

Settlement and recruitment of the barnacle *Balanus amphitrite* from a tropical environment influenced by monsoons

CHETAN A. GAONKAR AND ARGHA CHANDRASHEKAR ANIL
CSIR-National Institute of Oceanography, Dona Paula, Goa 403 004, India

Studies on the settlement and the subsequent recruitment of intertidal organisms are crucial steps in understanding their population structure in a particular bioregion. However, studying the recruitment of intertidal organisms such as barnacles, with two-phase life cycle, and understanding the determinants of recruitment is a complex problem. Many processes which operate during the pelagic pre-settlement phase and benthic post-settlement phase at different spatial and temporal scales can determine the fate of barnacle populations. In this study, observations were carried out on settlement and recruitment of the intertidal barnacle Balanus amphitrite from a tropical environment influenced by monsoons at spatial and temporal scales. Settlement and recruitment both showed significant temporal variations. In general, settlement and recruitment was lower during the monsoon season except during monsoon breaks. Consistency in settlement and recruitment was mostly observed during the pre-monsoon season, and it coincided with peaks in larval abundance observed during the same season. In general, settlement remained more or less similar on different types of substrata, whereas recruitment differed significantly. Temporal variations observed in settlement and recruitment of barnacles could be due to the influence of monsoons in this region, which leads to seasonal fluctuations in physical factors such as local hydrodynamics, that influence the retention and dispersal of larvae in the adult habitats, and could also be due to variations in the availability of food for the larvae and the settled populations.

Keywords: barnacles, *Balanus amphitrite*, settlement, recruitment, larval abundance, temporal variations, tropical environment, monsoons

Submitted 7 November 2012; accepted 25 November 2012; first published online 26 February 2013

INTRODUCTION

In barnacles, settlement is the culmination of cyprid metamorphosis to a juvenile, whereas recruitment is the survival of the individual to an adult. Successful settlement and subsequent recruitment in an area indicates its sustainability in that particular region. Metamorphosis of cyprids to juveniles and their further growth to adults depends on various pre- and post-settlement factors. Settlement rate, which is defined as the rate at which planktonic larvae establish a permanent contact with the substratum, depends on a number of factors which operate over a variety of spatial and temporal scales (Jenkins *et al.*, 2000). Settlement is influenced by both variations in physical factors, such as temperature, salinity and current patterns that may disperse the planktotrophic larvae, and biological factors, such as phytoplankton abundance, which is an important source of food for the larvae as well as adult populations (Anil *et al.*, 1995, 2001; Desai & Anil, 2002, 2005). Competition for space and predation by other intertidal organisms along with substratum cues and larval behaviour also play a significant role. Larval abundance in an area, which is another important source for the variations in settlement, is in turn influenced by variations in

reproduction and adult population of an area (Wellington & Victor, 1988). Physical transport processes such as local wind patterns and hydrodynamics, along with larval behaviour and substratum characteristics also determine the abundance of larvae in a particular area (Crisp, 1955; Gaines *et al.*, 1985; Minchinton & Scheibling, 1991; Pineda, 1994; Bertness *et al.*, 1996; Shanks, 1998; Thompson *et al.*, 1998).

To figure out the different factors which are responsible for the variations in a population from a particular bioregion, it is necessary to monitor them on a regular basis. An understanding of the scales at which variations in settlement and recruitment occur will allow identification of those processes most important in determining settlement and recruitment rates at any particular region (Levin, 1992; Jenkins *et al.*, 2000). Studies on settlement and recruitment of the barnacle *Balanus amphitrite* along the Indian coast are very much lacking, in spite of its dominance in the intertidal community (Desai & Anil, 2005). Barnacles from the region are mostly studied with respect to their importance in the macrofouling community (Daniel, 1954; Iyengar *et al.*, 1957; Karande, 1965; Nair, 1965; Menon *et al.*, 1977; Anil, 1986; Fernando, 1990). The aim of the present study was to elucidate the settlement and recruitment rates of the barnacle *Balanus amphitrite* at different spatial and temporal scales in this unique tropical region which is influenced by monsoons (Goa, west coast of India), and to figure out the possible factors governing the variations in settlement and recruitment of barnacles in this region.

Corresponding author:
A.C. Anil
Email: acanil@nio.org

MATERIALS AND METHODS

Study area

This study was carried out along the coast of Goa, west coast of India (Figure 1A, B).

Four different stations were selected for the monitoring of settlement and recruitment of barnacles (Dona Paula, Mormugao Port (MPT), INS-Mandovi and Arambol—Figure 1A) based on their distinctive positions. Station Dona Paula is situated at the mouth of the Zuari estuary. MPT is one of the busiest ports along the central west coast of India. INS-Mandovi is a naval jetty located near the mouth of the Mandovi estuary and Arambol is located at the northern end of Goa coast, which is directly exposed to the Arabian Sea, with a rocky shoreline. The local tidal amplitude in the region ranges from 0.25 m during neap tides to 2.5 m during spring tides. Larval abundance along with different environmental variables was also monitored at seven different stations in and around the coast on a bimonthly basis (Figure 1B). The study sites are influenced by the south-west monsoon. Based on the influence of this monsoon, a year can broadly be classified into pre-monsoon (February to May), monsoon (June to September) and post-monsoon (October to January) seasons (Anil, 1986).

Settlement and recruitment

Settlement and recruitment of the barnacle *Balanus amphitrite* was monitored at four different stations on a monthly basis. At stations Dona Paula and MPT the observations were made from June 2005 to May 2007, whereas at stations INS-Mandovi and Arambol, the observations were made from June 2006 to May 2007. In addition, at station Dona Paula, weekly observations of settlement and recruitment were also made from June 2005 to May 2007. Two different types of panels (aluminium and acrylic materials) of size 15 × 10 cm were used as substratum at stations Dona Paula, MPT and INS-Mandovi. Aluminium and acrylic panels have been used in the past to study the settlement and recruitment

of barnacles in the study area, and they provide a good picture of settlement and recruitment (Anil, 1986; Desai, 2002). The panels were attached to an aluminium strip with the help of a nut and bolts and were deployed at a depth of about 15 ft from a jetty piling. Every month, a new set of panels were immersed ($N = 3$) and six marked quadrates of size 25 cm² each were observed. At station Arambol, the observations of settlement and recruitment were made from a naturally available rocky substratum. Quadrates of 25 cm² were marked ($N = 3$) at the beginning of each month. The surfaces of the marked quadrates were manually cleaned for the existing fauna using a scraper and then by a nylon brush so that no cyprids remained on the cleaned surfaces. Settled and recruited barnacles on the panels as well as on the rocky substratum were counted at the end of a respective month with the help of a hand-held lens. Seasonal observations of settlement and recruitment were also made by retaining the respective month panels and the marked quadrates of the rocky substratum till the end of a particular season, which provided cumulative counts for three month periods. Sizes (rostrum-carinal basal diameter) of the recruits were also monitored on a monthly as well as seasonal basis. Below 2 mm size-class was considered as settlers and above 2 mm size-class as recruits. Settlement and recruitment of the barnacles are expressed in terms of numbers per decimetre square (No./dm²).

Larval abundance

Larval abundance was monitored at seven different stations (Figure 1B) for the period 2005–2007 (samples were collected during March 2005, May 2005, September 2005, November 2005, January 2006, March 2006, May 2006, September 2006, November 2006, January 2007, March 2007 and May 2007). Horizontal plankton tows were made using a Haron-Trantor net of mesh size 100 µm fitted with a flow meter. The volume of water filtered was calculated using the number of revolutions obtained from a flow meter. The samples were preserved in 5% formaldehyde on-board and later sorted out and counted in the laboratory using a

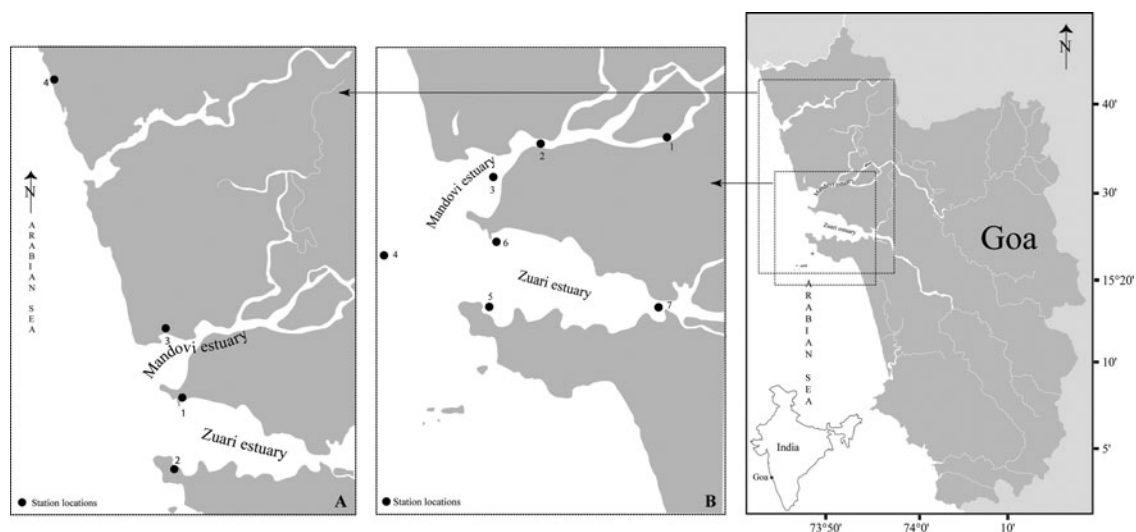


Fig. 1. Study locations for monitoring (A) barnacle settlement and recruitment (1. Dona Paula, 2. Mormugao Port (MPT), 3. INS-Mandovi, 4. Arambol) and (B) larval abundance and environmental variables (1. Old Goa, 2. Panjim bridge, 3. Miramar, 4. Offshore, 5. MPT, 6. Dona Paula, 7. Zuari bridge).

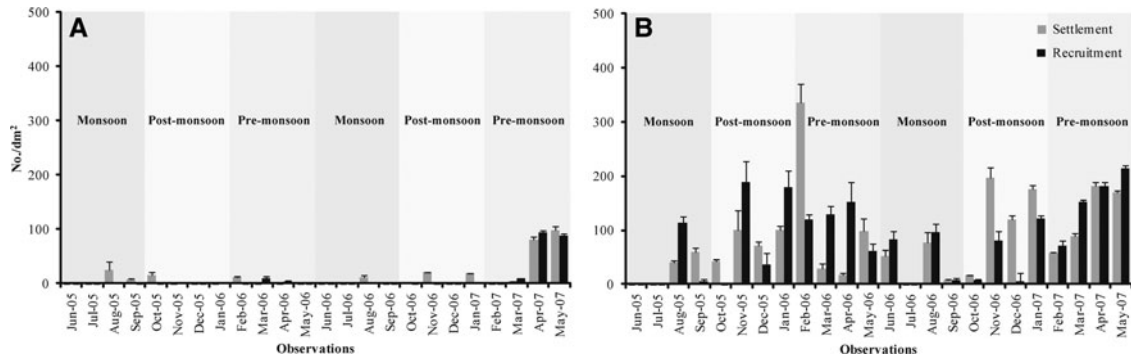


Fig. 2. Settlement and recruitment of the barnacle *Balanus amphitrite* at station Dona Paula on (A) acrylic and (B) aluminium panels. Error bar indicates standard deviation from the mean.

stereo-zoom microscope to determine larval abundance over time. Larval abundance is expressed in terms of numbers per 100 cubic meters (100 m³).

Environmental variables

Samples to measure environmental variables such as temperature, salinity, pH, dissolved oxygen (DO), nutrients (nitrate, nitrite, phosphate and silicate), chlorophyll-*a* and suspended particulate matter (SPM) for the period 2005–2007 were also taken from seven different stations (Figure 1B). Standard procedures were used for the analyses of these variables (Parsons *et al.*, 1984). The rainfall data for the study period were obtained from the Indian meteorological department to evaluate the influence of monsoons over the region.

Data analysis

Settlement and recruitment of barnacles along with larval abundance data which were collected during different months were log *x* + 1 transformed to ensure normality of means and homogeneity of variances. The log *x* + 1 transformed data were then subjected to one-way analysis of variance (ANOVA) (Sokal & Rohlf, 1981) to evaluate the variance between different sampling months (temporal variation) and also between different stations (spatial variation). For the analysis of spatial variations in settlement and recruitment of barnacles, station Arambol was excluded to nullify the effect of substratum (since at this station observations were taken from a naturally available rocky substratum).

Size ranges of barnacle recruits at different stations along with settlement and recruitment of barnacles on different types of substrata were also subjected to one-way ANOVA. Correlation analysis was performed between settlement and recruitment of barnacles versus environmental variables; settlement and recruitment of barnacles versus larval abundance and settlement versus subsequent recruitment of barnacles. Larval abundance during different sampling periods is presented as SURFER plots using SURFER 7 software.

RESULTS

Temporal variations in settlement and recruitment

Both settlement and recruitment varied significantly among the sampling months at all the four stations monitored during the period 2005–2006 and 2006–2007 (ANOVA: *P* < 0.05). In general, both settlement and recruitment was lower during the monsoon season when compared to post and pre-monsoon seasons (Figures 2A, B, 3A, B, 4A, B and 5).

Spatial variations in settlement and recruitment

Settlement did not vary significantly among the stations sampled during the period 2005–2006 on both aluminium and acrylic panels (ANOVA: *P* > 0.05), whereas it varied significantly among the stations sampled during the period

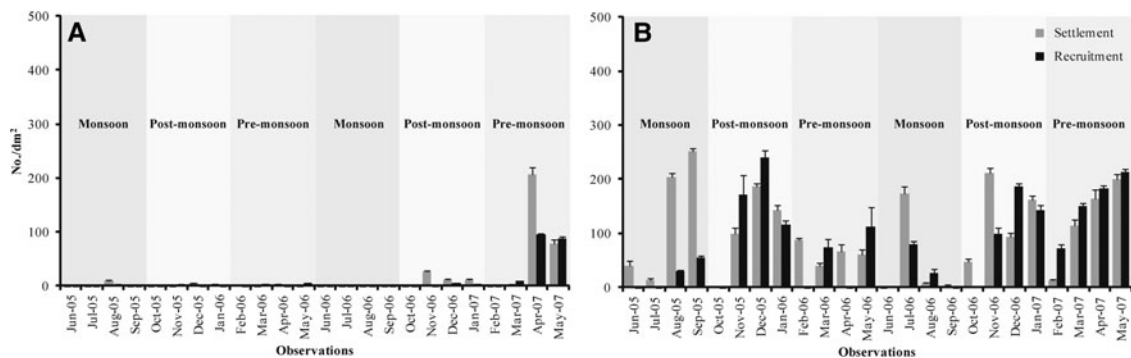


Fig. 3. Settlement and recruitment of the barnacle *Balanus amphitrite* at station Mormugoa Port on (A) acrylic and (B) aluminium panels. Error bar indicates standard deviation from the mean.

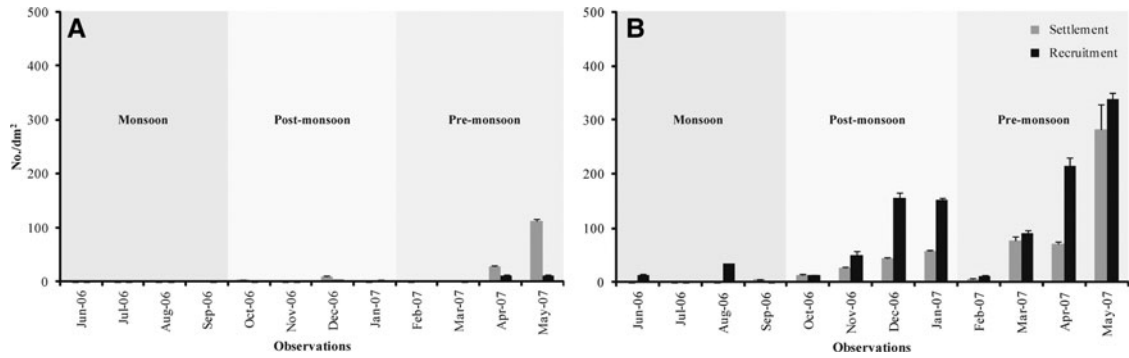


Fig. 4. Settlement and recruitment of the barnacle *Balanus amphitrite* at station INS-Mandovi on (A) acrylic and (B) aluminium panels. Error bar indicates standard deviation from the mean.

2006–2007 on aluminium panels (ANOVA: $P < 0.05$) and did not vary significantly on acrylic panels (ANOVA: $P > 0.05$).

Recruitment did not vary significantly among the stations sampled during the period 2005–2006 and 2006–2007 on both aluminium and acrylic panels (ANOVA: $P > 0.05$).

Seasonal observations of settlement and recruitment

Seasonal patterns of settlement and recruitment at stations Dona Paula, MPT and INS-Mandovi on aluminium and acrylic panels and at station Arambol during the period 2005–2006 and 2006–2007 are presented in Figures 6A–D, 7A–D, 8A, B and 9. Peak in recruitment was observed during 2005–2006 at station Dona Paula during post-monsoon season (Figure 6C). Not all the settled barnacles recruited themselves during 2005–2006 at station MPT during monsoon season (Figure 7C). Settlement and recruitment was found to be consistent during 2006–2007 period at all the stations monitored. In general, settlement to recruitment correlation was found to be weak during 2005–2006 compared to 2006–2007 period ($P > 0.05$).

Size-ranges (rostrum-carinal basal diameter) of barnacle recruits

MONTHLY OBSERVATIONS

Sizes of barnacles after one month period at station Dona Paula ranged between 3.4–10.0 mm on acrylic panels and

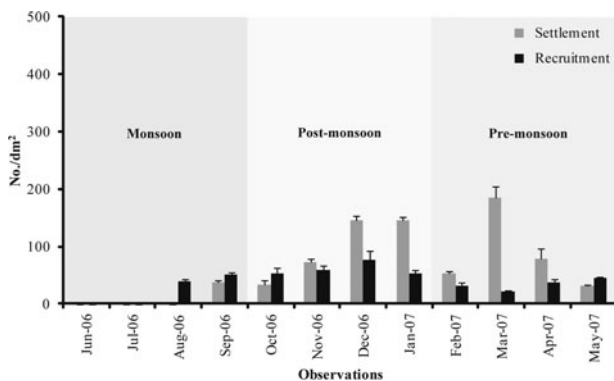


Fig. 5. Settlement and recruitment of the barnacle *Balanus amphitrite* on natural rocks at station Arambol. Error bar indicates standard deviation from the mean.

between 3.4–9.4 mm on aluminium panels (Figure 10A, B). At station MPT, it ranged between 2.6–5.6 mm on acrylic panels and 3.0–7.0 mm on aluminium panels (Figure 10A, B). At station INS-Mandovi, the size-range was between 3.0–5.6 mm on acrylic panels and 4.0–5.6 mm on aluminium panels (Figure 10A, B). At station Arambol, the size-range was 3.5–4.6 mm on natural rocks (Figure 11). Overall, the sizes of barnacle recruits varied significantly between different months at stations Dona Paula, MPT and INS-Mandovi on both acrylic and aluminium panels (ANOVA: $P < 0.05$), whereas it did not vary significantly at station Arambol on natural rocks (ANOVA: $P > 0.05$).

SEASONAL OBSERVATIONS

Size-ranges of recruits (maximum age of 3 months) on a seasonal basis at stations Dona Paula, MPT and INS-Mandovi on aluminium and acrylic panels, and at station Arambol on natural rocks, during the period 2005–2006 and 2006–2007 are presented in Figures 12A–D and 13. Size-ranges attained by the recruits were larger during 2005–2006 (3.4–14.0 mm) than 2006–2007 (2.8–7.6 mm) on both acrylic and aluminium panels at station Dona Paula. Sizes attained by the recruits were mostly found to be larger on acrylic (14 mm) than on aluminium (11.3 mm) panels at stations Dona Paula and MPT, whereas at station Arambol, the sizes attained by the recruits were between 3.5–5.6 mm.

Weekly observations of settlement and recruitment

Weekly observations of settlement and recruitment of the barnacles were carried out at station Dona Paula for a period of two years (2005–2007) on acrylic and aluminium panels and the results are presented in Figure 14A, B. Settlement and recruitment varied significantly on a temporal basis (ANOVA: $P < 0.05$). In general settlement and recruitment was found to be lower during the monsoon season except during monsoon breaks. Consistency in settlement and recruitment was mostly observed during the pre-monsoon season.

Substratum wise variations in settlement and recruitment

Settlement did not vary significantly when compared between natural rocks at station Arambol to that of aluminium and acrylic panels at station INS-Mandovi (Table 1A), whereas

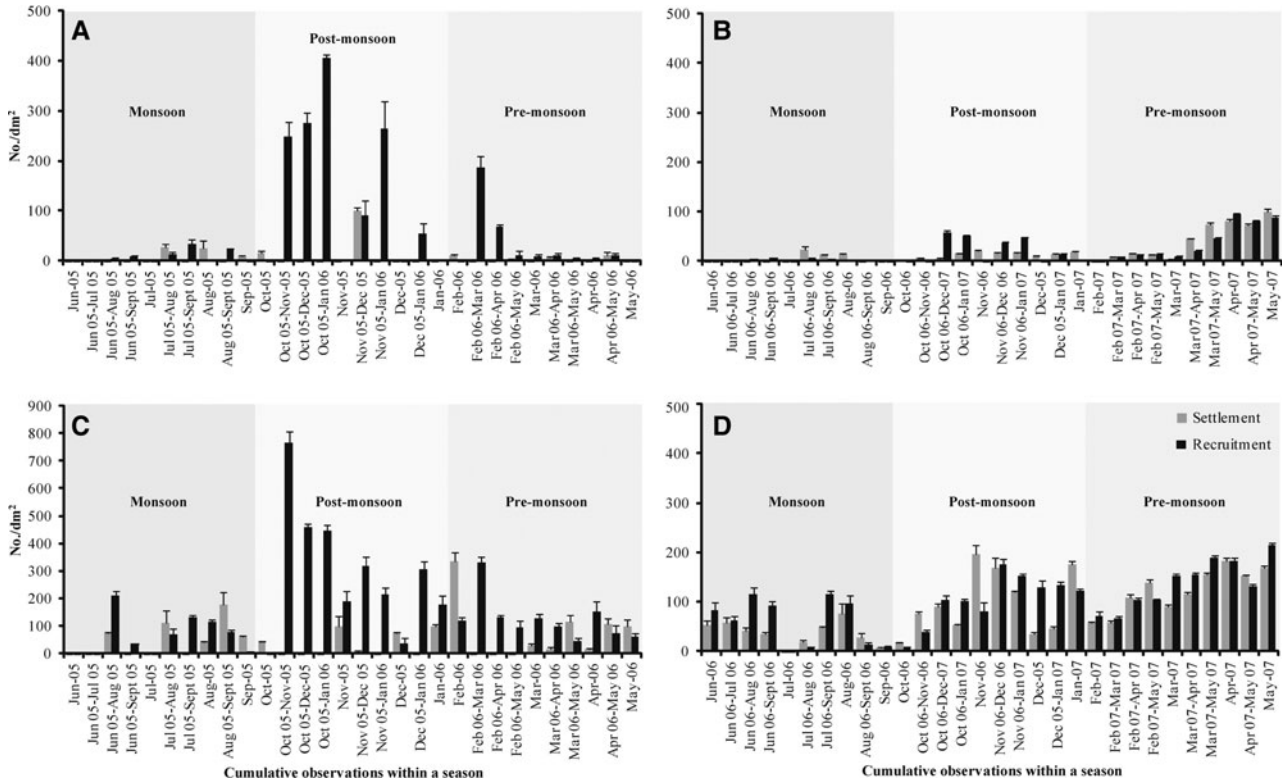


Fig. 6. Seasonal observations of settlement and recruitment of the barnacle *Balanus amphitrite* at station Dona Paula on acrylic panels during (A) 2005–2006 and (B) 2006–2007, and aluminium panels during (C) 2005–2006 and (D) 2006–2007 (cumulative observations for panels deployed for the whole season). Error bar indicates standard deviation from the mean.

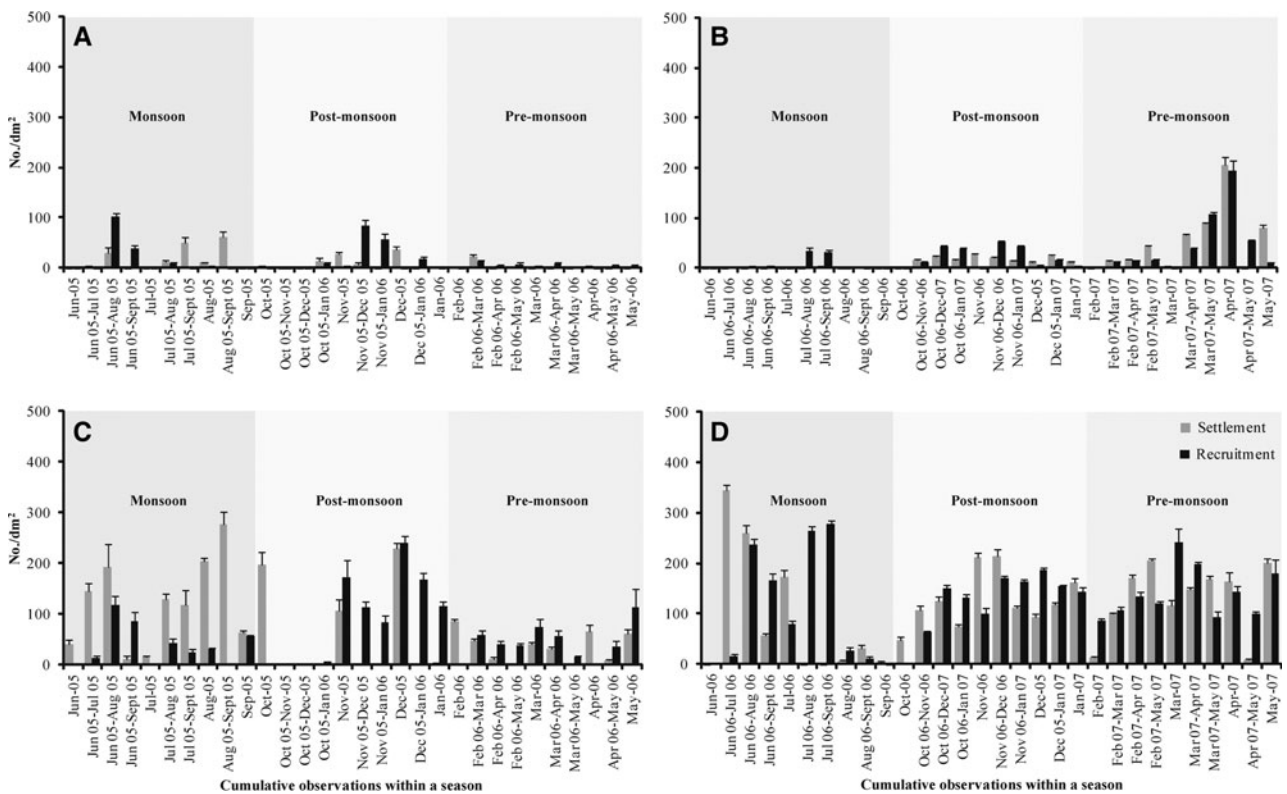


Fig. 7. Seasonal observations of settlement and recruitment of the barnacle *Balanus amphitrite* at station Mormugoa Port on acrylic panels during (A) 2005–2006 and (B) 2006–2007, and aluminium panels during (C) 2005–2006 and (D) 2006–2007 (cumulative observations for panels deployed for the whole season). Error bar indicates standard deviation from the mean.

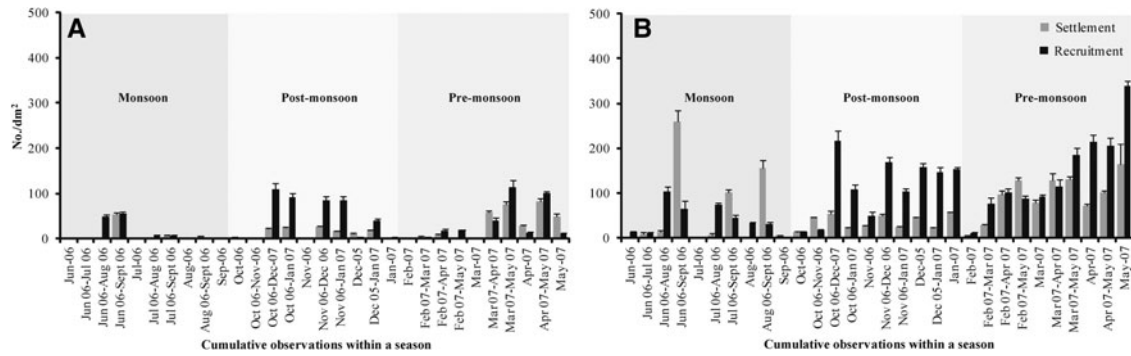


Fig. 8. Seasonal observations of settlement and recruitment of the barnacle *Balanus amphitrite* at station INS-Mandovi during 2006–2007 on (A) acrylic and (B) aluminium panels (cumulative observations for panels deployed for the whole season). Error bar indicates standard deviation from the mean.

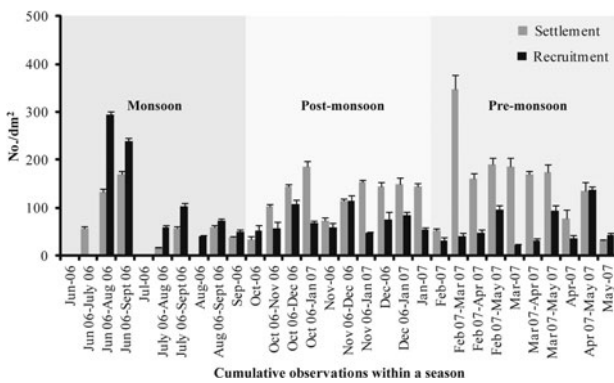


Fig. 9. Seasonal observations of settlement and recruitment of the barnacle *Balanus amphitrite* on natural rocks at station Arambol during 2006–2007 (cumulative observations for panels deployed for the whole season). Error bar indicates standard deviation from the mean.

recruitment varied significantly (Table 1B). However, settlement and recruitment varied significantly when compared between natural rocks at station Arambol to that of aluminium and acrylic panels at stations Dona Paula (Table 2A, B) and MPT (Table 3A, B).

When compared between aluminium and acrylic panels, settlement did not vary at station INS-Mandovi (Table 4A), whereas it varied at stations Dona Paula (Table 4B) and MPT (Table 4C) and recruitment varied significantly between

aluminium and acrylic panels at stations INS-Mandovi (Table 5A), Dona Paula (Table 5B) and MPT (Table 5C).

Larval abundance

Abundance of cirripede nauplii during different sampling months from different stations are presented in Figure 15. Naupliar abundance varied significantly on a spatial and temporal scale (ANOVA: $P < 0.05$). In general, cirripede nauplii were consistently observed during the pre-monsoon season (March 2005, May 2005, March 2006, May 2006, March 2007 and May 2007) at most of the stations, whereas their abundance was lower during the monsoon and early post-monsoon seasons (September 2005, November 2005, September 2006 and November 2006). Average larval abundance was found to be highest at station Dona Paula followed by stations Panjim jetty, Old Goa, Zuari bridge, Miramar, MPT and Offshore. Abundance of larvae during different months was significantly correlated with settlement and recruitment of barnacles ($P < 0.05$).

Environmental variables

Environmental variables observed during the period 2005–2007 from seven different stations are presented in Table 6. Temperature ranged between 27 and 36.2°C. Salinity ranged

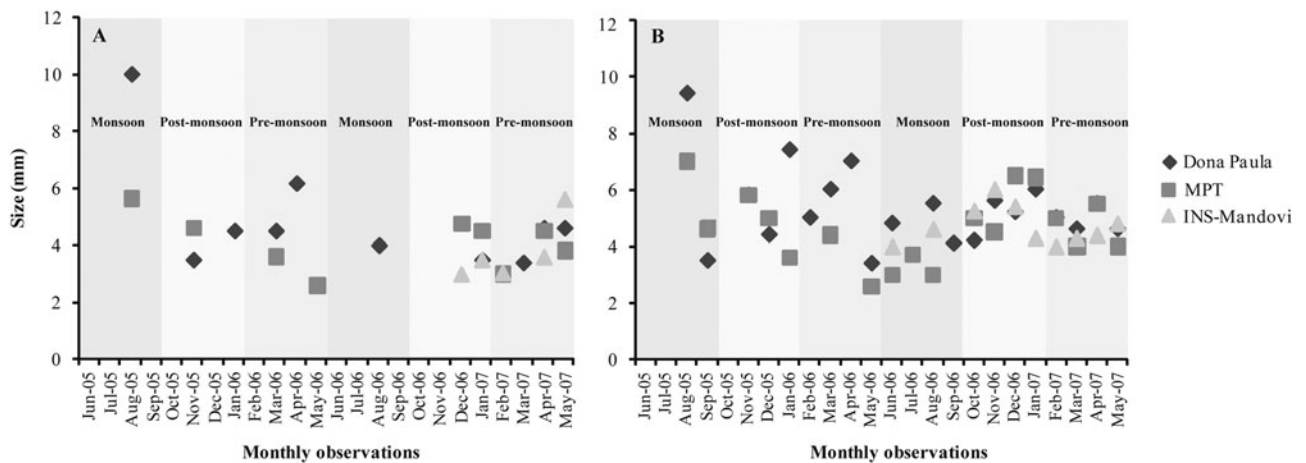


Fig. 10. Size of the barnacle recruits at a maximum age of one month period at stations Dona Paula, Mormugoa Port and INS-Mandovi on (A) acrylic and (B) aluminium panels.

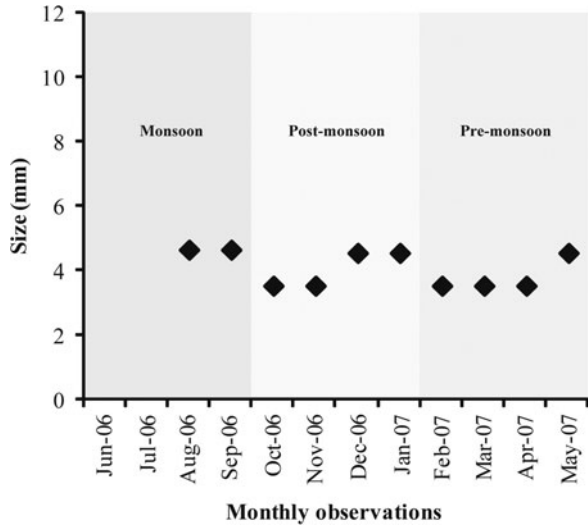


Fig. 11. Size of the barnacle recruits on one month period at station Arambol.

between 0.2 and 39.0 pH ranged between 7.1 and 9.2. Dissolved oxygen ranged between 2.45 and 7.57 ml.l⁻¹. Nutrients such as nitrate ranged between 0.04 and 13.21 μM, nitrite ranged between 0.03 and 12.60 μM,

phosphate ranged between 0.10 and 4.28 μM and silicate ranged between 0.93 and 76.41 μM. Suspended particulate matter ranged between 6.05 and 120.5 mg.l⁻¹ and chlorophyll-*a* concentration ranged between 0.45 and 11.51 mg.m⁻³. Settlement and recruitment of barnacles did not show any significant correlations with environmental variables except for salinity and chlorophyll-*a* concentrations at station Dona Paula (*P* < 0.05).

Daily rainfall patterns over the study region during the period 2005–2007 are shown in Figure 16. Rainfall per hour ranged between 0.025 and 6.40 mm during 2005 and 0.02 and 8 mm during 2006. During 2005 the peak in rainfall was observed during June and September, whereas during 2006, the peak in rainfall was observed at the end of May. In general there was a variation in rainfall patterns between the years.

DISCUSSION

Settlement and recruitment of barnacles varied significantly on a temporal scale monitored. In general, settlement and recruitment was lower during the monsoon season. Consistency in settlement and recruitment was mostly observed during the pre-monsoon season and it coincided

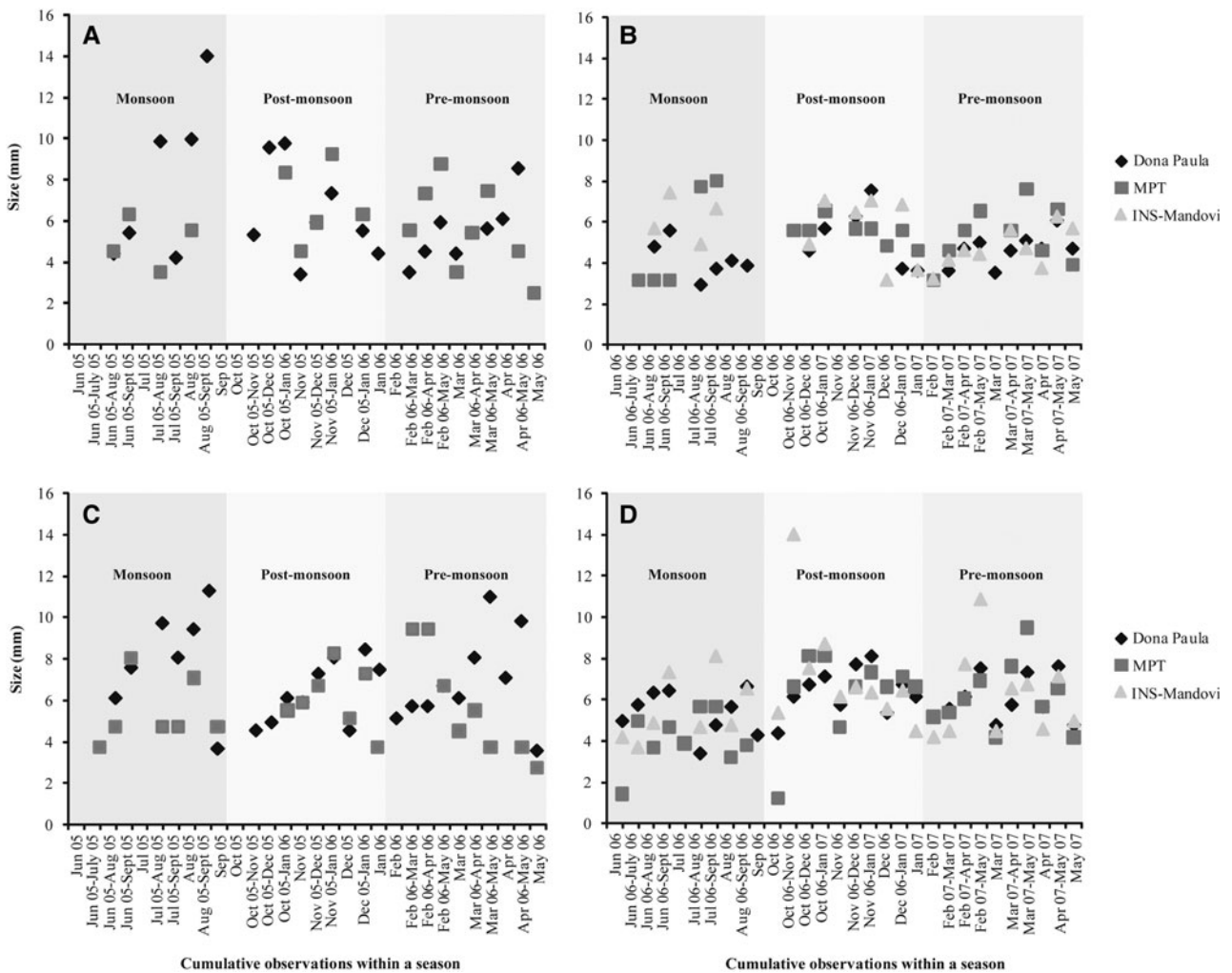


Fig. 12. Seasonal observations of sizes of barnacle recruits on acrylic panels during (A) 2005–2006 and (B) 2006–2007, and aluminium panels during (C) 2005–2006 and (D) 2006–2007.

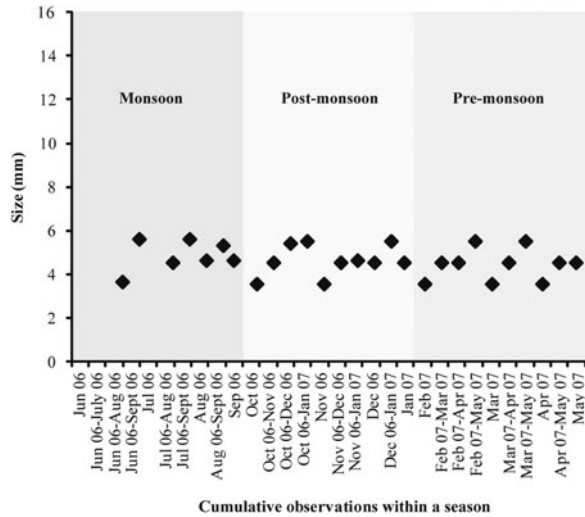


Fig. 13. Seasonal observations of sizes of barnacle recruits at station Arambol during 2006–2007.

with maximum larval abundance observed during the same season. Successful settlement and subsequent recruitment of barnacles in a particular region is governed by various pre and post-settlement factors which operate over different spatial and temporal scales. Physical transport processes can generate variations in settlement and recruitment of barnacles over different scales. Wind-induced larval transport can also cause variations in settlement and recruitment of barnacles. Differences in the retention or dispersal of larvae at different locations by area-specific hydrodynamic processes or by behavioural preferences of the larvae at settlement can also influence the recruitment of barnacles. In several studies, such variability in settlement and recruitment has been reported

(e.g. Connell, 1961a, b; Gaines *et al.*, 1985; Pineda, 1994; Jenkins *et al.*, 2000). A recent study carried out in the region on larval distribution and the resultant likely settlement using a coupled two-dimensional hydrodynamic and particle tracking model, by incorporating wind and tide data showed that the larval dispersal differed significantly between different seasons. The pattern of larval dispersal in the region varied with wind and resultant current patterns (Gaonkar *et al.*, 2012).

Once the larvae settle in a particular area by selecting a suitable substratum then the rate of recruitment depends not only on the factors which have an influence prior to settlement, but also on post-settlement factors (e.g. Connell, 1985; Minchinton & Scheibling, 1991; Jenkins *et al.*, 2000). Many studies have demonstrated a significant relationship between settlement inputs and their subsequent recruitment. Observations in this study also showed some degree of correlation between settlement and their subsequent recruitment, indicating that variations in recruitment may at least be related to factors which operate prior to settlement and post-settlement. Although recruitment is dependent on settlement inputs, not all of the variations in recruitment could be explained by variations in settlement. Such differences may be caused by differences in physical factors, such as temperature and salinity, and biological factors, such as predation pressure and competition for space by other intertidal organisms and a number of other such factors (Gosselin & Qian, 1997 and references therein).

Settlement and recruitment of the barnacles were both lower during the monsoon season, except during monsoon breaks. Larval abundance in the region was also lower during the monsoon season. However, adults with matured broods have been observed throughout the year in the vicinity (Desai *et al.*, 2006). During monsoon breaks, phytoplankton

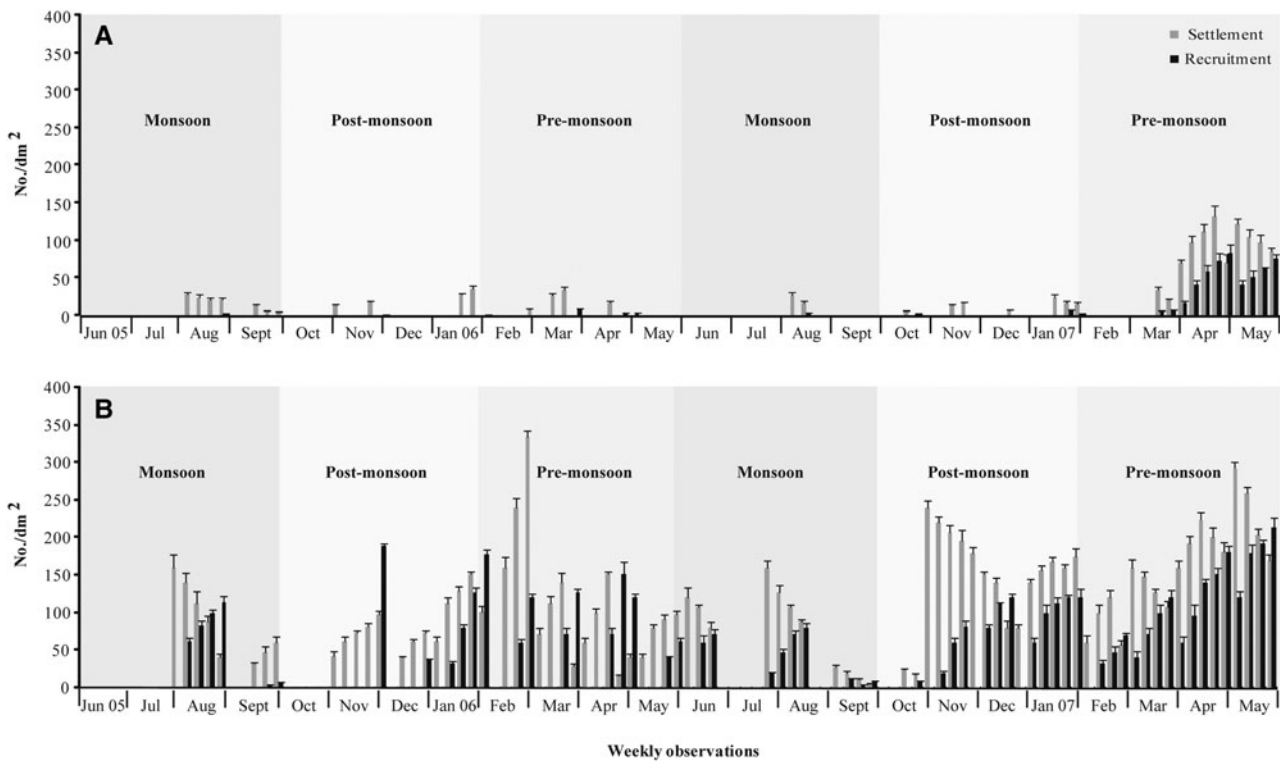


Fig. 14. Weekly observations of settlement and recruitment of barnacles on (A) acrylic and (B) aluminium panels at station Dona Paula.

Table 1. One-way analysis of variance for the (A) settlement and (B) recruitment of barnacles on different substrata (natural rocks, acrylic and aluminium panels) between stations Arambol and INS-Mandovi.

	(A)					(B)				
	df	SS	MS	F	P	df	SS	MS	F	P
Substrata	2	17084.96	8542.481	2.281731	0.117991	2	45879.73	22939.86	5.805871	0.006911
Error	33	123547.4	3743.86			33	130387.9	3951.149		
Total	35	140632.3				35	176267.7			

Table 2. One-way analysis of variance for the (A) settlement and (B) recruitment of barnacles on different substrata (natural rocks, acrylic and aluminium panels) between stations Arambol and Dona Paula.

	(A)					(B)				
	df	SS	MS	F	P	df	SS	MS	F	P
Substrata	2	34588.32	17294.16	5.056183	0.012149	2	29845.52	14922.76	6.410046	0.004447
Error	33	112873.1	3420.398			33	76824.91	2328.027		
Total	35	147461.5				35	106670.4			

Table 3. One-way analysis of variance for the (A) settlement and (B) recruitment of barnacles on different substrata (natural rocks, acrylic and aluminium panels) between stations Arambol and Mormugoa Port.

	(A)					(B)				
	df	SS	MS	F	P	df	SS	MS	F	P
Substrata	2	30217.36	15108.68	3.159349	0.055539	2	40867.19	20433.59	7.771802	0.001715
Error	33	157813	4782.212			33	86763.48	2629.196		
Total	35	188030.4				35	127630.7			

blooms are known to be triggered in the area. These blooms can serve as a food source for the newly released larvae and can also regulate the size of the larval pool in the region and determine the availability of cyprids at the shore (Desai & Anil, 2005). However, the settled barnacles did not recruit themselves successfully due to the onset of rains again after the short break periods. This indicates that the barnacles that settled during the monsoon break period were stressed due to the recurrence of low salinity and turbid conditions, indicating that synchronized release of larvae by the adults during bloom periods may not be a completely reliable mechanism in this region as discussed in detail by Desai & Anil (2005).

An inter-annual variation in settlement and recruitment of barnacles was also observed during the study period. In general consistency in settlement and recruitment was mostly observed during 2006–2007 when compared to 2005–2006. Correlation between settlement and subsequent recruitment was found to be weak during 2005–2006 when compared to 2006–2007. Such inter-annual differences observed in settlement and recruitment could probably be due to the pattern of rainfall observed between the years. There was a fluctuation in the amount of rainfall between the years. Such fluctuations in rainfall patterns could be due to the variations in the south-west monsoon winds. The resultant current patterns can lead to differential supply of larvae or the retention of released larvae in a particular locality, thereby leading to variations in settlement and recruitment of barnacles. Such variations in rainfall can also lead to differential water quality parameters such as temperature, salinity, turbidity and nutrient concentrations and this, in turn, can alter the phytoplankton abundances in the region which is

an important source of food for the larvae as well as juveniles and adult populations (Gaonkar *et al.*, 2010a, b; Gaonkar, 2012).

Feeding studies of barnacle larvae carried out in the region by monitoring the faecal pellets egested by freshly captured larvae indicated that the percentage of defecating larvae (an indicator of food consumed) was comparatively higher during the pre-monsoon season (Gaonkar & Anil, 2010). Generally this season is characterized by lower chlorophyll-*a* concentrations. However, the average number of faecal pellets defecated by a larva remained constant irrespective of the season (Gaonkar & Anil, 2010). The consistency observed in settlement and recruitment of barnacles during the pre-monsoon season coincided with higher percentage of defecating larvae and the absence of diatom frustules in the faecal pellets. This showed the capability of larvae to survive on food sources other than diatoms. Moreover, the gut fluorescence observations of larvae collected from the region indicated that the chlorophyll-*a* content of the larval gut was higher during the post-monsoon season when compared to pre-monsoon season (Gaonkar & Anil, 2012). This indicates that during the pre-monsoon season, larvae survived on food sources other than autotrophic forms. These studies showed the survival capabilities of larvae on a wide range of food sources and this can influence the settlement and subsequent recruitment of barnacles.

In general, settlement remained more or less similar on different types of substrata whereas recruitment differed significantly. Substratum variability is generally considered as one of the important factors that can influence the settlement and recruitment of biofouling organisms. In this study we used aluminium and acrylic panels as substratum

Table 4. One-way analysis of variance for the settlement of barnacles on different panels (acrylic and aluminium) at stations (A) INS-Mandovi, (B) Dona Paula and (C) Mormugoa Port.

	(A) df	SS	MS	F	P	(B) df	SS	MS	F	P	(C) df	SS	MS	F	P
Substrata	1	7608.907	7608.907	2.087429	0.162609	1	62942.15	62942.15	17.8121	0.000114	1	85261.02	85261.02	20.72829	0.000038
Error	22	80192.41	3645.109			46	162549	3533.675			46	189210.4	4113.269		
Total	23	87801.31				47	225491.2				47	274471.4			

Table 5. One-way analysis of variance for the recruitment of barnacles on different panels (acrylic and aluminium) at stations (A) INS-Mandovi, (B) Dona Paula and (C) Mormugoa Port.

	(A) df	SS	MS	F	P	(B) df	SS	MS	F	P	(C) df	SS	MS	F	P
Substrata	1	45472.02	45472.02	8.020645	0.009701	1	67425.02	67425.02	23.6219	0.000014	1	63607.79	63607.79	18.58947	0.000084
Error	22	124726.2	5669.372			46	131299.8	2854.344			46	157398.6	3421.71		
Total	23	170198.2				47	198724.8				47	221006.4			

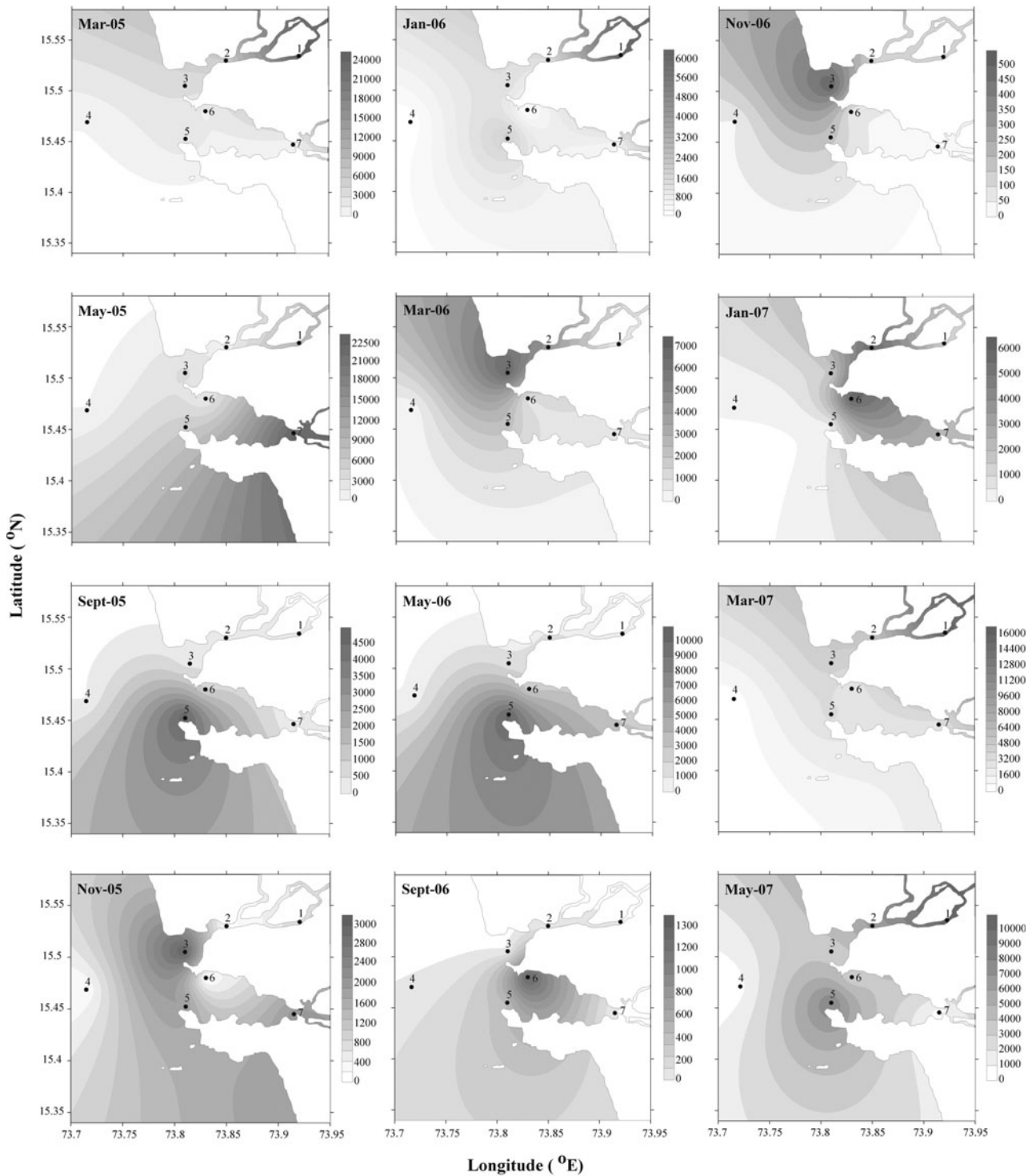


Fig. 15. Larval abundance (cirripede nauplii) (No./100 m³) in the field during different months at different stations for the period 2005–2007.

at three of the locations and naturally available substratum (rock) at one of the locations to evaluate the settlement and recruitment of barnacles, owing to different exposure settings available at these localities. In spite of this, the overall settlement and recruitment patterns remained the same irrespective of the type of substrata (significant temporal variations in settlement and recruitment of barnacles were observed on all types of substrata). However, little variations observed between different types of substrata at different stations could be due to the differential larval

retention patterns observed between these stations (Gaonkar *et al.*, 2012).

Density wise, settlement and recruitment was lower on acrylic compared to aluminium panels. However, the barnacles which settled on acrylic panels grew well at station Dona Paula. This could probably be due to less crowding on acrylic compared to aluminium panels. Size-ranges of the barnacles during August–September period were also found to be bigger (9–14 mm) compared to other months on both acrylic and aluminium panels (during 2005–2006 period) at station Dona

Table 6. Environmental variables from the study region during different sampling period (Stations: 1. Old Goa, 2. Panjim bridge, 3. Miramar, 4. Offshore, 5. MPT, 6. Dona Paula, 7. Zuari bridge).

	Stations/ months	March 2005	May 2005	September 2005	November 2005	January 2006	March 2006	May 2006	September 2006	November 2006	January 2007	March 2007	May 2007
Temperature (°C)	1	29.6	32.7	27.2	28.3	36.2	31.0	28.0	28.0	30.0	29.0	34.0	30.0
	2	29.2	31.1	28.3	28.4	26.4	29.6	29.0	29.2	30.0	27.0	33.0	31.5
	3	29.0	30.8	28.1	28.5	26.5	30.0	30.0	28.5	30.0	28.5	32.0	30.0
	4	28.7	29.9	28.3	28.2	27.7	29.6	30.0	28.0	30.0	29.5	32.0	31.0
	5	28.5	31.9	27.0	28.2	27.3	29.4	30.0	28.8	30.0	29.0	31.0	31.0
	6	29.3	31.5	28.1	28.7	27.0	29.8	30.0	28.6	28.0	29.5	31.0	30.0
	7	30.0	32.5	28.8	28.8	27.0	32.0	29.0	30.0	30.0	29.5	30.0	30.0
pH	1	8.3	8.3	7.1	8.2	8.4	8.0	8.4	7.5	7.2	7.5	8.2	8.4
	2	8.4	7.8	7.6	8.2	8.5	8.4	8.6	7.8	7.3	7.5	8.5	8.6
	3	8.5	8.0	7.9	8.3	8.5	8.3	8.8	7.9	7.2	7.6	8.3	8.8
	4	8.4	8.3	8.7	8.2	8.6	8.4	9.0	8.0	7.9	7.6	8.6	9.0
	5	8.5	8.0	8.6	8.4	8.6	8.4	8.7	8.0	8.0	7.5	8.6	8.8
	6	8.4	8.4	8.4	8.3	8.5	8.3	9.1	7.9	7.8	7.5	8.5	9.2
	7	8.3	8.0	8.3	8.0	8.1	8.0	9.0	7.5	8.0	7.6	8.2	9.0
Salinity (ppt)	1	30.0	33.3	0.2	18.0	23.2	24.3	0.4	0.2	14.0	25.0	28.0	33.3
	2	34.0	36.0	3.7	33.3	33.3	34.6	10.0	7.3	25.0	31.0	34.0	35.1
	3	34.2	35.3	5.5	33.3	33.0	33.9	17.0	17.8	30.0	35.0	37.0	35.3
	4	35.5	36.7	12.9	36.7	33.5	35.2	31.0	35.0	35.0	39.0	38.0	36.6
	5	34.4	36.0	17.9	36.0	34.1	34.6	31.0	20.6	34.0	37.0	36.0	36.0
	6	34.5	36.0	17.7	34.0	33.0	34.3	27.0	17.9	33.0	35.0	37.0	36.0
	7	33.2	34.7	3.9	32.0	26.7	28.4	21.0	10.0	29.0	28.0	35.0	34.7
Dissolved oxygen (ml. l ⁻¹)	1	2.45	3.64	3.19	2.85	4.55	4.10	4.67	2.90	2.50	3.76	2.85	4.10
	2	2.85	3.76	2.96	2.62	4.04	4.44	4.78	2.73	3.02	4.21	3.85	3.76
	3	2.79	3.76	3.19	2.62	4.55	3.98	5.63	3.41	3.56	4.50	2.85	3.87
	4	2.85	2.73	3.24	2.62	4.44	4.44	6.60	3.19	3.62	4.55	2.79	3.76
	5	2.85	3.76	2.73	3.02	4.21	4.21	5.46	3.19	2.85	4.55	2.45	3.64
	6	2.85	3.87	3.41	2.56	4.50	4.15	7.57	2.96	3.62	4.04	3.85	4.76
	7	2.85	4.10	2.90	2.50	3.76	4.55	7.00	3.24	2.62	4.44	3.85	2.73
Nitrate (μM)	1	1.27	0.07	0.05	0.25	0.84	1.59	0.09	8.5	0.25	0.2	1.74	9.4
	2	0.09	0.00	0.20	0.49	0.58	0.09	0.00	13.21	0.54	4.08	1.34	3.73
	3	0.09	0.42	0.08	0.66	0.59	0.08	0.30	5.34	0.25	3.22	1.22	2.93
	4	0.09	0.06	0.05	0.57	0.28	0.06	0.04	0.35	0.54	3.16	1.36	6.2
	5	0.08	0.30	0.17	0.25	0.2	0.09	0.06	2.04	0.57	1.42	0.86	1.9
	6	0.12	0.04	0.04	0.50	0.4	0.09	0.42	3.11	0.66	1.34	1.28	6.53
	7	0.06	0.04	0.08	0.54	1.77	0.12	0.04	4.68	0.50	0.11	0.49	1.8
Nitrite (μM)	1	0.00	0.44	6.44	2.25	3.34	0.69	1.35	0.25	2.79	0.24	0.67	1.35
	2	0.23	0.42	12.60	1.43	1.75	0.54	0.44	0.33	2.36	0.3	0.63	0.44
	3	0.25	0.63	3.67	1.63	1.83	0.38	0.36	0.24	2.38	0.51	0.32	0.36
	4	0.09	0.30	0.63	0.45	0.88	0.4	0.24	0.54	0.45	1.23	0.4	0.16
	5	0.00	0.18	9.82	0.79	1.08	0.28	0.28	0.27	0.98	0.55	0.24	0.51
	6	0.00	0.10	0.03	2.36	1.86	0.35	0.25	0.25	1.63	0.2	0.28	0.71
	7	0.00	12.53	2.01	2.67	3.7	0.76	12.33	0.33	1.43	0.55	0.83	1.27
Phosphate (μM)	1	0.24	0.13	0.57	0.78	1.36	0.35	0.63	0.8	1.58	0.76	0.43	0.54
	2	0.28	0.05	2.03	1.02	0.79	0.30	0.87	2.08	0.59	0.6	0.43	0.97
	3	0.20	0.18	0.60	4.17	0.63	0.20	0.89	2.03	1.28	0.54	0.32	0.97
	4	0.10	0.20	0.55	0.66	0.46	0.39	0.49	0.68	0.76	0.5	0.43	0.54
	5	0.15	0.26	0.98	0.49	0.49	0.39	0.30	1.55	1.10	0.58	0.43	1.84
	6	0.24	0.15	0.90	1.04	0.82	0.89	0.15	1.84	4.28	0.97	0.97	1.51
	7	0.23	0.20	0.18	1.41	1.39	0.25	0.38	1.79	0.98	1.25	0.22	1.62
Silicate (μM)	1	2.07	3.28	30.27	22.99	24.61	2.11	4.58	30.5	30.55	12.09	10.23	24.37
	2	1.93	5.93	76.41	9.22	5.26	1.18	7.93	64.95	10.32	4.5	5.77	9.3
	3	2.56	2.67	22.97	6.14	5.71	1.46	3.57	50.5	7.25	3.91	2.6	15.44
	4	4.17	5.25	15.59	4.74	4.49	4.15	6.90	25.05	5.75	7.25	0.93	11.72
	5	1.18	1.37	19.56	3.04	4.64	1.93	1.49	33.62	4.98	9.86	3.16	18.97
	6	1.46	1.32	15.00	5.61	9.16	2.56	1.61	33.24	6.85	8.45	2.79	15.44
	7	2.01	1.51	9.05	14.77	21.85	2.07	2.45	37.63	17.45	21.2	5.39	18.79
Suspended particulate matter (mg. l ⁻¹)	1	16.37	12.07	3.05	19.30	30.33	19.58	14.16	55.9	36.60	40.49	13.55	19.76
	2	15.53	14.87	5.60	25.83	40.13	15.67	19.00	120.5	37.13	36.25	17.67	16.66
	3	14.97	22.00	9.50	31.50	38.70	15.90	34.00	80.5	33.23	38.35	25.00	15.79
	4	13.73	6.05	10.28	30.33	30.80	14.97	12.75	12.55	23.96	40.13	19.05	15.90
	5	14.57	8.00	19.10	28.37	38.53	16.37	18.00	34.5	29.76	30.37	17.58	18.49
	6	14.77	9.00	11.95	33.10	35.13	15.53	17.77	25.5	35.40	36.25	16.87	17.48
	7												

Continued

Table 6. Continued

	Stations/ months	March 2005	May 2005	September 2005	November 2005	January 2006	March 2006	May 2006	September 2006	November 2006	January 2007	March 2007	May 2007
Chlorophyll- <i>a</i> (mg/m ³)	7	15.57	18.00	9.93	26.87	30.37	14.86	18.86	21.5	19.30	38.25	18.49	15.56
	1	4.08	9.35	0.45	7.25	9.83	3.47	4.73	0.50	3.40	5.67	4.57	4.40
	2	2.98	4.33	2.75	1.07	5.47	4.20	4.40	0.90	3.73	5.33	4.10	4.43
	3	3.54	8.89	2.04	3.87	5.98	4.23	3.90	1.20	5.77	6.67	3.40	4.30
	4	1.41	4.81	9.25	1.81	1.07	3.00	4.10	1.40	4.90	5.00	2.60	3.70
	5	2.83	6.01	11.51	3.95	1.89	3.07	4.27	1.50	4.93	4.63	3.73	4.23
	6	4.29	3.68	1.66	4.42	5.38	3.50	4.00	1.67	5.33	4.33	4.33	3.57
7	6.84	6.02	6.62	2.55	1.89	4.53	4.30	0.60	5.70	5.97	4.40	3.83	

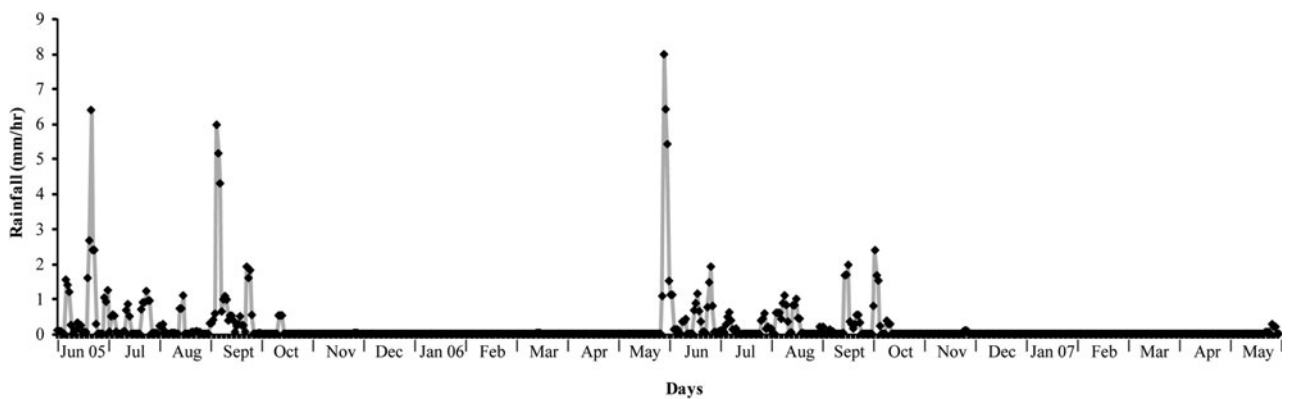


Fig. 16. Daily rainfall patterns over the study area during different sampling period.

Paula. In general barnacle recruits took 3–4 months to attain a maximum size-range of 6–10 mm, except at station INS-Mandovi, where they took 2 months to attain a maximum size of 14 mm during post-monsoon season. Settlement to recruitment proportions also changed during different seasons at most of the stations monitored. Not all of the settled barnacles metamorphosed to recruits. Such differences in settlement to recruitment proportions could be due to various post-settlement factors. At station MPT, the barnacles which settled during the monsoon season did not recruit at all. It is possible that turbidity and low saline conditions during the monsoon can play a significant role in the mortality of settled barnacles.

Wave action can be another cause for the variations observed in settlement and recruitment of barnacles. Sessile organisms like barnacles often become more vulnerable to dislodgement by waves as they age (Shanks & Wright, 1987). As a result, sites with different degrees of wave action will have differences in the settlement and recruitment of barnacles. On the other hand, there is also a possibility that on more exposed shores, water circulation is more intense and the amount of food available can be higher (Sanford *et al.*, 1994), resulting in higher rates of settlement and recruitment of barnacles. Temporal patterns observed among the stations could also be due to differences among the stations with different degrees of wave flushing during different seasons. The study sites in this investigation are also exposed to different degrees of wave actions. Station Dona Paula is located at the mouth of the Zuari estuary which experiences tremendous fluctuations in the intensity of incoming waves during different seasons due to its perennial connection with the Arabian

Sea, whereas station MPT is a port area which is exposed to less fluctuations in wave action due to wave barriers in the surroundings. Station INS-Mandovi is a naval jetty which is located near the mouth of the Mandovi estuary with considerably less degree of wave actions whereas station Arambol is an open rocky shore with direct exposure to incoming waves.

Field observations have shown higher larval abundance mostly at inshore stations during the pre-monsoon season. Simulation results have also shown maximum retention of larvae at these stations during the pre-monsoon season (Gaonkar *et al.*, 2012). Higher larval abundance observed during the pre-monsoon season, both in field and simulation studies coincided with consistency in settlement and recruitment of barnacles during the same season. Little is known regarding the variations in hydrodynamic processes in the near shore environment and the resultant effect on intertidal organisms in this study region, except for the recent study carried out in case of barnacles (Gaonkar *et al.*, 2012). Such processes will influence the settlement rates in addition to nutrients and food supply and thus may influence the population dynamics of intertidal organisms. The present study did not evaluate the effects of all the factors influencing settlement and recruitment of barnacles, suggesting that their effects may not be negligible. Complete understanding of the underlying processes operating in a particular bioregion is essential to scrupulously demonstrate the variations in settlement and recruitment of barnacles in a particular locality. This study points out some of the elemental factors which are responsible for the variations in settlement and recruitment of barnacles in this unique tropical region which is influenced by monsoons.

ACKNOWLEDGEMENTS

We are grateful to Dr S.R. Shetye, Director, National Institute of Oceanography, for his support and constant encouragements. Financial support provided by Ballast Water Management Programme, India (Directorate General of Shipping, Government of India) is gratefully acknowledged. We thank Dr S.S. Sawant, Mr K. Venkat, Mr Kaushal Mapari and other colleagues from the division for their ever-willing help and co-operation during this study. C.A.G. acknowledges the Research Fellowship provided by the Council of Scientific and Industrial Research (CSIR), India. This is a NIO contribution 5285.

REFERENCES

- Anil A.C. (1986) *Studies on marine biofouling in the Zuari estuary (Goa) west coast of India*. PhD thesis. Karnatak University, India.
- Anil A.C., Chiba K., Okamoto K. and Kurokura K. (1995) Influence of temperature and salinity on the larval development of *Balanus amphitrite*: implications in the fouling ecology. *Marine Ecology Progress Series* 118, 159–166.
- Anil A.C., Desai D. and Khandeparker L. (2001) Larval development and metamorphosis in *Balanus amphitrite* Darwin (Cirripedia: Thoracica): significance of food concentration, temperature and nucleic acids. *Journal of Experimental Marine Biology and Ecology* 263, 125–141.
- Bertness M.D., Gaines S.D. and Wahle R.A. (1996) Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series* 137, 103–110.
- Connell J.H. (1961a) Effects of competition, predation by *Thais lapillus* and other factors on natural population of the barnacle *Balanus balanoides*. *Ecological Monographs* 31, 61–104.
- Connell J.H. (1961b) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42, 710–723.
- Connell J.H. (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* 93, 11–43.
- Crisp D.J. (1955) The behaviour of barnacle cyprids in relation to water movements over a surface. *Journal of Experimental Biology* 32, 569–590.
- Daniel A. (1954) The seasonal variation and succession of the fouling communities in the Madras harbour waters. *Journal of Madras University* 24, 189–212.
- Desai D.V. (2002) *Studies on some ecological aspects of Balanus amphitrite (Cirripedia: Thoracica)*. PhD thesis. Goa University, India.
- Desai D.V. and Anil A.C. (2002) Comparison of nutritional status of field and laboratory reared *Balanus amphitrite* Darwin (Cirripedia; Thoracica) larvae and implication of starvation. *Journal of Experimental Marine Biology and Ecology* 280, 117–134.
- Desai D.V. and Anil A.C. (2005) Recruitment of the barnacle *Balanus amphitrite* in a tropical estuary: implications of environmental perturbation, reproduction and larval ecology. *Journal of the Marine Biological Association of the United Kingdom* 85, 909–920.
- Desai D.V., Anil A.C. and Venkat K. (2006) Reproduction in *Balanus amphitrite* Darwin (Cirripedia: Thoracica): influence of temperature and food concentration. *Marine Biology* 149, 1431–1441.
- Fernando S.A. (1990) Systematic status of some fouling barnacles of Indian coastal waters. Marine Biofouling and Power plants. In Nair K.V.K. and Venugopalan V.P. (eds) *Proceedings of the specialists meeting on Marine Biodeterioration with reference to power plant cooling systems*, IGCAR, Kalpakkam, 26–28 April 1989. Kalpakkam–Tamilnadu: Indira Gandhi Centre for Atomic Research, pp. 240–250.
- Gaines S., Brown S. and Roughgarden J. (1985) Spatial variation in larval concentration as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67, 267–272.
- Gaonkar C.A. and Anil A.C. (2010) What do barnacle larvae feed on? Implications in biofouling ecology. *Journal of the Marine Biological Association of the United Kingdom* 90, 1241–1247.
- Gaonkar C.A., Sawant S.S., Anil A.C., Venkat K. and Harkantra S.N. (2010a) Changes in the occurrence of hard substratum faunal composition: a case study from Mumbai harbour, India. *Indian Journal of Marine Science* 39, 74–84.
- Gaonkar C.A., Venkat K. and Anil A.C. (2010b) Changes in the abundance and composition of zooplankton from the ports of Mumbai, India. *Environmental Monitoring and Assessment* 168, 179–194.
- Gaonkar C.A. (2012) *Studies on settlement and recruitment of the barnacle Balanus amphitrite*. PhD thesis. Goa University, India.
- Gaonkar C.A. and Anil A.C. (2012) Gut fluorescence analysis of barnacle larvae: an approach to quantify the ingested food. *Estuarine, Coastal and Shelf Science* 111, 147–150.
- Gaonkar C.A., Samiksha S.V., George G., Aboobacker V.M., Vethamony P. and Anil A.C. (2012) Numerical simulations of barnacle larval dispersion coupled with field observations on larval abundance, settlement and recruitment in a tropical monsoon influenced coastal marine environment. *Journal of Marine Systems* 94, 218–231.
- Gosselin L.A. and Qian P. (1997) Juvenile mortality in benthic marine invertebrates. *Marine Ecology Progress Series* 146, 265–282.
- Iyengar S., Gopalkrishnan V. and Kelkar V.M. (1957) Studies on marine fouling organisms in Bombay Harbor. *Defence Science Journal* 7, 123–139.
- Jenkins S.R., Aberg P., Cervin G., Coleman R.A., Delany J., Della S.P., Hawkins S.J., LaCroix E., Myers A.A., Lindegarth M., Power A.M., Roberts M.F. and Hartnoll R.G. (2000) Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. *Journal of Experimental Marine Biology and Ecology* 243, 209–225.
- Karande A.A. (1965) On cirripede crustaceans (barnacles) an important fouling group in Bombay waters. *Proceedings of the Symposium on Crustaceans* 4, 1245–1252.
- Levin S. (1992) The problem of pattern and scale in ecology. *Ecology* 72, 1943–1967.
- Menon N.R., Katti R.J. and Shetty H.P.C. (1977) Ecology of marine fouling in Mangalore waters. *Marine Biology* 41, 127–140.
- Minchinton T.E. and Scheibling R.E. (1991) The influence of larval supply and settlement on the population structure of barnacles. *Ecology* 72, 1867–1879.
- Nair N.V. (1965) Marine fouling in Indian waters. *Journal of the Marine Biological Association of the United Kingdom* 24, 483–488.
- Parsons T.R., Maita Y. and Lalli C.M. (1984) *A manual of chemical and biological methods for seawater analysis*. Oxford: Pergamon Press.
- Pineda J. (1994) Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. *Marine Ecology Progress Series* 107, 125–138.
- Sanford E., Bermudez D., Bertness M.D. and Gaines S.D. (1994) Flow, food supply and acorn barnacle population dynamics. *Marine Ecology Progress Series* 104, 49–62.

Shanks A.L. (1998) Abundance of post-larval *Callinectes sapidus*, *Penaeus* spp., *Uca* spp., and *Libinia* spp. collected at an outer coastal site and their cross-shelf transport. *Marine Ecology Progress Series* 168, 57–69.

Shanks A.L. and Wright W.G. (1987) Internal-wave mediated shoreward transport of cyprids, megalopae and gammarids and correlated long-shore differences in the settling rate of intertidal barnacles. *Journal of Experimental Marine Biology and Ecology* 114, 1–13.

Sokal R.R. and Rohlf F.J. (1981) *Biometry*. 2nd edition. San Francisco, CA: W.H. Freeman.

Thompson R., Norton T. and Hawkins S. (1998) The influence of epilithic microbial films on the settlement of *Semibalanus balanoides*

cyprids—a comparison between laboratory and field experiments. *Hydrobiologia* 376, 203–216.

and

Wellington G.M. and Victor B.C. (1988) Variation in components of reproductive success in an undersaturated population of coral-reef damselfish—a field perspective. *American Naturalist* 131, 588–601.

Correspondence should be addressed to:

A.C. Anil
CSIR-National Institute of Oceanography, Dona Paula, Goa
403 004, India
email: acanil@nio.org