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RESEARCH ARTICLE

PARADIGM TO COMPLEX ECOSYSTEMS: COMPETITIVE INTERACTIONS BETWEEN CORALS AND *ACANTHASTER PLANCI* PREDATION

[1]Machendiranathan, M., [1]Senthilnathan, L., [1]Ranith, R., [1]Saravanakumar, A., *[1]Thangaradjou, T., [2]Ramana, I. V., [2]Choudhry, S. B. and [2]Sasamal, S. K.

[1]Centre of Advanced Studies in Marine Biology, Faculty of Marine Sciences, Annamalai University, Parangipettai – 608502, Tamilnadu, India
[2]National Remote Sensing Centre, Indian Space Research Organization, (Dept. of Space, Govt. of India), Balanagar, Hyderabad – 500625, Andhra Pradesh, India

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ABSTRACT

The presence of corallivore *Acanthaster planci* is most threatening to the coral reef ecosystems and worldwide most of the reports state that its aggressive feeding behavior degrades the life forms of coral reefs in the last few decades. However, its selective feeding behavior is only on *Pavona sp.* which indirectly helps to recover the long-lived massive forms of *Porites sp.* in the Lakshadweep atoll, Kavaratti lagoon corals. Benthic survey results reveal the reason behind this selective feeding by *Acanthaster planci* on *Pavono sp*. because of the single species (*Pavona sp.*) domination occuring via competitive interactions among the coral colonies. Observations clearly show that the higher competitive interactions (26.8%) among corals results in higher mortality (53.5%) of corals by the *Acanthaster planci*. The predation compensate the loss of species diversity due to dominating competitive interactions in the coral reef ecosystem, which is evidenced by the predation prey mediation analysis and the results indicate that the recovery level of *Porites sp.* against *Pavona sp.* is 0.785. This selective predation regulates the coral reef ecosystem as a balanced one by the crown of thorn starfish *Acanthaster planci* in Kavaratti lagoon corals.

INTRODUCTION

A Coral reef ecosystem is a highly dynamic and complex system (Nystrom and Folke, 2001; Dizon and Yep, 2006) among other marine ecosystems. It possesses more structural complexity regulated by a variety of competition, predation, allee effect and also physical factors of perturbation (Pimm, 1984; Paine *et al*., 1998). However, any of the above disturbances exerted in an environment lead to the domination of a particular community or conversion of unique species habitat (Knowlton, 1992). If the single species dominated ecosystem facing the perturbation, the ecosystem returns to the equilibrium (Dizon and Yep, 2006; Trapon *et al*., 2011; Adam *et al*., 2011). Competitive interactions of coral reefs vary with their adaptive mechanism of sweeper tentacle, mesentrial filaments and terpenoid compound released by them. Especially the scleractinian corals use aggressive/defensive sweeper tentacle and digestive mesentrial filaments to compete with the neighbour corals (Tanner, 1997; Abelson and Loya, 1999; Lapid and Chadwick, 2006).

Corresponding author: Thangaradjou, T.,
Centre of Advanced Studies in Marine Biology, Faculty of Marine Sciences, Annamalai University, Parangipettai – 608502, Tamilnadu, India

Instead non-scleractinian corals were using an allelopathy process of releasing terpenoid compound into the water, which reduces the light and reduces the growth of a competitor (Delbeek and Sprung, 1994). Soft corals are comparatively safer due to the support of environmental conditions (Dai, 1990; Alino *et al*., 1992). Notably, the competition directly depends upon the polyp size, abundance and the number of species present within the environment (Abelson and Loya, 1999). The result of competitive interactions among corals declines the structural complexity of coral reef ecosystem (Tanner, 1997; Lang, 1971), but predation devastates the coral coverage. For instance, the *Acanthaster planci* plays a key role in reducing the coral cover drastically (De'ath and Moran, 1998; Done, 1999; Pratchett *et al*., 2009). *Acanthaster planci* is recognized as a threat to the coral reefs only during 1950s (Moran, 1986). Outbreak of *A. planci* and its selective feeding behavior are more controversial, ambiguous and yet not clearly understood (Rotjan and Lewis, 2008; Kayal *et al*., 2012) but the laboratory and field studies reported that the branching corals like *Acropora spp*. are more favourable feed than the massive *Porites spp*. (Pratchett *et al*., 2009). But chemical compositions of corals are responsible for the selection of feed by a predator (Brauer *et al*., 1970; Ormond *et al*., 1973; Collins, 1974; Hanscomp, 1976). *A. planci* consumes 5-6

m^2/yr (Birkeland, 1989) of coral cover. While comparing the recovery processes, soft corals recover faster than the hard corals from the crown of thorn predation (Ammar *et al*., 2007). The present study was originally intended to know the density of *A. planci* and its predation on coral reef ecosystem of Kavaratti island, but the keen observation in the field showed a unique competitive interactions existing between and among different corals. Competitive interactions among corals lead to single species domination and it is balanced by the selective feeding of corallivore *A. planci*. Hence, competitive interactions among various corals were also taken into consideration in the benthic survey to find out the relationship between the predation and competitive interactions among coral reef ecosystem.

MATERIALS AND METHODS

Benthic survey

A typical coral reef feeding preference of *A. planci* (COTs - Crown of Thorn starfish) and the competitive interactions among the corals were observed during the end of May 2012 by the *in-situ* standard survey protocols, in the lagoon of Kavaratti Island (Fig.1) located at the latitude of 10° 33'N and longitude of 72° 28'E, 403 km away from the Cochin coast. Six monitoring stations were selected within the lagoon (depth varies from 2 to 6 m) and duplicate surveys were performed at all stations for maintaining the robustness of coral reef ecosystem. Competitive interactions between corals were observed along the 20 m line intercept transects (LIT) placed perpendicular to the shore (English *et al*., 1997) in all the stations. Random spot check methods (Nomura *et al*., 2001) were performed for estimating the number of predators (COTs), predator size and prey species of coral reefs.

Competition Index (CI)

Competitive interactions among coral reefs were differentiated in the field as direct interaction, overgrowth and standoff (Lang, 1973; Connell, 1976; Sheppard, 1979; Richardson, 1979; Wellington, 1980), where direct interaction between corals resulted in tissue damage by the way of using sweeper tentacle or mesentrial digestion was observed in the field and documented. But such authentic report of tissue damage because of overgrowth and standoff competitive interactions were not reported among coral reefs in the present study. In order to know the competitive ability among the various corals, competitive index (Dai, 1990) was calculated. It ranges from +1 which wins all interactions to -1 which loses all

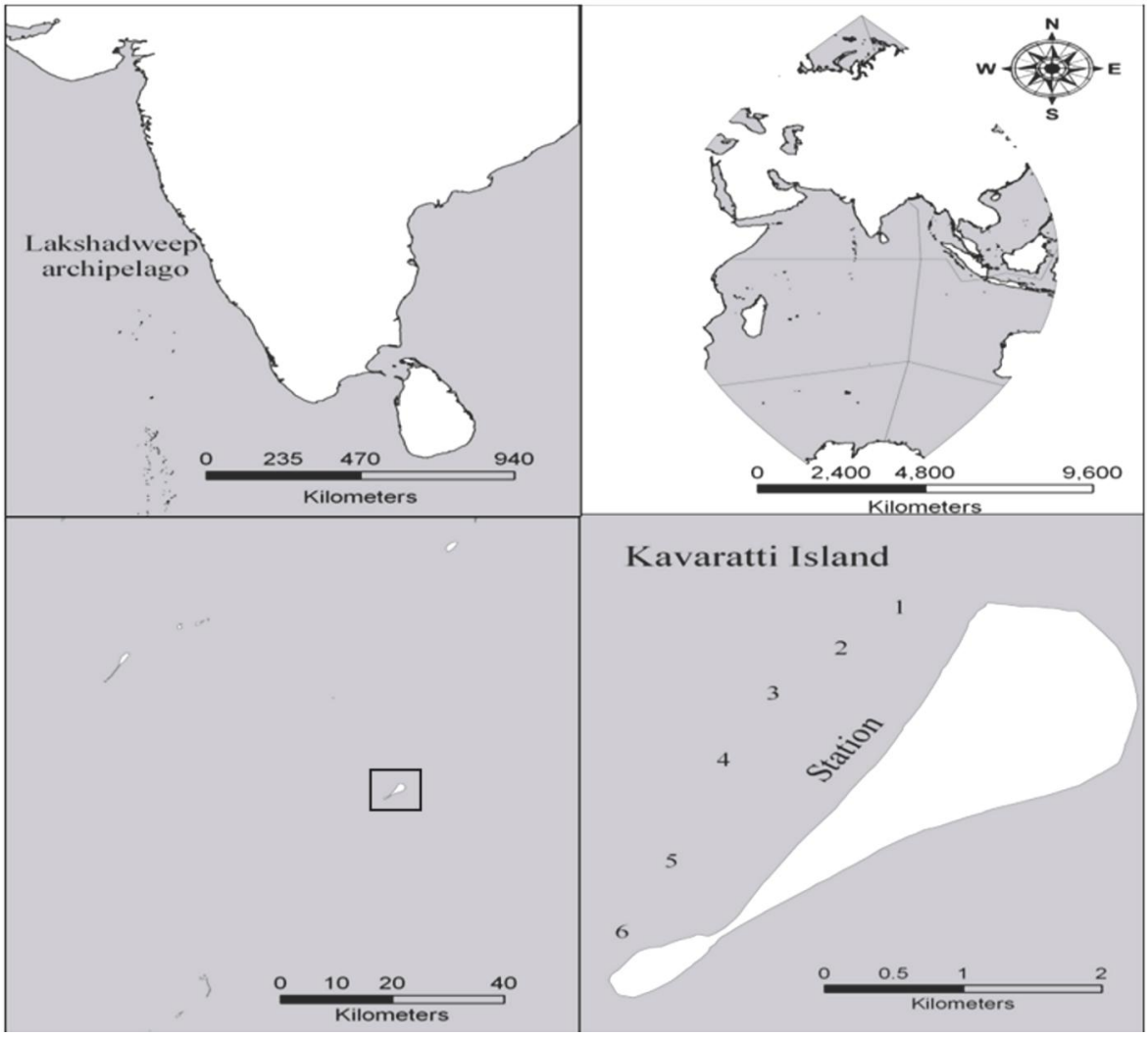

Fig. 1. Map showing the study area

interactions. Competitive interactions among the corals were recorded and categorized into five groups, aggressive 1 to 0.6, moderately aggressive 0.59 to 0.2, intermediate 0.19 to – 0.2, moderately subordinate -0.21 to -0.6 and subordinate -0.61 to -1 according to Dai (1990) scale of competition index. The below equation was used to calculate the competitive index (CI):

CI = (No. of wins – No. of losses) / Total no. of interactions
…… (Eq. 1)

Mediation Analysis

To determine the total effects due to the competitive interactions within the coral reef community and predator to the coral reef ecosystem were analysed by using the mediation analysis. Mediation analysis was performed only for predator-prey relationship not for the competitive interactions among corals, because observations from the field clearly indicated that all the interactions of competition were won by the *Pavona spp.* against *Porites spp*. Hence, it is neglected for this analysis, and competitive interactions between corals and total effect is treated as 1. On the other hand, the recovery level of ecosystem by the predation of *A.planci* on *Pavona spp.* in the ecosystem need to determine, so mediation analyses were performed. For performing mediation analyses to predator-prey (*Acanthaster planci-Pavona spp*.), variables of dominance rate of *Pavona spp.,* mortality rate of *Pavona spp.* and corallivore *A. planci* were used. A series of multiple regressions (consider the coefficient value of first linear regression as 'a' and second linear regression coefficient as 'b' as well as the standard error values consider as s_a and s_b respectively) was performed using the SPSS 16 statistical software and the results derived for Sobel test to conduct mediation analysis using online tool (http://www.quantpsy.org/Sobel/Sobel.htm) developed by the Kristopher J. Preacher (Vanderbilt University) and Geoffrey J. Leonardelli (University of Toronto). To ensure the influence of mediation among the variables, mediator, and the total effect among the variable was found using the following equation,

C = C`+ a*b ……. (Eq. 2)

(C` derived from the standard error value of the Sobel test result)

Where,

C = Total effect, C' = Direct effect, a*b = Indirect effect

Mediation Index (MI)

Mediation index determined the resultant effect of variables and mediation among the variables as partial or full. The index was computed by dividing the indirect effect by the total effect. Results beyond 50% indicated that effect among the variables is full, if it is less than 50 and it is treated as partial.

MI = (Indirect effect / Total effect)*(100) …… (Eq. 3)

RESULTS

Maximum mortality rate and predation were noticed at station 5, which possesses higher competitive interactions among coral reefs (Fig. 2), while predation and predator infestation were not recorded at station 3. Among the observed 382 coral colonies competitive interactions relate 23 genera of corals and it was 94.7% due to direct interactions, whereas overgrowth is represented by 5.2% and the standoff mode competition was not encountered. The results of competitive interactions were categorized directly into win/loss/interactions for different coral genera depicted in (Fig. 3).

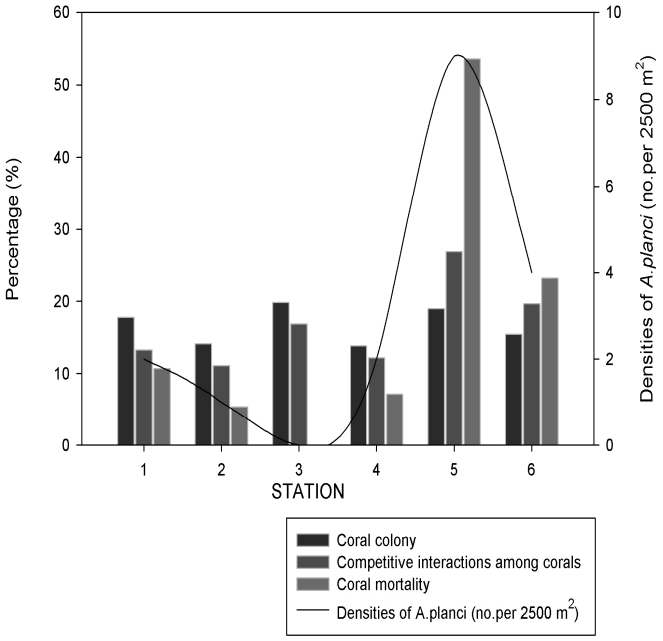

Fig. 2. Percentages cover of coral colony, competitive interactions among corals, coral mortality and density of *Acanthaster planci* at six stations along the Kavaratti Island. (Note: Right side y axis only for the densities of *Acanthaster planci*)

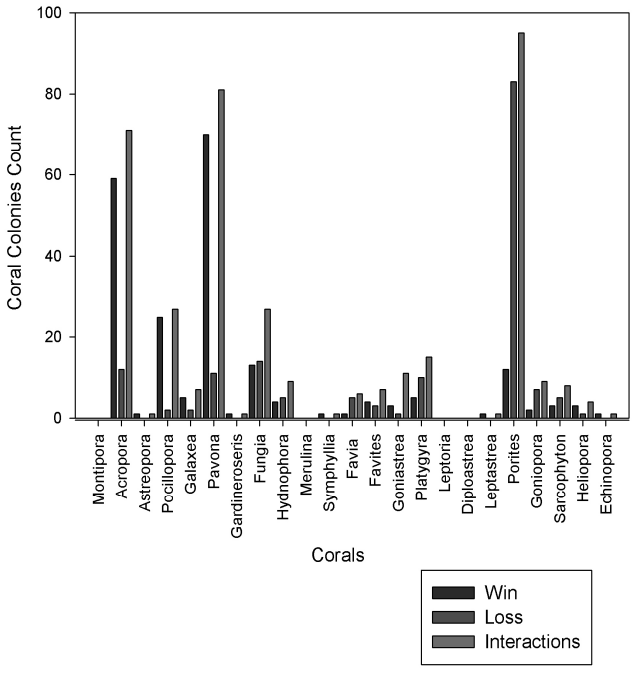

Fig. 3. Competitive interactions recorded for different corals

Among the corals more competitive interactions were observed between corals of *Acropora*, *Pocillopora*, *Pavona*, and *Porites*. However, *Pavona spp*. showed higher winning

and *Porites spp*. recorded higher losses in all the competitive interactions than any other competitive interaction among corals. Ability of corals was calculated based on the win, loss and interactions used in the competition index (Fig. 4), which found that corals, *Acropora, Pavona, Astreopora, Pocillopora, Gardineroseris, Symphyllia, Lepastrea* and *Echinopora* were the more aggressive and dominant all the time during a spat with the neighbour corals by the approach of direct interactions and over growth.

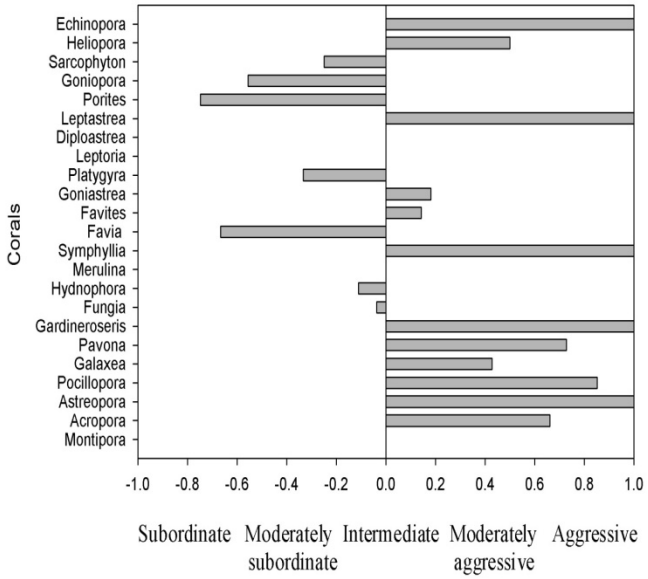

Fig. 4. The competition index value recorded for different corals (corresponding group values given in materials and methods)

While *Heliopora* and *Galaxea* were moderately aggressive, *Favites, Goniastrea, Platygyra, Leptoria, Diploastrea, Fungia, Hydnopora, Merulina and Montipora* were intermediated groups, *Goniopora* and *Sarcophyton* were moderately subordinate but *Porites* and *Favia* lost all competitive interactions and was thereby grouped under subordinate class. Competition index was recorded for *Acropora* (0.66), *Pocillopora* (0.85), *Pavona* (0.72) and *Porites* (-0.74) which are encountered with high competitive interactions among them, indicating that the first three corals are aggressive and overriding the ecosystem. In all the benthic survey transects, *Pavona spp*. showed a declining trend (Fig. 5) with that of infestation by *A. planci* predation, which indirectly made the way to sustain the *Porites spp*. in the ecosystem against *Pavona* populations. Station three was dominated by *Acropora spp*. which remains constant without any rapid change as it was not fed by the corallivore. Though selective dominates on a specific coral, the size of the predator was not playing a role in selective feeding. In general average diameter of all adults measured was greater than 28 cm and juvenile of *A. planci* was not recorded. Direct interaction of the competition between the coral *Pavona spp.* and *Porites spp*. (Fig. 6_a and 6_b) clearly illustrate the dominance of the encrusting *Pavona spp*. by overlapping. Before performing the mediation analyses of predator and prey relationship, initial check was made by subjecting the variable for bivariate correlation to test whether the variables are statistically significant or not. The results showed that the variables of competitive interactions such as

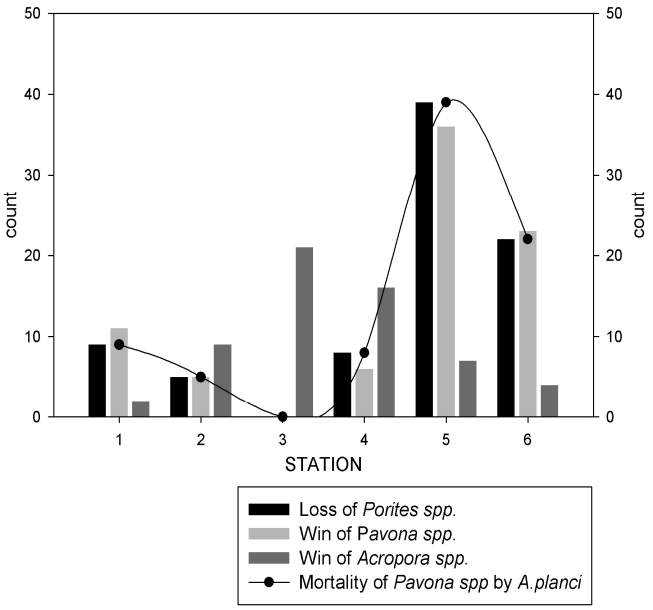

Fig. 5. Loss and win comparisons of competitive interactions for the corals *Porites*, *Pavona*, and *Acropora* to the mortality rate of *Pavona spp.* by *A.planci*

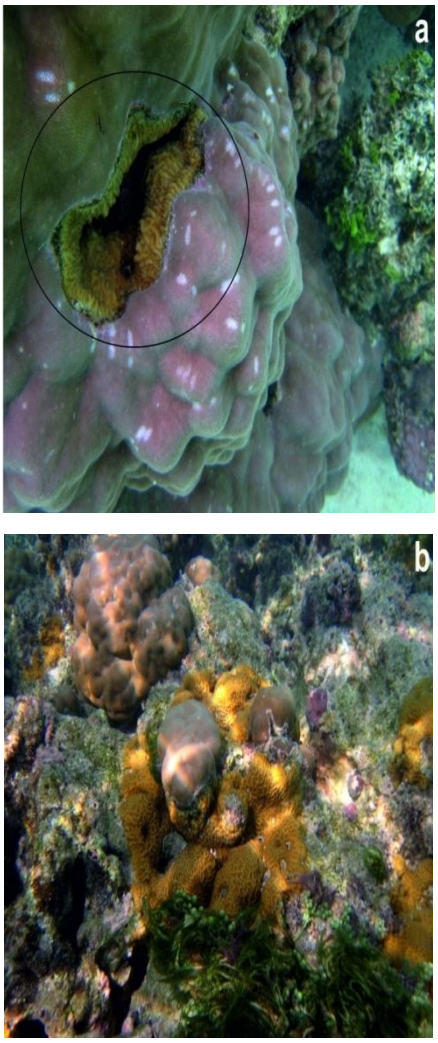

Fig. 6. (a). Initial stage of competitive interactions between the coral *Pavona spp.* to *Porites spp.* through the direct interaction and dominance (b) of *Pavona spp.* over the *Porites spp.*

dominance rate of *Pavona spp*., mediator (predator *A. planci*) and mortality rate of *Pavona spp*. were highly significant to each other. Bivariate level results confirmed the role of mediation among the variables; hence, the mediation analysis was performed (Fig.7). The values of the unstandardized coefficient and standard error for above variables were required for conducting the Sobel test. Hence, linear regressions were performed; the first linear regression results showed the association between the variables of competitive interactions between dominance rate of *Pavona spp.* (IV) and the Mediator (M) with a the unstandardized coefficient of 0.23 and standard error of 0.028. The second linear regression was performed between the mortality rates of *Pavona spp*. due to *A. planci* infestation (DV) (as a control) and the competitive interaction dominance rate of *Pavona spp*. against the predator (IV). The results showed unstandardized coefficient and standard error of 2.87 and 0.692 respectively.

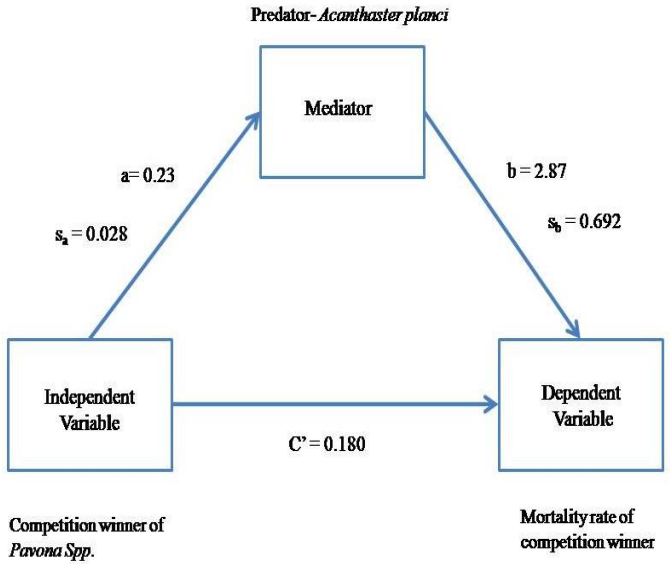

Fig. 7. Schematic diagram of mediation analyses for predator – prey relationship

To complete the Sobel test for mediation analysis, the values of the unstandardized coefficients were used. The simple mediation analyses clearly established the relationship among the competitive interaction winner *Pavona spp*., the mortality rate of competitive interaction winner *Pavona spp*. and to the mediator (predator *A. planci*). Sobel test was conducted online, and the results revealed the test statistics 3.71 with the p value of 0.0002. The Sobel test results also confirmed high significance among the variables because of the p value fall below the estimate alpha value of 0.05. From this result, it is evident that mediation plays a vital role between predator and prey in the coral reef ecosystem. The total effects caused by predation due to *A. planci* in the coral reef ecosystem were estimated to be 0.785 from the mediation analyses.

DISCUSSION

From the results of a benthic survey of Kavaratti island, it is clearly depicted that the increasing mortality (53.5%) of corals by the predator *A. planci* was recorded where the higher competitive interactions (26.8%) occurred (station 5) with a notable elevated predator infestation. Presence of predators was increasing with increasing competitive interactions between *Pavona spp.* to *Porites spp.* in the benthic ecosystem. Predation or even feeding mark of uniform stark-whiteness on the corals by the corallivore of *A. planci* was not recorded in and around the abundant branching coral (Fig. 8_a) colonies of *Acropora* species. In contrast to this, most of the field and laboratory studies reported from the Indo-Pacific, and Great Barrier reefs indicate *Acropora spp*. as the most favorable and suited prey to *A. planci* (De'ath and Moran, 1998; Pratchett *et al*., 2009; Keesing and Lucas, 1992). However, the present results witnessed that the predator-prey relationship in a coral reef ecosystem exists because of the competitive interactions between dominant encrusting coral *Pavona spp*. and the *Porites spp*. From the observations, the selective feeding of *Pavona spp*. might be due to the chemical cues of unique combined extracts released during the competition between *Porites* and *Pavona spp*. Competitions among corals were not stable around the Indo-Pacific regions (Abelson and Loya, 1999) which also supports the present results.

On the other hand, observation from the field showed that the modes of competition among the corals were fighting each other through a direct interaction approach which leads to drastic community structure changes alike to Taiwanese corals (Dai, 1990). Kavaratti lagoon corals competitive interactions are more of standoff approach and similar to the reefs from Okinawa, Japan (Rinkevich and Sakai, 2001). Variations in the competition of coral's ability toward domination, such as *Goniopora* were found to be more aggressive and *P. varians* were found intermediate in Indian Ocean (Sheppard, 1979) but the present results found it was moderately subordinate and aggressive. In the Pacific corals, *P. varians* noted as moderately aggressive and *Pocillopora damicornis* is found to be subordinate (Dai, 1990) but the present results found both as aggressive and dominated the ecosystem (Fig. 8_b). The corals such as *Leptoria, Diploastrea, Merulina* and *Montipora* colonies were found alone, thereby avoiding the competition (Fig. 8_c). Sheppard (1979) also reported *Montipora spp.* as non-aggressive, even touch with adjacent corals without any affects. Free living fungiid corals are also reported to be more aggressive (Dai, 1990) but they struggle to win and also fail to move into another place from the crevice of (Fig. 8_d) the massive corals.

The coral *Fungia* also like to move away quickly while in competitive interaction with the sponges from the experimental setup (Hoeksema and de Voogd, 2012). Hence, the settling of larvae away from the more associated colonies furthermore plays a role in competition within a complex system of corals and confirmed that the corals are selective in an ecosystem. As for as predation is concerned lonely settled corals, were untouched by the predator. From the observation the competitive interactions among the corals such as *Astreopora, Gardineroseris, Symphylia, Leptastrea* and *Echinopora* do not lose the competitions. Undoubtedly, the aggressive approach makes them never lose. From the reports (Lang, 1973; Sheppard, 1979; Richardson, 1979; Chornesky, 1983; Chadwick, 1987) it is evident that, *Porites spp*. was severely affected by the aggressive *Pavona varians* by both sweeper tentacles and mesentrial filaments. These occurrences

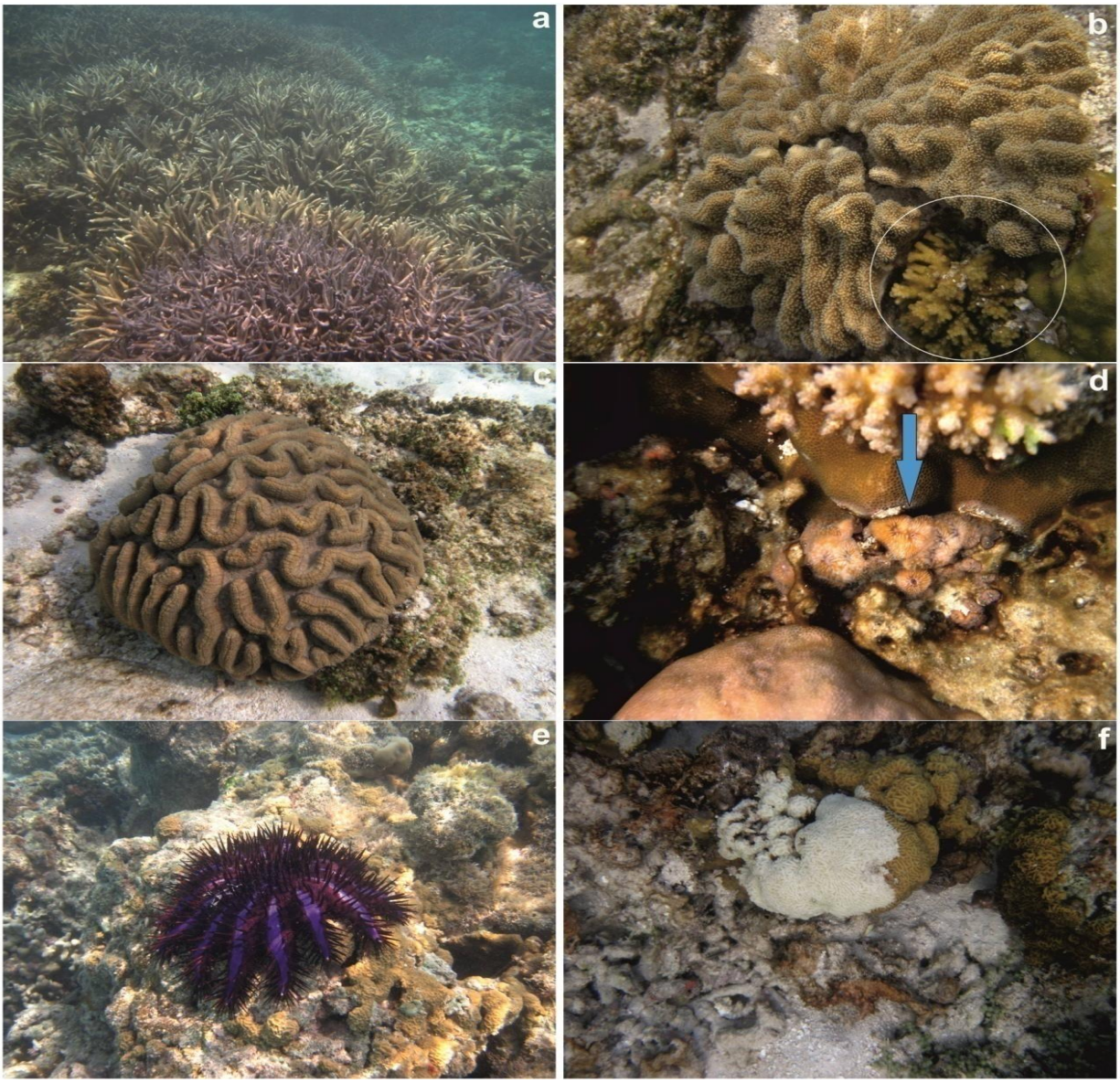

Fig. 8. The dynamics of coral reef ecosystem in Kavaratti island.
(a); Healthy branched coral colonies untouched by the corallivore *Acanthaster planci*, (b); Allelopathy process failed against the *Pocillopora damicornis* and severely affected soft coral of *Sarcopython spp.* (c); Example of avoiding competitive interactions, by the way, of growing away from more associated colonies noticed in *Symphyllia spp.* (d); Trapped fungiid loss their lives and survival among the corals, (e); Aggressive feeding of *Acanthaster planci* on *Pavona varians*, (f); Remaining white skeleton of *Pavona varians* after the feeding of *Acanthaster planci.*

were more frequent, tissue recognized by the adjacent coral might stimulate the competitive interactions and dominate over it (Chornesky, 1983), the same way *Pavona spp*. recognized and dominated against *Porites spp*. in all along the benthic survey. Notably the agonizing gaps between corals were observed to be 5mm, which is conspicuous in the field. Most of the studies observed that the preference of prey corallivore *A. planci* is mediated by chemical attachment rather than abundance and coverage. For instance, in Hawaii Kona reefs, *Pociillopora* is found as the more favourite prey than the abundant *Porites spp*. (Chess, 1997). The level of protein content plays a role in predation, low protein and energy content of Faviidae, Poritidae was untouched by *A. planci*; in contrast it fed only *Acropora* and *Pocillopora*, which possess high protein and energy content (Keesing and J. S. Lucas, 1992). Present competitive interactions among corals and predation results with the above indicate that the Favidae and Poridae were most subordinate but Acroporidae and Pocilloporidae were most aggressive. From this, it is evident that the suppressed species in competition are untouched by the predator *A. planci* and prefers the aggressive species. The phenomena of competitive interactions among corals and predation within the ecosystem dynamics, the role of competitive interactions declined the complexity of coral reefs in Kavaratti island but remarkably, predation by corallivore *A. planci* regulates the coral reef communities by selective feeding. Based on the above phenomena, the competitive interactions found the reduction of *Porites spp*. by the overgrowth of the *Pavona spp*. which leads to the single regime of *Pavona spp*. in the habitat. It is reduced by the selective feeding behavior of *A. planci* (Fig. 8_e). Occurrence of *Pavona spp*. with stark white color scares due to the predation

(Fig. 8_f) also supports this. Long living massive coral *Porites spp*. were highly affected during competitive interactions. Supporting to our results, Kayal *et al*. (2011) also reported the selective feeding behavior of *A.planci* in the island of Moorea, French Polynesia. However, the structural complexity of corals is indirectly maintained by the selective feeding preference of *A. planci*. Result of mediation index confirmed (82.3%) the effects by the predator *A.planci* is full and it is indirectly playing a major role in coral reef ecosystem. The total effect of competitive interactions between *Pavona* and *Porites spp*. in the coral reef ecosystem considered as 1 in the Kavaratti lagoon and its perturbation regained strongly by the activity of selective predation by *A. planci* at the level of 0.785 in the coral reef ecosystem. In a remarkable manner, the voracious predation by *A. planci* indirectly recovers the coral reef ecosystem from the single species dominated regime.

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