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ORIGINAL PAPER

The relationship between *Diadema* corallivory and macroalgae in a high-latitude coral community in Japan

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Abstract. Destructive corallivory by *Diadema* spp. on acroporid corals was observed in high-latitude coral communities in Japan, where high algal abundance is generally observed in winter and spring. Primarily, an herbivore *Diadema* turns omnivorously during times of food shortages, suggesting that corals could become an alternative food source for *Diadema* spp. when algae become scarce. This hypothesis was examined by quantifying algal abundance, *Diadema* abundance, and *Diadema* feeding scars on corals in the remnant coral population along the coast of Nishiura, Shizuoka, Japan. Incresing in the density of *Diadema* when algal abundance decreased suggested the correlation between the number of feeding scars with the density of *Diadema*. However, there was no correlation between algal abundance and the number of feeding scars on corals. Thus, the hypothesis that corals are an alternative food source for *Diadema* spp. was partially confirmed, although examination of *Diadema* gut content composition could help verifying whether the frequency of corallivory is inversely correlated with algal abundance.

Keywords: High-latitude corals, *Diadema*, Grazing, Algae.

1. Introduction

Depending on their densities, the herbivorous echinoids of the genus *Diadema* have been considered to have both positive and negative effects on corals, (Sammarco 1980). At intermediate density, they facilitate coral recruitment and growth in coral reefs~~,~~ by removing competitive macroalgae and providing suitable substrate for coral settlement and growth. Although coral reefs in the Caribbean dramatically changed from a coral-dominated to macroalga-dominated state in the 1980s, due to a combination of anthropogenic and natural factors~~,~~ including loss of *Diadema* (Hughes 1994), relatively high densities of juvenile corals were observed at sites with relatively high densities of *Diadema* in the late 1990s (Edmunds and Carpenter 2001; Carpenter and Edmunds 2006; Myhre and Acevedo-Gutiérrez 2007; Idjadi et al. 2010). It was suggested that an increase in *Diadema* density could be associated with a reduction in macroalgae and an increase in juvenile coral density in Caribbean reefs (Edmunds and Carpenter 2001; Carpenter and Edmunds 2006). However, primarily herbivorous *Diadema* also has omnivorous tendencies (Rodríguez-Barreras et al. 2015)~~,~~ when algae availability is limited (Bak and van Eys 1975). *Diadema* also incidentally graze on juvenile corals whose activities could damage corals at high sea urchin densities (Bak and van Eys 1975; Sammarco 1980).

Diadema corallivory has been reported in the southern Caribbean Sea (Bak and van Eys 1975), the Gulf of Thailand (Ruengsawang and Yeemin 2000), Hong Kong (Dumont et al. 2013; Qiu et al. 2014), and Japan (Kosaka et al. 2001). Bioerosion of massive corals by *Diadema* grazing has mostly been focused as one of the its negative effects on corals. Furthermore, grazing on branching acroporid corals has also been reported in the Caribbean Sea and Japan.

Destructive acroporid corallivory by *Diadema* spp. was observed in high-latitude coral communities along the coast of Nishiura, Shizuoka, Japan, as early as the mid-1990s (Kosaka et al. 2001). This area is known for the largest *Acropora pruionosa* population at the northern distributional limit of scleractinian corals. This population was first recorded in 1991, with a size of about 5000 m^2. However, it had shrunk to only 127 m^2 by September, 2016.

Due to extremely low seawater temperatures from January to March, heavy coral mortality was first observed in 1996. The population was bleached and then died. By autumn of that year, the population size had been approximately reduced by a half. Afterward, *Diadema* spp. came into the coral population and began to graze on corals. Usually, macroalgae start to grow in the area from December/January. They mature in April and then disappear by July (Yamanishi et al. 2013). Therefore, it was hypothesized that *Diadema* corallivory in the area might occur during the period of low algal cover corals could be an alternative food for *Diadema* spp. in this area. To verify this hypothesis, we investigated algal and *Diadema* abundance, and also *Diadema* feeding scars on corals at this remnant coral population.

2. Materials and Methods

Four 3 m x 3 m quadrats were employed in this study. Two were established at the remnant coral population (Coral sites A and B) and two other quadrats were located near the coral population (Non-coral sites A' and B') along the coast of Nishiura, Shizuoka, Japan (Figure 1). Each 3 m x 3 m quadrat was divided into nine 1 m x 1 m quadrats. Photographs were taken for each 1 m x 1 m quadrat to calculate algal covers. In addition, coral covers at the Coral sites were observed in September when algae had almost disappeared from the area. Photographs were analyzed using the free image-analyzing software, Image J (Schneider et al. 2012).

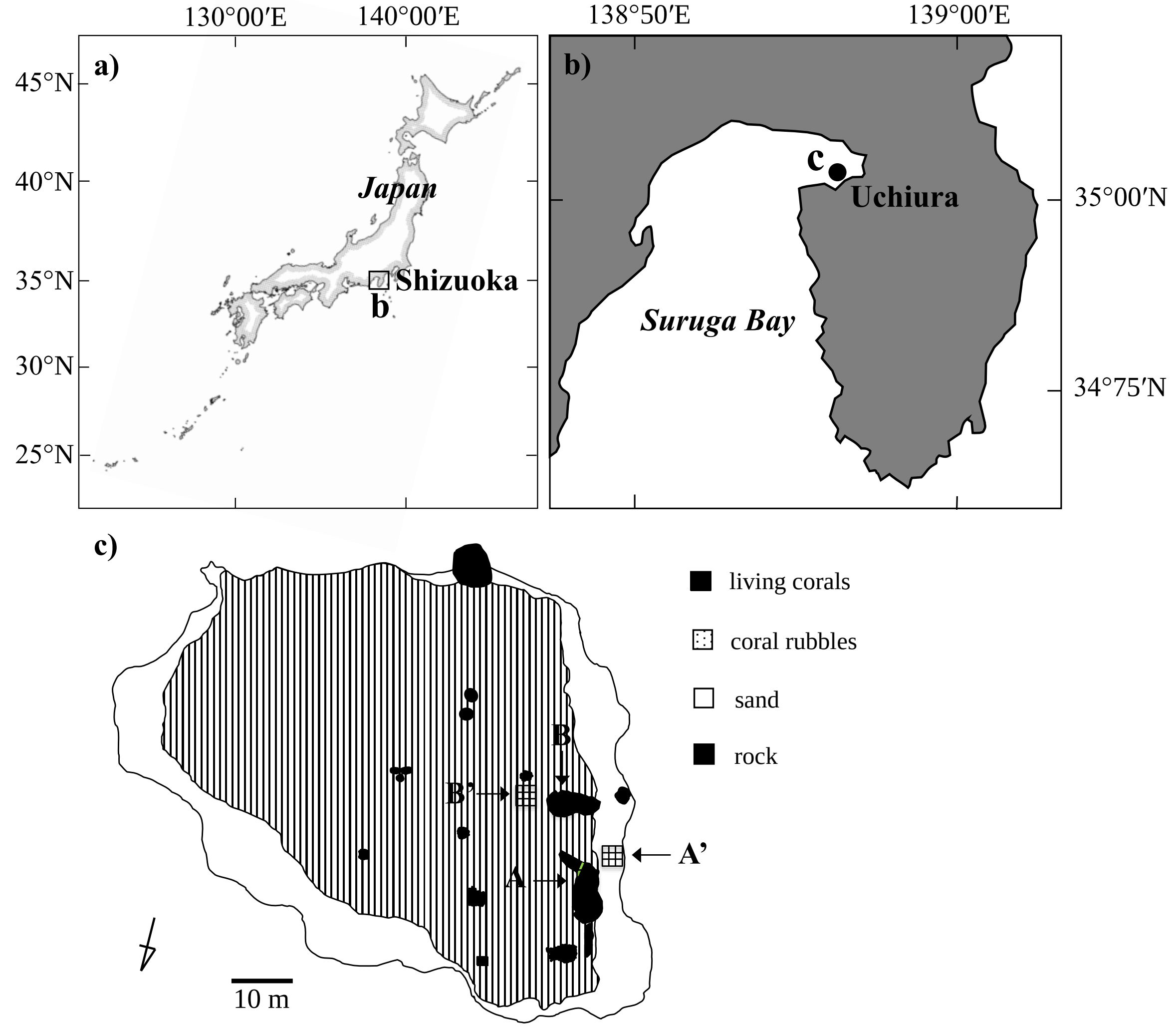

Figure 1. Study sites; a) Shizuoka, b) Nishiura, c) Coral sites (A, B) and Non-coral sites (A', B') along the coast of Nishiura

The numberof *Diadema* spp. was counted in each 1 m x 1 m quadrat. Moreover, the number of feeding scars of *Diadema* spp. on corals was counted in each 1 m x 1 m quadrat at the Coral sites. It has been observed that feeding scars were mended within a month (Atobe and Ueno 2001). Additionally, seawater temperatures at research sites were measured with a TidbiT v2 Water Temperature Data Logger (Onset Computer Corporation, USA). Data loggers were set at the Coral sites. Temperature was recorded hourly from May 2016 to December 2018.

Spatial and temporal variations in seawater temperature, algal cover, the number of *Diadema*, and the number of feeding scars of *Diadema* on corals were analyzed using non-parametric Kruskal-Wallis test. In addition, Spearman rank-order correlation was used to analyze the relationships between seawater temperature, algal cover, the number of *Diadema*, and feeding scars at the Coral site. Statistical analysis was conducted using the free statistical software, R (ver. 3.5.3, R Development Core Team 2019).

3. Results

Seawater temperatures varied among years and months (Kruskal-Wallis test, $p < 0.05$) (Figure 2). In 2016, average seawater temperature was 19.8 °C in May, however it exceeded 20° C in June, 25° C in August and September, and remained above 20° C until November. In 2017, average seawater temperature lowered to 14.8° C in March, and then increased to reach a maximum average temperature of 25.8° C in August. As in the previous year, average seawater temperature exceeded 20° C in June and 25° C in August and September. In 2018, the temperature decreased to about 15° C in January and remained approximately 15° C until March, and then increased. In April, 2018, the average seawater temperature exceeded 17°C, compared to 14° C in April 2017. Temperatures in May and June, 2018 were about 1° C higher than in the same month during the previous year. The temperature was higher than 25° C in July, 26° C in August and September, and 20° C in December, 2018

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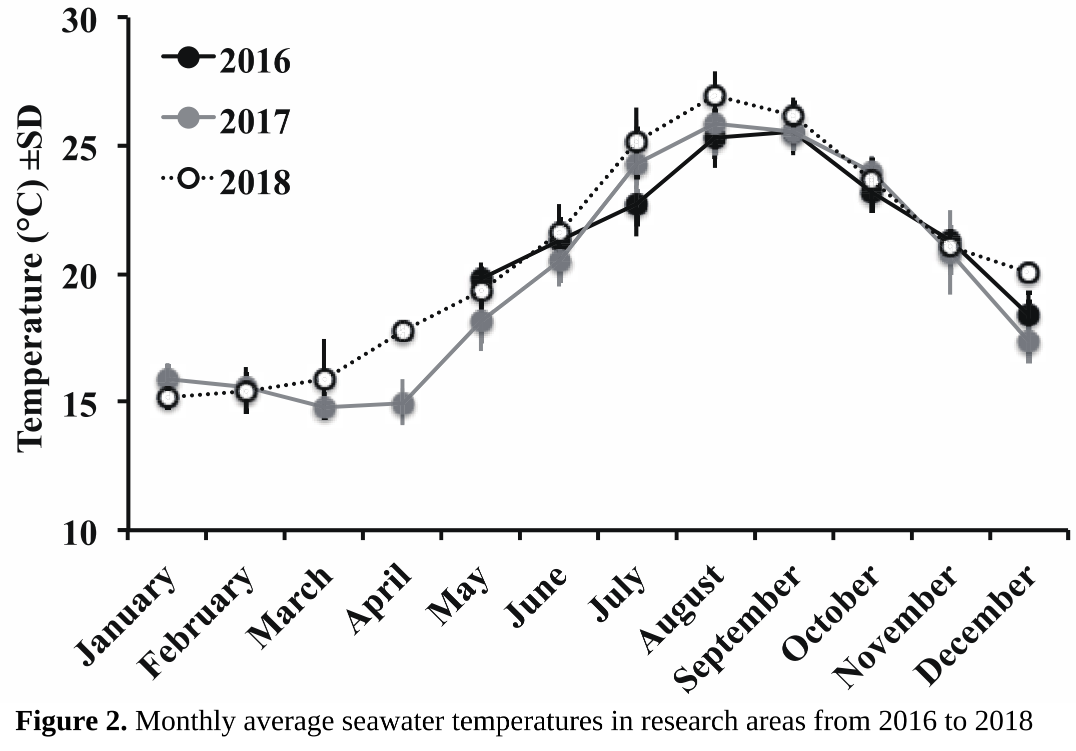

Figure 2. Monthly average seawater temperatures in research areas from 2016 to 2018

Mean algal cover varied significantly among months over three years between the Coral and Non-coral sites (Kruskal-Wallis test, $p < 0.05$) (Figure 3). At the Coral sites, algal cover was less than 10% from July to December in 2016, January to March and July to December in 2017, January in 2018, and July to December in 2018. At the Non-coral sites, algae were more abundant than at the Coral sites. Similar to the Coral sites, algal covers were less than 10% at the Non-coral site from July to December in 2016. However, algal covers were relatively higher in 2017 and 2018. Over 50% of algal covers were observed in January to April and June in 2017, in February to June in 2018, ~~and~~ in February to April and June to August in 2017, and January to June in 2018. Average coral covers at the Coral sites were 92.9 ± 6.08 % (mean ± SD) in 2016, 90.0 ± 10.4 % in 2017, and 89.4 ± 12.2 % in 2018.

Diadema densities significantly differed among months over three years between the Coral and Non-coral sites (Kruskal-Wallis test, $p < 0.05$) (Figure 4). *Diadema* were hardly observed in the Non-coral sites while being always observed in the Coral sites with fluctuation. They increased toward December 2016, decreased to June, then increased October, and decreased in December 2017. In 2018, lower than 2 / m^2 of the average densities were observed until June, and then increased in November.

Densities of feeding scars of *Diadema* spp. on corals significantly differed throughout 2016-2018 (Kruskal-Wallis test, $p < 0.05$) (Figure 5). In 2016, the density of feeding scars decreased until August, and then increased

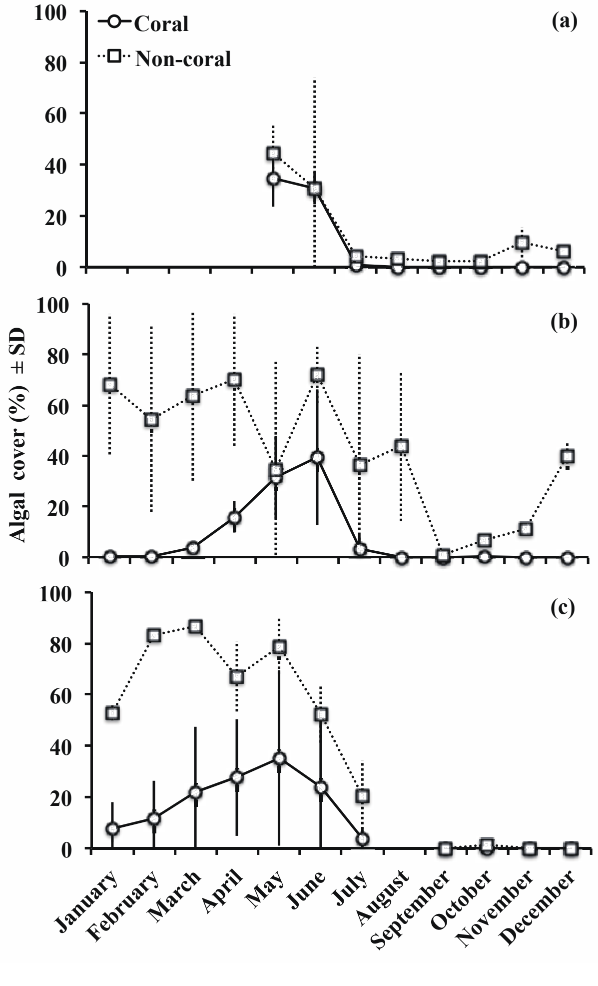

Figure 3. Monthly averages of algal cover (%) in the Coral sites and the Non-coral sites for 2016 to 2018. a)2016, b)2017, c)2018.

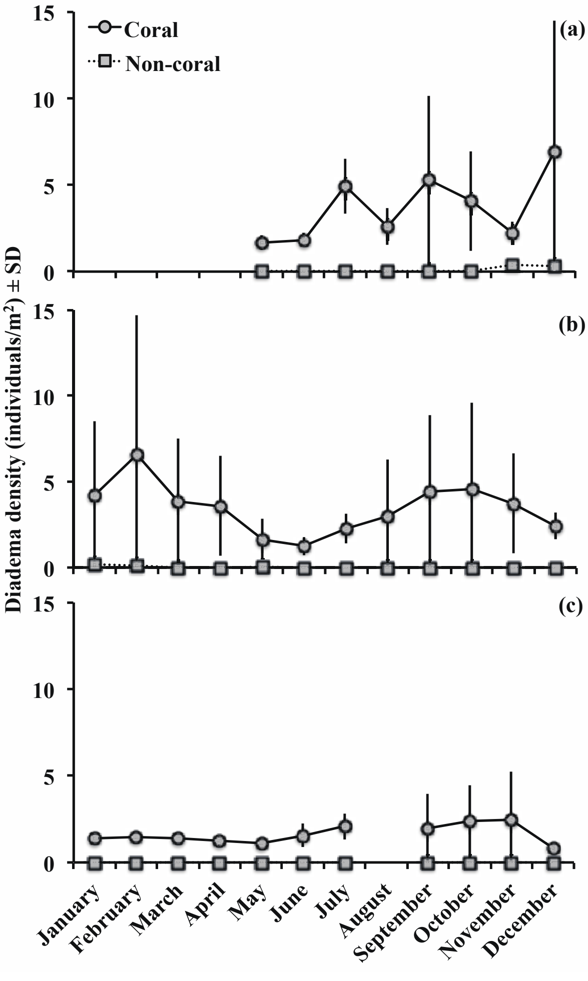

Figure 4. Monthly averages of *Diadema* densities in the Coral sites and the Non-coral sites in a)2016, b)2017, and c)2018.

in October. It gradually decreased as seen as 1.7 scars/ m^2 in May 2017. Later, less than 2 scars/ m^2 was continuously observed until September 2018, except for 4.4 scars /m^2 detected in September 2017. However, a slight increase was observed in October 2018.

At the Coral sites, statistically significant negative correlations were observed between seawater temperatures and algal covers ($r = -0.43$, $p < 0.05$), and between algal covers and the number of *Diadema* spp. ($r = -0.47$, $p < 0.05$). A significant positive correlation was also observed between numbers of *Diadema* spp. and feeding scars ($r = 0.49$, $p < 0.05$).

4. Discussion

During the periods of study, an increase in the number of feeding scars coincided with a decrease in algal abundance at the Coral sites; however, the trends were less obvious in 2017 and 2018. Therefore, no significant correlation between algal abundance and feeding scars was observed at the Coral sites. However, some indirect relationships were seen: (1) a seasonal negative correlation of algal abundance and seawater temperature; (2) *Diadema* the higher density at the Coral site during periods of low algal cover; (3) more abundance of feeding scars on corals when *Diadema* density were higher at the Coral site. On the other hand, the indirect relationship (3) was mostly observed in 2016. These results imply that *Diadema* corallivory is probably related to macroalgal abundance with varied effects among years. The decrease in *Diadema* predation on corals seems to be related to the increase in algal abundance at the Coral sites and surrounding Non-coral sites. As is well known, *Diadema* are primarily herbivorous, but show omnivorous tendencies during food shortages (Bak and van Eys 1975). Compared to 2016, algal abundance increased and the period of algal bloom was longer in 2017 and 2018 at the Coral sites and surrounding Non-coral sites, suggesting that *Diadema* did not need to prey upon corals in 2017 and 2018.

The hypothesis that corals could be an alternative food source for *Diadema* spp. during the period of low algal cover appeared partially supported by this study. Reduced corallivory in 2017 and 2018 could be resulted from relative abundance of algae during those years. Therefore, frequency of corallivory may change with algal abundance. As gut contents could be one of indicators for *Diadema* corallivory (Dumont et al. 2013), examination of the composition and abundance of gut contents of *Diadema* could document more precisely whether corallivory changes with algal abundance

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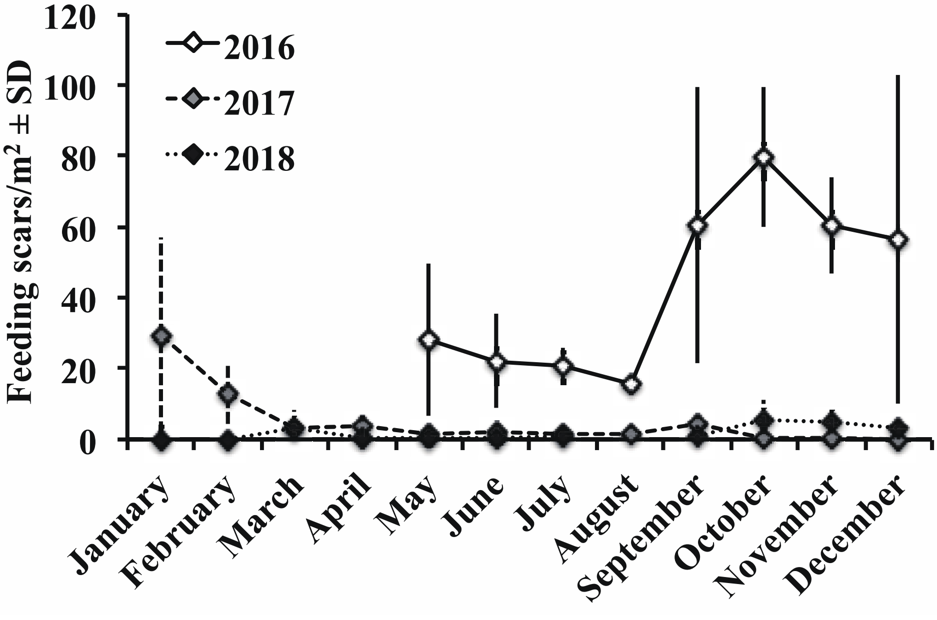

Figure 5. Monthly averages of *Diadema* feeding scars in the Coral sites for 2016 to 2018

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