

Consequences of crowding on life-histories of cheilostome bryozoans in Bombay waters

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In Bombay harbour waters cheilostome bryozoans *Electra bengalensis*, *Acanthodesia* sp., *Hippoporina indica*, *Membranipora annae* and *M. tenuis* occurred in that order of abundance. Field observations with the help of exposure coupons were carried out to examine the life-history of the species competing with one another for a limited space. Each species as an isolated colony achieved sexual maturity at specific size but in *M. annae* and *M. tenuis*, sexual reproduction was triggered by conspecific crowding. The incidence of breeding in all 5 species was more amongst interacting colonies as compared to isolated colonies of identical ages. Under the stress of crowding, the species showed between 25 to 50% suppression of zooid growth in interacting vector as compared to non-interacting vector of the colony. Different life-history characters may help different species in competing with one another. However, ability to breed continuously as noted in *E. bengalensis* seems to be a major factor that determines the success.

Community patterns developed on immersed substrates depend on factors such as animal morphology, environment, biota, availability and access to food, predation and several other conditions. The most important and limiting factor, however, is the availability of space. The constraint of space leads to interactions and the consequent overgrowths amongst encrusting bryozoans.

Overgrowth and competition involving analysis of distribution and abundance of encrusting bryozoans¹, interphyletic competition², competition and cooperation interactions³, disturbance and species diversity⁴, life histories and community developments⁵, predation and community development⁶, and over-growth competition have been reported. There are very few observations⁷ on the life histories of bryozoans with particular relevance to growth and death of zooids under the influence of crowding⁸. Present study has been undertaken to augment information on effect of interactions on growth, mortality and breeding in some endemic species of bryozoan.

Materials and Methods

The study was carried out at near-shore station in Bombay harbour (lat. 18°55' N; long. 72°50' E). Perspex coupons (25 × 15, 12 × 10 and 15 × 4 cm dimensions) were exposed 1 m below the low tide level. Over 300 coupons bolted to exposure frames were immersed and withdrawn at the end of 30 and 60 d to obtain both isolated and interacting colonies

of *Electra bengalensis*, *Acanthodesia* sp., *Membranipora annae*, *Membranipora tenuis* and *Hippoporina indica*.

For the examination of the coupons under microscope, a transparent perspex grid engraved accurately with 1 cm quadrates was superimposed on each coupon to record growth of colonies and zooids. The number of dead or live zooids, their dimensions, presence or absence of eggs and their number were recorded with the help of microscope under low power magnification. The number of zooids were counted along a single row in a vector of a colony from the point of larval settlement to the periphery of the colony.

The effect of interactions on the colony growth was ascertained by recording the state of zooids in growth vectors along which interaction had taken place. This was compared with the state of zooids in vectors along which colony continued to grow in the absence of any interaction with the other colony. Having known the dimensions of the zooids of each species⁹, the number of zooids covering dead and live areas of the entire colony were determined. Growth or dimension is referred here as the diameter of the colony.

Results

Influence of crowding on breeding—The observations were made to ascertain if onset of first breeding in 5 bryozoans encountered in Bombay waters was size or age dependent. The colonies were di-

vided into 5 arbitrary size classes and reproductive conditions of zooids of several colonies of each species were determined.

It was observed (Table 1) that among 5 species, *Acanthodesia* sp. as an isolated colony achieved sexual maturity at the smallest colony diameter of 3 mm. No colony of *E. bengalensis* was reproductive until it attained 6 mm size. *H. indica*, *M. annae* and *M. tenuis* became sexually mature when they achieved colony sizes of 15, 18 and 20 mm, respectively. *E. bengalensis* and *Acanthodesia* sp. had about 180 and 95 zooids respectively at their first maturity, whereas the other 3 species did not breed until they grew to colony sizes of over 1000 zooids (Table 1).

It was observed that crowding or contact triggered the onset of breeding earlier in *M. annae* and *M. tenuis* (Table 1). Crowding does not prepone maturity in *H. indica*, *E. bengalensis* and *Acanthodesia* sp. achieve maturity at quite early colony sizes and therefore the influence of crowding on them, if any, was undetectable. It was also observed (Table 1) that the incidence of breeding was higher among interacting colonies as compared to isolated colonies of all size classes of the 5 species examined.

Influence of interactions on the onset of breeding of *E. bengalensis*, was examined in detail. To obtain more data, coupons of all the three dimensions immersed for both 30 and 60 d were considered. In colonies measuring below 5 mm (Table 2) no mature

Table 1—Percentage of sexually matured colonies in various size classes of isolated (A) and interacting (B) cheilostome bryozoans

Colony size (dia in mm) and type	<i>Electra bengalensis</i>		<i>Acanthodesia</i> sp.		<i>Hippoporina indica</i>		<i>Membranipora annae</i>		<i>Membranipora tenuis</i>	
	%	n	%	n	%	n	%	n	%	n
1-5										
A	0	616	3.2	61	0.0	232	0	84	0	7
B	0	79	6.8	88	0.0	90	0	12	42.8	3
6-10										
A	5.9	235	7.6	13	0.0	45	0	32	0	7
B	8.9	347	25.8	93	0.0	98	28.5	7	58.3	7
11-20										
A	15.7	133	25.0	4	40.0	5	20.0	5	50.0	5
B	56.5	207	68.1	69	33.6	101	40.0	15	64.2	12
21-50										
A	58.8	34	100.0	5	*	*	40.0	5	57.0	7
B	75.5	258	83.3	6	100.0	3	53.8	13	64.2	28
Above 50										
A	*	*	*	*	*	*	*	*	*	*
B	100	27	*	*	*	*	100.0	8	100.0	4
	(6 & 180)		(3 & 95)		(15 & 1425)		(18 & 2700)		(20 & 2400)	

Figures in each parenthesis denote size and number of zooids at first maturity respectively

* = no colonies encountered; n = number of colonies examined

Table 2—Percentage of sexually matured colonies in various size classes of isolated (A) and interacting (B) *Electra bengalensis*

Period of exposure (d)	Colony size class (dia in mm)									
	1 - 5		6 - 10		11 - 20		21 - 50		Above 50	
	A	B	A	B	A	B	A	B	A	B
25 × 15 cm coupon										
30	0	0	13.4	68.4	40.8	87.8	83.3	86.0	*	100.0
60	0	0	5.5	4.3	17.6	39.3	75.0	78.3	100.0	100.0
12 × 10 cm coupon										
30	0	0	50.0	68.7	84.2	73.6	66.6	100.0	*	100.0
60	0	0	0	21.9	14.2	58.3	66.6	56.0	100.0	100.0
15 × 4 cm coupon										
30	0	0	20.0	42.8	100.0	100.0	100.0	80.0	*	*
60	0	0	11.7	35.2	75.0	73.6	100.0	100.0	*	100.0

A = isolated, B = interacted, * = no colonies encountered

zooids were found and that only the interacting colonies showed higher incidence of breeding. In all size classes of *E. bengalensis*, death of zooids was significantly higher than that recorded in isolated colonies (Table 3). The life history characters of this species as compared with those of the other species (Table 4) showed that, this species as a colony has a shorter life span but has ability to grow faster and breed perennially.

Table 5 summarises the data on the growth inhibition in 50 d old colonies of the 5 bryozoans encountering interspecific or intraspecific interactions^{7,9}. Three species among these *H. indica*, *M. annae* and *Acanthodesia* sp. as consequence of interactions showed between 25 — 35% reduction in zooid formation and therefore reduced breeding capacity. In *E. bengalensis*, zooid suppression was as high as 50% as also the highest percentage of dead zooids.

Discussion

Success of a sedentary organism in establishing itself at a given marine habitat depends on its ability to grow faster, mature earlier and breed as often and as longer as it can. A number of eggs produced in clutches and number of times they are produced would decide the number of generations produced in a single season and thus would determine the stability of a species in a given environment. The size of the zooids and consequently their number per unit area of the colony will also contribute to its success. Larger the number of zooids more would be the reproducing units in a colony. Death of older zooids and emergence of new zooids is a continuous process in encrusting bryozoans. A ratio between living zooids and the dead ones in a colony would decide the life-span of a species in a given environment.

The aforesaid factors would regulate life history of a sedentary colony while it exists as an isolated

Table 3—Influence of crowding on mortality of zooids of *Electra bengalensis* of various size classes

Colony size (dia in mm) and type	Dead zooids in a single contact vector (%)	SD	't' value	'P' value	Significance of crowding
5 - 10					
A	77.12	30.22	4.366	$P < 0.0005$	HS
B	29.13	17.18			
11 - 20					
A	84.28	22.01	5.479	$P < 0.00005$	HS
B	39.89	13.11			
21 - 30					
A	70.44	33.15	4.484	$P < 0.0001$	HS
B	33.86	12.87			
31 - 40					
A	61.28	29.13	1.935	$P < 0.10$	NS
B	36.4	16.25			
Above 41					
A	72.86	36.26	3.568	$P < 0.005$	HS
B	28.86	14.66			

A = interacting, B = isolated, HS = highly significant, NS = not significant

Table 4—Life history characteristics of isolated cheilostome bryozoans with reference to growth, life-span and breeding in Bombay harbour

Species	Isolated colonies					
	Growth (cm) in 60 days	Zooids (no. mm ⁻²)	Size at maturity (dia in mm)	Breeding frequency (1987)	Eggs (no. zooid ⁻¹)	No. live zooids No. dead zooids
<i>Electra bengalensis</i>	50	6.35 ± 0.3	6	12 month	7-23	2.9
<i>Acanthodesia</i> sp.	3	13.37 ± 0.4	3	3 month	8-12	11.9
<i>Hippoporina indica</i>	3	8.02 ± 0.2	15	5 month	Ovicells	20.2
<i>Membranipora annae</i>	38	10.58 ± 0.9	18	6 month	6-7	4.5
<i>Membranipora tenuis</i>	16	7.64 ± 1.1	20	*	7-12	6.4

* = Infrequent

entity, free from a severe crowding and therefore competition. Under a stressed environment created by crowding, some more factors other than these would be relevant (Table 5). Here ability of the sedentary organism to grow over its interacting competitor is very important. Further, endurance of the zooids located in interacting vectors and their ability to survive and reproduce for longer period would be an advantage. This is particularly true of 'tie' encounters where on contact, confronting colonies cease to grow and neither of the two colonies spread over the other¹⁰.

It is observed that *E. bengalensis* and *Acanthodesia* sp. in that order are the dominant species in Bombay harbour. Their success, however, cannot be attributed to any one factor like breeding, rate of growth, number of zooids or overgrowing ability. *E. bengalensis* is a fast growing species and therefore has a larger number of reproducing units. This species also produces generally larger number of eggs almost throughout the year⁹. *Acanthodesia* sp. on the other hand, may attain maturity at an early age like *E. bengalensis* but does not breed continuously. It has a larger number of zooids per unit area but since the species grows slowly, the number of reproducing zooids in a colony is smaller than in *E. bengalensis* of identical age. *Acanthodesia* sp. however scores over *E. bengalensis* in one respect in that its zooids both in isolated and crowded colonies show longer life-span, and this happens despite its poor overgrowth ability (Tables 4,5).

H. indica does not settle down in as much abundance as *E. bengalensis* or *Acanthodesia* sp. but its presence is noticeable. The growth of this species is slow, maturity is delayed and the breeding is infrequent. It, however, shows advantage over the other 7 endemic species⁹ in having superior overgrowing ability⁷ and also in having zooids with longer life spans. In this species a ratio between living zooids and dead zooids at any given point of time is higher than the rest of the species.

Of the 2 *Membranipora* species, *M. annae*, for instance, grows faster, if not as rapidly as *E. bengalensis*. At any given point of time, a good number of colonies show matured zooids, each having a sizeable number of eggs. The number of zooids per unit area is also high. This species is second only to *H. indica* in its ability to grow over the other interacting colonies. Despite all these advantages, the incidence of *M. annae* at the study station is less as compared to *E. bengalensis*, *Acanthodesia* sp. or *H. indica*. This can be attributed to its zooids achieving late sexual

Table 5—Life history characteristics of interacting cheilostome bryozoans (Figures denoting zooid death and zooid suppression are for a single contact vector)

Species	Interacting colonies		
	Over-growth ability*	Zooid death (%)	Zooid suppression (%)
<i>Electra bengalensis</i>	4	73.1	50.7
<i>Acanthodesia</i> sp.	5	33.9	25.9
<i>Hippoporina indica</i>	1	Nil	35.4
<i>Membranipora annae</i>	2	40.5	30.6
<i>Membranipora tenuis</i>	3	39.1	19.5

* = 1 denotes best overgrowing ability

maturity. The zooids, as it is, also have shorter life span as judged by living/dead ratio which is 4.5. The species, however, attains an early maturity under the stress of crowding. To what extent this faculty helps it to compete with the other species is not known. Harvell and Greene⁸ who identified a similar triggering of maturity in *M. membranacea* observe that indeterminacy in the timing of reproduction allows rapid occupation of substrate when available or early onset of reproduction in the absence of available substrata.

Present study suggests that it is difficult to attribute the success of a species to any one of the 8 or 9 life history characteristics presently examined. Different factors, singly or in combination, perhaps help each species in competing with the others. It is, however, very likely that the ability to breed continuously, as noted in *E. bengalensis*, is a single major factor that determines the success of organism in a given biotic community.

References

- 1 Jackson J B C & Winston J E, *J Exp Mar Biol Ecol*, 57 (1982) 135.
- 2 Woodin S A & Jackson J B C, *Am Zool*, 19 (1979) 1029.
- 3 Buss L W, *Science Wash*, 213 (1981) 1012.
- 4 Abugov R, *Ecology*, 63 (1982) 289.
- 5 Winston J E & Jackson J B C, *J Exp Mar Biol Ecol*, 76 (1984) 1.
- 6 Dayton P K, *Ecol Monogr*, 41 (1971) 351.
- 7 Karande A A & Swami B S, *Proc Indian Acad Sci (Anim Sci)*, 97 (1988) 141.
- 8 Harvell C D & Greene C, *Proc Sixth Internat Cong Mar Corr Foul*, (Comite International Permanent Pour la Recherche Sur la Preservation Des Matériaux En Milieu Marin, Athens, Greece), 1984, 261.
- 9 Udhayakumar M & Karande A A, *Indian J Mar Sci*, 18 (1989) 95.
- 10 Jackson J B C, *J Anim Ecol*, 48 (1979) 805.