

## **Resilience potential of an Indian Ocean Reef: An assessment through coral recruitment pattern and survivability of juvenile corals to recurrent stress events**

**Manikandan Balakrishnan<sup>1</sup>, Ravindran Jeyaraman\*<sup>1</sup>, Vidya Pottekkatt Jayabalan<sup>1</sup>,  
Shrinivasu Selvaraju<sup>2</sup>, Manimurali Rajagopal<sup>1</sup>, Paramasivam Kaliyaperumal<sup>2</sup>**

<sup>1</sup>CSIR- National Institute of Oceanography, Dona Paula, Goa- 403004, INDIA

<sup>2</sup>Marine Biology Regional Centre, Zoological Survey of India, Chennai – 600028, INDIA

\**Communicating Author*: Dr. J. Ravindran, email: [jravi@nio.org](mailto:jravi@nio.org); Phone no: +91-9791570076

### **Abstract**

Coral reefs are degraded by the synergistic action of climate and anthropogenic stressors. The coral cover in Palk Bay reef at Northern Indian Ocean largely declined in the past decade due to frequent bleaching events, tsunami and increased fishing activities. In this study, we carried out a comparative assessment to assess the differences in the recovery and resilience of three spatially distant reefs *viz.* Vedhalai, Mandapam and Pamban along Palk Bay affected by moderate, severe and low fishing pressure respectively. The assessment was based on the juvenile coral recruitment pattern and its survivability combined with availability of hard substratum, live coral cover and herbivore reef fish stock. Vedhalai reef has the highest coral cover ( $14.6 \pm 6.3\%$ ) and  $\geq 90\%$  of the live corals in Vedhalai and Mandapam were affected by turf algal overgrowth. The density of herbivore reef fish was low in Vedhalai and Mandapam reefs compared to Pamban reef with relatively few grazing species. The juvenile coral diversity and density were high in Pamban reef and low in Vedhalai and Mandapam reefs despite high hard substratum cover. In total, 22 species of juvenile corals of 10 genera were recorded in Palk Bay. Comparison of the species diversity of juvenile corals with adult ones suggested that the Pamban reef is connected with other distant reefs whereas Vedhalai and Mandapam reefs were self-seeded. There was no statistically significant difference in the survivability of juvenile corals between the study sites and in total  $\geq 90\%$  of the juvenile corals survived the high sedimentation stress triggered by the northeast monsoon and bleaching stress that occurred recurrently. Our results indicated that the human activities indirectly affected the juvenile coral recruitment by degrading the live coral cover and contributed to the spatial variation in the recovery and resilience of Palk Bay reef. Low species diversity of the juvenile corals will increase the vulnerability of Palk Bay reef to species-specific endemic threats.

**Keywords:** Coral, recruitment, resilience, bleaching, Palk Bay, community structure

## **Introduction**

Coral reefs are deteriorating worldwide (Pandolfi et al. 2011; Darling et al. 2013) due to the synergistic effects of natural (McClanahan et al. 2005; Palumbi et al. 2014) and anthropogenic stresses (Wolanski et al. 2009; Hughes et al. 2010) despite their values. Increasing frequency of natural stresses including bleaching, disease outbreaks, storms and cyclones along with anthropogenic stresses such as pollution, sedimentation, coastal development and overfishing have declined the coral cover in the reefs globally (Hughes 1994; Burke et al. 2006). Also, anthropogenic stress had reduced the ability of corals to cope up with the natural stresses and caused dramatic shifts in the species composition (Bak et al. 1984; Alvarado et al. 2004; Norstorm et al. 2009) that in turn affects the recovery and resilience of the reef. A deeper insight in to the synergistic effects of the climate change and anthropogenic stressors on the life history processes of corals such as coral recruitment will enable devising a sound, science based management strategy focussed on strengthening the resilience potential of the reefs.

High coral recruitment rate enables a degraded reef to recover quickly and remain coral dominant despite the type and severity of the disturbance event (Graham et al. 2011). However, variety of environmental stresses such as changes in the reef water quality, added nutrients from run-off waters, overexploitation and coastal development hampers coral recruitment through various processes such as altering the transmission of chemical signals involved in coral reproduction (Richmond 1997), promoting the macroalgal and turf algal growth (Hughes 1994; Szmant 2002; Kuffner et al. 2006) and reducing the coral larval fertilization success due to high sedimentation (Perez et al. 2014, Erftemeijer et al. 2012) respectively. In addition to adequate supply of coral larvae and high recruitment rate, the survivability of the juvenile corals, resisting the climate and local environmental stress also plays a critical role in determining the recovery and resilience potential of a reef.

The Palk Bay reef located in the northern Indian Ocean has the ecological footprints of both climatic and anthropogenic stresses. Palk Bay corals are affected by frequent bleaching events (Kumaraguru et al. 2003, Ravindran et al. 2012), seasonally reversing monsoonal patterns and associated sedimentation (Wilson et al. 2005). In addition, the shallow nature and close proximity of the reef to the shore enabled the local population to easily access the reef for fishing that in turn increased the human pressure on this reef by overfishing and careless boating practices (Manikandan et al. 2014). Collectively, these stressors reduced the overall coral cover, diversity and density of corals in this reef. Recent study by Venkataraman and Rajkumar (2013) revealed reduction in the species richness of corals from 63 species (Pillai 1969) to 31 species.

In this study, we used the recruitment pattern of the juvenile corals and their survivability to the natural stress amidst the human pressure, as an indicator of recovery and resilience. A survey on the juvenile coral assemblage (diversity, density and taxonomic composition), live coral cover and hard substratum cover was undertaken to determine the recovery and resilience of Palk Bay reef and to identify the potential difference in the recovery patterns at the selected study sites along Palk Bay that are influenced by different levels of fishing pressure. In addition, the diversity of adult coral colonies was measured and compared with the juvenile corals to know whether the reefs are self-seeded or connected with other reefs. The fishing pressure was assessed using the standing stock (density) of reef fishes.

## **1. Materials and Methods**

### *1.1. Study sites*

The study was conducted in Palk Bay reef, a part of Gulf of Mannar Marine Biosphere Reserve located at the northern Indian Ocean (9°55'-10°45' N and 78°58'- 79°55' E). The Palk Bay reef is a narrow discontinuous reef, running parallel to the shore, 200 – 600 m apart, in the west – east direction for 24 kms. Three spatially distant reefs, Vedhalai, Mandapam and Pamban, 2 - 4 km apart, at an average distance of 500 m away from the shore were selected along Palk Bay and fixed permanently for this study. Vedhalai, Mandapam and Pamban reefs were affected by moderate, severe and low level of fishing activities respectively (Manikandan et al. 2014) such as reef fishing, drifting of boats across the reef to locate fishing cages, trawl boat passage, boat cleaning and shore seine operations (Table 1). Two study sites, atleast 500 m apart, were observed each in Vedhalai (V1 & V2), Mandapam (M1 & M2) and Pamban (P1 & P2) reefs (Fig. 1) and all the samplings were carried out at an average depth of 2.5 m in Vedhalai and 1.5 m in both Mandapam and Pamban reefs using snorkelling and skin diving.

### *1.2. Live coral and hard substratum cover*

We quantified the average percent cover of live corals (LC), hard substratum components (HS) and macroalgae at the selected study sites using 20 m line transects (English et al. 1997). Average percent cover of hard substratum components were derived by pooling the average percent cover of other benthic components such as dead corals, crustose coralline algae and rocks. Four transects were established, two parallel and other two perpendicular to the shore at each study site. Live corals and other benthic forms that fall under the transect were recorded and their average percent cover was calculated. Live corals were identified to the maximum taxonomic resolution

possible using high-resolution photographs and the identification keys described by Veron (2000) and Venkataraman (2003).

### *1.3. Herbivore reef fish*

Reef fishing is dominant among the human induced stress to the corals of Palk Bay. Hence this study focussed only on the standing stock of herbivore reef fish. The standing stock of herbivore reef fishes was assessed following the reef fish visual census method on a 50 m belt transect with a width of 2 m on either side of the transect (English et al. 1997). The transect was left undisturbed for 15 minutes to enable the fishes to retain their normal behaviour. The density of reef herbivore fishes were enumerated by swimming slowly along the transect and recorded as total number of fishes in 200 m<sup>2</sup> area. The fishes were identified to the highest taxonomic resolution possible in the field and identified up to species level using photographs and videos. Survey on the standing stock of herbivore reef fish was conducted between March – September in 2014. Sea conditions during rest of the months in 2014 were unsupportive to conduct underwater observations.

### *1.4. Coral recruitment pattern*

Portable quadrats of size (1m X 1m) were used to determine the density and diversity of juvenile corals in the study sites. Corals,  $\leq 5$  cm in diameter were considered for this study with a presumed growth rate of 1-3 mm diameter every month (Moulding 2005; Bak and Engel 1979). In total, 20 quadrats were placed randomly within each study site, atleast 5 m apart and the number of juvenile corals within each quadrat was enumerated, measured to their nearest size (mm) and identified to the maximum taxonomic resolution possible underwater. The juvenile corals were also photographed using Olympus camera (Model:  $\mu$ tough 8000) in underwater macro mode for identification. The average density was expressed as number of juvenile corals m<sup>-2</sup> averaged over the total number of quadrats at each study site. The taxonomic composition was calculated and expressed as the average percentage of juvenile corals in each species relative to the total number of juveniles in other species.

### *1.5. Survivability of juvenile corals*

The survivability of juvenile corals was tested against the high sedimentation stress triggered by Northeast (NE) monsoon that falls between October to December every year and bleaching stress during the summer (March – June). Individual juvenile corals were tagged using numbered plastic tags in September 2013. In total, 600 juvenile corals were tagged by nailing the numbered polypropylene tags at a rate of 100 juveniles at each study site. The tagged juvenile corals were visually and digitally observed post- NE monsoon during April 2014 to estimate their survivability.

The survivability was assessed by visually counting the number of juvenile corals that were alive, dead and partially dead relative to the total number of juvenile corals that were tagged alive before the NE monsoon. The tagged juvenile corals were continuously observed every 8 days from March to September 2014 for their bleaching and recovery response. Vulnerability of juvenile corals to bleaching was expressed as the percentage of juvenile corals that were bleached and remained unresponsive to bleaching relative to the total number of juvenile corals tagged. The survivability of juvenile corals post bleaching was assessed following the same method described above for the sedimentation stress.

#### *1.6. Environmental conditions during the stress events*

Palk Bay reef is influenced by both Southwest (SW) and NE monsoon. During NE monsoon, the wind generated waves stir up the bottom sediments and leave them in suspension, thereby increasing the level of suspended sediments in the water column and the rate of sedimentation over corals. It is not possible to determine the rate of sedimentation by deploying sediment traps due to high wave action and poor visibility during NE monsoon. Hence, the amount of total suspended solids (TSS mg/l) in the water column was measured. Also, TSS was measured during the pre (June 13 – September 13) and post NE monsoon period (February 14 – May 14) to know the variation in the amount of TSS during different seasons. TSS was determined by filtering out 1 litre of seawater using pre-weighed Millipore filter papers and the filtration was carried out in triplicates. After filtration, the filtrates were dried in an oven at 50 – 60 °C and cooled to room temperature. TSS was calculated from the initial and final weights of the filter paper. Data on sea surface temperature (SST) was obtained from a daily 9 km optimum interpolated global SST (MODIS+TMI) dataset for the period of March 2014- August 2014 ([www.misst.org](http://www.misst.org)). The data was a merged product of both day and night in the Infrared and microwave wavelengths. From those data, average SST for every eight days was calculated and plotted.

#### *1.7. Analysis*

Variations in the average percent cover of different benthic components including live coral cover, density and diversity of juvenile corals, density of reef fish population was compared among study sites using One-way ANOVA with the study site as a fixed factor. Percent cover of various benthic components in each transect was pooled to derive the average percent cover of the benthic components representative of that site. Data on the average percent cover of the benthic components were arcsin square root transformed and checked for the assumptions of ANOVA using residual analysis. Similarly, data on the density of juvenile corals and reef fishes were log transformed before

analysis. We used a standard linear model to determine how juvenile coral density (response variable) was impacted by live coral cover, hard substratum cover, macroalgal cover and herbivore reef fish density (predictor variables). We started with the most complete linear model: Coral recruit density ~ Adult Coral Cover + Macroalgal Cover + Hard Substrate + Herbivore Fish Density. After examining the output, we simplified the model by dropping the least significant factor and running the analysis once again, choosing the most conservative model based on its AIC value. We continued with this process, dropping factors sequentially until we arrived at the most conservative model based on AIC values. The analysis was performed using the statistical software, R, using the package lmer.

Percentage of juvenile corals of different genera at each study site was arranged in a data matrix and it was fourth root transformed. A non-metric multidimensional scaling (nMDS) was used to analyze the juvenile corals assemblage between the study sites at Vedhalai, Mandapam and Pamban reef. Similarity percentage (SIMPER) analysis was used to determine the average dissimilarity between the study sites and the contribution of each species to the observed differences in the species composition of juvenile corals. Analysis was performed using the PRIMER statistical software (V. 6.1.15) described by Warwick and Clarke (1991) and Clarke (1993).

### 3. Results

#### 3.1. Live coral, Macroalgae and Hard Substratum cover

Overall, average live coral cover was  $8.2 \pm 5.8\%$  (Mean  $\pm$  SD) at Palk Bay reef and displayed a statistically significant variation among Vedhalai, Mandapam and Pamban reefs ( $p = 0.01 < 0.05$ ). Mean live coral cover was high in V2 ( $16 \pm 7.8\%$ ) followed by V1 ( $12.8 \pm 4.6\%$ ) and it was low in M2 ( $0.5 \pm 7.7\%$ ). The overall average cover of macroalgae at Palk Bay was  $18.9 \pm 9.6\%$ , comparatively higher than the live coral cover and it do not differ significantly between study sites ( $p$  value =  $0.2 > 0.05$ ). Average macroalgal cover ranges between a minimum of  $2.1 \pm 16.8\%$  to the maximum of  $27.9 \pm 8.92\%$  at the study sites M1 and V2 respectively. The cover of CCA and DCA, collectively termed as hard substratum, showed no significant variation among the Vedhalai, Mandapam and Pamban reefs ( $p$  value =  $0.3 > 0.05$ ) with the lowest cover at M2 ( $10.1 \pm 21.7\%$ ) and highest cover at V1 ( $47.3 \pm 15.5\%$ ). The average percent cover of different reef components at the study sites were presented in the Fig. 2. In total, 166 adult coral colonies of 19 species; 77 colonies of 13 species; and 168 colonies of 28 species were recorded along the transects in the study sites of Vedhalai, Mandapam and Pamban reefs respectively. The adult coral assemblage was dominated by *Leptastrea* sp and *Porites* sp in Vedhalai and Mandapam reefs and *Favites* sp in Pamban reef. The

taxonomic composition of adult corals at the study sites of Palk Bay were given in the supplementary table (ST1).

### 3.2. Herbivore fish population

The overall average density of herbivore reef fish recorded at Palk Bay was  $16.1 \pm 6.2\%$  and it differed significantly between Vedhalai, Mandapam and Pamban reefs ( $p$  value =  $0.01 < 0.05$ ). The density of herbivore fish was low at Mandapam reef, with the highest densities recorded at Pamban reef and it varied from  $7.8 \pm 1.6$  to  $24.3 \pm 8.2$  ( $200 \text{ m}^{-2}$ ) at the study sites (Fig. 3). In total, 14 species of herbivore fishes were recorded from Palk Bay with high diversity at Pamban reef (14 species) and low diversity at Vedhalai reef (8 species). The distribution of different species of herbivore reef fish in the vedhalai, mandapam and pamban reef was provided in supplementary table (ST2).

### 3.3. Juvenile coral assemblage

The average density of juvenile corals ( $\leq 5$  cm in diameter) varied spatially along the Vedhalai, Mandapam and Pamban reefs, ranging from  $1.4 (\pm 2.1 \text{ SD})$  to  $6.2 (\pm 2.1)$  recruits  $\text{m}^{-2}$  and it showed a statistically significant variation ( $p$  value =  $0.0005 < 0.05$ ). The density of juvenile corals was low at Mandapam reef, with highest densities recorded at Pamban reef (Fig. 4). In total, 97 juveniles of 16 species; 68 juveniles of 14 species and 118 juveniles of 22 species were recorded from the quadrats at Vedhalai, Mandapam and Pamban reefs respectively. The species richness of the juvenile corals varied across the study sites from a maximum of 22 species (P2) to a minimum of 9 species (M1). The juvenile coral assemblage was dominated by *Leptastrea* spp. in both Vedhalai and Mandapam reefs. Whereas, *Goniastrea* spp. and *Favites* spp. were abundant in the Pamban reef (Table 2).

Based on the results of standard linear model, the density of juvenile corals was significantly influenced by the herbivore reef fish density and macroalgal cover (Table 3) compared to the other factors at the study sites (ST 3). The juvenile coral density was positively related to the herbivore reef fish density. Whereas, the density of juvenile corals was low at the study sites with high macroalgal cover. There was a high concordance between the study sites V2 and M2 followed by P1 and P2 in their juvenile coral taxonomic composition, as these sites were grouped together in the ordination space with  $>80\%$  and  $>70\%$  similarity respectively (Fig. 5). Results of SIMPER analysis revealed that the juvenile coral assemblage at Pamban reef differed from Vedhalai and Mandapam reefs with an average dissimilarity value of  $31.37\%$  and  $37.93\%$  respectively. Juveniles of *Goniastrea* spp. and *Acropora* spp. have largely contributed to the observed variation in the juvenile coral assemblage between Pamban reef and Vedhalai and Mandapam reefs (Table 4). Vedhalai and

Mandapam reefs differed with an average dissimilarity of 25.01% with a major contribution from *Favites* spp. and *Cyphastrea* spp. to the observed differences.

#### 3.4. Sedimentation stress and survivability of juvenile corals

TSS recorded at the study sites of Vedhalai, Mandapam and Pamban reefs do not differ significantly (p value = 0.6 > 0.05) and it was pooled across the study sites to derive the average TSS, representative of Palk Bay and compared between NE monsoon, pre-NE monsoon and post-NE monsoon. Average TSS levels in the water column during NE monsoon differed significantly from their levels during pre-NE monsoon and post-NE monsoon (p value = 0.001 < 0.05). Average TSS values fluctuated between a maximum of 126.3 mg l<sup>-1</sup> in November 2013 to a minimum of 34 mg l<sup>-1</sup> in April 2014 (Fig. 6a). Overall mortality rate among juvenile corals in response to the sedimentation stress at Palk Bay is 6.8 ± 1.9% and it ranged from 9 ± 2.2% to 4 ± 2.8% between the study sites (Fig. 7a). The mean mortality rate among juvenile corals was high in Pamban reef (7.5 ± 0.68) compared to the Vedhalai (6 ± 0.83) and Mandapam reefs (7 ± 0.17) and it is not statistically significant (p value = 0.7 > 0.05). *Favites* spp. and *Leptastrea* spp. were highly susceptible to sedimentation stress with an average mortality rate of 9.7 ± 2.8% and 7.4 ± 0.5% respectively (Fig. 7b). Individual corallites of the juvenile corals were covered with sand and sediment particles (Fig. 8) suggesting mortality occurred due to the smothering effect of sediments.

#### 3.5. Bleaching stress and survivability of juvenile corals

The average SST at Palk Bay was 28.5 °C during March 2014 and it gradually increased to a maximum of 31.4 °C during the first week of May 2014. The average SST was > 30 °C till the second week of July 2014 and it gradually decreased to a minimum of 28.8 °C by the end of July 2014 (Fig. 6b). Overall, there were statistically significant differences in the proportion of juvenile corals affected by bleaching between the study sites at Palk Bay reef (p value = 0.006 < 0.05). The mean proportion of juvenile corals affected by bleaching ranged from 47 to 63% and the mortality rate varied from a maximum of 3 ± 1.5% to a minimum of 1 ± 0.5% across the study sites and the variation in mortality rate was not statistically significant (p value = 0.13 > 0.5). Both bleaching sensitivity and mortality rate among juvenile corals was high in Pamban reef compared to the Vedhalai and Mandapam reefs (Fig 9a). The common slow growing corals of the genus *Porites* spp. and *Favites* spp. were highly susceptible to bleaching. In total, 76.6 ± 30.6% of the juveniles of *Porites* spp. and 61.7 ± 25.7% of the juveniles of *Favites* spp. were bleached. In contrast, juveniles of the genus *Acropora* spp. and *Cyphastrea* spp. were unresponsive to bleaching and retained their



normal colour. The rate of mortality was high among the *Porites* spp. ( $2.9 \pm 1.6\%$ ) and *Favia* spp. ( $1.1 \pm 0.2$ ) (Fig. 9b).

#### 4. Discussion

The Palk Bay reef is unusual among other Indian reefs in that the close proximity and the shallow nature had enabled the local population to access the reef at low expense. This in turn had increased the fishing pressure that had substantially reduced the overall density of reef fishes in Palk Bay reef. Though the human activities have no direct impact over the reproductive and recruitment potential of the corals, it can indirectly affect the coral recruitment by depleting the coral larval sources (Goreau et al. 2000), altering the water currents and larval dispersal routes, by creating local pollution barriers that reduce the survivability of the coral larvae (Richmond 1993) and by reducing the availability of hard substratum

The overall live coral cover and species diversity of corals in Palk Bay was low compared to the other major reefs in India. Our estimates of live coral cover (LC= 8.2%) was comparatively lower than the earlier records of Palk Bay (LC = 26.7%) (Kumaraguru et al. 2005) and it showed spatial variation across the reef fishing intensity gradients. In general, heavily fished reefs are characterized by low coral cover and low substratum complexity (McClanahan et al. 2001). Like many other reefs in the world, the Palk Bay reef suffered catastrophic coral mortality during the 1998 and 2010 global bleaching events (Arthur 2000; Ravindran et al. 2012). Thereafter, the recovery of Palk Bay reef was not quantified and it suffered from the annual bleaching events and continuous anthropogenic pressure that have caused marked declines in the live coral cover and its diversity.

The species diversity of corals was severely reduced from their earlier record of 63 species (Pillai 1969) to 31 species (Rajkumar and Venkataraman 2013) and the live corals were dominated by the massive coral forms belonging to *Porites*, *Favia* and *Favites* spp. that are stress tolerant (Baker et al. 2008). The morphology of these massive coral forms contribute less to the overall structural complexity of the reef and reduce the refugium available for other reef associated organism such as reef fish (Komyakova et al. 2013). Presence of diverse and healthy coral colonies in a reef enhances its resilience by inhibiting the settlement of other species that reduce coral growth and survival (Philips et al. 2014). In the current scenario, chances that the live coral cover will contribute to the recovery and resilience of Palk Bay reef is low and it requires an adequate supply of coral larvae from other pristine reefs to restore its lost coral diversity.

The density of juvenile corals reported in this study ( $1.4 - 6.2$  recruits  $m^{-2}$ ) was closer to those values reported in Mesoamerican barrier reef (Ruiz-Zarate and Arias Gonzalez 2004);

Biscayne National park (Miller et al. 2000) and Gulf of Thailand (Yeemin et al. 2009). However, juvenile coral densities of 28 to 59.5 recruits  $m^{-2}$  have been reported from other undisturbed reef ecosystems such as Chagos archipelago (Sheppard et al. 2008) and Palmyra atoll (Roth and Knowlton 2009). Variation in the juvenile coral density between Pamban, Vedhalai and Mandapam reefs demand an explanation. Such spatial variations are often explained by numerous factors that include larval production in the parent reef, larval mortality, larval dispersal, their settlement and survival (Underwood and Keough 2001), herbivory (Edmunds and Carpenter 2001), low turbidity and low sedimentation rate (Ruiz-zarate and Arias Gonzalez 2004). Apparently, any of these processes could contribute to the low density of juvenile corals in Vedhalai and Mandapam reefs compared to Pamban reef. The density of the juvenile corals was not dependent on the abundance of adult coral colonies in a reef (Edmunds 2000). In accordance, the density of juvenile corals was low in Vedhalai reef despite the high live coral cover compared to Pamban reef in this study.

Macroalgal cover and reef herbivore fish density showed significant relationships with the density of juvenile corals. Though there is no substantial difference between the macroalgae and hard substratum cover between the Vedhalai, Mandapam and Pamban reefs, the juvenile coral densities showed a marked difference with highest density at Pamban reef and lowest at the Mandapam reef. These spatial variations are likely a consequence of availability of hard substratum that is suitable for the settlement of juvenile corals. The overall density of herbivore reef fishes recorded from Palk Bay ( $16.1 \pm 6.2\%$   $200 m^{-2}$ ) in this study was comparatively lower than GoM reef where reef fishing was banned ( $233 \pm 4.5\%$   $200 m^{-2}$ ) (Manikandan 2015). An earlier study by Manikandan et al. (2014) have revealed the abundant growth of turf algae over the live coral colonies and other hard substrates such as dead coral standing colonies and rocks in the Vedhalai and Mandapam reefs due to low density of reef herbivore fishes. The turf algae, with their ability to trap the suspended sediments (Birrell et al. 2005) from the water column make these hard substratum components unsuitable for the settlement of coral larvae.

Comparison of the diversity of adult coral colonies with juvenile coral diversity revealed that Vedhalai and Mandapam reefs are mostly self-seeded and the Pamban reef is connected to other distant reefs in addition to self-seeding. Specifically, juveniles of *Porites*, *Leptastrea*, *Favia* and *Favites* spp. were more prevalent along the entire Palk Bay reef. Whereas juveniles of *Acropora*, *Goniastrea*, *Galaxea* and *Hydnophora* spp. were recorded only from the Pamban reef. The adult colonies of these species were absent in Pamban reef implying that the larvae of these particular species might arrived from other distant reefs most possibly from the Gulf of Mannar (GoM) reef. The Palk Bay reef is separated from the adjacent coral islands of GoM by the Rameswaram

Island and the waters of GoM and Palk Bay mix through the Pamban pass channel and also through a series of submerged banks between India and Srilanka during NE and SW monsoon respectively (NIO 2012). Flow of water from GoM to Palk Bay and vice versa might facilitate the transport of coral larvae between these reefs. Absence of *Acropora* spp. and *Goniastrea* spp. in Vedhalai and Mandapam reef suggest that these species are often unsuccessful in human- dominated reef environments.

The mortality rate was low among juvenile corals in response to high sedimentation and bleaching stress which occurs recurrently in a short time interval. Majority of the juvenile corals were settled on the vertical substrate and few under the holes and crevices (Personal Observations). The settlement position of the juvenile corals had contributed to their success against high sedimentation during NE monsoon. The juvenile coral colonies were bleached in response to increase in the SST  $\geq 31$  °C. Analysis of the average SST of Palk Bay region since 2006 revealed that the average SST was consistent  $\geq 29$  °C and the values recorded in 2014 is at par with the values recorded during the 2010 El-nino bleaching event (ST 4). During such warm years the growth of juvenile corals is slowed down with subsequent mortality (Edmunds and Gray 2014). However in Palk Bay, the juvenile corals recovered from bleaching with relatively low mortality rate ( $\leq 3\%$ ) and juveniles of *Acropora* spp. showed no signs of bleaching, indicating their adaptive potential.

In conclusion, results of this study suggest that human activities indirectly influenced the diversity and distribution of juvenile corals and contributed to the spatial variation in the recovery patterns of Palk Bay reef. The spatial variation in the recruitment pattern of juvenile corals could have serious implications over the community structure and resilience potential of the Palk Bay reef in future. The factors contributing to the observed variation in the juvenile coral recruitment pattern and its survivability needs further research. The chances that the existing live coral cover will contribute to the recovery and resilience of the Palk Bay reef is very low due to the continuous decrease and increase in the live coral and macroalgal cover respectively. However, the current study found the evidence of reef connectivity in the Pamban reef of Palk Bay which will aid in restoring the lost coral diversity. Survivability of juvenile corals in response to the prevailing stress conditions in Palk Bay is a promising factor of reef resilience and will contribute in restoring the live coral cover. However, less diversity of corals will increase the vulnerability of Palk Bay reef to the species-specific endemic diseases. Loss of corals in such cases will severely affect the Vedhalai and Mandapam reefs where the coral recruitment occurs mostly by self-seeding.

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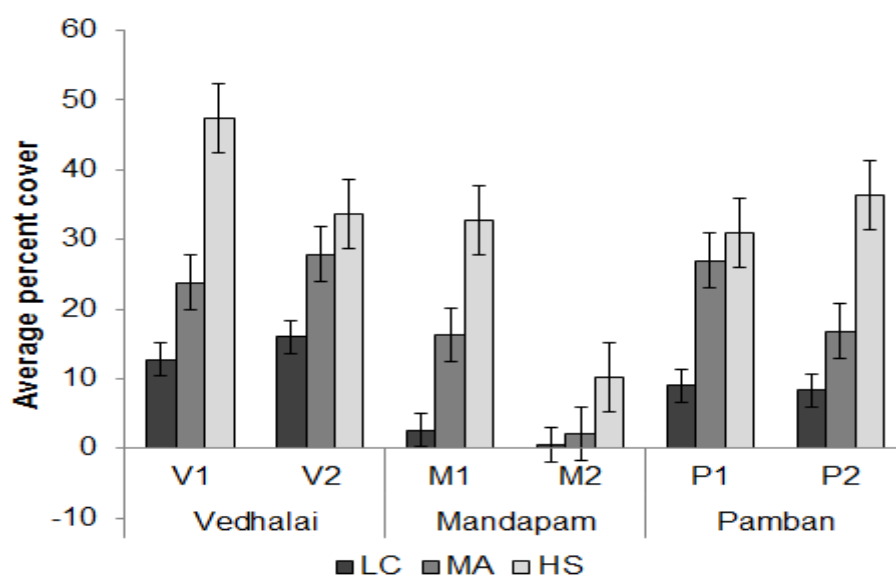
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## Figures

**Fig.1** Map of Palk Bay showing the location of the study sites. (V1 & V2 – Vedhalai reef; M1 & M2 – Mandapam reef; P1 & P2 – Pamban reef).

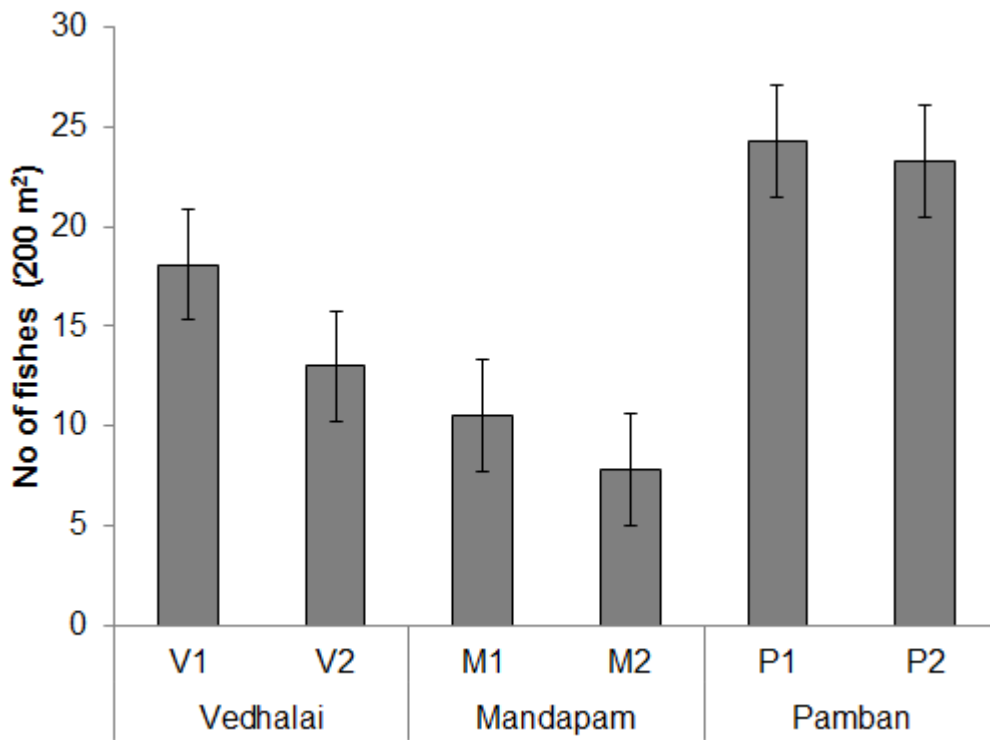


**Fig. 2** Average percent cover of different benthic types at the study sites of Palk Bay. Live corals (LC), Macroalgae (MA) and Hard Substratum components (HS).. Error Bars indicate standard error.

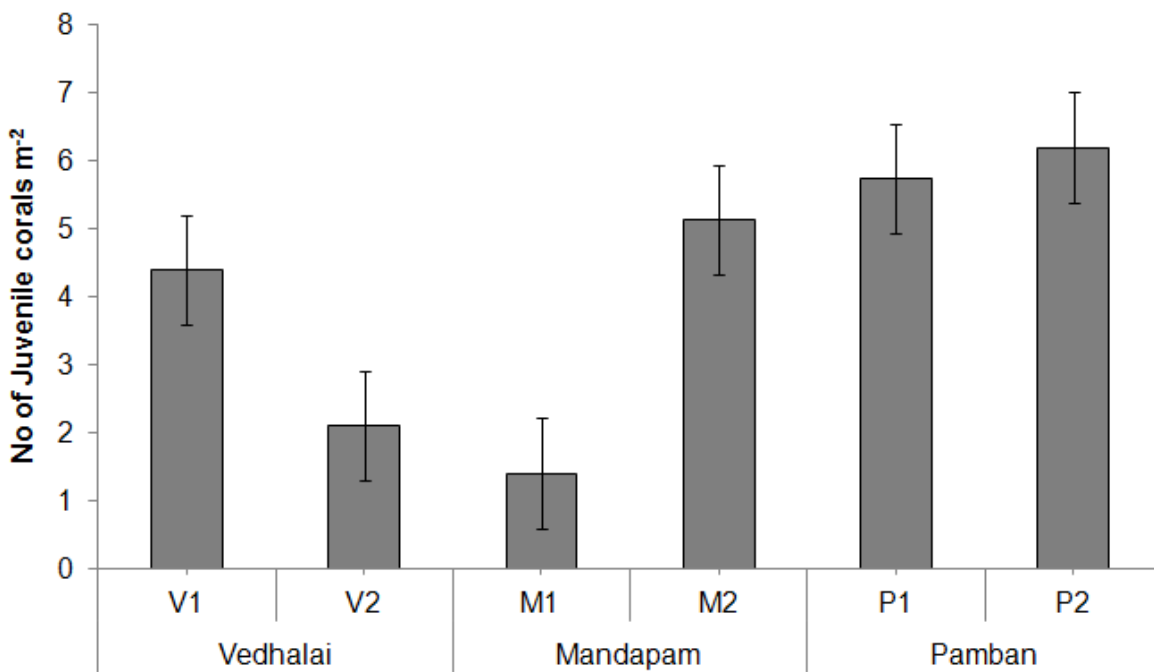




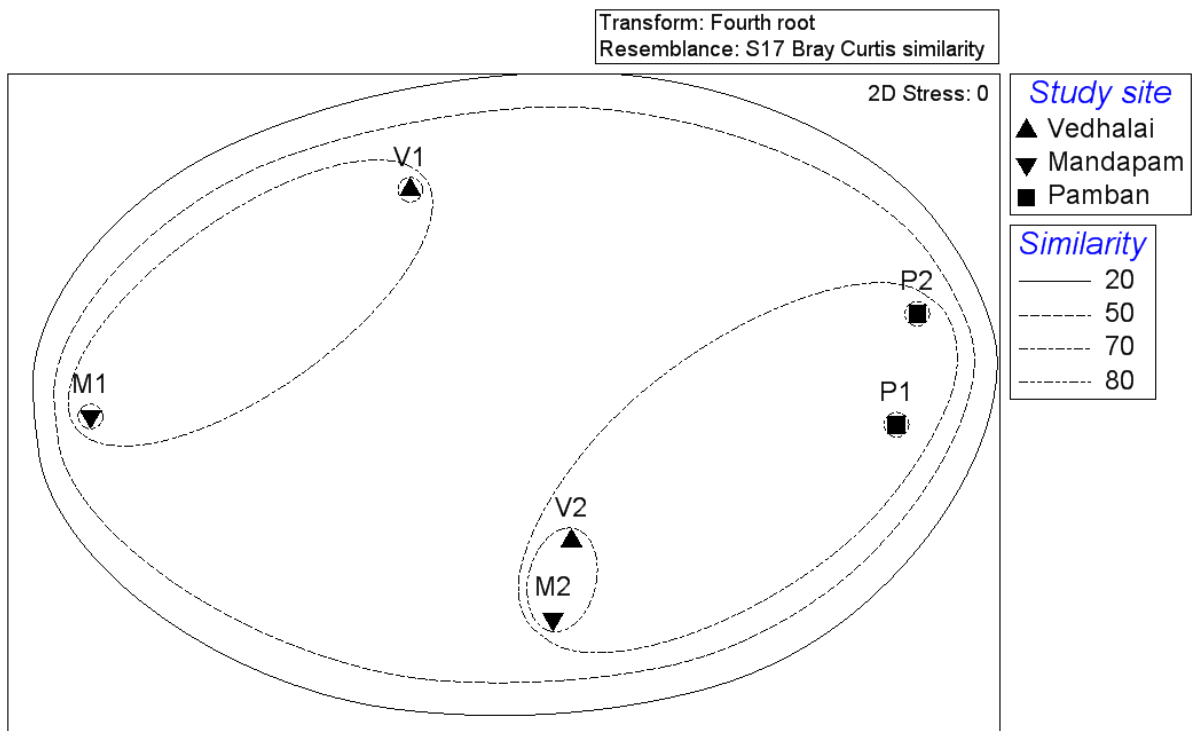
**Fig. 3** Average density of herbivore reef fishes at Palk Bay. Error bars indicate standard error.



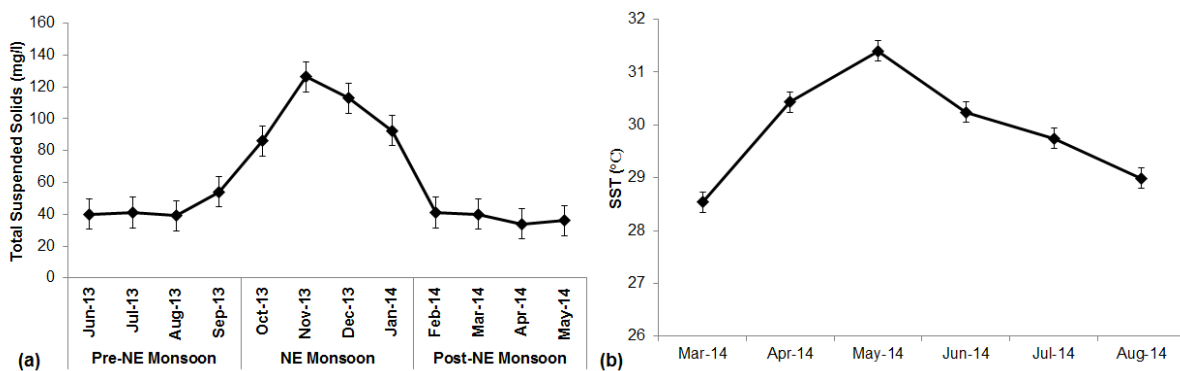
**Fig. 4** Average density of juvenile corals at the study sites of Palk Bay. Error Bars indicate standard error.



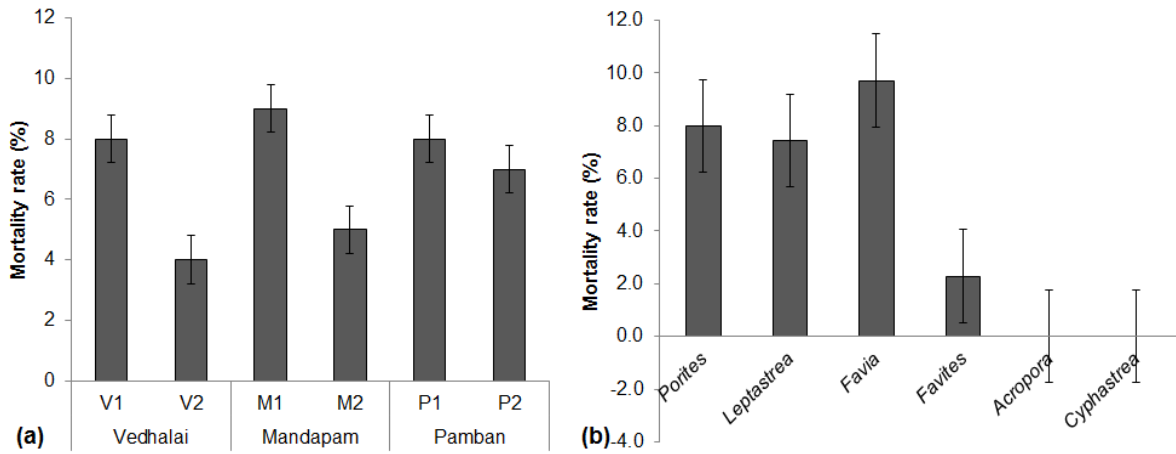
**Fig. 5** non-metric Multidimensional scaling (nMDS) analysis of the study sites at Palk Bay.



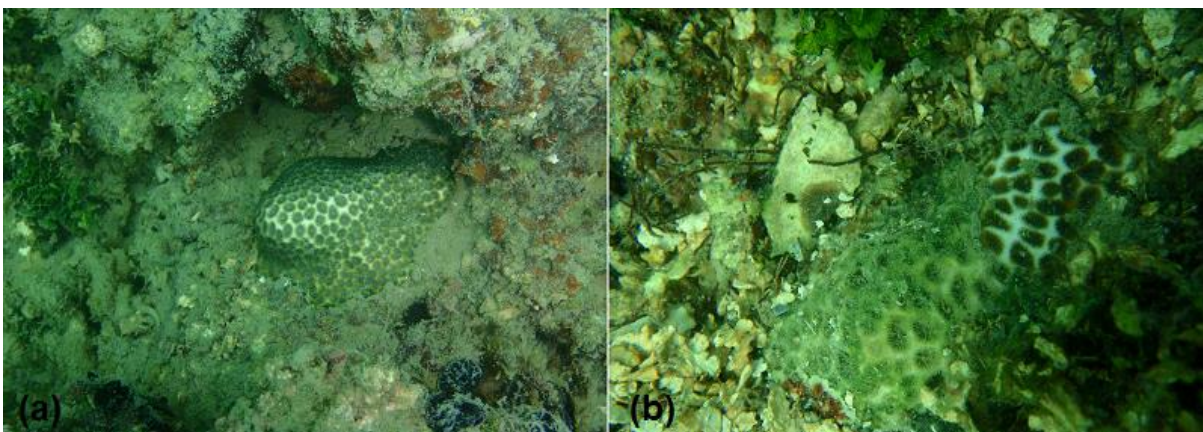
**Fig. 6** Environmental conditions during the stress events. (6a) – Average Total Suspended Solids (TSS mg/l) recorded at Palk Bay; (6b) – Average Sea Surface Temperature (SST) recorded at Palk Bay in 2014. Error bars indicate standard bar.



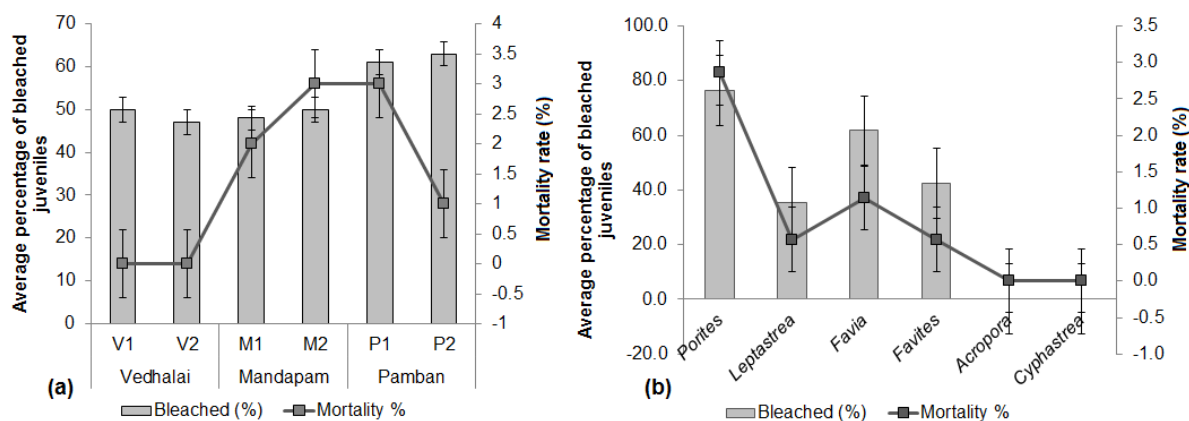
**Fig. 7** Juvenile coral mortality rate in response to sedimentation stress at the study sites Palk Bay (7a); between different species of juveniles recorded from Palk Bay (7b). Error bars indicate standard error.



**Fig. 8** *Leptastrea* sp tagged alive before Northeast (NE) monsoon (8a) observed partially dead after NE monsoon (8b). Individual corallites of the coral colony were covered with sand particles.



**Fig. 9** Average percentage of bleached juveniles and the mortality rate in response to bleaching stress at the study sites of Palk Bay (9a); between different species of juveniles recorded from Palk Bay (9b). Error bars indicate standard error.



**Table 1:** Different types of anthropogenic pressure in Palk Bay

Reef Site	Disturbance Level	Types of Disturbance
Vedhalai	Moderate	Reef fishing, Drifting boats over corals; Macroalgae culturing using bamboo rafts
Mandapam	Severe	Reef fishing, boat drifting, trawl boat operations, boat cleaning, sewage discharge; shore seine operations, trap net fishing
Pamban	Low	Reef fishing using traditional methods

**Table 2:** Taxonomic composition of juvenile corals at the study sites of Palk Bay

<b>Species</b>	<b>V1</b>	<b>V2</b>	<b>M1</b>	<b>M2</b>	<b>P1</b>	<b>P2</b>
<i>Acropora cyatherea</i>	0	0	0	0	1.8	8.3
<i>Acropora digitifera</i>	0	0	0	0	0	5.7
<i>Acropora formosa</i>	0	0	0	0	0.4	5.2
<i>Cyphastrea sp</i>	1.5	6.5	0	2	0	4.9
<i>Favia albidus</i>	0.6	1.5	0.4	1	4.8	2.1
<i>Favia lizardensis</i>	0.8	1.8	0	0	3.6	0.7
<i>Favia pallida</i>	1	2.3	3.1	3.5	6.2	4.3
<i>Favia rotumana</i>	0	0.9	0.1	0.4	4.3	2.4
<i>Favia speciosa</i>	0.4	1.7	1.8	1.1	5.1	3.8
<i>Favia veroni</i>	0.2	1.5	0.3	0.1	2.1	1.3
<i>Favites complanata</i>	0	2.3	0	2.5	3.1	8.3
<i>Favites halicora</i>	1.2	3.1	0	3.2	1.9	4.7
<i>Favites russeli</i>	1.8	2.6	0	5.7	3.8	6.3
<i>Favites vasta</i>	0	1.7	0	4.9	2.1	2.7
<i>Galaxea fascicularis</i>	0	0	0	0	0	2.4
<i>Goniastrea retiformis</i>	0	0	0	0	32.6	4.9
<i>Goniopora minor</i>	1.5	0	0	0	0	2.4
<i>Hydnophoramicroconus</i>	0	0	0	0	0	2.4
<i>Leptastrea aequalis</i>	63.2	31.6	54.9	8.3	6.1	7.4
<i>Leptastrea purpurea</i>	18.6	13.6	31.9	3.9	3.9	7.2
<i>Porites lutea</i>	5.1	19.2	4.1	19.3	8.8	5.2
<i>Porites sp</i>	4	9.8	3.4	44	8.6	7

**Table 3:** Standard Linear model results of the reef factors that impact juvenile coral density at the study sites of Palk Bay

<b>Juvenile coral density</b>	<b>R<sup>2</sup></b>	<b>F ratio</b>	<b>p value</b>	
Model	0.507	10.81	<0.001	
<i>ANOVA table</i>	<i>Sum sq</i>	<i>Df</i>	<i>F value</i>	<i>p</i>
Macroalgae	17.895	1	7.03	<0.01
Herbivores	51.91	1	20.41	<0.01

**Table 4:** Results of SIMPER analysis on the taxonomic composition of juvenile corals at the study sites of Palk Bay reef.

<b>Vedhalai vs Mandapam</b>					
Average dissimilarity = 25.01					
<i>Coral species</i>	<i>Average abundance</i>		<i>Average dissimilarity</i>	<i>% contribution</i>	<i>Cum %</i>
	<i>Vedhalai</i>	<i>Mandapam</i>			
<i>Favia lizardensis</i>	1.05	0	3.04	12.15	12.15
<i>Cyphastrea</i> sp	1.35	0.59	2.44	9.76	21.91
<i>Favites russeli</i>	1.21	0.77	2.37	9.49	31.40
<i>Favites vasta</i>	0.57	0.74	2.09	8.36	39.77
<i>Favites halicora</i>	1.19	0.67	2.09	8.36	48.13

<b>Vedhalai vs Pamban</b>					
Average dissimilarity = 31.37					
<i>Coral species</i>	<i>Average abundance</i>		<i>Average dissimilarity</i>	<i>% contribution</i>	<i>Cum %</i>
	<i>Vedhalai</i>	<i>Pamban</i>			
<i>Goniastrea retiformis</i>	0	1.94	4.25	13.54	13.54
<i>Acropora cyatherea</i>	0	1.43	3.03	9.67	23.21
<i>Acropora formosa</i>	0	1.15	2.43	7.74	30.95
<i>Leptastrea aequalis</i>	2.60	1.61	2.15	6.86	37.81
<i>Favites complanata</i>	0.62	1.51	1.97	6.29	44.10
<i>Favia rotumana</i>	0.49	1.34	1.91	6.10	50.20

<b>Mandapam vs Pamban</b>					
Average dissimilarity = 37.93					
<i>Coral species</i>	<i>Average abundance</i>		<i>Average dissimilarity</i>	<i>% contribution</i>	<i>Cum %</i>
	<i>Mandapam</i>	<i>Pamban</i>			
<i>Goniastrea retiformis</i>	0	1.94	4.57	12.05	12.05
<i>Acropora cyatherea</i>	0	1.43	3.26	8.59	20.64
<i>Favia lizardensis</i>	0	1.15	2.70	7.11	27.75
<i>Acropora formosa</i>	0	1.15	2.60	6.87	34.62
<i>Favites complanata</i>	0.63	1.51	2.13	8.43	40.23
<i>Favites russeli</i>	0.77	1.49	1.96	5.16	45.40

**Supplementary Table 1:** Taxonomic composition of adult coral colonies at the study sites of Palk Bay reef.

Species	Vedhalai		Mandapam		Pamban	
	V1	V2	M1	M2	P1	P2
<i>Cyphastrea microphthalma</i>	3.8	7.0	4.3	0.0	5.2	2.2
<i>Favia albidus</i>	2.5	4.7	0.0	6.7	2.6	1.1
<i>Favia fragrum</i>	0.0	1.2	0.0	0.0	2.6	1.1
<i>Favia lizardensis</i>	2.5	1.2	0.0	0.0	0.0	2.2
<i>Favia pallida</i>	3.8	5.8	6.4	6.7	0.0	2.2
<i>Favia rotumana</i>	0.0	1.2	0.0	0.0	1.3	1.1
<i>Favia speciosa</i>	3.8	4.7	0.0	0.0	2.6	2.2
<i>Favia veroni</i>	2.5	0.0	0.0	0.0	1.3	2.2
<i>Favites complanata</i>	6.3	0.0	0.0	20.0	14.3	9.9
<i>Favites halicora</i>	5.0	7.0	2.1	10.0	7.8	7.7
<i>Favites pentagona</i>	0.0	1.2	0.0	3.3	6.5	8.8
<i>Favites russelli</i>	7.5	7.0	0.0	0.0	7.8	9.9
<i>Favites vasta</i>	6.3	4.7	4.3	10.0	10.4	5.5
<i>Goniopora minor</i>	0.0	0.0	0.0	0.0	3.9	2.2
<i>Hydnophoramicroconus</i>	2.5	1.2	0.0	3.3	0.0	3.3
<i>Leptastreaequalis</i>	18.8	12.8	38.3	6.7	10.4	6.6
<i>Leptastrea purpurea</i>	15.0	17.4	27.7	23.3	5.2	9.9
<i>Montastrea colemanii</i>	0.0	0.0	0.0	0.0	0.0	2.2
<i>Montastrea valenciennesi</i>	0.0	0.0	0.0	0.0	1.3	1.1
<i>Platygyra deadalia</i>	0.0	0.0	0.0	0.0	1.3	0.0
<i>Platygyra sinensis</i>	0.0	0.0	0.0	0.0	2.6	0.0
<i>Pleasantreaversipora</i>	0.0	0.0	0.0	0.0	0.0	3.3
<i>Porites asteroides</i>	3.8	3.5	4.3	0.0	1.3	2.2
<i>Porites lobata</i>	6.3	8.1	6.4	0.0	5.2	5.5
<i>Porites lutea</i>	10.0	11.6	6.4	10.0	2.6	2.2
<i>Symphyllia recta</i>	0.0	0.0	0.0	0.0	2.6	1.1
<i>Turbinaria frondscens</i>	0.0	0.0	0.0	0.0	1.3	2.2
<i>Turbinaria peltata</i>	0.0	0.0	0.0	0.0	0.0	1.1

**Supplementary Table 2:** Distribution of reef fishes recorded at Palk Bay. (+) indicates presence; (-) indicates absence.

S. No	Species	Vedhalai	Mandapam	Pamban
1	<i>Abudefdufseptemfasciatus</i>	+	+	+
2	<i>Abudefdufvaigiensis</i>	+	-	-
3	<i>Acanthurusleucosternon</i>	-	+	+
4	<i>Acanthurusmata</i>	+	+	+
5	<i>Acanthurusnigrofuscus</i>	-	-	+
6	<i>Canthigastersolandri</i>	+	+	+
7	<i>Chaetodondeccusatus</i>	-	+	+
8	<i>Chlorurusgibbus</i>	-	+	+
9	<i>Scarusghobban</i>	+	+	+
10	<i>Scarusgibbus</i>	+	+	+
11	<i>Scarusrubroviolaceous</i>	-	-	+
12	<i>Siganuscanaliculatus</i>	+	+	+
13	<i>Siganusjavus</i>	+	+	+
14	<i>Siganuslineatus</i>	-	+	+

**Supplementary Table 3:** Akaike Information Criterion (AIC) values of the models used to analyse the impact of various factors on coral recruit density. Results of the model with the lowest AIC value were considered.

Model No	Parameters estimated	AIC value
1	Coral recruits ~ Coral cover + Macroalgae + Herbivores + Hard substrate + Human Pressure	100.058
2	Coral recruits ~ Macroalgae + Herbivores + Hard substrate + Human Pressure	99.447
3	Coral recruits ~ Macroalgae + Herbivores + Human Pressure	97.546
4	Coral recruits ~ Macroalgae + Herbivores	96.481



**Supplementary Table 4:** Average SST (°C) recorded in Palk Bay region since 2006

<b>Months</b>	<b>2006</b>	<b>2007</b>	<b>2008</b>	<b>2009</b>	<b>2010</b>	<b>2011</b>	<b>2012</b>	<b>2013</b>	<b>2014</b>
March	29.98	29	28.51	29.66	29.83	29	29.18	29.19	28.81
April	31.09	30.52	30.2	30.55	31.27	30.26	30.55	30.88	31
May	30.35	30.56	29.67	30.17	30.7	29.8	29.67	30.44	30.6
June	29.71	29.55	29.29	29.23	29.45	29.61	29.5	29.02	30.1
July	28.48	28.34	28.92	28.38	29.15	29.4	29.52	28.55	29.5
August	28.57	28.72	28.41	28.72	28.68	28.78	29.28	28.49	28.9
September	28.8	29.12	29.16	29.01	29.1	29.2	29.64	28.85	29.3
<b>Average</b>	<b>29.57</b>	<b>29.40</b>	<b>29.17</b>	<b>29.39</b>	<b>29.85</b>	<b>29.44</b>	<b>29.62</b>	<b>29.35</b>	<b>29.74</b>