Jackson, J. B. C. 1979a Morphological strategies of sessile animals. In *Biology and systematics of colonial organisms* (ed. G. Larwood & B. R. Rosen), pp. 499–555. London: Academic.
- Jackson, J. B. C. 1979b Overgrowth competition between encrusting cheilostome ectoprocts in a Jamaican cryptic reef environment. *J. Anim. Ecol.* **48**, 805–823.
- Jackson, J. B. C. & Buss, L. 1975 Allelopathy and spatial competition among coral reef invertebrates. *Proc. Natl Acad. Sci. USA* **72**, 5160–5163.
- Jackson, J. B. C. & Herrera Cubilla, A. 2000 Adaptation and constraint as determinants of zooid and ovicell size among encrusting ascophoran cheilostome Bryozoa from opposite sides of the isthmus of Panama. In *Proc. 11th Int. Bryozoology Association Conf.* (ed. A. Herrera Cubilla & J. B. C. Krebs), pp. 249–258. Panama City: Smithsonian Tropical Research Institute.
- Krebs, C. J. 1985 Do changes in spacing behaviour drive population cycles in small mammals? In *Behavioural ecology* (ed. M. Sibly & R. H. Smith), pp. 295–312. Oxford: Blackwell Scientific.
- Lopez Gappa, J. J. 1989 Overgrowth competition in an assemblage of encrusting bryozoans settled on artificial substrata. *Mar. Ecol. Prog. Ser.* **51**, 121–130.
- McGuinness, K. A. 1990 Physical variability, diversity gradients and the ecology of temperate and tropical reefs. *Aust. J. Ecol.* **15**, 465–476.
- McKinney, F. K., Lidgard, S., Sepkoski, J. J. & Taylor, P. D. 1998 Decoupled temporal patterns of evolution and ecology in two post-paleozoic clades. *Science* **281**, 807–809.
- Maughan, B. 2000 Ecology of encrusting epifauna at Lough Hyne marine nature reserve, Co. Cork, Ireland. Unpublished PhD thesis, University College Cork, Ireland.
- Menge, B. A. & Sutherland, J. P. 1987 Community regulation: variation in disturbance, competition and predation in relation to environmental stress and recruitment. *Am. Nat.* **130**, 730–757.
- Mileikovsky, S. A. 1971 Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Mar. Biol.* **10**, 193–213.
- Nandakumar, K. 1995 Competitive interactions among sessile organisms in Tomioka Bay, South Japan: importance of light conditions on the panel surface. *Mar. Biol.* **121**, 713–719.
- Pearse, J. S., McClintock, J. B. & Bosch, I. 1991 Reproduction in Antarctic benthic marine invertebrates: tempos, modes and timing. *Am. Zool.* **31**, 65–80.

- Pianka, E. R. 1966 Latitudinal gradients in species diversity: a review of concepts. *Am. Nat.* **100**, 33–46.
- Quinn, J. F. 1982 Competitive hierarchies in marine benthic communities. *Oecologia* **54**, 129–135.
- Roughgarden, J. 1986 A comparison of food-limited and space-limited animal competition communities. In *Community ecology* (ed. J. Diamond & T. J. Case), pp. 492–516. New York: Harper & Row.
- Roy, K., Jablonski, D., Valentine, J. W. & Rosenberg, G. 1998 Marine latitudinal diversity gradients: tests of causal hypotheses. *Proc. Natl Acad. Sci. USA* **95**, 3699–3702.
- Rubin, J. A. 1982 The degree of intransitivity and its measurement in an assemblage of encrusting cheilostome Bryozoa. *J. Exp. Mar. Biol. Ecol.* **60**, 119–128.
- Russ, G. R. 1982 Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. *Oecologia* **53**, 12–19.
- Schmidt, G. H. & Warner, G. F. 1986 Spatial competition between colonial ascidians: the importance of stand-off. *Mar. Ecol. Prog. Ser.* **31**, 101–104.
- Schoener, T. W. 1983 Field experiments on interspecific competition. *Am. Nat.* **122**, 240–285.
- Sebens, K. P. 1986 Spatial relationships among encrusting marine organisms in the New England subtidal zone. *Ecol. Monogr.* **56**, 73–96.
- Stanwell-Smith, D. & Barnes, D. K. A. 1997 Benthic community development in Antarctica: recruitment and growth on settlement panels at Signy Island. *J. Exp. Mar. Biol. Ecol.* **212**, 61–79.
- Stebbing, A. R. D. 1973 Competition for space between the epiphytes of *Fucus serratus*. L. *J. Mar. Biol. Assoc. UK* **53**, 247–261.
- Tanaka, M. & Nandakumar, K. 1994 Measurement of the degree of intransitivity in a community of sessile organisms. *J. Exp. Mar. Biol. Ecol.* **182**, 85–95.
- Turner, S. J. & Todd, C. D. 1994 Competition for space in encrusting bryozoan assemblages: the influence of encounter angle, site and year on outcome variability. *J. Mar. Biol. Assoc. UK* **74**, 603–622.
- Wagnon, K. A., Loy, R. G., Rollins, W. C. & Carrol, F. D. 1966 Social dominance in a herd of Angus, Hereford and shorthorn cows. *Anim. Behav.* **14**, 474–479.

As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.