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Overgrowth competitions amongst encrusting cheilostomes

A A KARANDE and B S SWAMI
Biology Division, Naval Chemical and Metallurgical Laboratory, Tiger Gate, Bombay 400 023, India

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Abstract. The overgrowth interactions and spatial relationships amongst 7 interacting bryozoan species in the coastal waters of Bombay were studied. All interspecific encounters involved overgrowth, there being a total absence of ties. On the other hand, in intraspecific encounters, occurrence of ties was quite high. It was observed that a superior overgrowth of any species did not determine its relative abundance. None of the 7 species studied won in all its overgrowth interactions with the others. It was further observed that the success of cheilostome species to dominate over the others did not depend on their ability to grow over through any one particular encounter angle. Ranking of competitive overgrowth abilities amongst the 7 species studied did not form a simple hierarchial sequence but instead formed a competitive network.

Keywords. Epibenthic; bryozoa; competitive interactions; community structure.

1. Introduction

Any hard substratum immersed in sea water is readily colonised by a variety of solitary and colony forming marine organisms. The community patterns developed on these substrates depend on several factors such as predation, morphological features, availability and access to food, physical and chemical characteristics of the environment, composition of the biota and several other factors. The most important and limiting factor that influences the community development is the availability of space. When space for growth becomes a constraint, it is the competitive ability of the participating organisms for overgrowth that decides the community structure on hard substrates.

In recent years, a good amount of work on overgrowth competition involving an analysis of distribution and abundance of encrusting organisms (Jackson and Winston 1982) and on other related aspects such as inter-phyletic competition amongst marine benthos (Woodin and Jackson 1979), competition and cooperation interactions (Buss 1981), temporal pattern of disturbance and species diversity (Abugov 1982), life-histories and their influence on community development (Winston and Jackson 1984) and on predation and community development (Dayton 1971) have been published. Amongst these, Buss and Jackson (1979) have reported particularly on the community development of encrusting bryozoans, while the observations of Jackson (1979) refer to cryptic reef environment. Rubin (1982) who examined the interactions amongst shallow water bryozoans has also commented on the method of measurements.

The present work was carried out in the coastal waters of Bombay where the encrusting cheilostomes are perennially and abundantly present. It was felt that availability of such a material would give an opportunity to investigate the outcome of overgrowth interactions and spatial relationships amongst the 7 cheilostome species prevailing in this water. In the present study, a ranking of competitive overgrowth abilities of the 7 species was made. It was also found out if this ranking was a simple hierarchial sequence or a competitive network (Buss 1980). Overgrowth interactions amongst cheilostomes are found to be complex and one of the factors that influences these interactions is the encounter angle formed by the interacting species. In the present study this aspect is also examined in detail.

2. Materials and methods

The test coupons made of PERSPEX, admeasuring 15 × 16 cm were immersed along the jetty in Bombay harbour (18° 55′ N lat. and 72° 50′ E long). This environment is characterised by the presence of encrusting cheilostomes, 7 species of which are encountered here seasonally and some amongst them perennially. The site also supports the growth of a few species of ascidians, sponges, serpulids and balanids. However, these species fail to compete with cheilostomes which are recruited here in overwhelming quantity.

The test coupons, numbering over 300, withdrawn from the exposure frames after 45–50 days were air-dried and washed with fresh water to remove the detritus. The coupons were studied using a stereomicroscope for the outcome of the interspecific encounters. The encounter angle is defined as an angle between the directions of the growth of the overgrown colony and the overgrowing colony (Jackson 1979). Three encounters illustrated in figures 1 and 2 are defined as follows:

(i) *Frontal encounter*: This is an head-on encounter where the growths of two interacting colonies are in opposite directions and an encounter occurs in 121–180° (181–240°) section.
(ii) *Rear encounter*: When one colony overgrows another from behind, their growth directions are similar and the encounter occurs in 0–60° (0–300°) section.
(iii) *Flank encounter*: In this encounter, one colony overgrows along the flank of the other colony. Here the encounter occurs between 61–120° (241–300°) section.

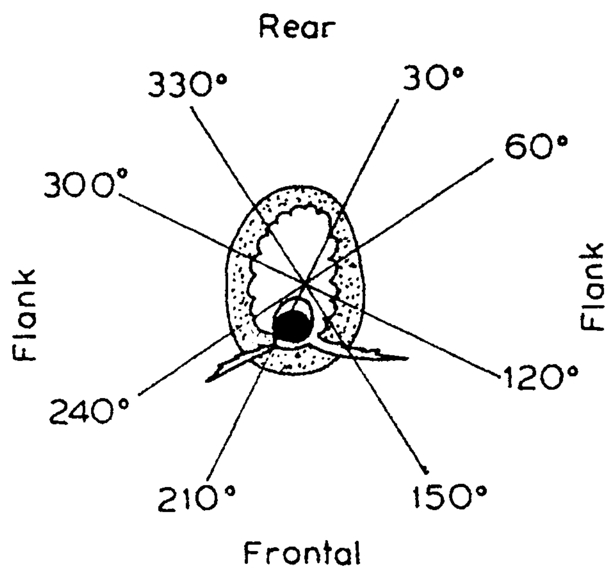

Figure 1. Categories frontal (121–180° and 181–240°), rear (0–60° and 0–300°) and flank (61–120° and 241–300°) encounters made according to the angle of encounter observed between interacting zooids in rows of colonies.

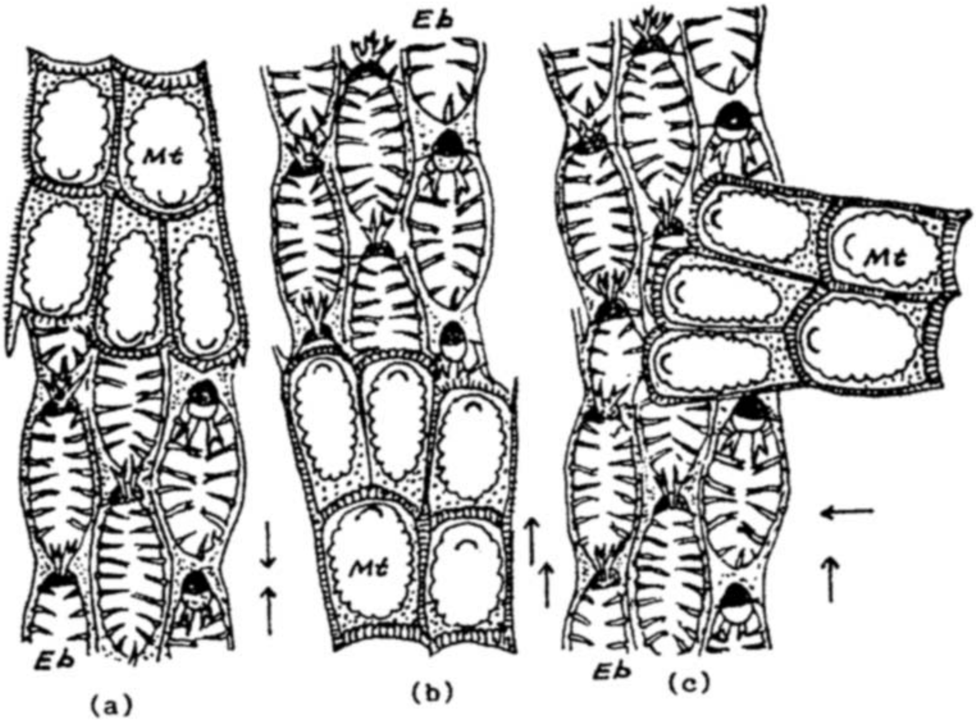

Figure 2. Categories of encounter angles between directions of growth of two cheilostomes *Membranipora tenuis* (Mt) and *Electra bengalensis* (Eb). Arrows point in direction of growth of each colony. Mt drawn as overgrowing Eb (**a**) frontally, (**b**) rearly and (**c**) along the flanks.

The frontal over-growth involves growing edge to growing edge encounters. The flank and rear overgrowths involve growing edge to non-growing edge encounters. Figure 3 illustrates the patterns of cheilostome encounters. The angle of encounter, that is the angle between growth directions of any two interacting colonies, was measured with the help of a microscope by rotating the ocular containing a cross-hair reticle and reading the degrees of rotation from an external scale marked at 10° intervals.

3. Results

3.1 *The biota*

The bryozoans cover between 50 and 70% of the area of coupons immersed at this site in Bombay harbour. Seven species to which the present data refer to are, *Electra bengalensis*, *Electra angulata*, *Membranipora tenuis*, *Membranipora annae*, *Hippoporina indica*, *Celleporaria pilaefera* and *Acanthodesia* sp.

Two species *E. bengalensis* and *Acanthodesia* sp. together cover 65·54% of the area covered by the bryozoans. The area covered by other species individually, does not exceed 6·58% of the coupon area.

3.2 *Overgrowth competition*

The number of encounters, both interspecific and intraspecific are recorded in table 1. All inter-specific encounters involve overgrowths, there being a total absence of

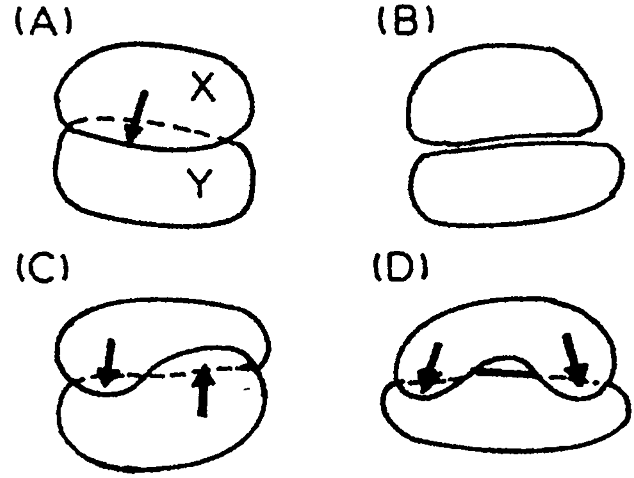

Figure 3. Patterns of cheilostome encounters. **A.** Single encounter, colony X growing over Y. **B.** Tie encounter. **C.** Colony X growing over Y and Y growing over X forming a single encounter line. **D.** Colony X growing over Y at two points showing two separate encounter lines.

Table 1. Summary of species percentage cover on test-coupons, the frequency of cheilostome-cheilostome encounters and outcome of cheilostome-cheilostome overgrowth interactions.

Species	Percentage cover (cm²)	Number of encounters: Inter-specific	Number of encounters: Intra-specific	Total	Outcome of interspecific overgrowth interactions: Wins	Losses	W/L ratio	Ranking according to W/L ratio
Electra bengalensis	25·9	84	50	134	35	49	0·71	6
Acanthodesia sp.	16·18	64	32	96	Nil	64	0	7
Membranipora annae	6·58	47	9	56	32	15	2·13	4
Electra angulata	4·55	44	3	47	34	10	3·4	2
Membranipora tenuis	4·11	37	10	47	25	12	2·08	5
Hippoporina indica	3·6	34	10	45	25	9	2·8	3
Celleporaria pilaefera	3·28	14	24	38	11	3	3·7	1
	64·2%	324*	138	462	162	162		

*Total encounters

ties. On the other hand, in intraspecific encounters, occurrence of ties is quite high. During this study no fusion of the colonies, both inter and intraspecific was recorded. A total of 300 cheilostome-cheilostome encounters were recorded. Of these 162 were interspecific and 138 intraspecific. This gives over 4·5 cheilostome-cheilostome encounters per 100 sq cm of the submerged surface.

Table 1 also gives the percentage area covered by individual species of these sheetlike cheilostomes and the number of interactions encountered. It is very clear from this table that more the area covered by a given species, more are the interactions, both interspecific and intraspecific. The Kendall rank order correlation of the per cent cover of each cheilostome species and the number of encounters each species involved in is $\tau = +1$ ($P < 0{\cdot}0002$). This is expected of the encrusting species which grow flat and closer to the substratum.

Table 2. Pairwise (162) overgrowth interactions amongst 7 cheilostome species involved in more than 10 encounters .

	Species B						
Species A	*C. pilae-fera*	*E. angu-lata*	*H. indica*	*M. annae*	*M. tenuis*	*E. benga-lensis*	*Acantho-desia* sp.
Celleporaria pilaefera		—	100 (1)	—	—	77 (13)	
Electra angulata	—		100 (1)	17 (6)	(0)	72 (14)	100 (22)
Hippoporina indica	(0)	(0)		78 (9)	34 (6)	88 (8)	100 (9)
Membranipora annae	—	83 (6)	22 (9)		50 (6)	78 (18)	100 (8)
Membranipora tenuis	—	100 (1)	66 (6)	50 (6)		53 (15)	100 (9)
Electra bengalensis	23 (13)	28 (14)	12 (8)	22 (18)	47 (15)		100 (16)
Acanthodesia sp.	0	0	0	0	0	0	

*Data are percentage overgrowth interactions in which A overgrows B (number of interactions in parentheses).

The contact matrix of 162 pairwise overgrowth interactions in which species A grows over species B are given in table 2. The number of interactions between the species pairs ranged from 0–22. These are indicated in the parentheses in the table.

Figure 4 illustrates 7 cheilostome species ranked in decreasing order of their wins/losses (W/L) ratios. This W/L ratio for any given species is defined as the number of interactions in which species A overgrows all other cheilostome species divided by number of interactions in which the other cheilostomes overgrew species A (Jackson 1979). Overall differences in the number of wins and losses for these species are highly significant (2×2 contingency table; $P < 0{\cdot}0001$).

The 7 cheilostome species studied here can be divided into 3 categories on the basis of their overgrowth abilities. These are super, moderate and inferior overgrowth dominants. Three species *C. pilaefera*, *E. angulata* and *H. indica* are clearly super overgrowth dominants. Two species, *M. annae* and *M. tenuis* are moderate dominants and in the third category of inferior dominants are *E. bengalensis* and *Acanthodesia* sp. (see figure 4).

None of the 3 super growth dominants however, covers much space (3·3–4·6% of the available area) though their W/L ratios are between 2·8 and 3·7 (table 1). Moderate dominants like *M. annae* and *M. tenuis* also do not cover much space but have W/L ratios greater than 1. Two species viz *E. bengalensis* and *Acanthodesia* sp. which fall in the third category of inferior dominants, though they occupy the maximum space (together about 42%) have W/L ratios below 1. It is evident therefore that the abilities of the species to overgrow the others need not necessarily help them to occupy larger surface. On the other hand species like *E. bengalensis* and *Acanthodesia* sp., despite their handicap in overgrowing the others, succeed in occupying maximum space on the substrate.

The above observations suggest that overgrowth ability in the cheilostome-cheilostome encounters has not been an important determinant of the relative abundance of a particular cheilostome species, unlike noted by Jackson (1979) for the species assemblage he had studied in Jamaican waters. A larger the surface covered by a given species, more is the probability of its interactions with the others but not necessarily an increase in its W/L ratio.

Figure 4 will further show that none of the 7 cheilostome species wins in all its overgrowth interactions with the others. *Acanthodesia* sp. amongst these never

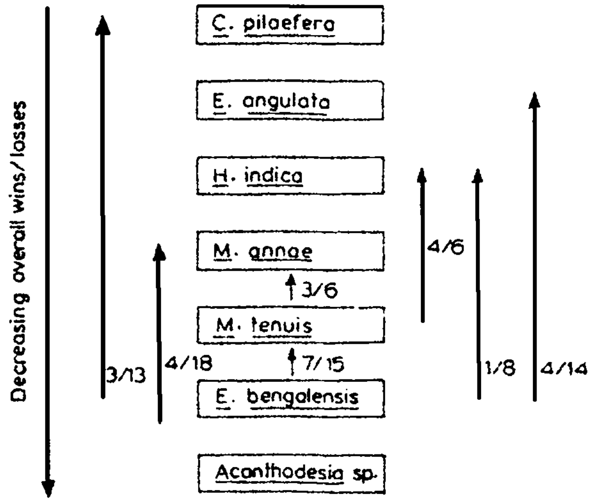

Figure 4. Ranking of 7 cheilostomes based on their W/L ratios. Upward pointing arrows indicate reversal, i.e. *E. bengalensis* out of total 13 encounters has overgrown 3 times on *C. pilaefera*.

scored a single win and was always overgrown by other species. Of the 80 pairwise overgrowth interactions between these 7 species, there were 26 reversals, i.e. cases in which the lower ranked species were observed to have grown over the species ranked above them.

It is seen from figure 4 again, that the higher ranked *C. pilaefera* is overgrown by one of the two lower ranked species, viz *E. bengalensis* during 3 of their 13 encounters. The other super-ranked species *E. angulata* is also overgrown by *E. bengalensis*. *H. indica* which is placed third in overall ranking is overgrown by two lower ranked species. *M. annae* which is ranked as moderately dominant species, is overgrown by *M. tenuis*, a species of its equal ranking and also by *E. bengalensis* that belongs to a category of inferior overgrowth dominants.

3.3 *Encounter angle and dominance*

Jackson (1979) has noted that the variations in outcome of overgrowth interactions are frequently related to (i) orientation or growth directions and associated encounter angles between colonies and their overgrowth competitions and (ii) to the conditions of the cheilostome colony surface in the region of overgrowth. In the present study, the influence of orientation factor between two competitors in their overgrowth interactions was alone examined.

The frequency of overgrowths of earlier defined 3 encounter angles for the 7 cheilostome species, (each involving in more than 10 encounters) is given in table 3. The overgrowth interaction measurements were made along the continuous encounter line between two interacting colonies. Therefore a single overgrowth may involve frontal and flank overgrowth and/or rear and flank overgrowth. Because of this, interactions recorded between two colonies, the number of rear, flank and frontal overgrowths may be more than the total number of interactions recorded.

Table 3. Outcome of interspecific overgrowth interactions at different encounter angles for 7 cheilostome species*.

Species		Percentage overgrowth interactions at each angle			Total overgrowth inter-actions
		Rear	Flank	Frontal	
Celleporaria pilaefera	Won	18 (2)	9 (1)	100 (11)	11
	Lost	0 (0)	0 (0)	100 (3)	3
	W/L	2·0	—	2·2	3·66
Electra angulata	Won	65 (22)	56 (19)	26 (9)	34
	Lost	70 (7)	50 (5)	50 (5)	10
	W/L	3·0	3·8	1·8	3·4
Hippoporina indica	Won	40 (10)	52 (13)	36 (9)	25
	Lost	33 (3)	67 (6)	33 (3)	9
	W/L	3·3	2·2	3·0	2·8
Membranipora annae	Won	47 (15)	84 (27)	37 (12)	32
	Lost	33 (5)	80 (12)	40 (6)	15
	W/L	3·0	2·3	2·0	2·13
Membranipora tenuis	Won	56 (14)	52 (13)	44 (11)	25
	Lost	91 (11)	33 (4)	42 (5)	12
	W/L	1·3	3·3	2·2	2·11
Electra bengalensis	Won	91 (32)	23 (8)	51 (18)	35
	Lost	57 (28)	57 (28)	57 (28)	49
	W/L	1·14	0·28	0·64	0·71
Acanthodesia sp.	Won	—	—	—	—
	Lost	61 (39)	40 (26)	30 (19)	64
	W/L	—	—	—	—

*Values for each angle given as percentages of total overgrowth interactions (number of interactions in parentheses). A sum of the components adds to more than 100% because any overgrowth interaction often involves more than one encounter angle.

Table 3 illustrates the percentage of encounters for each of the 7 species at the 3 encounter angles. Of the 162 interspecific, pairwise over growth interactions recorded, 44% involved frontal overgrowths, 50% flank overgrowths and 59% rear overgrowths.

Table 3 gives the outcome of interspecific overgrowth interactions at different encounter angles for the 7 species. Values given for each angle, that is rear, flank and frontal are percentage of total overgrowth interactions recorded along the 3 angles are more than the number of overgrowth interactions. For instance, for the bryozoan *E. angulata*, total interactions are 34, while total overgrowth interactions at different encounter angles are 50.

It is evident from the observations recorded in table 3 that the success of two super-dominant species viz *C. pilaefera* and *E. angulata* can not be attributed to any one particular encounter angle. In the former, W/L ratio for overgrowth interaction is higher because of frontal interactions, whereas in the latter, it is mainly due to the rear and the flank interactions. In *H. indica*, where the W/L ratio for total overgrowth interaction is 2·8, the species seems to overgrow onto others along all the 3 angles.

It is likely therefore that the success of cheilostome species to dominate over the other does not depend on its ability to grow over from any one particular encounter angle. In other words, progressing from any one particular angle does not decide the organism's dominance. The failure of *E. bengalensis*, the prolific space occupier, in overgrowing the others, is therefore not due to its inability to overgrow through a particular encounter angle but is due to its general lack of overgrowing ability.

4. Discussion

The observations on the interactions amongst the 7 encrusting cheilostome species abundantly present in harbour waters were made. The competition for the space among these cheilostomes was very severe and one cheilostome-cheilostome encounter, either inter or intraspecific, was recorded per 22 sq cm of area. For this assemblage of 7 cheilostomes, it was observed that more the area covered by a given species, more were the interactions it encountered.

The species can be divided into 3 categories like super, moderate and inferior dominants on the basis of overgrowth abilities as decided by their win over loss ratios. The ability to dominate by any species, however, is not related to its ability to cover the space. The species *E. bengalensis* and *Acanthodesia* sp. despite their low W/L ratios occupied the maximum space. The overgrowth ability therefore did not decide the abundance of the species as noted by Jackson (1979) in the assemblage he studied. The continuous recruitment and abundance of *E. bengalensis* lead to its covering the maximum space.

The 7 species can be ranked on the basis of their competitive overgrowth abilities and it was noted that these did not form a simple hierarchial sequence but instead formed a competitive network. None of the 7 cheilostome species won in all its overgrowth interactions with the others. The higher ranked species like *C. pilaefera* was overgrown by a lower ranked species *E. bengalensis*. Outcome of the overgrowth interactions between colonies of the same two species was not the same nor was the outcome between two species of the same genus. These observations therefore, support the view of Osman (1977) that 'it is extremely unlikely that the outcome of any two species interaction involving sessile colonial animals will always be the same'. As stated by Jackson (1979) 'no species is likely to win all of its competitive interactions and rankings of species, competitive abilities will rarely, if ever, form a simple hierarchial sequences'.

Jackson (1979) has noted that interactions between encrusting cheilostomes are complex and that variations in outcome are significantly correlated with the encounter angle formed by the intersection of the growth direction/vectors of interacting colonies. The present study involving an assemblage of 7 species shows that the success of any cheilostome species to dominate over the others does not depend on its ability to grow over from any one particular encounter angle.

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