Octocorals outcompete scleractinian corals in a degraded reef

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Abstract. Competition among benthic organisms plays an important role in coral population dynamics in degraded reefs. In this study, interspecific interactions between scleractinians and octocorals and larval settlement of scleractinians near selected octocorals in Lucero, a degraded reef in Bolinao, Pangasian, northwestern Philippines were assessed. Competitive index (CI) was computed based on species interactions (i.e., direct interaction, overgrowth) observed on the reef. The coral settlement near alcyonacean octocorals (i.e., Sarcophyton, Sinularia), blue coral (Heliopora), and substrate without octocorals (control) were monitored by deployment and retrieval of settlement plates on the reef in February and May 2018. Results showed that octocorals were more aggressive towards other species (CI between 1.00 and 0.20). Heliopora was subordinate (CI = -0.10) to octocorals, but relatively competitive than scleractinians. Scleractinian coral settlement is inhibited by octocorals and is reduced near Heliopora. Interspecific interactions indicate that octocorals present in the study site are more tolerant than other species; hence, it might be attributed to its higher competitive ability. Settlement inhibition by octocorals and Heliopora is indicative of the production of allelochemicals, a substance known to deter settlement. Considering the growth advantage of Heliopora over Sarcophyton and Sinularia, it is likely that Heliopora will dominate over scleractinians in a degraded reef of Lucero. However, this necessitates long-term monitoring using permanent quadrats to detect the large-scale effects of competition for space on the community structure of disturbed reefs.

1. Introduction

Worldwide coral reef degradation is primarily attributed to global climate change and exacerbated by localized threats such as destructive fishing methods, siltation, and eutrophication [1]. These factors have been known to contribute deleterious effects on health and may reduce populations of scleractinians and octocorals within ecosystems [2]. As an effect, newly opened spaces become available, promoting opportunity for space colonization on benthic substrates [3]. Occupancy and distribution of marine organisms within these zones are controlled by physico-chemical factors (e.g., temperature, salinity, nutrients, and light) and biological processes such as predation, grazing, and competition [4-11].

Scleractinian and octocorals compete for space for survival and territory expansion. To ensure this, some corals release allelopathic chemicals or use sweeper tentacles to deter settlement and kill other organisms [5, 8, 12]. While some coral species affect others through allelochemical production, other species have direct aggressive mechanisms for competition. These mechanisms have been evident among Indo-Pacific corals [10, 13]. Field experiments conducted by [4] showed the competitive superiority of Briareum octocoral by overgrowth on scleractinian Acropora within the natural
environment. Specialized sweeper tentacles are also found in some scleractinian coral species which are used for territorial protection, successful food hunting, and destruction of tissues of neighboring corals [14]. These interspecific interactions were believed to have contributed to the development of coral adaptive mechanisms [5, 8, 11]. Here, the competitive ability of corals is assessed using an index categorizing interspecific interactions as direct, overgrowth, and stand-off [8].

Aside from territorial expansion and food hunting, another factor affecting population dynamics, as well as the resilience of the reef ecosystem on varying environmental perturbations, is a successful settlement [5, 15]. Several studies reported the potential of octocorals to inhibit the successful settlement of scleractinian recruits [5, 16, 17]. Since interspecific competitions and reef disturbance were considered to be intense within the tropics [3, 18], it is imperative to investigate how relevant these interactions are in the structuring reef community. To date, there are limited studies on coral competition in degraded reefs in the Philippines. Thus, this study was conducted to understand the role of interspecific interactions among scleractinians and octocorals. Besides, larval settlement inhibitory strength of various octocorals was also examined. The results of this study will give insights on the effects of disturbances on community structure coral and coral recovery potential of disturbed reefs.

2. Materials and methods

2.1. Site description

The Bolinao reef in northwestern Luzon is one of the most studied reefs in the Philippines [4, 5, 19-23]. It has been reported to be a degraded reef due to nutrient inputs from submarine water discharge and eutrophication-sedimentation brought by unconsumed feeds and fecal matter from mariculture areas that have proliferated over the years [23]. The reefs in the area have also experienced other disturbances such as bleaching [24] and overfishing [25]. Lucero, a degraded fringing reef in Bolinao, Pangasinan, northwestern Philippines (16.41057° N; 119.90409° E), was selected to understand the interspecific competition of corals (Figure 1).

![Figure 1. Location of the Lucero reef, Bolinao, Pangasinan, northwestern Philippines (modified map from dela Cruz and Harrison [26]).](image-url)

2.2. Competitive interactions of scleractinians and octocorals

Field observations were conducted in February 2019. All competitive interactions of scleractinian-octocoral colony pairs (≤ 8cm) encountered through SCUBA diving along approximately 100 × 10 m transect, at depths between 3 to 5 m, were recorded. Interspecific interactions were scored following the protocol of [8]. Interactions between adjacent octocoral-octocoral and octocoral-scleractinian were characterized as direct (i.e., presence of dead margins on portion in contact with one of the coral pairs); overgrowth (i.e., growth of one specimen on the other with no evident tissue damage); and stand-off (i.e., coral colonies at ≤ 8 cm proximity without direct interaction or overgrowth). Interacting
scleractinians and octocorals were identified up to the genus level. Octocorals were identified using morphological descriptions published by Roxas [27]. Here, octocorals were categorized as Alcyonaceans and Heliopora. Competition index was computed only for the coral genera with at least six recorded interactions (exclusively based on direct interaction and overgrowth) using the following formula:

\[
CI = \frac{\text{number of wins} - \text{number of losses}}{\text{Total number of interactions}}
\]

Relative competitive abilities were categorized as 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) and was based on calculated coral competition index values [8].

2.3. Effects of octocorals, Sarcophyton, Sinularia, and Heliopora on scleractinian coral settlement
The Scleractinian larval settlement was monitored near (≤ 5 cm) Sarcophyton, Sinularia, and Heliopora, and bare substrate (control). The following species were selected due to their abundance based on the benthic cover assessment conducted. Heliopora species has been previously reported by [5] to inhibit the settlement of coral recruits within its radius. Ten fiber-cement settlement plates (10 × 10 × 0.6 cm) were hammered 3 cm above the substrate. These were deployed on the reef in February and retrieved in May 2018. This period was selected to capture coral spawning within the study site, as previously reported by Vicenturan et al. [28]. Retrieved settlement plates were bleached overnight in 10% house bleach solution, rinsed with fresh water, and air-dried at the Bolinao Marine Laboratory, Marine Science Institute, University of the Philippines. Coral recruits on the settlement plates were examined under stereo zoom microscope (Motic®, SMZ-171) at 20× magnification for identification. Each coral recruit found was photographed using the camera (Moticam 1080) attached to the microscope and identified to the lowest taxonomic level possible using the identification key of Babcock et al. [29]. Unidentifiable recruits (i.e., broken, highly eroded, and lack distinguishable features) were designated as ‘others.’

3. Results

3.1. Competitive interaction of scleractinians and octocorals
A total of 195 interactions involving six octocorals and 17 scleractinian genera were observed and scored. All of the six octocoral genera (i.e., Briareum, Clavularia, Heliopora, Lobophytum, Sarcophyton, Sinularia) identified and only three scleractinian genera (i.e., Favia, Favites, Porites) were regarded as major species (with six or more recorded repetitive interactions). Out of 195 recorded interactions, 86 cases were between other octocorals and scleractinians; 63 cases from Heliopora and scleractinians; 44 from Heliopora and octocorals; and two cases from interactions of both octocoral genera. Twenty-two percent (42 cases) of major coral interactions observed were direct interactions; 44% (86 cases) overgrowth; and 34% (67 cases) were recorded as stand-offs. Coral interactions observed with both overgrowth and direct interaction was recorded as direct interactions since it is known to precede the former, following the protocol of Dai [8]. Table 1 shows the relative competitive ability of octocorals (aggressive Briareum; CI = 1) and scleractinian (subordinate Porites; CI = -0.68) based on calculated CI values. Competitive interactions between major coral genus encountered, with emphasis on octocoral-octocoral, and octocoral-scleractinian interactions were recorded. Winners and losers, as well as the type of competitive interactions involved for each pair, are summarized (Figure 2).
Table 1. Competitive index value and relative competitive ability of scleractinians and octocorals in Lucero reef, Bolinao, Pangasinan, northwestern Philippines.

| Major coral groups | Family   | Competitive index value | Relative competitive ability |
|--------------------|----------|-------------------------|------------------------------|
| Scleractinians     | Faviidae | -1.00                   | Favorable                     |
|                    | Merulinidae | -0.30                 |                             |
|                    | Poritidae  | -0.68                   |                             |
| Octocorals         | Briareidae | 1.00                    | Briareum                     |
|                    | Clavulariidae | 1.00               | Clavularia                   |
|                    | Helioporidae | -0.10                  | Heliopora                    |
|                    | Alcyoniidae | 0.42                    | Lobophytum                   |
|                    |           | 0.79                    | Sinularia                    |

Figure 2. Field observations of interspecific interactions between coral species observed at 3 - 5 m depths. Each axis represents coral genera encountered with at least six recorded interactions. Arrowheads point toward the winner of each interaction.

4. Discussion

Community structure (i.e., diversity, abundance) in reefs is strongly governed by interspecific interactions. Competition for space and predation is known to be intense between octocorals and scleractinians [3, 4, 8]. It was revealed in this study that scleractinians were subordinate to Heliopora and other octocorals by overgrowth, a common direct aggressive competitive behavior exhibited by octocorals. These observed patterns of scleractinian subordination were among scleractinians with particularly massive growth forms and slow growth rates (e.g., Porites, Favia) [10, 11].

Octocorals have higher tolerances to different disturbances than many scleractinian species [30, 31]. Few species of alcyonaceans were observed to be superior to other species in interspecific interactions and even having the adaptability to increased nutrient loads [32]. Thus, there might be a probability of octocorals dominating a disturbed reef. The tolerance of species to multiple disturbances might affect its competitive advantage on other species. This higher tolerance to disturbance by octocorals compared to scleractinians can be attributed to their ability to release allelopathic
chemicals, called terpenoids, during times of stress. Terpenoids have a variety of functions for different octocoral species [33]. This is the main mechanism behind the low predation on octocorals since terpenoids can serve as an ichthyotoxin and feeding deterrent to other organisms [34]. During conditions with high nutrient levels, which can promote growths of algae, octocorals may release terpenoids and serve as algicide to prevent algal growth on their surface. Terpenoids may also have allelopathic effects on neighboring benthic organisms, such as scleractinian corals [11]. Aside from having a chemical defense mechanism, other octocorals are resilient to disturbances because of their morphological characteristics. For example, species of *Lobophytum* can adapt to conditions with high sedimentation because of the presence of high ridges on their upper surface creating a large proportion of the surface not covered by sediment, so photosynthetic activity will be affected [35].

The settlement of scleractinians was inhibited by octocorals. Among octocorals, *Sarcophyton* has a higher inhibitory effect on larval settlement than *Heliopora*. This inhibition on a larval settlement near *Heliopora* was also observed near the study site [5]. It should be noted that although there was no settlement near *Sinularia*, only one tile was retrieved (Figure 3). Maida et al. [17] have observed reduced settlement of scleractinians on settlement tiles placed adjacent to the *Sinularia flexibilis* and *Sarcophyton glaucum* due to allelopathic interactions. Several studies have documented the chemical defense mechanisms of octocorals and how this decreases competition to other substrate settlers such as scleractinians [3, 16, 33]. The presence of octocorals might have led to the negative preference of coral planulae to settle near the treatment colonies. However, it must be taken into consideration that allelopathic interactions are species-specific and that the effectiveness of the influence of octocorals may vary with respect to the local environment [36]. Composition scleractinian coral settlement on tiles deployed near *Heliopora* has lesser generic richness than those retrieved within the control site. If such a situation persists, the ecological opportunity may arise for *Heliopora* and other octocorals to fill up niches that are left open by the retreating scleractinian corals in disturbed reefs [37].

Ecological models predict community shifts from scleractinian-dominated reefs, to reefs dominated by octocorals and sponges under locally stressed conditions [32, 38]. The dominance of any taxa or group of organisms varies depending on their competitive ability. Competition among benthic organisms might vary and could be species- and site-specific depending on the prevailing environmental conditions and disturbances. In this study, octocorals have competitive advantage overabundant genera (i.e., *Favites*, *Favia*, and *Porites*) present in Lucero reef. Considering the relatively slower growth of octocorals and lower larval settlement success than scleractinians [39], scleractinian dominance is less likely to happen. The dominance of octocoral might also not be realistic in the study area because of the octocoral genera present, the Alcyoniids. Alcyoniids, which include the major octocorals (i.e., *Sinularia, Sarcophyton, Lobophytum*) present in the study site, are k strategists, which means slower growth rates [40] and few offspring compared to r strategists such as Xeniids [41].

*Heliopora* is more competitive than scleractinians in the study site. *Heliopora* is known to be greatly resistant to coral bleaching. This was observed to be least susceptible to the 1997 and 1998 bleaching events in southern Ryukyus, NW Pacific [31]. In addition, coral larvae of *Heliopora* were observed to be resilient to increased sea surface temperature (SST) (author’s personal observation). Its high tolerance to increased SST makes it even more competitive over other scleractinians. Given that aclyoniids present in Lucero reef have slower growth than *Heliopora* and scleractinians, it is highly possible that *Heliopora* might dominate in Lucero reef when prevailing disturbances persist.

In conclusion, octocorals are superior to scleractinians in terms of their competitive ability. Scleractinian settlement inhibition was greatly observed in aclyonaceans, followed by *Heliopora* and less observed in scleractinians, probably through allelopathic interactions. Therefore, the potential impact of octocorals such as *Heliopora, Lobophytum, Sarcophyton*, and *Sinularia* to community structure may lead to its dominance over scleractinians. Moreover, *Heliopora* is predicted to dominate over other organisms present in Lucero reef. Long term monitoring using permanent quadrats is recommended to evaluate interspecies competition at various types and levels of disturbances.
Figure 3. Mean settlement of coral spats near *Sarcophyton* (n=5), *Sinularia* (n=1), *Heliopora* (n=8) and control (n=9).

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