

Overgrowth Competition Between Clades: Implications for Interpretation of the Fossil Record and Overgrowth Indices

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Abstract. Overgrowth interactions (2693 in total) were observed among three major groups (arguably clades) of bryozoans—cheilostomatids (57 species), ctenostomatids (3 species), and cyclostomatids (14 species). The bryozoans studied here occur in shallow water at high-temperate polar latitudes where they encrust hard substrata such as rock piles. The main study site was the intertidal and infralittoral zones of Kodiak Island, Alaska, but observations were also made in similar zones of South Georgia Island and the Falkland Islands in the South Atlantic Ocean. Cheilostomatids dominated the number of species, individuals, and interactions at all depths. Intraclade interactions formed 73.7% of the encounters for cheilostomatids, 1.6% for ctenostomatids, and 5.7% for cyclostomatids. The competitive ranking of the three clades was broadly ctenostomatids > cyclostomatids > cheilostomatids. Significantly, these results contradict all previous quantitative studies of bryozoan overgrowth, in which cheilostomatids are reported to overgrow cyclostomatids at a higher rate. From these studies and the literature, we calculated win indices to vary from 0 to 0.42 for living cyclostomatids, from 0.08 to 0.9 for living cheilostomatids, and from 0.25 to 0.75 for living ctenostomatids. The win indices of cyclostomatid and cheilostomatid clades show significantly more variation in living assemblages than in fossil assemblages. This disparity may be due to differential preservation (polar and subpolar assemblages last less than 4 years). The diversity was very high in terms of both species richness and interaction types (outcomes between competitor pairs). Comparison with the literature suggests the possibility that nearshore diversity of bryozoans may be bimodal (have two peaks) between high arctic

and antarctic latitudes. Indices of success in overgrowth competition have been constructed in various ways. For cheilostomatids, the method of calculation had little influence on the ranking of representatives. In contrast, the apparent success of ctenostomatids and cyclostomatids varied hugely with how the index was calculated. This inconsistency is due to the use of very different strategies in overgrowth competition; among the two latter groups, many interactions involve tied outcomes.

Introduction

Cyclostomatida, Ctenostomatida, and Cheilostomatida are the major groups of the Phylum Bryozoa (the fourth is exclusively fresh water). For convenience, we will use the term “clade” to refer to these major groups of marine bryozoans, but this is not entirely accurate. Although the Cyclostomatida and the bulk of the Cheilostomatida probably represent monophyletic groups, or clades, Ctenostomatida is probably a paraphyletic group (Todd, 2000), better referred to as a “grade.” Representatives of these groups occur together in most benthic assemblages, where frequently the encrusting members are directly competing for space and food (*e.g.*, Stebbing, 1973; Sebens, 1986; Lopez Gappa, 1989). Cheilostomatids generally dominate the bryozoan component of assemblages in space occupied, numbers of species, numbers of colonies, and overgrowth performance. As a result of such dominance, most studies of competition between encrusting benthos have either documented cheilostomatid interactions with representatives of other benthic phyla (Quinn, 1982; Sebens, 1986) or have been restricted solely to cheilostomatid-cheilostomatid interactions (*e.g.*, Jackson, 1979a; Buss, 1980; Palumbi and

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Jackson, 1983; Tanaka and Nandakumar, 1994; Barnes and Rothery, 1996). A few studies have shown that representatives of the Ctenostomatida may be high or mid-ranked in overgrowth performance against the cheilostomatid representatives (Stebbing, 1973; Turner and Todd, 1994). Cyclostomatids, in contrast, have been found to be almost always overgrown by cheilostomatids in the few studies of Recent (living) competition between the two clades (Harmelin, 1976; Buss and Jackson, 1979; Lopez Gappa, 1989; McKinney, 1992). Analysis of the fossil record has shown that competitive performance has been stable for the last 100 million years, with cheilostomatids overgrowing cyclostomatids in about 66% of encounters (McKinney, 1995a). Although broad trends have been described, many factors contribute to the outcome of interactions between any pair of competitors.

Phylum membership is the principal factor determining overgrowth ability, with ascidians > sponges > bryozoans > unitary forms such as barnacles, annelids (Buss and Jackson, 1979; Russ, 1982; Sebens, 1986). Growth form is also important, with foliaceous forms > encrusting sheets > stoloniferous types (Buss, 1979; Barnes and Rothery, 1996), and bryozoans that have the capability of frontal budding overgrowing those that lack it (Lidgard and Jackson, 1989; McKinney, 1992; 1995a). To explain the competitive advantage that cheilostomatids have over cyclostomatids, McKinney (1992; 1993; 1995a, b) has described a number of attributes, including higher growth rates and larger colonies and feeding structures. The crucial features of cheilostomatids, however, are probably (1) rapid ontogenetic development resulting in full-sized zooidal skeletons (and feeding structures) at colony margins, (2) labile morphogenetic responses at colony margins (raised growing edges, frontal budding, stolon production and others), and (3) water excurrents that leave around the colony margin, potentially into the area of uptake for a cyclostomatid competitor. These features may explain the great radiation that, since the mid-Cretaceous period, the cheilostomatids have undergone relative to the cyclostomatids (Lidgard *et al.*, 1993), or this may be due to unrelated factors such as the acquirement of planktotrophic larvae (Taylor, 1988). It seems likely that an increase in encounters with a superior competitor would contribute to the decline of cyclostomatid species richness from the end of the Cretaceous to Recent periods (Lidgard *et al.*, 1993; McKinney, 1995a; Sepkoski *et al.*, 2000).

Studies involving interpretation of competitive interactions between major groups or clades of the same phylum are rare for both living and fossil assemblages, and this is the case with the Bryozoa. Consequently, our knowledge is biased to the results of the few studies carried out and the limited distribution of the localities of these studies. Many studies are based on relatively few interactions between many species pairs and even fewer between clades, and thus

a synoptic interpretation of overall outcomes is difficult. Problems of interpretation are compounded by differences in the way performance is measured (*e.g.*, wins compared to losses, or wins compared to total interactions) and by the way contact matrices are analyzed (that is, by using transitivity indices) (see Petraitis, 1979; Rubin, 1982; Tanaka and Nandakumar, 1994). Perhaps the largest barrier to meaningful comparison, though, is that the three marine bryozoan clades have not, to date, been evaluated in the same study (at a single locality).

In this study we investigate intraspecific and interspecific competitive encounters among representatives of the bryozoan clades Cyclostomatida, Ctenostomatida, and Cheilostomatida from the intertidal and infralittoral zone of Kodiak Island, Alaska. The boreal/subpolar region is unusually diverse with respect to many taxa, but particularly bryozoans (see Barnes and Dick, 2000; Dick and Ross, 1986; 1988), and provides an opportunity for comparing interactions between abundant representatives of the three clades. We compare the outcomes using different methods of competitive strength calculation, and we evaluate these methods. We also compare win indices and rankings of the clades with unpublished work involving interactions among the clades at two south Atlantic localities: the Falkland Islands and South Georgia Island. Win indices and rankings from other localities and time periods were extracted from the literature for comparisons with our results.

Materials and Methods

Study site and species

Bryozoan overgrowth interactions were analyzed on 110 rocks from 14 sites at Narrow Strait, Kodiak Island (57° 54'N, 152° 27'W) in the Alaskan boreal-Arctic (see Dick and Ross, 1988, for more detail). Four tidal levels or depths were represented by a number of rock-pile sites: upper midlittoral (2), lower midlittoral (4), upper infralittoral (3), and lower infralittoral (5). Rock surface area was measured using a nonelastic grid of square centimeters as per Barnes and Rothery (1996), but percent cover and colony size were not measured. All competitors were identified into the three orders of bryozoans present and to genus or species level where possible. Poor taxonomic resolution in the initial stages of the study led to uncertainty about the particular species involved in interactions within the genera *Caulorhamphus* (5 species), *Microporella* (4 species), *Celleporella* (2 species), and *Alcyonidium* (2 species). The cyclostomatids from Narrow Strait have not been worked up taxonomically and here were identified to ordinal level only, with the exception of a common lichenoporidae designated *Lichenopora* sp.

Table 1

Mean number of species per rock and proportion of rocks (in parentheses) colonized by species occurring rarely at the study sites, Alaska

Tidal cover/depth	Mean no. species per rock		
	Cyclostomatids	Ctenostomatids	Cheilostomatids
Upper midlittoral	0	0.25 (0.13)	4.88 (0.49)
Lower midlittoral	0.88 (0.31)	0.75 (0.09)	6.81 (0.49)
Upper infralittoral	1.54 (0.72)	0.54 (0.25)	10.7 (1.00)
Lower infralittoral	4.25 (0.94)	0.73 (0.30)	13.0 (0.63)

Measurement of interactions

All colony-to-colony interactions between representatives of the three clades of bryozoans were recorded from each rock and site, along with the number of intraspecific and interspecific encounters within clades. When the growing edge of competitor A covered the apertures of competitor B, A was determined to have overgrown B. Only "frontal" overgrowth interactions between two living competitors, without direct settlement onto one of the competitors, was counted as overgrowth for the purposes of this study (see Rubin, 1982; Turner and Todd, 1994; Barnes and Rothery, 1996). The actual scores were tabulated into a competitor-contact matrix (as Turner and Todd, 1994; Barnes and Rothery, 1996). Measurements of overgrowth performance were calculated for each competitor that took part in more than 20 between-clade interactions. Various measurements of overgrowth performance were used: a score system in which a win = 3, a tied outcome = 1, and a loss = 0 (wins rated much higher than ties because ties often prevent further growth and development of colonies, see Barnes and Clarke [1998]); the number of wins divided by the total number of interactions for that competitor; the number of losses divided by the total number of interactions for that competitor; the number of wins divided by the number of losses for that competitor; and an aggregate measure in which the mean of the rankings from all methods was obtained. The rankings in Table 2 are those calculated from raw data. These may differ from true population rankings because the number of encounters with each competitor was not the same for each species, and some potential competitors did not meet. The rankings were standardized by multiplying all pairwise interactions such that each had a total value of 100, then recalculating the total wins, losses, and ties for each competitor identity.

Results

Between-species interactions

A total of 74 species of bryozoans were recorded during the study: 57 cheilostomatids, 3 ctenostomatids, and the

remainder cyclostomatids (later analyzed to be 14 species). The mean number of cheilostomatid and cyclostomatid species per rock increased with depth of rocks (Table 1), the former dominating the number of species at all depths. The proportion of ctenostome species was small with respect to the total number of bryozoan species, and it varied inconsistently with depth. The mean number of interactions increased with depth for all clades (Fig. 1). Cheilostomatids were involved in 2653 interactions, of which 73.7% were within the clade; ctenostomatids were involved in 367 interactions, of which 1.6% were within the clade; and cyclostomatids were involved in 384 interactions, of which 5.7% were within the clade. All cheilostomatids that encountered ctenostomatids or cyclostomatids on more than 20 occasions are illustrated in a species-contact matrix (Table 2). The remaining cheilostomatid species are pooled because fewer than a total of 20 competitive interactions were not considered to be representative. Certain pairs of competitors had anomalously higher frequencies of encounters, such as *Alcyonidium* spp. and *Porella alba*. The cheilostomatid species *Callipora craticula* encountered only ctenostomatids and cyclostomatids, despite the overwhelming numerical dominance of cheilostomatids and being involved in 30 interspecific interactions.

Most (99.3%) of the intra-clade encounters observed were interspecific interactions. Over 80% (114) of the possible competitor-pair interactions (136 in the matrix Table 2) and 44 of the 45 between-clade interactions were observed (but these represented only a small proportion of the 74×74 species interactions theoretically possible). The proportion of indeterminate outcomes (neither competitor won all encounters) from competitor pairs was significantly higher within the clade of cheilostomatids (15.9%) than between cheilostomatids and other clades (5.1%) (Mann-Whitney *U* test, $P < 0.01$). The proportion of tied outcomes or standoffs in competitor pairs was significantly higher between clades than within clades (Mann-Whitney, $P < 0.001$). The proportion of ties was also significantly

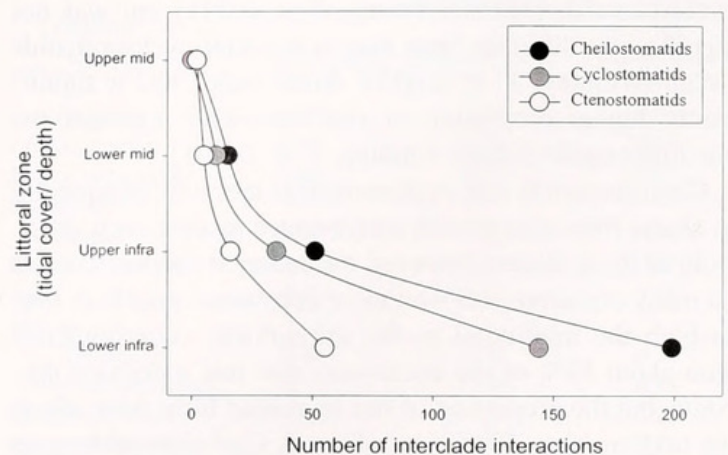


Figure 1. Mean number of interactions per clade with depth. All data are presented as mean with standard error.

Table 2

Matrix of competitive interactions for Alaskan cheilostomatid, ctenostomatid, and cyclostomatid bryozoans (latter two groups are gray shaded)

	<i>T. armifera</i>	<i>T. aquilirostris</i>	<i>M. plana</i>	<i>Caulorhamphus</i> sp.	Cyclostomatids	<i>M. californica</i>	<i>T. artica</i>	<i>Lichenopora</i> sp.	Cheilostomatids	<i>Microporella</i> sp.	<i>C. annulata</i>	<i>P. alba</i>	<i>Alcyonidium</i> sp.	<i>Celleporella</i> sp.
<i>Tegella armifera</i>	2 5 4 3 2 1	9 16 3 10 1 4	0 11 0 0	10 13 2 3 2 4	1 2 1 0 1 1	3 0 1 3 2 2	0 1 4 27 31 13 17	6 7 44 51	8 1 7	10 19 25	8 1 7	10 19 25	8 1 7	10 19 25
<i>Tegella aquilirostris</i>		8 19 1 1	4 7 1 2 6 7	2 4 16 19 6 8	3 5 0 0 5 2	4 5 9 5 0 0	5 2 35 5	20 2 9	7 16 24	5 0 11	3 8 41	20 2 9	7 16 24	5 0 11
<i>Myriozeolla plana</i>		3 3	7 14 5 6 0 4	0 3 34 43 37 51	11 11 8 15	3 8 41	20 2 9	7 16 24	5 0 11	3 8 41	20 2 9	7 16 24	5 0 11	3 8 41
<i>Caulorhamphus</i> sp.			1 3 2 6 3 9	1 12 21 39 9 25	4 9 11 51	2 24 77	4 3 1 3 1 1	6 8 12 14 14 14	6 2 6 3	3 1 8	3 7 39	2 1 2	5 2 2	0 7 26
Other Cyclostomatids			3 7 2 6 2 4	1 15 16 42 20 48	5 13 10 19	3 7 39	2 1 2 0 1 3 0 0	0 2 9 2	5 2 2	0 7 26	1 1 3 3 2 5 0 0	5 3 14 0 5	2 4 16	5 21
<i>Microporella californica</i>			6 9	0 2 3 7 1 1	0 2 16 27	0 7 26	1 1 3 3 2 5 0 0	5 3 14 0 5	2 4 16	5 21	8 53 7 9 58 47	14 11 18	9 17 94	6 34
<i>Tegella artica</i>				11 1 6 2 7 1 8 0	4 1 16	5 21	5 17 7 15 3 11 5 13	0 5 13	0 5 21	8 53 7 9 58 47	14 11 18	9 17 94	6 34	7 89
<i>Lichenopora</i> sp.				8 53 7 9 58 47	14 11 18	9 17 94	6 34	7 89	9 10	5 14	9 14	61 24 40	16 100 73	5 1 34
Other Cheilostomatids				49 110 4 20 43 148	9 17 94	6 34	7 89	9 10	5 14	9 14	61 24 40	16 100 73	5 1 34	1 6 39
<i>Microporella</i> sp.				7 26 27 102	6 27 89	5 3 10	1 9 14	61 24 40	16 100 73	5 1 34	1 6 39			
<i>Cribilina annulata</i>				9 6	5 3 10	1 9 14	61 24 40	16 100 73	5 1 34	1 6 39				
<i>Porella alba</i>				5 20	1 9 14	61 24 40	16 100 73	5 1 34	1 6 39					
<i>Alcyonidium</i> sp.														
<i>Celleporella</i> sp.														

Data are displayed in standard form—see Turner and Todd (1994), Barnes and Rothery (1996). If row = competitor A and columns = competitor B, for each cell the top left, top right, and bottom left 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.

higher in the ctenostomatids than in the non-*Lichenopora* cyclostomatids (Mann-Whitney, $P < 0.001$) but was not significantly different from that in the total cyclostomatids (Mann-Whitney, $P = 0.053$). Both clades had a significantly higher proportion of tied outcomes than did the cheilostomatids (Mann-Whitney, $P < 0.001$).

Ctenostomatids and cyclostomatids met too infrequently to assess their overgrowth performance against each other. Both of these clades, however, encountered cheilostomatids on many occasions and won more encounters than they lost. In both the midlittoral to the infralittoral, ctenostomatids won about 55% of the encounters that had a decided outcome, but the proportion of ties increased from 4% in the midlittoral to 58% in infralittoral. Cyclostomatids were better competitors against cheilostomatids, winning 87% of midlittoral encounters and 62% of infralittoral encounters.

As with ctenostomatid-cheilostomatid encounters, the proportion of tied outcomes increased from the midlittoral to the infralittoral, but less dramatically, from 31% to 35%.

The overall transitivity of the assemblage measured using the index of Tanaka and Nandakumar (1994) was 0.62. This was 25% lower than the value obtained for interactions just within the clade of cheilostomatids (0.83—Barnes and Dick, unpubl. data). This value indicates a generally hierarchical system (Buss, 1980; Russ, 1982) but, as predicted by Jackson (1979b), one that is more intransitive between clades than within the clade of cheilostomatids.

The competitors involved in interactions could be ranked in a sequence of overgrowth performance from several typically overgrown by others (cheilostomatids) to several typically overgrowing others (also cheilostomatids). Overgrowth performance can be and has been measured in a

Table 3

Ranking of competitive ability in Alaskan cheilostomatid, ctenostomatid, and cyclostomatid bryozoans (latter two clades are in bold), with names listed in descending order of initial number of wins

Taxon identity and coding		Standardized ranking					Aggregate
		Initial	Win-tie scored	W/T	L/T	W/L	
<i>Tegella armifera</i>	(Ta)	Ta	Tq	Tq	Tq	Ta	Tq
<i>Tegella aquilirostris</i>	(Tq)	Tq	Ta	Ta	Li	Tq	Ta
<i>Myriozeolla plana</i>	(Mp)	Mp	Mp	Mp	Ta	Mp	Mp
<i>Cauloramphus</i> sp.	(Ca)	Ca	Ca	Tr	Mp	Ca	Ca
Cyclostomatids	(Cy)	Cy	Cy	Cy	Ca	Li	Tr
<i>Microporella californica</i>	(Mc)	Mc	Tr	Ca	A	Tr	Li
<i>Tegella arctica</i>	(Tr)	Tr	Mc	Mc	Tr	Cy	Cy
Lichenopora spp.	(Li)	Li	Li	M	Mc	Mc	Mc
Cheilostomatids	(C)	C	M	C	Cy	A	A
<i>Microporella</i> sp.	(M)	M	C	Cn	Cn	M	M
<i>Cribrilina annulata</i>	(Cn)	Cn	A	Li	Pa	C	Cn
<i>Porella alba</i>	(P)	P	Cn	A	M	Cn	C
Aleyonidium spp.	(A)	A	P	Pa	C	Pa	Pa
<i>Cylindroporella tubulosa</i>	(Ct)	Ct	Ce	Ce	Ce	Ce	Ce
<i>Celleporella</i> spp.	(Ce)	Ce	Ct	Ct	Ct	Ct	Ct

Rankings are Initial (number of wins) and Standardized (multiplied up so every competitor meets each other on the same number of occasions). Standardized rankings are win-tie scored (wins score 3, ties score 1), W/T (proportion of wins over total number of interactions), L/T (proportion of losses over total number of interactions), W/L (proportion of wins over losses), and aggregate (of W/T, L/T, and W/L).

"Cheilostomatids" in the species-identity column refers to the remainder of the cheilostomatid species present but not listed.

number of ways (Table 3). A ranking based on the number of wins (actual overgrowth of the competitor) placed some cyclostomatids as intermediate competitors but others (*Lichenopora* sp.) and the ctenostomatids as poor competitors. In contrast, lichenoporidae cyclostomatids and, to a lesser extent, ctenostomatids were good competitors when assessed by the ratio of losses to total interactions (they were rarely overgrown). Cheilostomatids spanned the whole range of competitor performance, but those that scored highly in the win index also scored highly on the loss index (i.e., good overgrowers were rarely overgrown; poor overgrowers were usually overgrown). The average ranking change for a competitor between these different indices was 1.4 for cheilostomatids, but 6 for ctenostomatids and 6.5 for cyclostomatids. At the level of species, the performance of selected cheilostomatids against the combined representatives of each clade is illustrated in Table 4. All performed better against other cheilostomatids than against ctenostomatids or cyclostomatids, but most performed better against cyclostomatids than against ctenostomatids (e.g., *Microporella californica*), although a few (e.g., *Porella alba*) did the converse. A good competitor against one clade was generally a good competitor against the other, but some (e.g., *Microporella californica*) had quite different performances against competitors from different clades (Table 4).

The between-clade win index of the three clades varied (Table 5) between the Alaskan site and others we analyzed from County Cork (Ireland) and the Falkland Islands and South Georgia Island (both South Atlantic). Other literature

and unpublished data in Table 5 for which between-clade win scores have been calculated show the overgrowth scores of cyclostomatids in Alaska and County Cork to be the highest recorded.

Table 4

Performance of various Alaskan cheilostomatid species in overgrowth interactions with other cheilostomatids, ctenostomatids and cyclostomatids; values are the probability of a win for competitor A against competitor B

Competitor A identity	Competitor B		
	Cheilostomatids	Ctenostomatids	Cyclostomatids
<i>Tegella aquilirostris</i>	0.76	0.44	0.55
<i>Tegella armifera</i>	0.71	0.53	0.65
<i>Myriozeolla plana</i>	0.66	0.38	0.41
<i>Laganicella neosocialis</i>	0.60	—	0.29
<i>Cauloramphus</i> spp.	0.52	0.08	0.07
<i>Tegella arctica</i>	0.51	0.30	0.38
<i>Microporella californica</i>	0.46	0.00	0.33
<i>Cribrilina annulata</i>	0.34	0.09	0.13
<i>Microporella</i> spp.	0.32	0.22	0.25
<i>Porella alba</i>	0.29	0.16	0.11
<i>Celleporella</i> spp.	0.22	0.14	0.12
<i>Callipora craticula</i>	—	0.06	0.14

Table 5

Between-clade overgrowth competition performance scores and rankings in the three bryozoan clades (all other rankings are cheilostomatids)

Location	Latitude	Ctenostomatids vs. cheilostomatids		Cyclostomatids vs. cheilostomatids vs. ctenostomatids*		Cheilostomatids vs. cyclostomatids vs. ctenostomatids*
		Win index	Ranking	Win index	Ranking	Win index
Alaska (USA) ^a	57 N	0.24	7/12	0.42 (0.25*)	6/13	0.21 (0.18*)
Scotland	56 N	0.5	5/18	—	—	(0.32*)
Ireland ^{site 1}	51.5 N	—	—	0.41	6/8	0.56
Ireland ^{site 2†}	51.5 N	0.56	1/6	—	—	(0.37*)
England	50 N	0.75	1/5	—	—	(0.08*)
Croatia	43 N	—	—	0.08	—	0.78
Jamaica	18 N	—	—	Low	10/10	~0.9
Mozambique†	12 S	—	—	0.2	13/15	0.60
Australia	38 S	—	—	0.0	8/8	0.74
Argentina	47 S	—	—	0.33	9/12	0.62
Falkland Is	52 S	—	—	0.32	7/10	0.44
South Georgia†	54 S	0.4	1/7	0.18 (0.08*)	6/7	0.6 (0.32*)
Signy Is†	60.5 S	—	—	0.1	22/22	0.73

Data are taken from Stebbing (1973), Buss and Jackson (1979), Russ (1982), Lopez Gappa (1989), McKinney (1992), Turner and Todd (1994), Maughan and Barnes (in press), Barnes and Lehane (unpubl. data), present study (^a) and unpublished sources (†).

Discussion

Amongst the major groups of the phylum Bryozoa, cheilostomatids are generally the major space occupiers, the most speciose, and the superior overgrowth competitors (see, for example, Buss and Jackson, 1979). Sometimes they may even locally dominate the macrobenthic community—for example, on shells (Kay and Keough, 1981), on reef rubble (Jackson and Winston, 1982), on floating debris (Barnes and Sanderson, 2000), in mid-latitude shelf waters (James *et al.*, 1992), and on Antarctic shallow-water hard substratum (Barnes, 1995). When present, the rarer ctenostomatids may effectively compete against cheilostomatids (Stebbing, 1973), but cyclostomatids are typically overgrown in meetings (Buss and Jackson, 1979). Overgrowth of calcified benthos by soft-bodied forms such as ctenostomatid bryozoans or ascidians may not, however, always prove lethal to the overgrown competitor (Todd and Turner, 1988). In this study, the first to encompass all three “clades,” at the same localities, cheilostomatids were the major space occupiers, were involved in most interactions, and were the most speciose of the three clades, as found elsewhere (Table 1). They were, however, outcompeted by ctenostomatids at all three localities, and at Kodiak Island, Alaska, they were uniquely outcompeted by cyclostomatids (Table 5).

McKinney analyzed living and Recent relict (1992; 1995b) and fossil (1995a) cyclostomatid and cheilostomatid interactions and found that living and Recent relict assemblages in Rovinj, Croatia, were similar to those over the last

105 million years. The win index of fossil cheilostomatids oscillated around a value of 0.66 (66% win rate), and that of cyclostomatids at around 0.29. In the Alaskan assemblage studied here the win index of cyclostomatids was nearly 1.5 times greater and the win index of cheilostomatids 3 times lower. The win index of clades varied with site (Table 5) or possibly latitude (Fig. 2). In the living assemblages studied here (from Alaska, the Falkland Islands, and South Georgia Island) and other indices taken or calculated from the literature, the win indices of cyclostomatids varied from 0 to 0.42. The win indices of living cheilostomatids varied be-

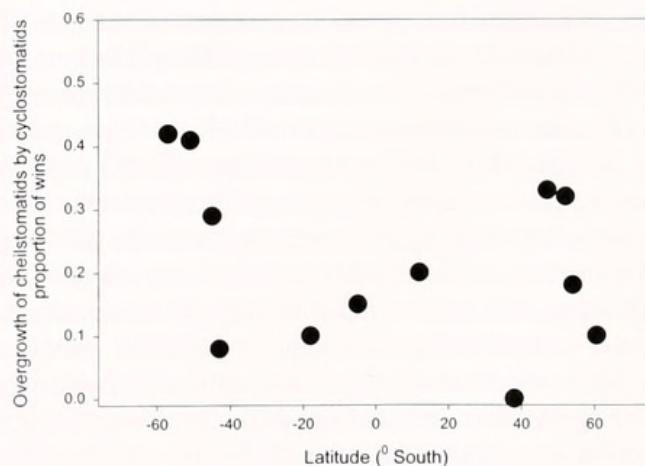


Figure 2. Magnitude of overgrowth (%) of cyclostomatids by cheilostomatids in Mesozoic and Cenozoic periods, adapted from McKinney (1995).

tween 0.08 and 0.9 and those of living ctenostomatids from 0.25 to 0.75 from the few studies carried out (Table 5). There is significantly more variation (Fig. 3) in the living assemblages that have been studied than in the fossil assemblages that have been studied in both the cyclostomatid clade (homogeneity of variance test, $F = 7.6$, $P < 0.01$) and the cheilostomatid clade ($F = 24.0$, $P < 0.01$). The sample size in both the living and fossil assemblages is reasonable (though not high in the former). McKinney (1995b) has shown that, through careful consideration of differential preservation of overgrower and overgrown, analysis of fossil assemblages probably gives an accurate representation of conditions at the time of preservation. Either there is more variation today than over the past 100 million years or we are getting some information from living assemblages that we are not getting from fossil assemblages. There is some evidence for both of these explanations.

The highest values of cyclostomatid win index and the lowest values of cheilostomatid win index are from high (50° – 60°) latitude localities (this study and Maughan and Barnes, unpubl. data). The high values for the cheilostomatid win index are generally from studies in mid to low latitudes (and typically from more sheltered sites) (e.g., Buss and Jackson, 1979; McKinney, 1992). Thus the high range of modern index values is probably partly due to the range of exposure of localities. Antarctic (high latitude)

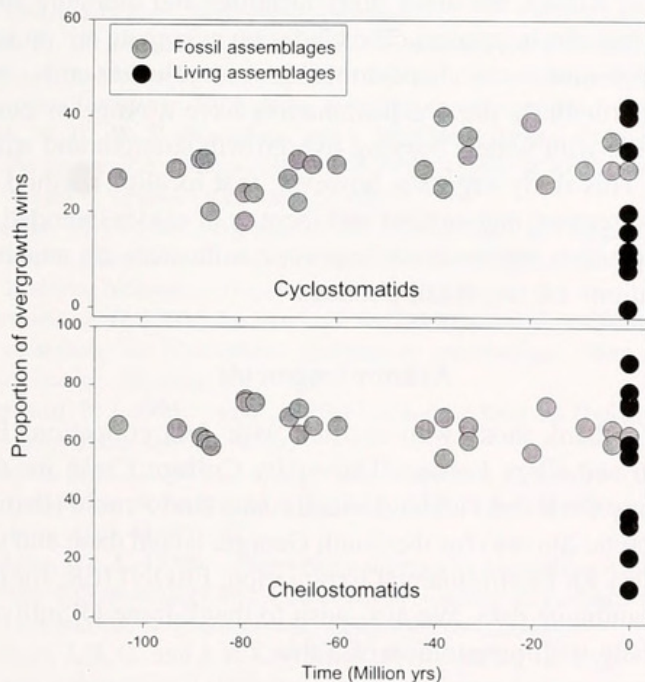


Figure 3. Non-cheilostomatid (ctenostomatid and cyclostomatid) species richness of rock-pile habitats with latitude. Data points are from Powell and Crowell (1967), Gordon (1980), Winston (1982), Cook (1985), Rao and Ganapati (1985), McKinney (1992), Barnes *et al.* (1996), Barnes and Arnold (1999), Maughan and Barnes (unpubl. data), present study, and unpublished sources.

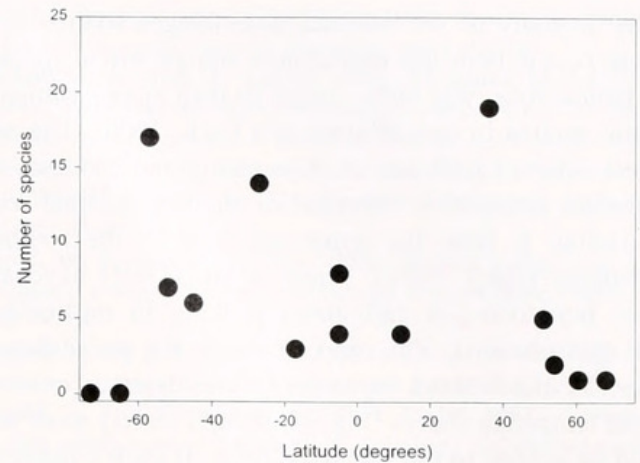


Figure 4. Cyclostomatid win index with latitude. Data points are from Buss and Jackson (1979), Russ (1982), Lopez Gappa (1989), McKinney (1992), Barnes and Rothery (1996), Maughan and Barnes (in press), present study, and unpublished sources.

values (from data from Barnes and Rothery, 1996; Barnes, unpubl. data), however, also showed high values for the cheilostomatid win index (Fig. 4). The geologically recent succession of glaciation periods, cooling of the poles, and separation of continents has probably resulted in higher levels of disturbance through wave action and ice-scour than before. So the range of nearshore conditions may be greater than in the past 100 million years. Depth is a potential confounding factor because most interaction data that has been recorded from fossil communities is from deeper water shelf environments (see Taylor and Allison, 1998), whereas most modern data sets of similar nature are from shallow water (see Buss and Jackson, 1979; Russ, 1982; Turner and Todd, 1994; Barnes and Rothery, 1996). However, studies of fossil assemblages such as those by McKinney (1992) are largely from mid latitudes, suggesting that conditions for fossilization of communities seem to be most prevalent in mid-latitude conditions (Taylor and Allison, 1998). The survival of encrusting communities (and, more specifically, bryozoan colonies) becomes progressively shorter with increasing latitude within the Southern Ocean, such that the longest survival time of any individual (even skeletal material) at 68° S is just 4 years (Barnes and Arnold, 1999). Additional support is provided by the high win-index values, similar to those in the fossil record, of cheilostomatids in mid to low latitudes and in sheltered localities (Buss and Jackson, 1979; McKinney, 1992). Thus it is possible, and even probable, that a broad range of index values have occurred throughout the last 100 million years but have not been preserved because the very conditions that yield extreme values prevent preservation (Lescinsky, 1993; McKinney, 1995b). This situation makes judgments about the evolutionary ecology and historical position of clades and the non-escalation of competition problematical (Liddell and Brett, 1982; McKinney (1992; 1995a, b).

The diversity of the Alaskan assemblages studied here, with respect to both species richness and variety of species-pair interactions, was high—more so than at any comparable site studied to date (Barnes and Dick, 2000). The next highest value of both non-cheilostomatid and cheilostomatid species richness in intertidal or shallow subtidal rock-pile habitat is from the temperate zone of the southern hemisphere (Russ, 1982). James *et al.* (1992) have also shown bryozoan-rich carbonates peaking in mid-latitude shelf environments. This finding raises the possibility of two peaks in nearshore bryozoan species diversity centered around temperate shores (Fig. 4), though clearly more data would be needed to test this hypothesis. If such a pattern is mediated through frequency of disturbance, one would expect the peak in the northern hemisphere to be at a higher latitude than that in the south because the continental effect of Antarctica increases the range of latitude influenced by ice scour in the southern hemisphere. Species richness typically increases towards the tropics (Thorson, 1957; Kendall and Aschan, 1993), but may peak around subequatorial levels (Silva, 1992). Bryozoans (along with polychaetes) are one of the few taxa that have a diversity center in Antarctic waters (Clarke, 1992; Hayward, 1995).

The definition of a win or tie in overgrowth competition has undergone some evolution (Jackson, 1979a). A tied outcome has been found to represent a variety of situations including a cessation of growth (*e.g.*, Stebbing, 1973), minor overgrowth (Russ, 1982), mere stalling of a future win for one of the two competitors (Sebens, 1986), mutual overgrowth (McKinney, 1992), fusion of colonies (intraspecific meetings), and redirection of growth (Barnes and Rothery, 1996). Tanaka and Nandakumar (1994) argued that a tied outcome was a result equal in importance to a win or a loss and should be included in index calculations. The method of win index tabulation, analysis, and interpretation has also changed dramatically, but for bryozoans has typically been based around cheilostomatids (Petraitis, 1979; Buss and Jackson, 1979; Rubin, 1982; Tanaka and Nandakumar, 1994). In this study, the various methods of ranking competitors in overgrowth competition indicate that the type of index of success used has little influence on the relative or absolute positions of cheilostomatids. In contrast, the apparent success of ctenostomatids and cyclostomatids varies hugely with how the index is calculated because they use a very different strategy in overgrowth competition; many interactions result in tied outcomes. The strategy is essentially defensive rather than offensive, involving not many wins but not many losses. Such a strategy may pay off better where encounters and superior competitors are rare, because either a win or a tie may result in persistence, but a loss can be lethal (though not necessarily to the genet). In very exposed environments, such as that in the present study and in Antarctic assemblages, encounters and good competitors are rare due to habitat ephemerality, so even poor

competitors may dominate assemblages (Barnes and Clarke, 1998). The non-lichenopodid cyclostomatids have a higher number of wins, but also a higher number of losses, than lichenopodids. Most cheilostomatids also have mostly determinate interactions, which may be a better strategy where habitats are more stable and competition is more intense. To tie with one competitor would not ensure persistence, as sooner or later an even better competitor will arrive. Although the assemblages studied here have not been followed through time, ties involving cyclostomatids cannot be considered likely to be delays on cheilostomatid wins (see Rubin, 1982; Sebens, 1986). This is partly because the majority of decided outcomes between these clades involved a win for the cyclostomatid competitor and partly because the majority of tied outcomes observed in other similarly exposed latitudes (*e.g.*, South Georgia Island [Barnes and Arnold, 1999]; Signy Island [Barnes and Rothery, 1996]) had remained as “standoffs” for a period of years. The disadvantages of cyclostomatids compared to cheilostomatids, in functional body plan and feeding or water flow dynamics (McKinney, 1992), may be reasons for achieving a defensive rather than aggressive strategy in overgrowth competition. There may, however, be other explanations, such as differential growth rates or budding patterns between environments; and other selective forces, such as the frequency of disturbance, may be more important.

Although the cyclostomatids are marginally superior to the cheilostomatids in overgrowth competition at Kodiak island, Alaska, the other study locations and literature suggest that this is atypical. The clades on aggregate are ranked ctenostomatids > cheilostomatids > cyclostomatids, but all, particularly the cheilostomatids, have a range of competitors with widely varying overgrowth strength and strategy. This study suggests, however, that locality, method of measurement, and number and identity of clades included in competition studies have important influences on and implications for the result obtained.

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