

**Differential growth forms of the sponge *Biemna fortis* govern the abundance of its associated brittle star *Ophiactis modesta***

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**Abstract:**

Marine intertidal regions are physically stressful habitats. In such an environment, facilitator species and positive interactions mitigate unfavorable conditions to the benefit of less tolerant organisms. In sponge–brittle star association, sponges effectively shelter brittle stars from biotic and abiotic stresses. The sponge, *Biemna fortis* (Topsent, 1897) was examined from two intertidal regions Anjuna and Mhapan along the Central West Coast of India for associated brittle star *Ophiactis modesta* (Brock, 1888) during 2013-2014. The study sites varied in Suspended Particulate Matter (SPM). *B. fortis* at the high SPM habitat (Anjuna) had partially buried growth form and at the low SPM habitat (Mhapan) had massive growth form. *O. modesta* was abundantly associated with the massive growth form (50-259 individuals per 500ml sponge) but rarely occurred in association with partially buried growth form (6-16 individuals per 500ml sponge). In laboratory choice assay *O. modesta* showed equal preference to the chemical cues from both the growth forms of *B. fortis*. In addition, *O. modesta* showed significant preference to *B. fortis* compared to other sympatric sponges. These observations highlight the involvement of chemical cues in host recognition by *O. modesta*. Massive growth forms transplanted to the high SPM habitat were unable to survive but partially buried growth forms transplanted to the low SPM habitat were able to survive. Differential growth forms of the host sponge *B. fortis* at different abiotic stresses affect the abundance of the associated brittle star *O. modesta*.

**Key Words:** Marine Sponge, Brittle star, Association, Abiotic factors, Growth forms, Oscula, *Biemna fortis*, *Ophiactis modesta*.

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## **Introduction**

Intertidal regions experience high physical disturbances. The presence of facilitator species and positive interactions mitigate the harsh conditions for the less tolerant organisms (Bertness and Leonard, 1997; Hacker and Bertness, 1999). Facilitator species allow the co-existence of organisms that generally would not survive in such environments hence expanding their realized ecological niche (Hacker and Bertness, 1999; Michalet et al., 2006; Filotas et al., 2010; Sanjerehei et al., 2011). Many studies supporting the stress gradient hypothesis (SGH) have found that facilitation and direct positive interaction like symbiosis and mutualism to be more common in high-stress environments (Bertness and Callaway, 1994; Stachowicz, 2001; Kawai and Tokshi, 2007). However, other studies suggest that facilitation is increased under moderate stress conditions compared to high-stress conditions (Maestre and Cortina, 2004; Maestre et al., 2006; Holmgren and Scheffer, 2010). In marine environments, sessile organisms like corals, gorgonians, and sponges are considered to be habitat-forming species (Bell, 2008) causing a high impact on community organization and dynamics (Airoldi et al., 1998).

Sponges are ubiquitously distributed in aquatic ecosystems (Wulff, 2006) and are known to serve as hosts to many organisms (Turon et al., 2000). Sponge morphology and size affect the number and abundance of associated organisms (Firth, 1976; Koukouras et al., 1996; Hultgren and Duffy, 2010). Sponges have phenotypic plasticity and can adapt morphology depending on the environment they inhabit (Carballo, 2006; Palumbi, 1986; Kaandorp, 1999). Morphology can influence in the distribution pattern of sponges as delicate forms avoid high disturbance environments; for example, an arborescent sponge is unlikely to be suited to a wave-exposed environment (Bell and Barnes 2000). Morphological diversity of sponge assemblage decreases with increasing environmental disturbances such as current flow (Bell and Barnes 2001) and sedimentation (Carballo, 2006).

Spatial distribution of ophiuroids with strong habitat preferences is limited by the presence of suitable habitat (Lewis and Bray, 1983). Some brittle star species associate with several different sponge species (Komkham et al., 2007) while some species show a species-specific preference to the host sponge and can recognize and locate the host by chemical cues (Henkel and Pawlik, 2011). Characteristic chemical and morphological features of the host sponge seem to have a significant role in these associations. Among sponge habitats with similar morphological features, brittle stars actively select and prefer particular sponge species as host even if the chosen sponge has no chemical defence to offer (Henkel and Pawlik, 2005). Brittle stars do not select sponge habitat for any associational chemical defense (Henkel and Pawlik, 2005). This observation indicates the presence and influence of other factors on the brittle star (Hendler, 1984). Considering the common

occurrence of the sponge and brittle star association, this spatial relationship provides an ideal opportunity for studying the inter-specific interaction between sessile invertebrate and cryptic fauna (Henkel and Pawlik, 2005).

*O. modesta* is distributed throughout the Indo-Pacific including the Gulf of Thailand and Andaman Sea (Putchakam and Sanchaeng, 2004), Inaca islands, Africa (Balinsky, 1957), Dampier, Western Australia (Marsh and Morrison, 2004), Kii Peninsula Japan (Murakami, 1963) and Hawaii (Mackay, 1945). *O. modesta* is not exclusively a sponge-dwelling brittle star, and when associated with sponges it is not species specific. Individuals have been observed and collected from rocks and corals (Price and Rowe, 1996; Marsh and Morrison, 2004). *O. modesta* has been reported to be associated with sponge *Spirastella inconsfans* (James, 1982; James, 1983) and also aggregating in sponges at the island of Oahu in the Hawaiian Islands (Mackay, 1945).

Protection of fragile coastal ecosystems has recently become a global priority (Halperm et al., 2009). Ocean ecosystems experience a cumulative impact of multiple stressors on local as well as global scale (Brown et al., 2014). The Central West Coast of India is characterized by pocket beaches flanked by rocky cliffs, estuaries, bays and mangroves and a major part of this coastal zone is exposed to environmental and anthropogenic pressures (Nayak and D'Souza, 2010). We studied the sponge-brittle star association of *B. fortis* and *O. modesta* at two rocky intertidal sites, Anjuna and Mhapan, along the central west coast of India. During monthly intertidal field trips over two years (2011 and 2012), we observed that *B. fortis* at the two sites had different growth form. *B. fortis* growth form at Mhapan showed a high abundance of associated brittle stars, but the *B. fortis* growth form at Anjuna showed an almost total absence of associated brittle stars, except for some occasional instances. To investigate the uneven distribution of sponge-brittle star association between the two sites, we examined the (1) monthly variation in the size and abundance of the brittle stars associated with the two growth forms of sponge *B. fortis*, and environmental parameters (Feb 2013 to Jan 2014); (2) abundance, morphology and volume of the host sponge; and (3) reciprocal transplantation of the host sponge *B. fortis* between the two habitats to test the influence of environmental conditions on the *B. fortis* growth forms and associated brittle stars. Additionally, in a laboratory experiment, Y-tube choice assays were used to determine the involvement of sponge chemical cues and the chemosensory ability of the brittle star *O. modesta* in host location. We examined chemotactic recognition by *O. modesta* to assess if the brittle star showed any variation in its preference to the *B. fortis* growth forms.

## 2. Materials and Methods

### 2.1 Study sites and Physico-Chemical Parameters

The study sites, Anjuna (15°33'57. 51"N 73° 44'30. 39"E) and Mhapan (15°55'28. 16"N 73°33'26. 69"E) are both situated along the Central West Coast of India (Fig. 1). Both sites consist of rocky intertidal habitat with interspersed shallow sandy patches. The seawater temperature, salinity and pH were measured on a monthly basis, using a multiparametric probe (OAKTON PCD 650). Every month three water samples were collected from each study site to measure the suspended particulate matter (SPM) by the filtration method of Neukermans et al., (2012). As the physicochemical parameters did not have normal distribution, significant difference in the temperature, salinity, pH and SPM at the two locations was assessed using a non-parametric Mann–Whitney U test.

### 2.2. Abundance of Host Sponge

Ten transects each of 30 m length, perpendicular to the coast and 10 m away from each other were selected at both sites. Three quadrats (1 m<sup>2</sup>) were placed along each transect at regular intervals. All the sponge species within each quadrat were recorded and checked for associated brittle stars. Non-sponge habitats like algae; sea anemones and rubble situated within the quadrats were also examined for any free-living brittle stars. Sponge community composition at the two habitats was analyzed using the one-way analysis of similarities test (ANOSIM). The differences between groups of samples were tested through randomization methods on a resemblance matrix. A similarity matrix was constructed using the Bray-Curtis coefficient (Legendre and Legendre, 1998) after square root transformation (Clarke and Warwick, 2001) was applied to the sponge abundance data from the study sites. The study sites and sponge species were ordered using non-metrical multidimensional scaling (MDS) (Clarke and Warwick, 2001). SIMPER (percentage similarity) analysis was done to determine which sponge species contributed most to between-site differences and within site similarity. All analyses were carried out in software PRIMER 6 (Plymouth Routines in Multivariate Ecological Research).

### 2.3. Occurrence of sponge-associated brittle stars

The sponge specimens were collected every month, in triplicates, during low tides from each location (from February 2013 to January 2014). Individual sponges were placed in separate plastic bags and brought to the laboratory. Sponge volume was determined by volumetric displacement of seawater. The number of oscula was recorded for all individuals collected from the two study sites. Sponges were opened up, and brittle stars from the sponge surface and inside the canals were retrieved. Isolated brittle stars were counted, photographed and examined under a microscope and the disk size

was measured on the aboral surface to the nearest 0.01mm using an ocular micrometer under a stereomicroscope. Measurements were taken from the base of an arm midway between the outer edges of the two radial shields to a point straight opposite on the disk periphery (Packer et al., 1994). The monthly density of *O. modesta* was calculated as the number of individuals per 500 ml of sponge. The significant difference in the sponge volume of both the growth forms was assessed with non-parametric Mann–Whitney U test, as the data showed non-normal distribution. Spearman rank correlation ( $r_s$ ) was used to evaluate if the abundance of associated brittle stars was related to the number of oscula in the host sponge and the sponge volume. The relation between the number of oscula and sponge volume was also assessed with Spearman rank correlation ( $r_s$ ).

#### 2.4. Reciprocal Transplantation

Reciprocal transplantation experiment was carried out with the massive and the partially buried growth forms from the two study sites in June 2013. Six sponges of similar size (volume=1.5-2 Liters) were collected from each of the two locations and transplanted to the other site within 3-4 hours. Sponges were transported in aerated seawater. Simultaneously, three control sponges were removed and replanted in their original habitat at both the sites. All the sponges used in transplantation were examined superficially for associated brittle stars. Partially buried growth forms had no associated brittle stars, massive growth forms ~50 brittle stars were observed and removed. Sponges were planted by placing them on the ground in their natural orientation. Uprturned meshed plastic baskets (mesh size 5 cm) were used to cover the planted sponges. Baskets were pegged down to the ground with iron rods to immobilize them. The transplanted sponges were monitored weekly at both the sites. In the earlier attempts of transplantation experiment, it was observed that the transplanted massive growth forms could not survive for more than two weeks at the new site. Hence the transplantation experiment was continued for only two weeks, and sponges from two locations were recovered after 15 days.

#### 2.5. Choice assays

Sponges growing on small to medium sized boulders and rocks were collected along with the substratum and were immediately transported to the laboratory in aerated seawater. In the laboratory, sponges were maintained in tanks (50 l) with aerated seawater. The choice assays were conducted on the same day. Live *O. modesta* were carefully isolated from separate sponges (massive growth forms) and kept in separate glass tanks with aerated seawater that had not been exposed to sponges.

Sponge conditioned seawater, control seawater and further choice assays were carried out following the method described by Henkel and Pawlik (2011). Seawater used in the choice assays was filtered

through a 500 $\mu$ m mesh. Sponge conditioned sea water was prepared by placing a live sponge (1 l) in filtered and aerated sea water (6 l) for four h. Similarly, control sea water was prepared without the addition of sponge tissue.

The Assay chamber was made using tygon tubing with an inner diameter of 2.5 cm. Two pieces of tygon tubes (14 cm long) were connected to the arms of a 120° PVC Y-connector, and the third piece of tygon tube (6 cm long) was attached to the base of the Y that served as the entrance for the test animal. An L-connector with a tygon tube (6 cm long) at one end was connected to each 14 cm tube attached to the Y-connector. L-connectors were positioned perpendicular to the plane of the Y-connector. The treatment and control seawater was delivered into the upright arms of the L-connectors with a flow rate of 48 ml/min-1. The assay chamber was placed in a shallow pan of control seawater and covered with a black waterproof paper to conduct the choice assays in the dark, as the brittle stars are negatively photo- sensitive.

*O. modesta* choice assay were first tested with seawater conditioned with *B. fortis* partially buried growth form and massive growth form (n=32). Additional choice assays were carried out between (1) *B. fortis* –partially buried growth form and control seawater (n=31); (2) *B. fortis* –massive growth form and control seawater (n=24); (3) *B. fortis* –massive growth form and *C. cavernosa* (n=45); and (4) *C. cavernosa* and control seawater (n=22). *C. cavernosa* was sympatric and the second most abundant sponge found at the study sites. Each test animal was acclimatized for 2 minutes in the assay pan before each trial. The test animal was placed inside the entrance tube after the acclimatization period, and the water flow was started. A choice occurred when the brittle stars oral disk passed into 1 of the two treatment arms of the Y-connector. Each animal was used only once in any choice experiment, and the assay chamber was washed with filtered seawater after each treatment. Only replicates in which a brittle star made a choice were used in the analyses. For the choice assay chi-square goodness of fit test was used to examine whether the brittle star's choice preferences deviated from the expected equal probability of selecting either arm of the Y-tube.

### **3. Results**

#### *3.1. Study sites and physico-chemical parameters*

Mann-Whitney test analysis indicated a non-significant difference in the pH, temperature and salinity between the two locations. However suspended particulate matter (SPM) was significantly different between the two sites (Anjuna, median = 15.80 mg/100 ml, SD  $\pm$ 4.34; Mhapan, median = 10.48 mg/100 ml, SD  $\pm$ 1.81, U= 100, p<0.001) and was consistently higher at Anjuna (Fig. 2). The temperature of the seawater at the high SPM site varied from 31.0° C in February to 24.8° C in

August. Although average salinity was 28.42 ‰, salinity dropped dramatically to 8.36 ‰ – 16.31 ‰ during the monsoon season (June-September) due to the fresh water inflow. At the low SPM site the seawater temperature varied from 32.5° C in February to 24.1° C in August. Average salinity was 27.53 ‰, which dropped to 9.52 ‰ – 16.61‰ during the monsoon season. The mean pH at the high SPM site and the low SPM site was 8.11 and 8.09 respectively.

### 3.2. Abundance of host sponge

Three sponge species *B. fortis*, *C. cavernosa* and *Haliclona* sp. were found at both sites. *B. fortis* was the most abundant sponge species followed by *C. cavernosa* (Fig. 3). ANOSIM analysis of the sponge community at the two habitats indicated low variation in the sponge communities at the two study sites. MDS plot of sponge abundance per quadrat along the selected transects at the two locations did not show any segregation (refer to Fig. 4). The SIMPER analyses showed that mean community similarity within high SPM site was 50.53%. *Biemna fortis* contributed about 82.11% of the total similarity, followed by *C. cavernosa* 16.56%. The mean community similarity within low SPM site was 43.84%. *Biemna fortis* contributed about 53.10% of the total similarity, followed by *C. cavernosa* 42.07%. The mean dissimilarity between the two locations was 56.22%. The greatest dissimilarity was generated by *B. fortis* (44.23%) followed by *C. cavernosa* (39.12%) and *Haliclona* sp. (16.66 %). Two growth forms of *B. fortis* were observed, partially buried and massive growth form, predominating at high SPM site and low SPM site, respectively (Fig. 5-A & C). A Mann-Whitney test indicated that the massive growth forms (Median = 1000 ml) had a significantly higher volume than the partially buried growth forms (Median = 550 ml)  $U = 87.5$ ,  $p < 0.001$ . The partially buried growth form had most of the base buried in the substratum and only small stub-like projections growing above the ground (Fig. 5-B). The underground portion of the partially buried growth form incorporated inorganic matter like pebbles, shells and debris. The buried sponges had sparsely distributed, ramose and arborescent stub like growth visible above the ground (Fig. 5-B). The massive growth form of *B. fortis* had prominent growth above ground (Fig. 5-D). The massive growth form did not have any buried portion growing in the substratum, and no sediment inclusions were found within the sponge. Within each quadrat, all other organisms and substrate like algae, seaweeds and rubble were carefully inspected, but no free-living individuals of *O. modesta* were found. *O. modesta* (Fig. 6) was always found to be in direct contact with the sponge.

### 3.3. Occurrence of sponge-associated brittle stars

The brittlestar *O. modesta* was found to be associated with *B. fortis* in all the monthly samples of massive growth form, whereas brittle stars were present intermittently with the partially buried

growth form (Fig. 7). Most of the brittle stars were found inside the sponge oscula except few individuals on the surface. The highest peak in the monthly abundance of associated brittle stars on both the growth forms was observed in the same season, partially buried growth form (February, n=16) and massive growth form (January, n=284). The lowest number of associated brittle stars on the massive growth form was recorded in April (n=50), and this was also one of the instances when no associated brittle stars were observed on the partially buried growth form. Most of the individuals on both the growth forms were less than 3 mm (Fig. 8 and 9). Throughout the study period the size range of *O. modesta* associated with the partially buried growth form was between 0.5-4 mm and on the massive growth form the *O. modesta* size range was between 0.5-6.5 mm. Largest specimens (6.3 mm) were observed in the massive growth form in October and November (Fig. 9). Sponge volume of partially buried and massive growth forms had significant positive relationship with the number of oscula (partially buried growth forms:  $r_s = 0.53$ ,  $P < 0.01$ ; massive growth form:  $r_s = 0.669$ ,  $P < 0.01$ ) and the number of associated brittle stars (partially buried growth forms:  $r_s = 0.55$ ,  $P < 0.01$ ; massive growth form:  $r_s = 0.47$ ,  $P < 0.01$ ). The number of associated brittle stars had significant positive correlation with the number of oscula in massive growth forms ( $r_s = 0.597$ ,  $P < 0.01$ ) but the correlation was not significant for partially buried growth forms (Fig. 10).

#### 3.4. Reciprocal Transplantation

*B. fortis* –massive growth forms transplanted from the low SPM site to the high SPM site (n=6) could not survive for more than 15 days. However the *B. fortis* –partially buried growth forms transplanted from the high SPM site to the low SPM site (n=6) and the control sponges (n=3) planted at both the study sites survived well throughout the transplantation experiment. After retrieval, the transplanted sponges were taken back to the laboratory and checked for associated brittle stars. The number of brittle stars found on the partially buried growth forms transplanted to the low SPM site was higher (31 individuals in 500 ml sponge volume,  $SD \pm 10.53$ ) than the number of brittle stars found on the partially buried growth forms at the high SPM site (7 individuals in 500 ml sponge volume,  $SD \pm 10.39$ ). The massive growth forms planted to the high SPM site were heavily covered with sediments and debris. After 15 days, there were no brittle stars in the massive growth forms planted to the high SPM site.

#### 3.5. Choice assay

*O. modesta* choice preferences were tested in total five assays (Table 1). Between control seawater and *B. fortis*, the brittle star showed significant preference to *B. fortis*, partially buried growth form ( $\chi^2_{31}=7.25$ ,  $P=0.007$ ) and massive growth form ( $\chi^2_{24}=4.16$ ,  $P=0.041$ ). *O. modesta*, however, exhibited



no significant distinct preference for chemical cues from partially buried growth form or the massive growth form ( $\chi^2_{32}=2$ ,  $P=0.15$ ). Between *C. cavernosa* (low SPM site) and *B. fortis* the brittle star showed significantly higher preference for *B. fortis* ( $\chi^2_{45}=8.02$ ,  $P=0.004$ ). *O. modesta* showed significantly higher preference for controlled seawater when given a choice against *C. cavernosa* ( $\chi^2_{22}=8.90$ ,  $P=0.002$ ).

#### 4. Discussion

The sites studied (Anjuna and Mhapan), situated along the Central West Coast of India (Fig 1) share many morphological features; both have a rocky intertidal zone with adjacent cliffs. Geomorphologically both the beaches are described to be stable with seasonal changes and annual cyclicality (Chandra Mohan et al., 1992). However, the suspended particulate matter (SPM) levels were significantly different between the two study locations (Fig. 2). The study site with consistently high SPM levels (Anjuna) is characterized for high erosional activity (Nayak and Souza, 2010). High SPM level indicates turbidity, which could be either due to re-suspension or deposition caused due to tides, local water current regimes or winds.

Sponges modify their morphology to the local conditions of water movement, light penetration, substratum suitability and space competition (Palumbi, 1986; McDonald et al., 2002). *B. fortis* showed different growth forms at the two locations. *B. fortis* at the high SPM site had a partially buried growth form (Fig. 5 B and D). Most of the sponge growth extended downward into the ground around small and medium sized pebbles, with only small stubs visible above the ground. The partially buried growth form had high amount of debris and substrate incorporated inside the sponge. *B. fortis* is known to grow into the ground in the sand and between crevices to form a buried underground body with only low oscula visible above ground (Cerrano et al., 2007; Longakit et al., 2005; Kelly, 1986). Sponges incorporate sediments and debris to get anchorage and stability (Cerrano et al., 2007). *Biemna* sponges are reported from habitats with strong tidal currents (Hooper, 1996), and on a sandy substratum *B. fortis* incorporate rocks and rubble to anchor itself against the wave action (Cerrano et al., 2002). However in less turbulent environment, their growth form is different. The inhalant papillae elevate and grow above the substrate (Kelly, 1986). At the low SPM site *B. fortis* had a massive growth form, most of the sponge mass was above ground, growing over boulders and sand with little or no underground growth and very few sediment inclusions (Fig. 5 A and C).

Only three sponge species were recorded at both the study sites and SIMPER analysis revealed the sponge community structure at two study sites was highly similar. The study sites consisted

primarily of *B. fortis* and *C. cavernosa*. *Haliclona* sp. was rare, and only three individuals were observed at both the sites. This similarity could be attributed to the low heterogeneity between the two locations. A more heterogeneous substrate supports higher species diversity (Sara and Vacelet, 1973). Shallow environments exposed to waves and high light intensity have low species richness and density, which gradually increases with depth (Sara and Vacelet, 1973; Zea, 2001). *B. fortis* was commonly found on the sandy bottom and in the intertidal rock pools at both the locations with highest frequency and abundance followed by *C. cavernosa* (Fig. 3). In symbiotic relationships, it is important that the host should be easy to find and hence host abundance is one of the major factors for symbiosis to evolve (Roughgarden, 1975). Sponge brittle star association involves mutualistic and symbiotic relationship (Hendler, 1984). Relative abundance of the host and microclimatic variations play a major role in the distribution pattern of plant-fungus symbiosis (Gilbert et al., 2007). Our observations conform with the previous studies on sponge-brittle star association where host sponge was found to be common and abundant (Henkel and Pawlik, 2005).

The brittle star *O. modesta* (Fig. 6) was common on the massive growth form but rarely occurred in the partially buried growth form. *O. modesta* was usually found on the surface and inside the canals. Brittle stars were never found in the buried sponge. This explains the low abundance of *O. modesta* on the partially buried growth form. *O. modesta* associated with the massive growth form showed high abundance in monsoon (August, n=178) and post-monsoon (January, n=259) (Fig. 7). A sudden decline in the abundance was observed pre-monsoon (April, n=53). In tropical regions, such a semiannual pattern has been recognized in many invertebrates due to the influence of monsoons (Giese and Pearse, 1974). Sponge-associated brittle stars maintain their population by asexual reproduction by fission, which occurs throughout the year, and also by sexual reproduction, which is seasonal (Chao and Tsai, 1995). The size histogram (Fig. 8 and 9) indicated juveniles dominated the brittle star population. Juvenile ophiuroids are known to concentrate in refuge substrates and can shift among microhabitats (Turon et al., 2000). Food capturing abilities of juveniles are limited and seem to be assisted by the filtering activity of the sponges and are suggested to benefit the brittle star by increased growth rates as a result of the trophic relationship (Turon et al., 2000).

Massive growth forms transplanted from the low SPM site to the high SPM site did not survive after transplantation. However partially buried growth forms from the high SPM site were able to survive well at the low SPM site. Sediments have a high impact on sponges and influence them in a variety of ways (Bell et al. 2015). Siltation stress is known to have a negative effect on sponges (Roberts et al., 2006; Tjensvoll et al., 2013). Ingestion of fine particles can impact sponge physiological processes by clogging the aquiferous system (Bakus, 1968). Due to high water movement sediments

can cause abrasion to the external tissue (Nava and Carballo, 2013). Although we could not assess the effect of the cage on the transplanted sponges all the control sponges caged in similar conditions were able to survive at both the sites, which suggests the conditions were acceptable. Cages with a similar mesh size (5 cm) employed in previous other sponge studies were found to have no significant effect on the flow (Hill, 1998). The mesh size was sufficiently large for brittle stars to leave or move into the transplanted sponges. The partially buried growth forms retrieved from the low SPM site had a higher number of brittle stars (31 brittle stars per 500 ml sponge), compared to the partially buried growth forms at high SPM habitat (7 brittle stars per 500 ml sponge). Sponge-associated brittle stars are capable of emigration and immigration from the host sponge habitat (Henkel and Pawlik, 2005). Massive growth form retrieved from the High SPM site were dead and did not have any associated brittle stars. Sponge-associated brittle stars actively search and prefer live sponge habitat to similar non-living predator refuge or sponge skeletons, suggesting a mechanism for sponge habitat recognition (Henkel and Pawlik, 2005). Sponge-dwelling brittle stars display a chemotactic recognition for the host sponge (Henkel and Pawlik, 2011) and in the present investigation, *O. modesta* was able to detect *B. fortis* in the choice assays (Table 1).

Interactions among species can vary in time and space according to the available physical and biotic conditions (Loh and Pawlik, 2009). Sponge-brittle star symbiosis is known to shift from commensalism to larvivory (Henkel and Pawlik, 2014) when the brittle star feed on the host sponge larvae (Henkel, 2008). Production of secondary metabolites is one of the major self-defence mechanisms used by the sponges (Thakur and Müller, 2004; Taylor et al., 2007). Secondary metabolites from sponges show spatial and temporal variations, which are influenced by the physical and ecological conditions (Page et al., 2005). In the choice assays *O. modesta* showed equal preferences for the waterborne chemical cues of *B. fortis* from both the habitats (Table 1). The brittle star *O. modesta* association with sponges is not species specific. *O. modesta* associated with *Spirastella inconspans* and other sponge species is reported (James, 1982; James, 1983; Mackay, 1945) however at our study site among all the available sponges, *O. modesta* was found to be associated only with *B. fortis*. The *O. modesta* used in the choice assay were all collected from the *B. fortis* tissue, and this could have possibly biased their preference in the choice assay. Although *O. modesta* specimens have been collected from rocks and coral (Price and Rowe, 1996; Marsh and Morrison, 2004), in the present investigation no individuals were found on non-sponge substrate, and it would be interesting to check the choice preference of free-living individuals of *O. modesta*. *O. modesta* showed a negative chemotactic response to the *C. cavernosa* chemical cues in the choice assays. *C. cavernosa* was abundantly present at both the study sites and is reported to have bioactive

metabolites with antiviral and cytotoxic activity (Singh and Thakur, 2015). Considering the overall number of experimental trials, *O. modesta* made a choice very infrequently, which was similar to the observations made by Henkel and Pawlik (2011) in their experimental choice assays involving brittle star *Ophiothrix lineata* and sponge *Callyspongia vaginalis*. A positive response to *B. fortis* chemical cues in choice assay does indicate the involvement of chemical cues in host location. However, since *O. modesta* is not an exclusive sponge-dwelling brittle star or an obligate associate of sponge *B. fortis* the choice preference is not sufficient to infer if it's a species – specific response to host sponge or a general feeding response to sponge metabolite.

In harsh environments, facilitator species offer protection to less tolerant species from stresses like rough conditions and predators (Hacker and Gaines, 1997). Direct positive interactions like symbiosis and commensalism are related to species diversity by the role mediated by the facilitator species (Hacker and Gaines, 1997). Theoretical models estimate the relative importance of positive interactions, may vary inversely across gradients of abiotic stress (Bertness and Callaway, 1994; Brooker and Callaghan, 1998). However, later studies suggest that facilitation may decrease with high abiotic stress (Maestre and Cortina, 2004; Maestre et al., 2010; Holmgren and Scheffer, 2010). In the high abiotic stress conditions, the limiting resources are so scarce that the benefits bestowed by the facilitator cannot overcome its own requirements (Maestre and Cortina, 2004; Maestre et al. 2010; Holmgren and Scheffer, 2010). In the sponge - brittle star association, sponges protect the brittle stars from predators and provide greater access to food particles (Henkel and Pawlik, 2005; Henkel and Pawlik, 2014). Sponges are also suggested to provide protection to the associates from physical stress like wave action during high tide and desiccation during low tide exposures (Firth, 1976). Sponges show morphological modifications that are induced by environmental perturbations and predators (Hill and Hill, 2002; De Voogd and Cleary, 2007; Manconi and Prouto, 1991). Sponge growth and morphology governed by the water movement, siltation and food supply influence the distribution of sponge-associated fauna (Peattie and Hoare, 1981; Ávila and Ortega-Bastida, 2014). *B. fortis* growth forms vary at different environmental stress conditions. *B. fortis* had partially buried growth form at the high SPM site. The rare occurrence of the brittle star *O. modesta* on the partially buried growth forms of *B. fortis* can be explained by the reduced availability of habitat space due to decreased sponge volume. The high abundance of *O. modesta* on the massive growth forms suggests the availability of habitat space due to high volume and a greater number of oscula. *O. modesta* showed positive chemotaxis to *B. fortis* chemical cues from both the growth forms. The present investigation indicates that sponge growth forms under different abiotic conditions govern the abundance of the associated brittle star.

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## Highlights

Morphological modification helps sponges acclimatize to the local environmental conditions.

Variations in the sponge growth form under different environmental conditions are important for survival.

Variations in the sponge growth form affect the abundance of associated brittle stars.

*Ophiactis modesta* showed positive chemotaxis to host sponge *Biemna fortis*.

## Tables

### Table 1

Response of *Ophiactis modesta* in the choice assays in which *O. modesta* was presented with seawater conditioned with *Biemna fortis*-partially buried growth form vs. *Biemna fortis*-massive growth form, *Biemna fortis* vs. control seawater. *Biemna fortis*-massive growth form vs. *Cinachyrella cavernosa* and *Cinachyrella cavernosa* vs. control seawater.

Choice experiment	No. of trials	No. of times choice made (n)	Percentage of choice made
<i>Biemna fortis</i> - partially buried growth form vs <i>Biemna fortis</i> - massive growth form	67	32	<i>B. fortis</i> -partially buried growth form=37.5% <i>B. fortis</i> - massive growth form=62.5%
<i>Biemna fortis</i> - partially buried growth form vs control seawater	53	31	<i>B. fortis</i> -partially buried growth form =74.1%
<i>Biemna fortis</i> - massive growth form vs control seawater	62	24	<i>B. fortis</i> - massive growth form=70.8%
<i>Biemna fortis</i> - massive growth form vs <i>Cinachyrella cavernosa</i>	60	45	<i>B. fortis</i> - massive growth form=71.1% <i>C. cavernosa</i> =28.9%
<i>Cinachyrella cavernosa</i> vs control seawater	36	22	<i>C. cavernosa</i> =18.2%

## Figure Legends

**Fig. 1.** Study sites along the central west coast of India, Anjuna and Mhapan.

**Fig. 2.** Monthly variation in Suspended Particulate Matter (SPM) of the two study sites at habitats with partially buried growth forms (Anjuna) and habitat with massive growth forms (Mhapan). ( $\pm$ error bars are the standard deviation).

**Fig. 3.** Sponge density at the high SPM (Anjuna) and low SPM (Mhapan).

**Fig. 4.** Multidimensional scaling ordination based on Bray-Curtis similarities of square-root transformed sponge abundance per quadrat on the transects selected at each of the two study sites.

**Fig. 5.** *Biemna fortis* growth forms. A) *Biemna fortis* growing at high SPM site (Anjuna) photographed in situ B) Partially buried growth form, with the underground, buried body mass C) *Biemna fortis* growing at low SPM site (Mhapan) photographed in situ D) Massive growth form, most of the growth is above surface. Black arrows indicate the portion above ground surface, white arrow indicates the sediment inclusion in the buried body mass. (scale =7 cm).

**Fig. 6.** Brittle star *Ophiactis modesta* found in sponge *Biemna fortis*. A) Dorsal view (scale bar =1mm) B) Ventral view (scale bar = 1 mm) C) Dorsal view of arm (scale bar= 0.5 mm) D) Jaw (scale bar = 0.2mm) E) Ventral view of arm (scale bar= 0.5 mm).

**Fig. 7.** Abundance of *Ophiactis modesta* found in association with Sponge *Biemna fortis*, partially buried and massive growth forms. Brittle stars per 500 ml of sponge volume. (error bars are standard dev).

**Fig. 8.** Monthly disc size variation in *Ophiactis modesta* (n=24), found on partially buried growth forms of *Biemna fortis*.

**Fig. 9.** Monthly disc size variation in *Ophiactis modesta* (n=24), found on massive growth forms *Biemna fortis*.

**Fig. 10.** Relationships between sponge volume and (A) abundance of associated brittle stars and (B) number of oscula (partially buried growth form). Relationships between sponge volume and (D) abundance of associated brittle stars and (E) number of oscula (massive growth form). Relationship between number of oscula and abundance of associated brittle stars (C) partially buried growth form and (F) massive growth form.

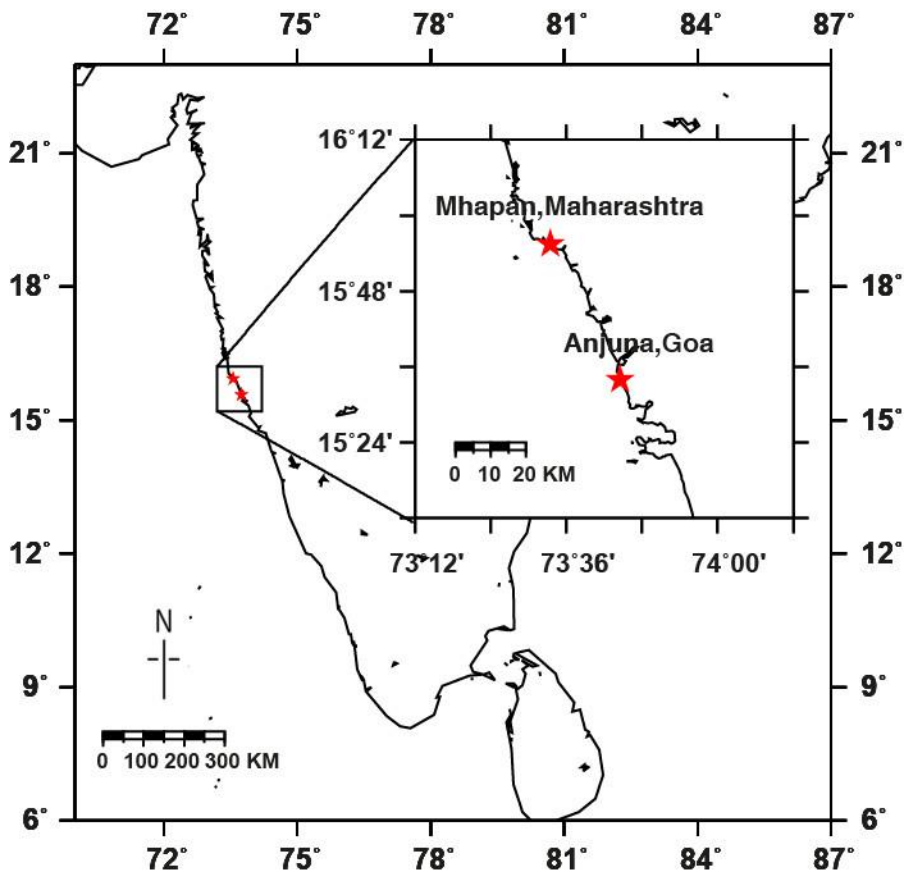


Fig 1

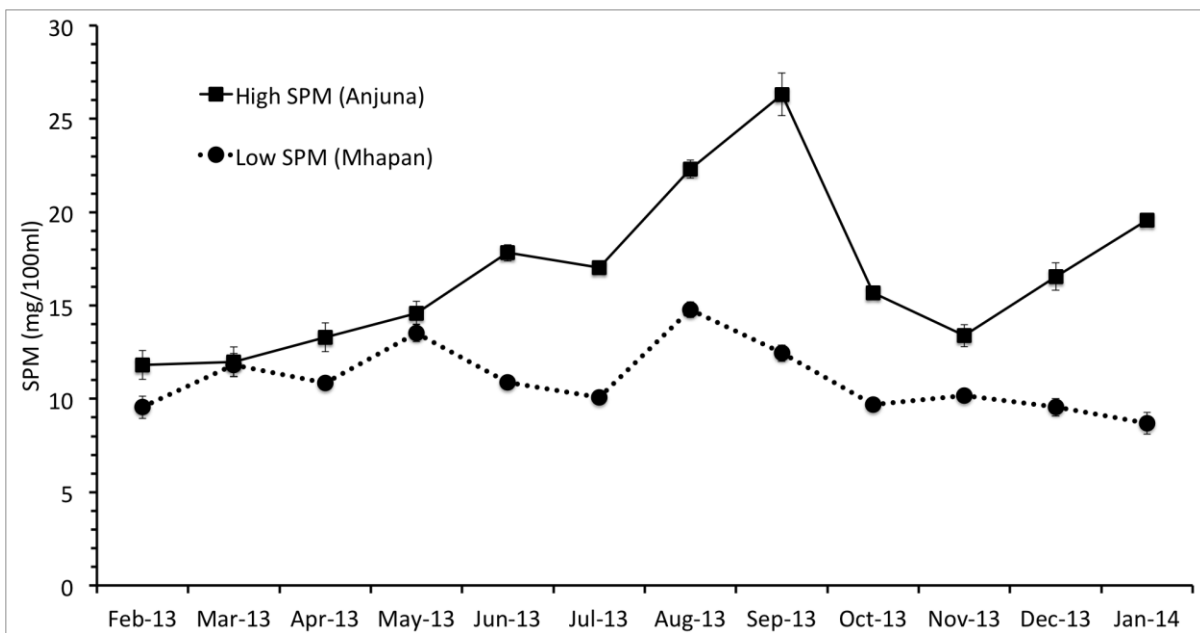


Fig 2

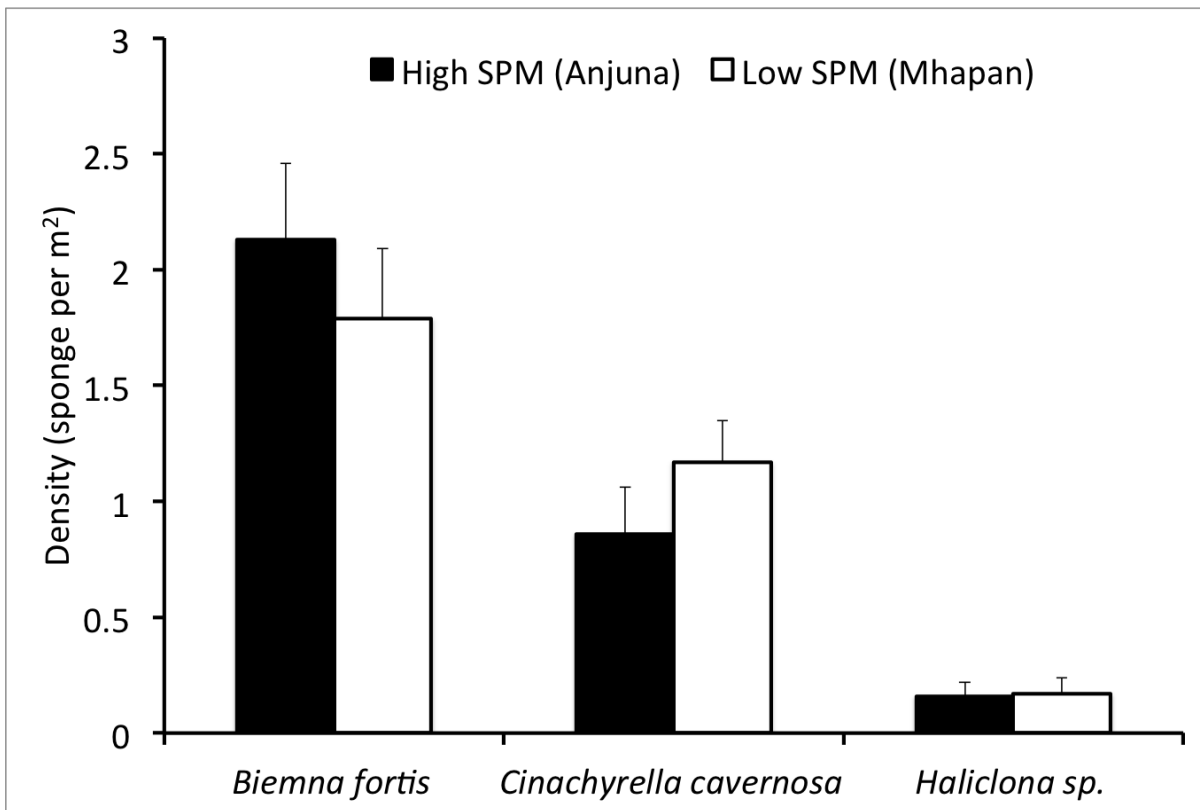


Fig 3

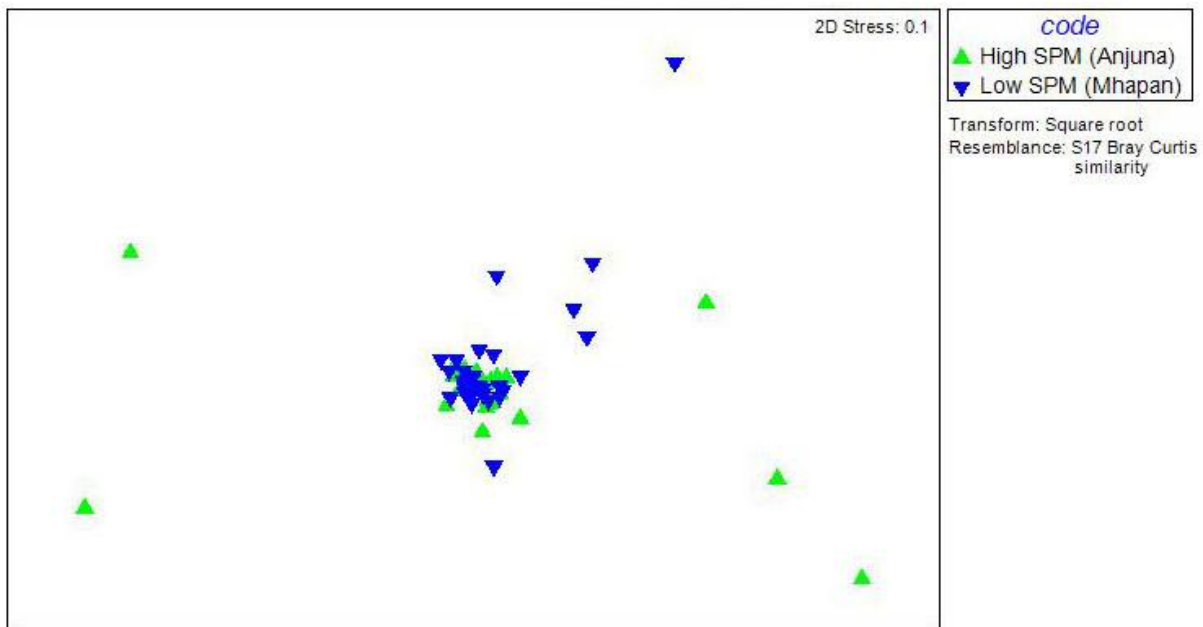


Fig 4

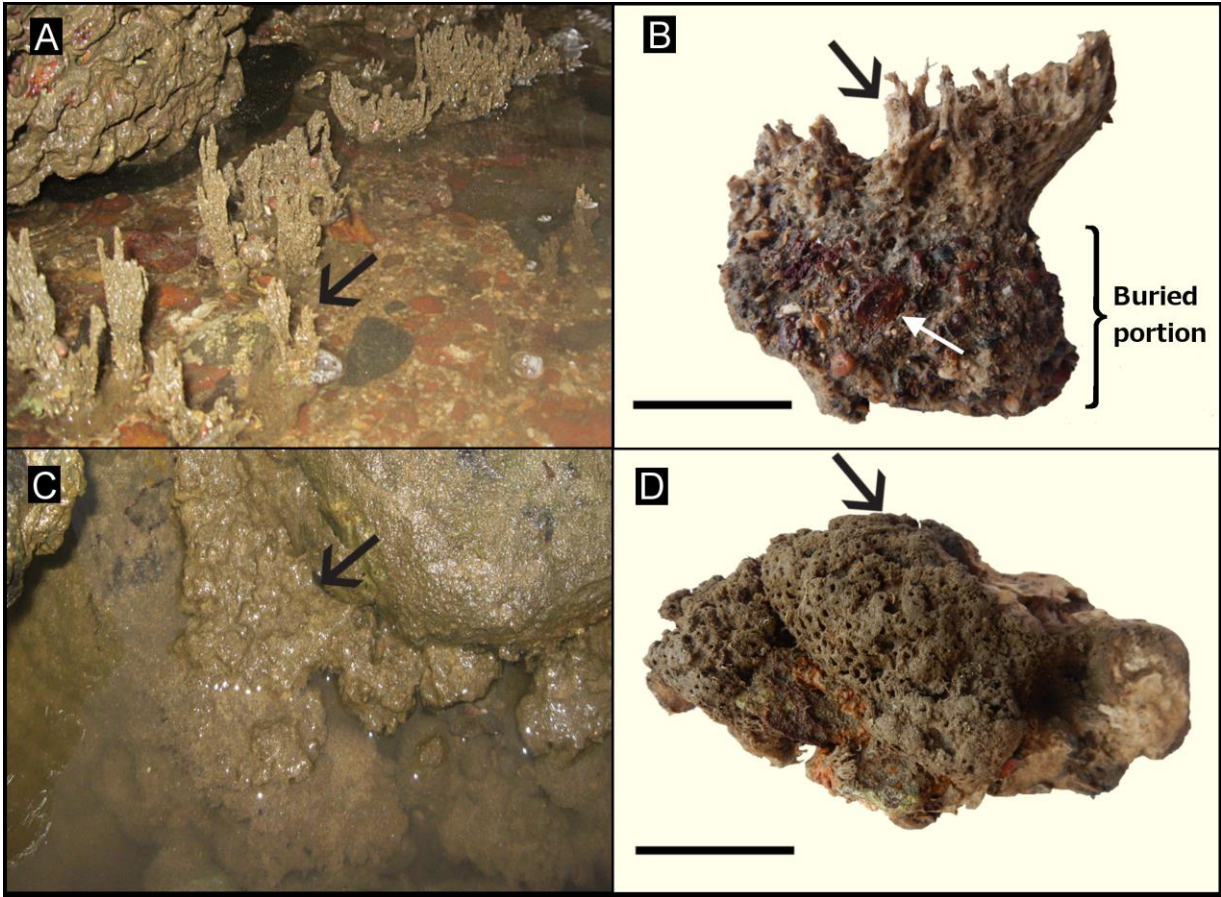
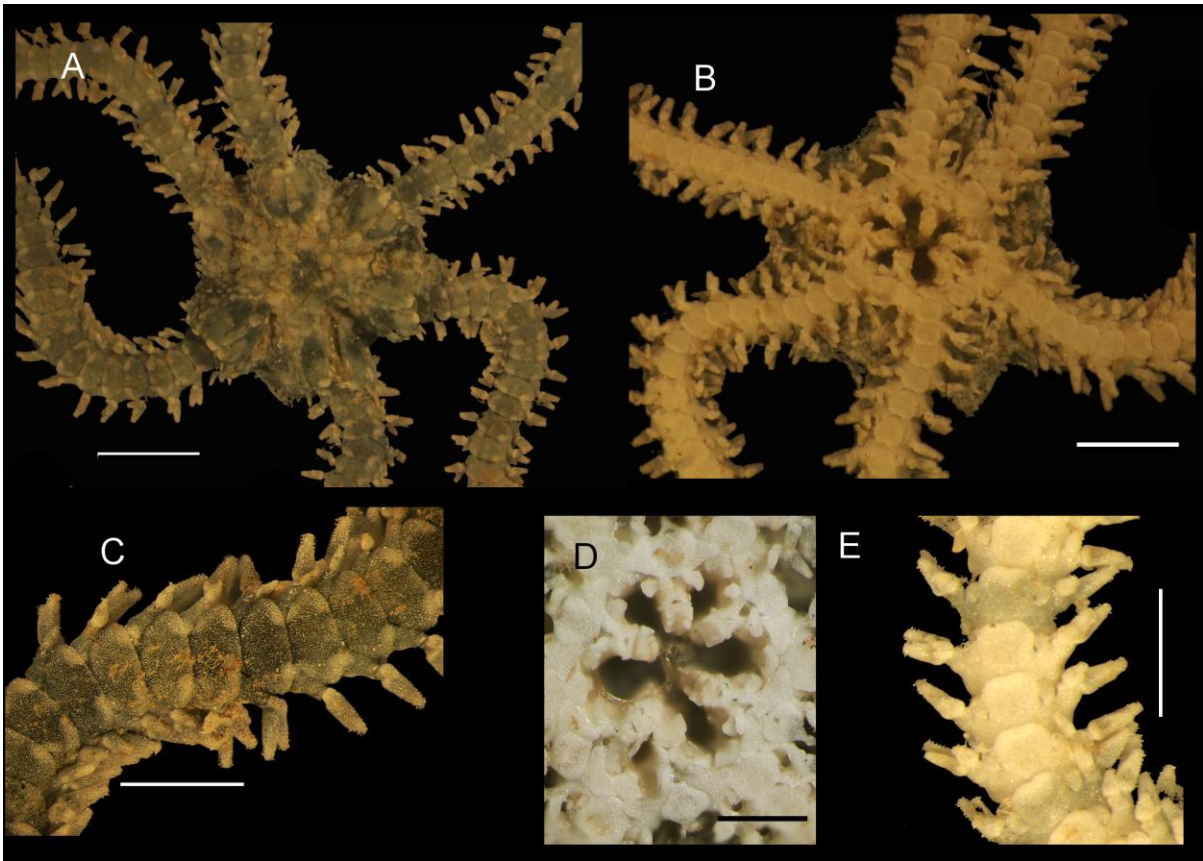
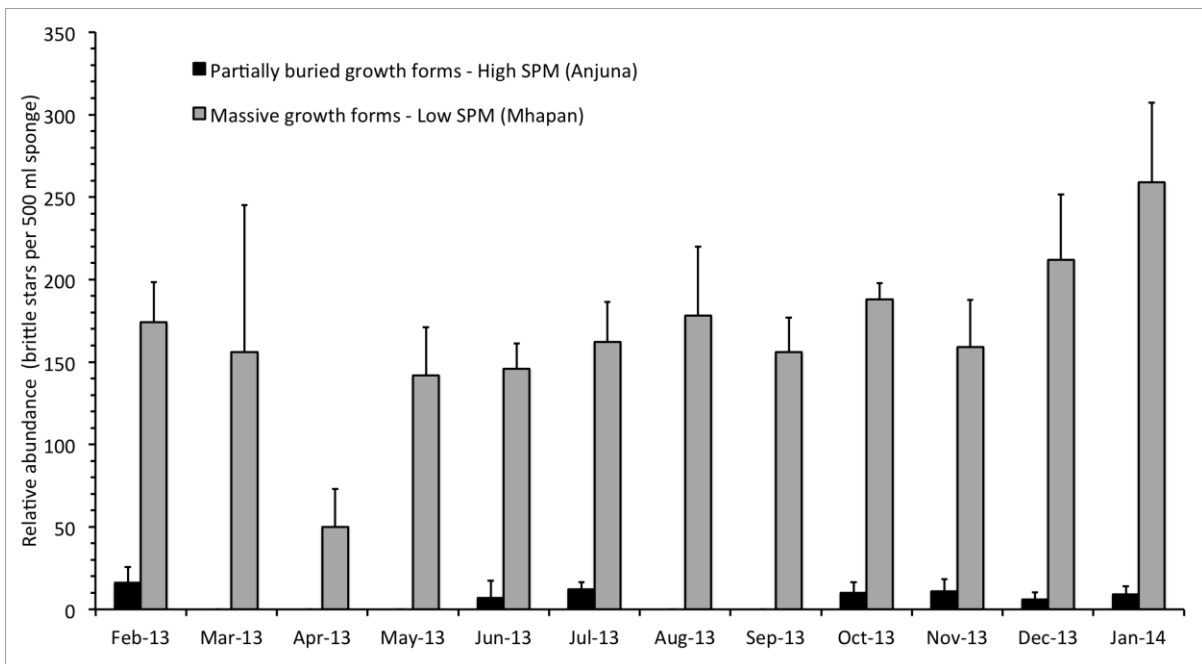


Fig 5



**Fig 6**



**Fig 7**

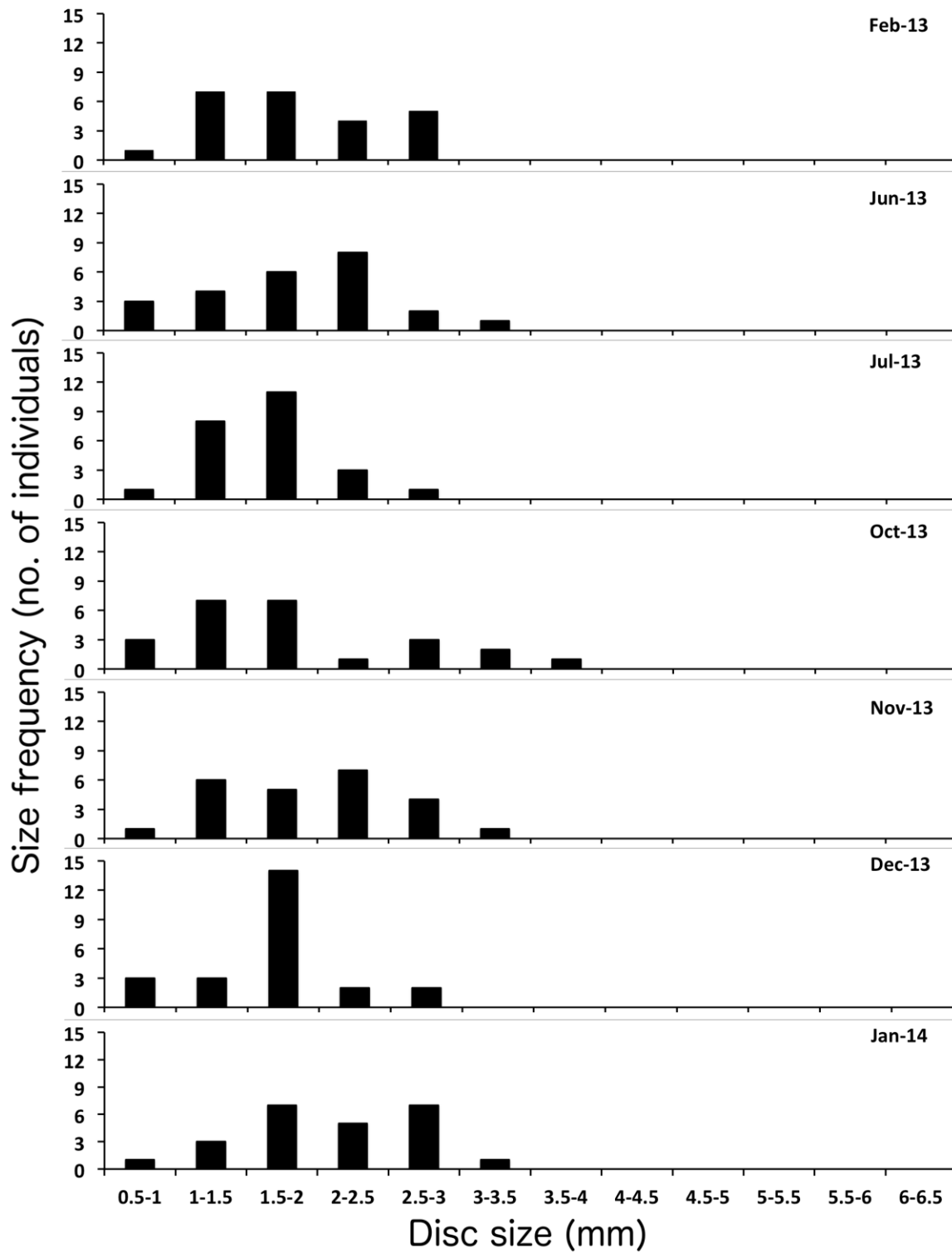


Fig 8



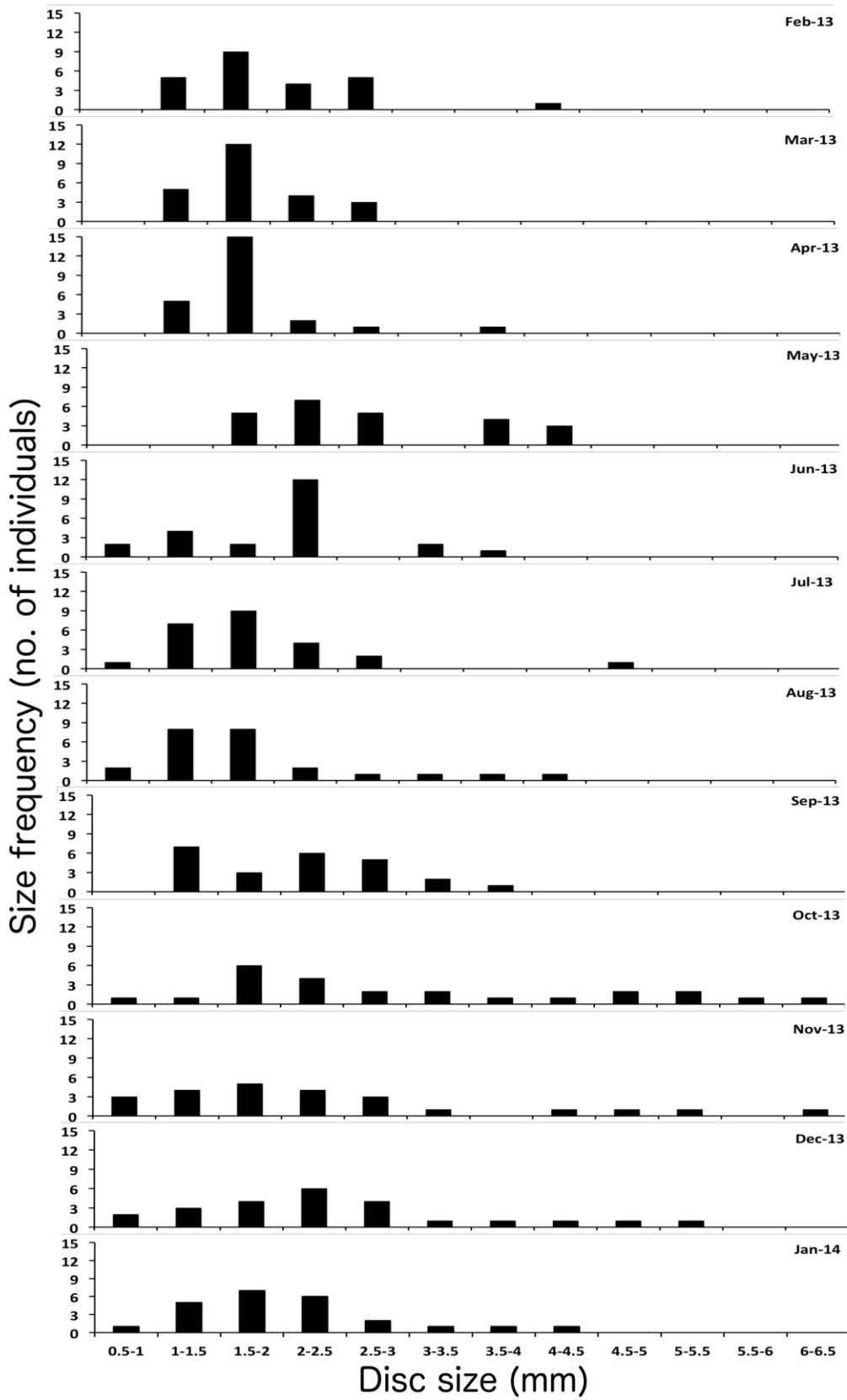
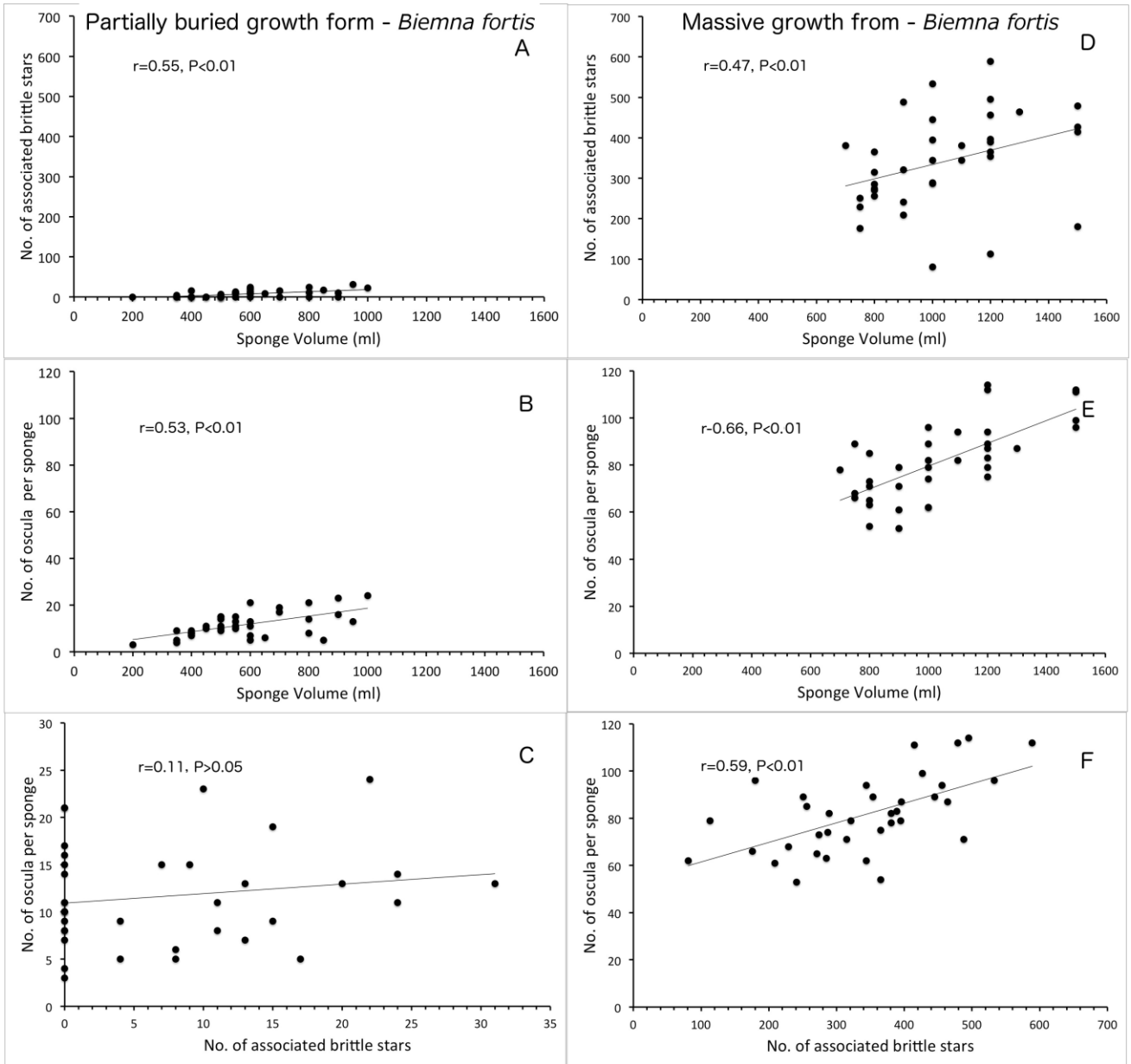


Fig 9



**Fig 10**