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Recruitment of the barnacle *Balanus amphitrite* in a tropical estuary: implications of environmental perturbation, reproduction and larval ecology

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Phytoplankton blooms are known to influence barnacle recruitment and in boreal regions spring blooms work as an important trigger. Close to the west coast of the sub-continent of India, blooms tend to be triggered by breaks in the monsoon and the recurrence of the monsoon after a short break can stress the new recruits. The recruitment of *Balanus amphitrite*, an acorn barnacle, at Dona Paula Bay at the mouth of Zuari estuary, Goa, India was studied. Observations included variations in recruitment, larval abundance, development and reproduction. Adult conditioning and inter-brood variations were important factors in the larval ecology of this organism. The results indicate that the impulsive release of larvae during breaks between monsoons could be a short-sighted luxury for *Balanus amphitrite* in these waters. Temporal variations or recruitment failure in such environments can be attributed to inappropriate cue synchronization.

INTRODUCTION

Barnacles are one of the important components of the intertidal community and also of the marine macrofouling community. *Balanus amphitrite* Darwin, an acorn barnacle, is a dominant fouling organism. The larval phase includes planktotrophic naupliar stages, followed by a pre-settling, non-feeding cypris larva. The key factor that influences the final destination of the larva during dispersal is the duration of its planktonic phase. Pechenik et al. (1998) also reported that the larval experience influences juvenile performance.

Laboratory experiments have reported the settlement of *B. amphitrite* cyprids to vary with respect to bacterial films, conspecific settlement factors, surface wetability, pharmacological agents etc. (Rittschof et al., 1984; Maki et al., 1988, 1990; Rittschof & Costlow, 1989; Holm, 1990a; Clare et al., 1995; Khandeparker et al., 2002). Holm et al. (2000) reported that the attachment of cyprids vary among families and indicated that physiological processes regulate metamorphosis. Thus recruitment of barnacles is governed by events during planktonic larval development and substratum cues. Recruitment is reported to vary with flow velocity, cues offered by the substratum, light conditions, contour, space and time (Bourget, 1988; Chabot & Bourget, 1988; Thiyagarajan et al., 1997). Local larval abundance, which is considered as an important cause of variation in recruitment can be influenced by variation in levels of reproduction in adult populations (Wellington & Victor, 1988). Recruitment is also influenced by the variations in physical factors such as water temperature, salinity, current patterns that may disperse the planktotrophic larvae, and biological factors such as phytoplankton abundance, which is a source of food for the larvae.

Considerable research has been carried out on the biological aspects of marine foulers from European and Pacific waters. In India, research on *B. amphitrite* has been carried out with respect to its importance in the fouling community (Daniel, 1954; Iyengar et al., 1957; Karande, 1965; Nair, 1965; Menon et al., 1977; Anil, 1986; Fernando, 1990). However, there is a lack of recruitment related studies in the natural environment in this tropical habitat and a study was undertaken at the Dona Paula Bay situated at the mouth of the Zuari estuary, west coast of India. The objectives of the study were to evaluate: (1) temporal and spatial (tidal level) variations in the recruitment of *B. amphitrite*; (2) effects of environmental perturbations on the recruitment of *B. amphitrite*; and (3) the linkages between reproduction, cirriped larval abundance, larval survival and metamorphosis in the recruitment process.

MATERIALS AND METHODS

Study location

The intertidal area of Dona Paula Bay (15°27.5′N 73°48′E) situated at the mouth of the Zuari estuary along the central west coast of India was selected as the study site. The local tidal amplitude ranges from 0.25 m during neap tides to 2.5 m during spring tides. Perennial connections of this estuary with the Arabian Sea result in a rhythmic exchange of marine and estuarine plankton populations (Devassy & Goes, 1989). The study site is influenced by the monsoons from the south-west. Based on the influence of monsoons, a year can broadly be classified into pre-monsoon (February to May), monsoon (June to September) and post-monsoon (October to January) seasons. The surface-water temperature during the study period ranged from 22°C to 31°C, and the salinity ranged from 4 to 36 psu. The rainfall data during the study period were obtained from the Indian meteorological department.

Recruitment

The recruitment of the barnacle *Balanus amphitrite* was studied at two tidal levels, mid-tide (1 m above the lowest low water (LLWM) of spring tides) and high-tide (2 m above LLWM) from June 1998 to September 1999. Concrete boulders used to protect the jetty in the bay were used as substratum. Three quadrats of 25 cm^2 were marked each month on concrete blocks at both the tidal levels, after which the surfaces were mechanically cleaned for the existing fauna using a scraper and then by a nylon brush so that no cyprids were present on the cleaned surface and left undisturbed till the end of the study. The marked quadrats were assayed for recruitment at the beginning of each month. Every month new quadrats were cleared and observations on recruitment, size and mortality were made on both new and old quadrats every subsequent month. We counted live and dead (shell remains) barnacles as well as spat (0–2 mm) using a magnifying lens. In total, 90 quadrats were marked (45 at each level). Observations on recruitment were not made in June 1999 due to bad weather conditions.

We refer to absolute recruitment as the new recruitment that occurred each month. Cumulative abundance was the total number of barnacles observed following the cleaning of fauna from a quadrat.

The sizes (rostrocarinal and basal diameter (RCB)) of the live and dead barnacles were taken using a Vernier caliper. The percentage area covered by the barnacles was calculated by using the individual's basal diameter assuming it to be circular. For observations on growth, solitary (5 nos) and crowded (5 nos) barnacles were marked at mid-tide level on the November 1998 quadrat exposed for one month and monitored for growth every succeeding month. At the end of 6–7 months all the marked barnacles were dead. These mortalities can be attributed to increases in temperature, lack of food and early setting of monsoon.

Observations on the development of egg masses were carried out from June 1998 to September 1999. Individuals were randomly collected from the intertidal area and the egg masses were classified. In this paper, we present the percentage of barnacles with broods ready to hatch (where the ovarian tissue was dark brown in colour).

Plankton samples were collected once a month from June 1998 to September 1999. Horizontal plankton tows were made at a depth of 0.5 m, using a conical Heron–Tranter net of 100-μm mesh fitted with a flow meter. The amount of water filtered ranged from 25 to 170 m^{-3}. The samples were brought back to the laboratory to count the cirripede larvae. Some of the larvae isolated from plankton were used for rearing in the laboratory.

Larvae isolated from the plankton samples and those collected from the adult broods every month were reared individually (N=24) in multiwells (Nunclon delta-143982) at 25 ($\pm$1)°C temperature and 35 ppt using *Chaetoceros calcitrans*, a unicellular diatom, at a concentration of 2×10^5 cells ml^{-1} as food. Each larva was reared with 2 ml of media with an antibiotic dosage of 0.3 ml l^{-1} of crystamycin (300 mg of penicillin G and 500 mg of streptomycin in 4 ml of distilled water). Rearing wells were maintained at 12L:12D cycle.

Observations on the moults were taken every day prior to changing the food. The total naupliar duration and percentage survival of nauplii to cyprids was measured. As cyprids appeared they were put into the individual multiwells containing 2 ml of filtered seawater (0.22 μm). The settlement of these cyprids was observed to evaluate the percentage metamorphosis of cyprids to juvenile.

Data analysis

The data on recruitment of barnacles during different months on freshly cleaned quadrats exposed for one month was subjected to cluster analysis. The dissimilarity level was measured using the squared euclidean distance and group average method. The X-axis groupings are based on the clusters that are dissimilar beyond mid-point of highest dissimilarity observed. The data were log transformed before subjecting them to cluster analysis. This was followed by non-metric multidimensional scaling (nMDS) to produce two dimensional ordinates and months were grouped. The data on the abundance of cirripede larvae and the percentage of barnacles with the ripe ovaries were also subjected to cluster analysis. Two-way analysis of variance (ANOVA) (months×number of recruits for one month on fresh quadrat) was applied to assess the variation in recruitment of barnacles with different exposure months and also between the months and tidal heights. The data were log transformed before applying the two-way ANOVA (Sokal & Rohlf, 1987). Similarly ANOVAs were carried out for the percentage survival and metamorphosis between plankton collected larvae and those collected from the broods and also data on growth of solitary and crowded barnacles.

RESULTS

Recruitment

The pattern of recruitment of *Balanus amphitrite* on a freshly cleaned quadrat exposed for one month between June 1998 and September 1999, at both mid-tide and high tide levels, are shown in Figure 1A&F (mid-tide) and Figure 1C&H (high tide). Two prominent clusters, one comprising four months (July 1998, September 1998, October 1998 and February 1999) and the other ten months were evident. August 1998 (43 ind dm^{-2}) was the most dissimilar month at the mid-tide level (Figure 1A&F). The results of the cluster dendrogram among the seasons indicated the 1999 monsoon with higher recruitment to be most dissimilar, thus indicating it was different from the 1998 monsoon. Post-monsoon and pre-monsoon seasons indicated almost similar recruitment (Figure 1B&G). At high tide such a differentiation was not evident, and the intensity of recruitment was similar throughout the year (Figure 1C&H). A two-way ANOVA indicated that the recruitment of barnacles significantly varied with the month and tide level (Table 1).

Recruitment at mid-tide level during different seasons

Monsoon season

During monsoon, settlement spurted on the quadrat freshly exposed in August 1998 (Figure 2C). However, we did not observe recruitment in August on surfaces cleaned 2–3 months earlier (initiated in June and July 1998). The

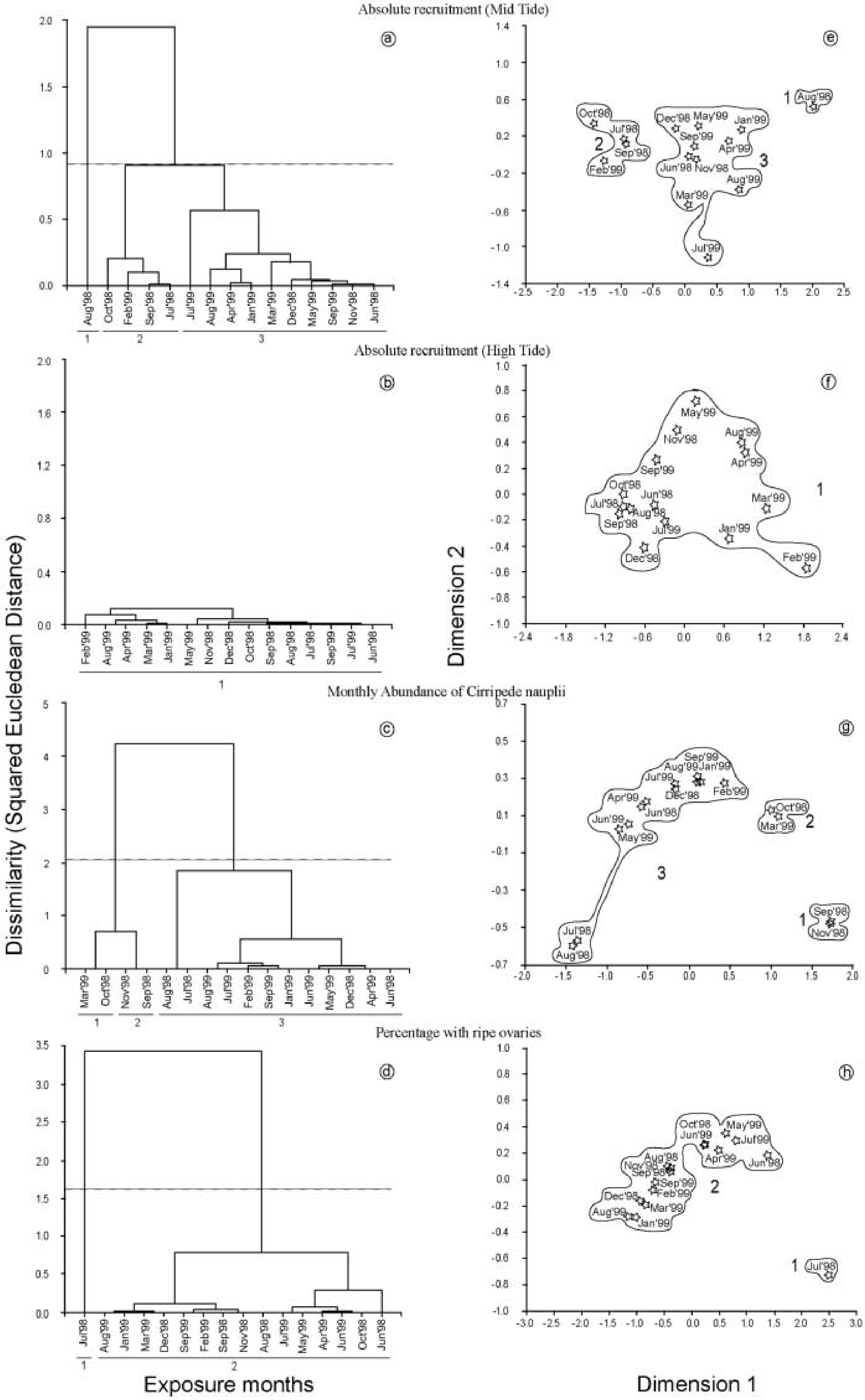

Figure 1. Cluster dendrograms and nMDS plots for absolute recruitment at mid-tide level (A&F), seasonal recruitment (B&G), absolute recruitment at high-tide level (C&H), monthly abundance of cirripede nauplii (D&I), percentage of *Balanus amphitrite* with mature brood (E&J). The dashed lines in A, B, C, D & E indicate the 50% dissimilarity from the highest dissimilarity level.

Table 1. *Two-way ANOVA of the absolute recruitment of* Balanus amphitrite *at mid-tide and high tide level.*

	df	SS	MS	Fs	p
Months	14	2.4	0.174	8	0.001
Tide level	1	14	13.9	679	0.001
Months×treatments	14	2	0.137	7	0.001
Within subgroup error	60	1.2	0.020		
Total	89	19.6			

df, degree of freedom; SS, sum of squares; MS, mean of squares; Fs, Fisher constant; p, probability.

newly settled barnacles on the August 1998 quadrat included a large number of spat (0–2 mm). The numbers of dead barnacles were considerable and most were spat (Figure 2C). Absolute recruitment was observed during

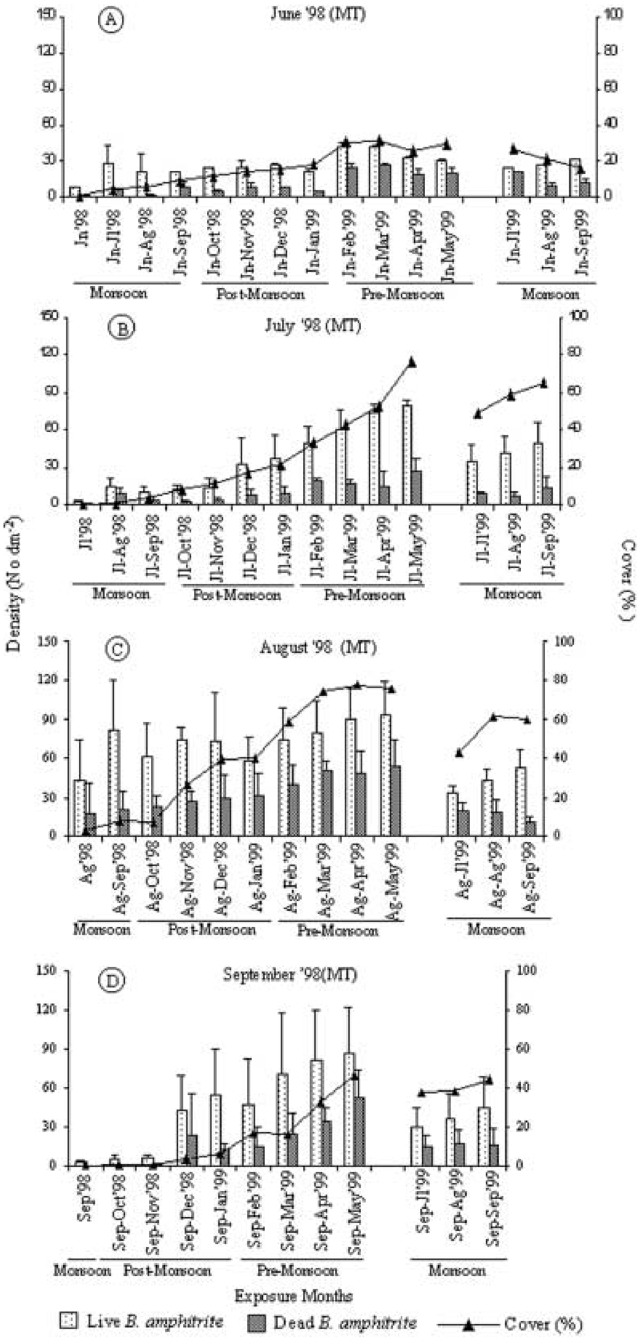

Figure 2. (A–D).

July on the 1–5 month old quadrats. Quadrats that were more than 5 months old showed dislodgment (the decrease in the number of recruited barnacles from the previous observation on any given quadrat exposed for a particular period), indicated by decreasing densities (Figure 3A). In August and September, absolute recruitment was observed on all the quadrats exposed for 1–15 and 1–16 months respectively (Figure 3A). A comparison of two monsoon seasons indicated that during the 1998 monsoon, recruitment was high in August 1998 (43 ind dm^{-2}), whereas,

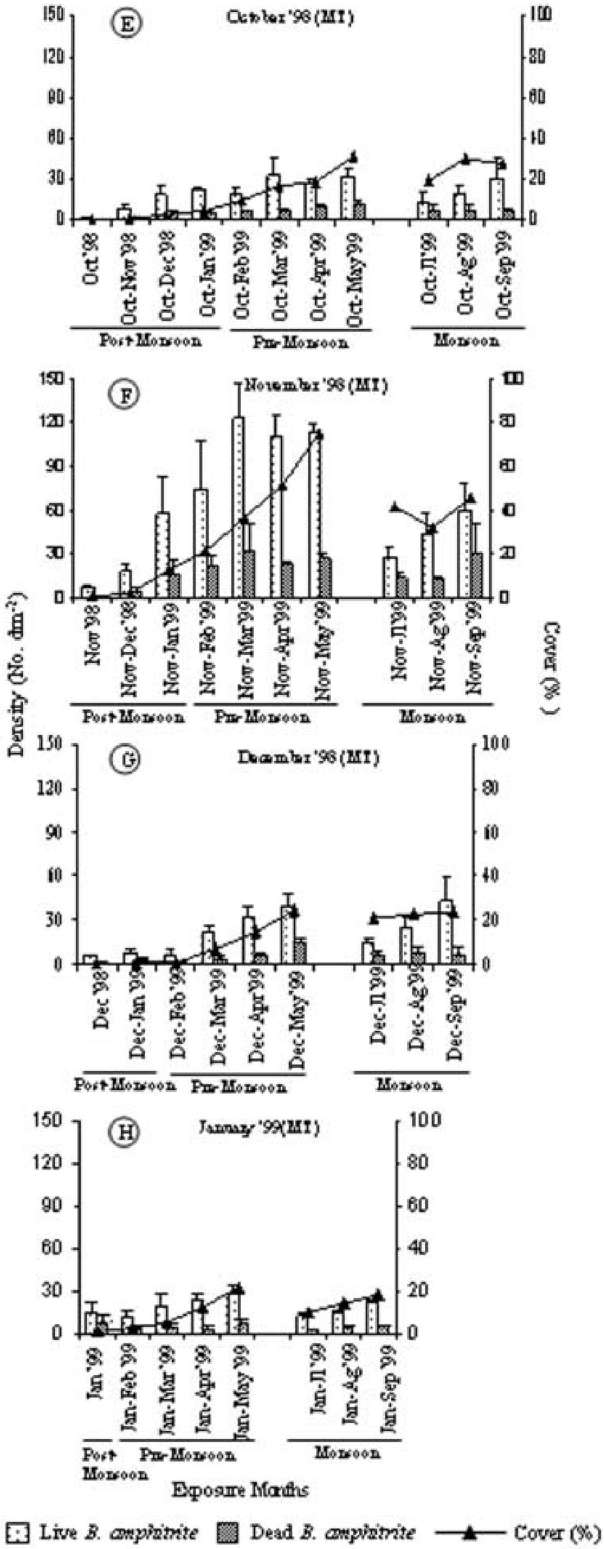

Figure 2. (E–H).

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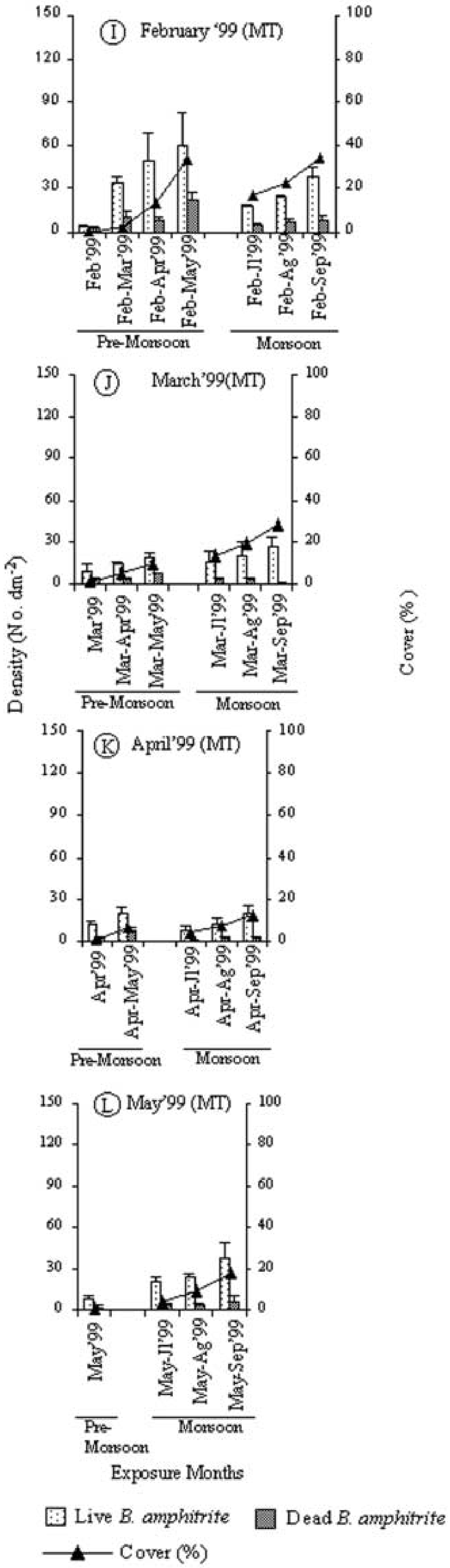

Figure 2. (I–L).

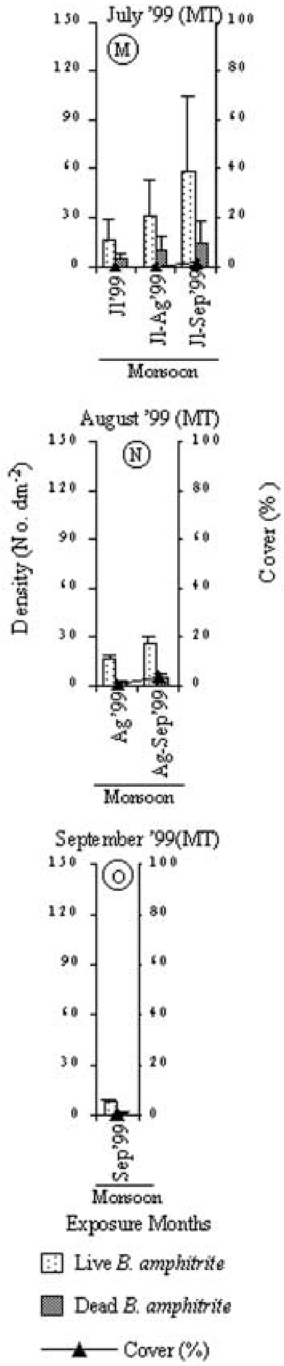

Figure 2. (A–O) Cumulative abundance of live and dead *Balanus amphitrite* and cover of barnacle at mid-tide level.

during 1999 recruitment was seen during both July and August (17 ind dm^{-2}) (Table 2). The observations on cumulative number of barnacles revealed that the recruitment continued through post and pre-monsoon months and declined at the beginning of the monsoon season. The per cent area coverage also indicated a similar trend (Figure 2A–D).

Post-monsoon season

Absolute recruitment peaked during January 1999 (15 ind dm^{-2}) (Table 2). In October the absolute recruitment was comparatively low and was almost similar on surfaces exposed for different periods (Figure 3B). In November

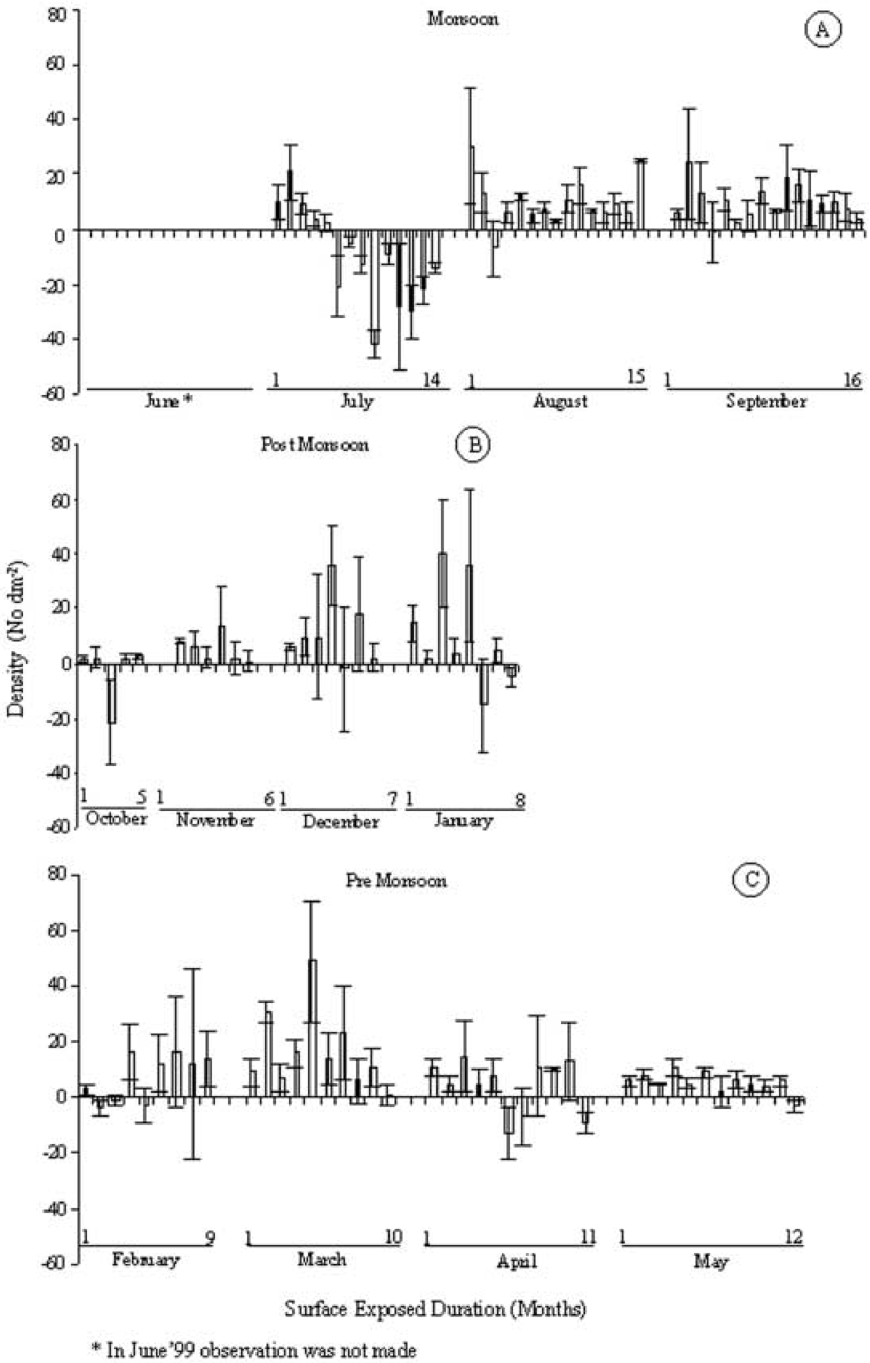

Figure 3. Absolute recruitment or dislodgment of *Balanus amphitrite* during different months on the quadrats aged for different duration at mid-tide level. (A) Monsoon; (B) post-monsoon; and (C) pre-monsoon. Vertical lines indicate the standard deviation from the mean.

1998, December 1998 and January 1999 absolute recruitment increased on 1- to 5-month old surfaces and then it decreased or showed dislodgment on older surfaces (Figure 3B). Cumulative abundance peaked during the pre-monsoon season on the November 1998 quadrat followed by ~70% decrease in the abundance with the onset of the 1999 monsoon indicating dislodgment (84 ind dm^{-2} Figure 2F; Table 2). The per cent area coverage remained uniform for 1–3 months and it further increased (Figure 2E–H). The number of dead barnacles also was quite low (Figure 2F). The cumulative abundance indicated a similar trend for October 1998, December 1998 and January 1999 (Figure 2E,G & H).

Pre-monsoon season

In March peak absolute recruitment was observed on a five month exposed surface, whereas in May the recruitment was almost uniform irrespective of the surface exposure duration (Figure 3C). The absolute recruitment peaked in March 1999 (2 months old; 31 ind dm^{-2}) followed by April 1999 (3 months old; 15 ind dm^{-2}) (Figure 3C). Cumulative abundance peaked on quadrats initiated in February 1999 (Figure 2I), whereas, the subsequent month initiations maintained a lower profile (Figure 2J–L). Similar results were highlighted by the data on percentage coverage. It was observed that during the late pre-monsoon month

Table 2. *Absolute recruitment, mortality and dislodgment of barnacles during different months at mid-tide level.*

Exposure duration		June 98	July	August	September	October	November	December	January 99	February	March	April	May	June	July	August	September
		Monsoon				Post-Monsoon				Pre-Monsoon				Monsoon			
Monsoon																	
1	L	8	3	43	3	2	8	6	15	3	9	12	8	NS	17	17	8
	D	1	1	17	0	0	0	1	8	2	3	3	2	NS	5	3	2
2	L	21	11	39	2	6	10	2	0 (−4)	31	5	8	NS		14	9	
	D	5	7	3	1	2	4	3	0 (−4)	9	0	5	NS		5	3	
3	L	0 (−7)	0 (−3)	0 (−19)	1	10	40	0 (−1)	7	15	5	NS	12		28		
	D	0 (−4)	0 (−4)	2	0	4	12	0 (−2)	0	0 (−3)	4	NS	1		5		
4	L	0	1	14	36	4	16	15	5	11	NS	0 (−12)	4				
	D	6	0 (−1)	5	22	0 (−1)	5	2	0 (−1)	14	NS	0 (−7)	0				
Post-monsoon																	
5	L	3	2	0	12	0 (−2)	49	8	5	NS	0 (−3)	4	13				
	D	0 (−3)	1	2	0 (−11)	1	11	3	6	NS	0 (−4)	2	3				
6	L	1	18	0 (−12)	0 (−4)	14	0 (−13)	9	NS	0 (−43)	5	8					
	D	3	4	3	3	1	0 (−8)	8	NS	0 (−17)	0	0					
7	L	2	5	16	23	0 (−5)	2	NS	0 (−16)	8	5						
	D	0	10	8	9	2	4	NS	0 (−5)	2	0 (−1)						
8	L	0 (−5)	12	6	11	6	NS	0 (−26)	3	14							
	D	0 (−4)	1	10	7	3	NS	0 (−9)	1	1							
Pre-monsoon																	
9	L	20	11	10	5	NS	0 (−84)	11	7								
	D	21	0 (−2)	0 (−2)	21	NS	0 (−13)	2	1								
10	L	0	13	4	NS	0 (−19)	16	19									
	D	2	0 (−2)	6	NS	0 (−5)	0 (−1)	0 (−1)									
11	L	0 (−9)	6	NS	0 (−56)	7	16										
	D	0 (−9)	12	NS	0 (−38)	0 (−1)	17										
12	L	0 (−1)	NS	0 (−60)	6	11											
	D	2	NS	0 (−35)	3	0											
Monsoon																	
13	L	NS	0 (−44)	9	9												
	D	NS	0 (−18)	18	0 (−1)												
14	L	0 (−27)	6	10													
	D	1	0 (−2)	0 (−7)													
15	L	25	8														
	D	0 (−11)	7														
16	L	4															
	D	2															

Numbers in the parentheses indicate the number of barnacles dislodged. L, live; D, dead; NS, not sampled.

(May 1999) the early setting of monsoon resulted in mortality.

Recruitment at high tide level

Recruitment of barnacles at high tide level was lower than at mid-tide level. There was a spurt in settlement during August 1998 (Table 2) at mid-tide level, but not at high tide level. At high tide level mortality and dislodgment was maximum during the pre-monsoon months, whereas, at mid-tide level it was during early monsoon months. Continued exposure (ageing of the surface) did not influence the abundance.

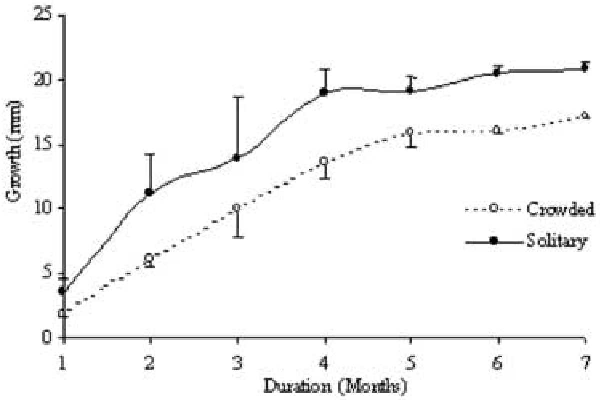

Figure 4. Variation in the growth of identified *Balanus amphitrite* during different exposure months, occurred as solitary and crowded individuals.

Table 3. *Two-way ANOVA for the growth of crowded and solitary* Balanus amphitrite.

	df	SS	MS	Fs	p
Months	6	1324	221	65	0.001
Tide level	1	127	127	37	0.001
Months×treatments	6	11	2	0.5	n.s.
Within subgroup error	28	95	3		
Total	41	1557			

df, degree of freedom; SS, sum of squares; MS, mean of squares; Fs, Fisher constant; p, probability; n.s., not significant.

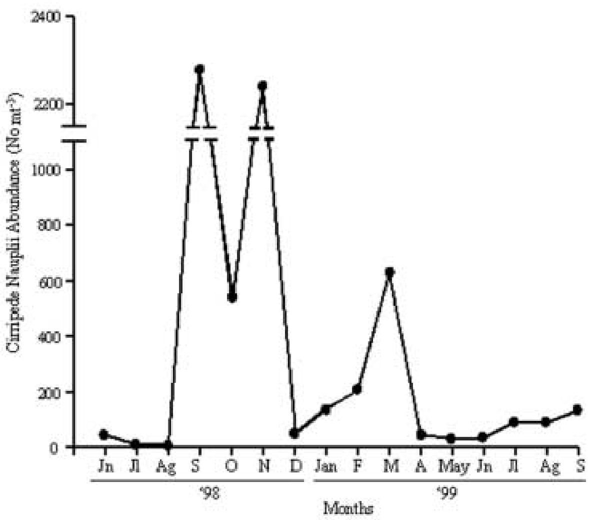

Figure 5. Monthly variation in the abundance of cirripede nauplii in the plankton.

Growth

Barnacles attained a maximum size of 6–8 mm on surfaces exposed for 2–3 months irrespective of the season. Further growth varied with seasons and time of

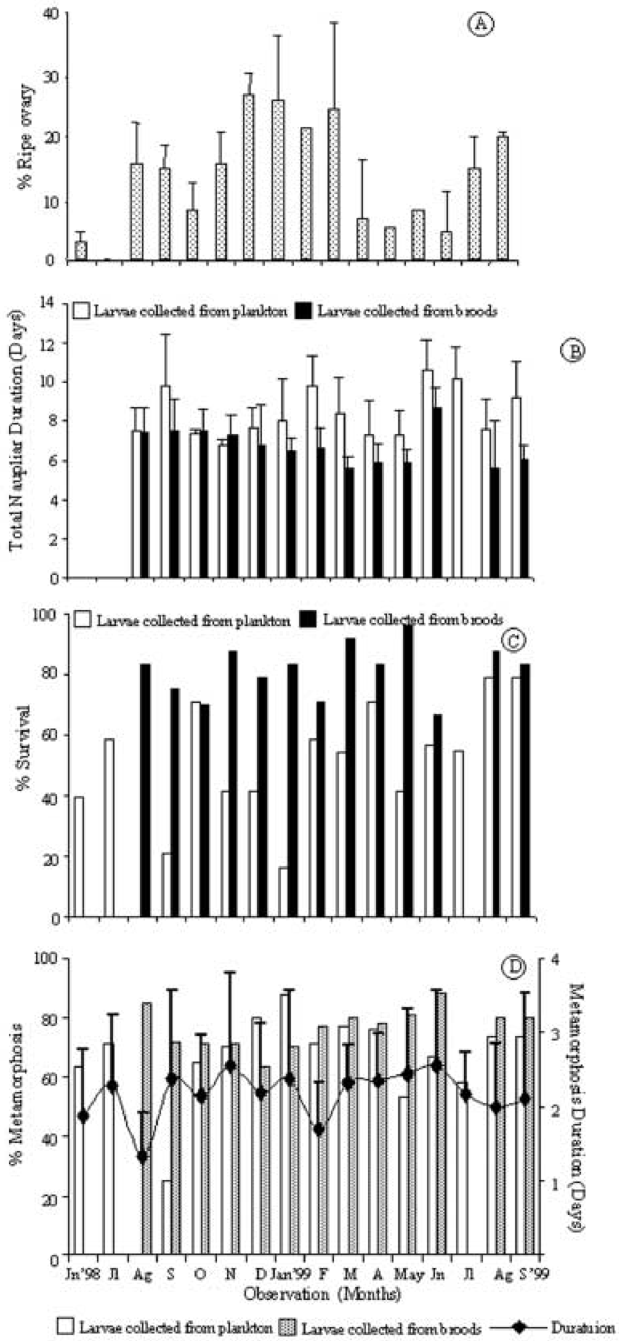

Figure 6. (A) Monthly variation in the percentage of *Balanus amphitrite* with mature brood; (B) monthly variation in the total naupliar duration; (C) monthly variation in the percentage survival of the nauplii to cyprid reared during different months; and (D) Y1-axis; monthly variation in the percentage metamorphosis of the cyprid to juvenile of the nauplii collected from plankton and from broods and Y2-axis; monthly variation on the duration of metamorphosis of cyprid to juvenile for the nauplii collected from plankton.

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Table 4. *Two-way ANOVA of the percentage survival of nauplii to cyprids of plankton collected larvae and larvae collected from broods, reared in the laboratory. Treatments (plankton collected and brood collected larvae).*

	df	SS	MS	Fs	*P*
Months	15	34871	2325	22112	0.001
Treatments	1	7062	7062	67173	0.001
Months × treatments	15	38676	2578	24525	0.001
Within subgroup error	64	7	0.10		
Total	95	80616			

df, degree of freedom; SS, sum of squares; MS, mean of squares; Fs, Fisher constant; p, probability.

recruitment. The individuals recruited during the monsoon season took longer (8–10 months) to attain a size of 16–20 mm, whereas those recruited in post-monsoon months took 6–8 months. The maximum size attained by the adults ranged from 20 to 22 mm. The larger size-groups were found in lower numbers. The growth rate of barnacles at mid-tide level was faster. At high tide level individuals attained a maximum size of 14–16 mm. The mortality of the barnacles marked for growth was observed after 6–7 months. Solitary individuals showed higher growth rate than the crowded ones. Solitary individuals grew at a faster rate (0.17 ±0.03 mm d^{-1}) than crowded individuals (0.1 ±0.06 mm d^{-1}) (Figure 4). Two-way ANOVA indicated significant variation in the growth rate of the barnacles when they occurred either as solitary or crowded individuals (Table 3).

Cirripede larvae

Cirripede larvae were observed throughout the study period. They were present in large numbers during September and November 1998 (2300 and 2200 100 m^{-3}) (Figure 5), while during October 1998 (500 100 m^{-3}) and March 1999 (600 100 m^{-3}) they were considerably less. The minimum numbers of cirripede larvae were observed in monsoon and late pre-monsoon months (June 1998 to August 1998 and April 1999 to September 1999). The results of the dendrogram to identify the pattern in the monthly abundance of cirripede larvae showed three clusters (Figure 1D&I). The first peak during September 1998 and November 1998 formed one cluster, followed by a second peak during October 1998 and March 1999. The remaining months, which had fewer larvae, grouped separately (Figure 1D&I).

Reproduction

The percentages of individuals with a mature brood were maximum during December 1998 (50 ±16). In August and September 1998 the percentage of barnacles with mature brood was 23 and 22.5 ±5% respectively. In monsoon months lower percentage of barnacles had mature brood (Figure 6A). The cluster dendrogram results indicated two clusters (Figure 1E&J). July 1998, which did not show ripe ovaries, was the most dissimilar and the other months, which had mature brood percentage ranging from 4–50%, grouped into one cluster (Figure 1E&J). The size of the barnacles at maturity varied with the months and the minimum size was 3.2 mm and maximum was 7.2 mm.

Rearing of larvae

The total naupliar duration was longer for the nauplii collected from plankton than those released from the broods (Figure 6B). The nauplii collected from plankton and reared in the laboratory showed lower per cent survival to the cyprid stage than larvae released from the broods (Figure 6C). Two-way ANOVA indicated significant variation in the percentage survival of nauplii to the cyprid stage in different months and between plankton and brood collected larvae (Table 4). Metamorphosis of cyprids raised from both these collections was comparable in most of the months (Figure 6D). The duration of cyprid metamorphosing to juvenile also varied with the month of collection, the minimum duration being in August 1998 (Figure 6D).

Rainfall

The rainfall data show that in the first year (1998) the peak monsoon was during the third week of July and in the second year (1999) this was during mid June. Throughout the monsoon considerably long break periods were observed (Figure 7).

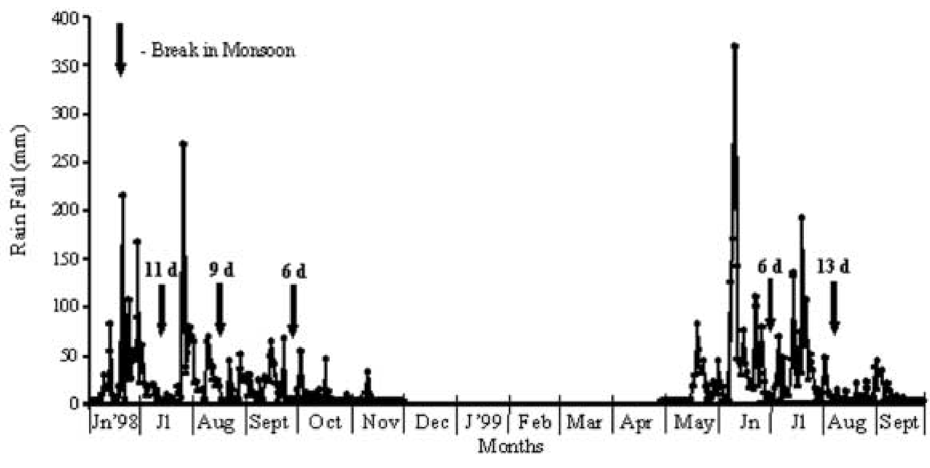

Figure 7. Daily rainfall during the year 1998–1999.

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DISCUSSION

Recruitment of organisms in boreal regions varies greatly according to the initiation of season, whereas, in the tropics, recruitment may be largely non-seasonal, unless the environment is influenced by meteorological factors such as fresh water run-off arising from monsoon conditions (Barnes, 1972). Recruitment density can serve as an accurate indicator of settlement density, and population age-structure may directly reflect past settlement, despite density-dependent mortality of settlers, especially when settlement density is low (Holm, 1990b).

Balanus amphitrite is an euryhaline and eurythermal species (Crisp & Costlow, 1963; Iwaki, 1981; Anil et al., 1995) and is known to breed year round in Indian waters (Karande, 1967). The observations made in this study showed that, in general, during monsoon months (with the exception of monsoon breaks), recruitment was low compared with non-monsoon months. The numbers of cirripede larvae in the plankton were also low during monsoon seasons. However, gonad conditions indicated that reproduction is not totally halted during the monsoon season. In fact, during August and September 1998, percentages of individuals with mature broods were high. Although there is a lull in recruitment during the monsoon season, a sudden spurt was observed during August 1998, and high recruitment was seen in July 1999. This shift in recruitment might have occurred due to conditions such as a break in the monsoon. During the monsoon considerably long break periods were observed. It has been reported that phytoplankton blooms occur along the west coast of India during the monsoon season. These blooms are generally caused by factors associated with the rainfall (Bhimachar & George, 1950; Subrahmanyan, 1954; Prakash & Sarma, 1964; Devassy, 1983). By the advent of monsoon, blooms of *Skeletonema costatum* and *Ceratium furca* are reported in this estuary (Devassy, 1983). Gopinathan (1974) reported the dominance of *S. costatum* immediately after or following a break in the monsoon. Starr et al. (1991) identified coupling of naupliar release in barnacles with phytoplankton blooms—a parallel strategy similar to that of spawning in urchins and mussels. Spawning at the onset of a bloom may represent a trade-off between an adequate food supply for the larvae and renewing of reserves in the adult (Starr et al., 1991). This is also supported by Barnes' (1962) data for 15 years at Millport, Scotland; the release of *Semibalanus balanoides* nauplii was closely associated with the spring *Skeletonema costatum* outburst. Barnacle larvae become planktonic soon after release and it would be favourable if the larvae were released in a food-rich environment. In temperate regions with clear seasonal changes, such a signal can work in favour of successful recruitment. However, a burst of phytoplankton in the middle of monsoon followed by reoccurrence of unfavourable conditions can lead to improper signal synchronization causing stress to new recruits. This was possibly the case in August 1998 where the maximum numbers of spat (0–2 mm rostrocarinal and basal diameter (RCB)) were dead.

Recruitment did not peak with the peak in larval abundance. A spurt in settlement was observed in August 1998, whereas, during the same month, the number of larvae was low in spite of the considerable number of barnacles with a ripe ovary. Thus, recruitment, larval abundance and the percentage of barnacles with ripe ovaries were not synchronized (Figure 1). A lack in synchrony among gonad condition, larval abundance and recruitment can be attributed to larval dispersion due to physical forces and biological processes. The Zuari estuary being a tidal stream is more or less homogenous from the surface to bottom during the non-monsoon months when fresh water flow is insignificant (NIO, 1979). With the onset of the south-west monsoon (June–September), increased freshwater inflow results in stratification. The stratification and physical factors such as currents may increase the chance of larval dispersal and could be one of the reasons for low recruitment during the monsoon season.

Maximum larval abundance was observed during September and November 1998, however, recruitment did not peak during these months. The larvae collected from plankton during September 1998 and reared in the laboratory showed low naupliar survival to cyprid and metamorphosis of cyprid to juvenile. The total duration of development was also longer. However, the same trend was not observed when larvae were collected from adult broods and reared in the laboratory; the results were reversed. It is possible that the quality of the larvae collected from plankton and those collected from broods were from different brood stock. Qiu & Qian (1997) inferred from their laboratory experiments, that the larvae from a single brood responded to food concentration in the same manner as larvae from multiple broods. However, in our experiment, the larvae collected during different months responded in a different manner. *Balanus amphitrite* breeds frequently (5–9 day brood^{-1}) (El-Komi & Kajihara, 1991), such a short breeding interval will have an impact upon the larvae released, as there might be a change in quality and quantity of food available during the inter-breeding interval. It was observed in *Balanus balanoides* by Barnes & Barnes (1967) that ovarian development is dependent upon adequate food supply and interruptions in the food supply led to reabsorption of tissue. The ability of adults to postpone hatching may therefore have important implications for the energy reserves and viability of newly hatched larvae. Thus, it is possible that poor ambient food availability during the monsoon season can influence the quality of the larvae released at the end of the monsoon. The larvae collected during the other peak, November 1998, were larger than those collected during September 1998. With the ending of the monsoon season, the environment returns to a stable condition; and this change can lead to a better condition for adults and new larvae released. Thus, the differences in the development and survival of larvae collected during different seasons indicate adult conditioning and inter-brood variation to be important factors in the larval ecology of this organism.

Factors such as food concentration, temperature and salinity influence the duration of larval development and also the ability of the larvae to metamorphose (Anil et al., 1995, 2001). In an earlier work, it was observed that *B. amphitrite* larvae reared in the field took longer to reach the cyprid instar than those reared in the laboratory (Dattesh & Anil, 2002). The phytoplankton population in this estuary is reported to be high after monsoons, moderately high prior to monsoons and there is a sharp decline during the peak monsoon months (Devassy, 1983). The differences in phytoplankton abundance can change the rate of larval development and metamorphosis and in turn govern temporal changes in recruitment.

Gosselin & Qian (1996) concluded through their study that intertidal barnacles could suffer substantial mortality during a brief period after settlement and they indicated this might neither be due to interactions with other recruits (density-dependent mortality), desiccation, grazers, or wave action, nor could it be explained by size-dependent changes in vulnerability. They stated that it might be the result of an interaction between two factors, e.g. energy reserves and ambient temperature.

Differences in the recruitment of barnacles with tidal height were evident, and can be attributed to the duration of substratum immersion. During both non-monsoon and monsoon seasons the amplitude of the semi-diurnal tides remains unchanged. Thus, the mid-tide quadrats would be submerged about 60 times a month (twice a day), whereas, surfaces exposed at high-tide would remain immersed for a minimum of 16 to a maximum of 26 times (i.e. once in 2 to 1.7 days) in a month. Hence, the surface conditioning and time available for cyprids to explore the surface and settle could depend on the duration of substratum immersion. Qian et al. (2003) showed that the *Balanus amphitrite* cyprids preferred mid-intertidal height over high intertidal or subtidal heights for settlement. It has been suggested that intertidal barnacles can possibly identify tidal height by detecting variation in biofilm components along the intertidal zone (Strathmann et al., 1981; Thompson et al., 1998; Miron et al., 2003).

The growth rate of barnacles was low during the monsoon season compared with post and pre-monsoon seasons. Slow growth during monsoons can be correlated to low food availability. It is also true that the greater land run-off during monsoons increases suspended load, which may interfere with the feeding mechanism and respiratory organs, thereby reducing the growth rate (Santhakumaran, 1989). Seasonal changes in water temperature and other environmental factors can also cause differences in growth rate. Pechenik et al. (1993) also reported that the growth rate of newly metamorphosed *B. amphitrite* slows down significantly if cyprids are prevented from metamorphosing for as few as three days. Higher growth rate after monsoons can be attributed to stable marine conditions. In this estuary, the maximum abundance of diatoms is reported during the post-monsoon season (Mitbavkar & Anil, 2002). During pre-monsoon, air temperature and surface-water temperature increase by about 10°C from that in the post-monsoon season. It was observed by Southward (1955) that surface-water temperature affects growth rate of barnacles through its influence on the rate of cirral beat and feeding. Slow growth during summer can also be attributed to less food and the rise in air and sea-surface temperatures to above optimum (Ritz & Crisp, 1970). The implication of these factors on adult energy reserves is yet to be illustrated in the tropical scenario.

In the present context, the settlement of barnacles that occurred during the monsoon break period was stressed with the recurrence of low saline and turbid conditions indicating that synchronized release of larvae in food rich environment, may not be a completely reliable mechanism in such environments. Release of larvae in response to diatom blooms could be a poor strategy for *B. amphitrite*. It is important to understand the impact of such environmental purturbances on sustenance of a population. The probable decrease or recruitment failure in an environment such as the one we studied can be attributed to inappropriate cue synchronization.

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