Effect of sea urchin (*Diadema setosum*) density on algal composition and biomass in cage experiments

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Abstract: This study examines the effects of the sea urchin *Diadema setosum* on algal composition, coverage and biomass on barren ground. In cage experiments, the effects of *D. setosum* density were examined at 5 levels over the range of 0–8 ind. m⁻². Algal coverage and number of species, densities and lengths of *Sargassum* spp. on experimental blocks in each cage were measured monthly. In the cage without *D. setosum*, algal coverage and biomass were higher than in cages with *D. setosum*. For *D. setosum* density of 1 ind. m⁻² and higher, decreased algal coverage and decreased biomass and density of *Sargassum* spp. were observed. *D. setosum* at a density higher than 2 ind. m⁻² had a negative effect on algal species numbers. Consequently, algae could grow when the *D. setosum* density was fewer than 2 ind. m⁻². This study revealed that grazing by *D. setosum* has a great effect on the seaweed bed ecosystems along the coast of central Japan.

Key words: *Diadema setosum*, algal flora, cage experiment, sea urchin, barren ground

Introduction

Sea urchins play a key role in the benthic ecology of coastal ecosystems, particularly in barren grounds and coral reefs (Harrold & Reed 1985, Watanabe & Harrold 1991, Coyer et al. 1993, Tegner et al. 1995, Korzen et al. 2011). In sea urchin-dominated barren grounds around the globe, algal coverage and biomass increase following the removal of sea urchins (McClanahan 1996, Maciá et al. 2007, Kurashima et al. 2014, Ling et al. 2015).

Grazing by sea urchins *Diadema* spp. has important and varied effects on the ecology of reefs and algal communities (Sammarco 1982, Muthiga & McClanahan 2013). *Diadema antillarum* Philippi was shown to effectively enhance scleractinian coral recruitment and growth by grazing on algae that compete with coral in the Caribbean Sea (Idjadi et al. 2010). However, high densities of *Diadema setosum* Leske (Qju et al. 2014) and *D. antillarum* (Bak & van Eys 1975) can cause serious damage to scleractinian coral due to grazing on living coral. Reduction in grazing intensity can alter algal biomass and scleractinian coral recruitment. This effect was evident after the mass mortality of *D. antillarum* in 1983–84, the most extensive die-off of a marine invertebrate ever reported (Levitan 1988, Lesios 1988, Carpenter 1990, Muthiga & McClanahan 2013) in an epidemic that covered more than 2000 km of the Caribbean Sea. The dramatic reduction of *D. antillarum* population densities by 95–99% (Lesios 1988) resulted in a release from the grazing intensity by *D. antillarum* and an increase in algal biomass by 22–439% along with decreased abundance and recruitment of scleractinian coral (Carpenter 1990, Muthiga & McClanahan 2013).

In the Canary Islands, grazing by *Diadema africanum* Rodriguez et al. plays an important role in the structure of the shallow benthic algal assemblages (Tuya et al. 2004, Hernández et al. 2008). The assessment of *D. africanum* populations, algal coverage of barren grounds, and algal composition by a spatio-temporal approach revealed a negative relationship between the density of *D. africanum* and macroalgal coverage (Hernández et al. 2008). The ecological effects of *D. antillarum* and *D. africanum* have been well studied. However, the Pacific *Diadema* spp., including *D. setosum*, have not received as much attention. A small number of detailed studies have been carried out on the ecological effects of *D. setosum* (McClanahan et al. 1996, Dotsu et al. 2002, Muthiga & McClanahan 2013, Kurashima et al. 2014). McClanahan et al. (1996) reported...
increases in the coverage of algae and seagrass after removal of sea urchins, including *D. setosum*, compared to control plots. As a consequence of increasing algal food resources, fish biomass nearly tripled, the population density increased by 65% and species richness increased by 30% compared with the control plot (McClanahan et al. 1996). We previously reported that *Diadema*-dominated barren grounds in Haidaura Bay (Mie Prefecture, central Japan) transitioned seaweed beds after removing *D. setosum* and *Diadema* sp. (Kurashima et al. 2014). Algal coverage in this area increased when *Diadema* density decreased to 2 ind. m$^{-2}$ or lower.

Cage experiments have been widely used in the field to test the interactions of various organisms (Castro & Huber 2000), including sea urchin-algae interactions (Carpenter 1981, Dotsu et al. 2002, Alves et al. 2003, Jessen & Wild 2013). However, there have been no studies utilizing cage experiments to examine the relationships between *Diadema* density and algal biomass. This study aims to examine the effects of *D. setosum* density on algal flora, coverage and biomass in barren grounds using cage experiments with 5 levels of *D. setosum* density.

**Materials and Methods**

**Study site**

Haidaura Bay is located in central Japan at 33°59′ N and 136°15′ E; the bay has a wide mouth facing the Pacific Ocean and a narrow inner part extending inland (Fig. 1). In previous surveys, seaweed beds consisting of *Sargassum* spp. and *Eckloniopsis radicosa* (Kjellman) Okamura were found in the mouth of the bay, while the inner area was characterized by barren ground (Kurashima et al. 2001). Recently, seaweed beds have recovered in barren ground areas as a result of removing *Diadema* spp. (Kurashima et al. 2014). The present study was performed at the point marked “study site” in the inner area of Haidaura Bay (Fig. 1).

**Water temperature**

Water temperature was recorded at a depth of 5 m using a data logger (UTBI-001, Onset Computer, Co.) attached to a stainless steel post secured by a rock. Temperature was recorded every 30 min from September 2013 to June 2014.

**Field cage experiments**

Field cage experiments were performed at the study site between September 2013 and June 2014. At the start of the experiment in August 2013, concrete blocks (dimensions, 0.39×0.19×0.10 m) were set at a depth of 5 m in an area with a sandy bottom. For each of the 5 experimental cages, 6 blocks were set. On them, 5 blocks were arranged as shown in Fig. 2. A single cage was used for each treatment, and measurements were taken individually on the blocks in the upper layer. Each experimental unit was enclosed within a cage (dimensions, 1×1×1 m) made by stretching polyethylene netting over a frame made from polyvinyl chloride pipes (Fig. 3). In September 2013, 0, 1, 2, 4, or 8 individuals of *D. setosum* (diameter mean±SD, 46.9±3.3 mm) were added to each of the cages to reach...
densities of 0, 1, 2, 4, or 8 ind. m\(^{-2}\). The polyethylene netting was changed at monthly intervals; at this time, the \(D. \) setosum were counted and new individuals were added if the density had decreased. In the 4 ind. m\(^{-2}\) cage, 2 individuals were added in October and 1 was added in each of November and December, while 1 individual was added to the 8 ind. m\(^{-2}\) cage in November and March. No additions were needed in the other cages.

**Measuring and sampling**

In each cage, algal coverage on the top surface of each of 5 upper blocks was quantified monthly using a 0.2 m\(\times\)0.2 m quadrat; algal species on the five blocks were also recorded. The number of \(Sargassum\) spp. on each block was counted and their lengths were measured using ruler monthly. At the end of the experimental period, algae were collected from the upper surface of the 5 blocks and brought back to Mie University (Tsu City, Mie Prefecture). The collected algae were washed with fresh water and dried at 60°C for 48 h. The dry weight of the algae was measured. Algal biomass and \(Sargassum\) spp. counts on each block were divided by the surface area of the block to determine densities per square meter.

**Results**

**Water temperature**

The average daily temperature and daily temperature range between September 2013 and June 2014 are shown in Fig. 4. The highest temperature of 26.3°C recorded was on 23 September 2013 and the lowest of 13.4°C was recorded on 27 January 2014; the mean water temperature was 18.2°C during the study period.

**Algal coverage**

Algal coverage on the blocks at each \(D. \) setosum density is shown in Fig. 5. Algal coverage on the blocks in cages with 0, 1, and 2 ind. m\(^{-2}\) increased from September to April. The maximum algal coverage occurred in the 0 ind. m\(^{-2}\) cage in April at 95.2\(\pm\)5.3% (mean\(\pm\)SE), in the 1 ind. m\(^{-2}\) cage in June at 35.6\(\pm\)4.2%, and in the 2 ind. m\(^{-2}\) in April at 54.2\(\pm\)8.4%. The maximum algal coverage in the 4 ind. m\(^{-2}\) cage was 8.0\(\pm\)0.2% in May, and coverage was low throughout the study period. Algae were not observed in the 8 ind. m\(^{-2}\) cage throughout the study period. At the end of the experiment, algal coverage in the 0 ind. m\(^{-2}\) cage was higher than in the other cages; the difference in algal coverage in the 1 and 2 ind. m\(^{-2}\) cages was low, and algal coverage was lower in the 4 ind. m\(^{-2}\) cage than in the 0, 1 and 2 ind. m\(^{-2}\) cages.

Algal coverage on blocks in the cages with \(D. \) setosum densities of 4 ind. m\(^{-2}\) or lower decreased slightly or showed almost no change after April. Change in coverage of \(Colpomenia \) sinuosa (Mertens ex Roth) Derbès & Solier and other algae on blocks in each of the cages are shown in
Effect of D. setosum density on algal biomass

Fig. 6. In all cages with D. setosum density of 8 ind. m\(^{-2}\) or lower, C. sinuosa first appeared in December, and coverage rapidly increased until April. After April, coverage of C. sinuosa decreased. Total algal coverage was strongly dependent on that of C. sinuosa, as this species dominated throughout the study period.

Algal biomass

Algal biomass at the end of the experiment at each D. setosum density is shown in Fig. 7. Algal biomass on blocks in the 0 ind. m\(^{-2}\) cage was higher than in the other cages, and few differences were observed in pairwise comparisons of the cages with D. setosum density of 1, 2, or 4 ind. m\(^{-2}\). Algal biomass on blocks was 437.5±78.9 g dw m\(^{-2}\) (mean±SE) in the 0 ind. m\(^{-2}\) cage, 42.9±7.2 g dw m\(^{-2}\) in the 1 ind. m\(^{-2}\) cage, and 34.6±8.2 g dw m\(^{-2}\) in the 2 ind. m\(^{-2}\) cage. Only C. sinuosa was recorded in the 4 ind. m\(^{-2}\) cage, and the algal biomass was 0.9±0.4 g dw m\(^{-2}\). Algae were not observed on blocks in the 8 ind. m\(^{-2}\) cage. Padina arborescens Holmes (392.2±74.0 g dw m\(^{-2}\)) and Sargassum alternato-pinatum Yamada (30.1±14.0 g dw m\(^{-2}\)) comprised the largest proportions of algae in the 0 ind. m\(^{-2}\) cage. P. arborescens (22.1±7.3 g dw m\(^{-2}\)) and C. sinuosa (8.7±2.9 g dw m\(^{-2}\)) predominated in the 1 ind. m\(^{-2}\) cage, and P. arborescens (16.8±8.8 g dw m\(^{-2}\)) and C. sinuosa (16.7±10.7 g dw m\(^{-2}\)) comprised a large proportion of the algae in the 2 ind. m\(^{-2}\) cage.

Algal species

Algal species present at the end of the experiment are shown in Table 1. The number of algal species was 12 in the 0 ind. m\(^{-2}\) cage, 14 in the 1 ind. m\(^{-2}\) cage, and 11 in the 2 ind. m\(^{-2}\) cage. Only C. sinuosa was observed in the 4 ind. m\(^{-2}\) cage, and no algae were observed in the 8 ind. m\(^{-2}\) cage. There were few differences in the numbers of species among the 0–2 ind. m\(^{-2}\) cages.

Change in density of Sargassum spp.

Changes in densities of Sargassum spp. on the blocks over the course of the experiment are shown in Fig. 8. Sargassum spp. were observed on blocks in the 0–4 ind. m\(^{-2}\) cages after October. The following densities of Sargassum spp. were recorded in the various cages: 99.9±22.8–423.8±68.0 ind. m\(^{-2}\) (mean±SE) in the cage with 0 D. setosum m\(^{-2}\); 2.7±2.7–83.7±7.9 ind. m\(^{-2}\) in the cage with 1 D. setosum m\(^{-2}\); 8.1±5.5–64.8±9.9 ind. m\(^{-2}\) in the cage with 2 D. setosum m\(^{-2}\); and 0–2.7±2.7 ind. m\(^{-2}\) in the cage with 4 D. setosum m\(^{-2}\) cage. Sargassum spp. were not observed in the 8 ind. m\(^{-2}\) cage throughout the study period.

The densities and lengths of Sargassum spp. on blocks
in each cage at the end of the experiment are shown in Fig. 9. The majority of the Sargassum individuals on the blocks belonged to S. alternato-pinnatum, although a few S. micracanthum (Kützing) Endlicher were observed. At the end of the experiment, the density of Sargassum spp. in the cage with D. setosum density of 0 ind. m$^{-2}$ was higher than in the others, and few differences were present between the 1 and 2 ind. m$^{-2}$ cages. The densities of Sargassum spp. on blocks in cages with 0 or 1 D. setosum m$^{-2}$ were 124.2±23.1 and 21.6±6.9 ind. m$^{-2}$, respectively. The density of Sargassum spp. in the cage with 2 D. setosum m$^{-2}$ was 10.8±2.7 ind. m$^{-2}$ and the frequency of adult Sargassum spp. (>2 cm) was lower than in the 0 and 1 D. setosum m$^{-2}$ cages. No Sargassum spp. were observed on the blocks in cages with 4 or 8 D. setosum m$^{-2}$.

### Table 1. Algal species present at the end of each Diadema setosum density cage experiment.

| Species       | Density of D. setosum (ind. m$^{-2}$) |
|---------------|----------------------------------------|
|               | 0   | 1   | 2   | 4   | 8   |
| Ulvophyceae   |     |     |     |     |     |
| Ulva intestinalis | o  |     |     |     |     |
| Ulva lactuca  |     |     |     |     |     |
| Ulva sp.      |     |     |     |     |     |
| Phaeophyceae  |     |     |     |     |     |
| Padina arborescens | o  |     |     |     |     |
| Colpomenia sinuosa | o  |     |     |     |     |
| Sargassum alternato-pinnatum | o  |     |     |     |     |
| Sargassum micracanthum | o  |     |     |     |     |
| Sargassum sp. |     |     |     |     |     |
| Rhodophyceae  |     |     |     |     |     |
| Amphiroa zonata | o  |     |     |     |     |
| Gelidium elegans |     |     |     |     |     |
| Grateloupia sp. |     |     |     |     |     |
| Hypnea saidana |     |     |     |     |     |
| Gracilaria incurvata |     |     |     |     |     |
| Gracilaria parvispora |     |     |     |     |     |
| Gracilaria textorii |     |     |     |     |     |
| Champia parvula |     |     |     |     |     |
| Ceramium sp.  |     |     |     |     |     |
| Laurensia sp. |     |     |     |     |     |

Number of species:

| Density of D. setosum (ind. m$^{-2}$) |
|----------------------------------------|
| 12 | 14 | 11 | 1 | 0 |

**Fig. 8.** Change in Sargassum spp. densities on blocks in each cage. Error bars show SE.

**Fig. 9.** Densities and lengths of Sargassum spp. on blocks in each cage at the end of the experiment. Error bars show SE.
Discussion

Dotsum et al. (2002) conducted experiments by setting *D. setosum* in experimental cages without roofs, but *D. setosum* often escaped from the caging. In this study, we specifically used cages with roofs to contain the sea urchins, and only 0–2 individuals escaped per month. In the present study, since grazing intensity of sea urchins depends on their size (diameter) (Barker et al. 1998), we used uniformly sized *D. setosum* to analyze the effects of density. In the analysis of grazing by sea urchins, consideration of not only density but also diameter is required.

Alves et al. (2003) set exclusion cages on *D. africanum*-dominated barren ground in the northeastern Atlantic Ocean and found that algal coverage within the exclusion cages was higher than in the uncaged control areas. Benayahu & Loya (1977) reported a significant negative correlation between the annual turf-algae coverage and density of *D. setosum* from field surveys in the Red Sea. Our results showed the highest algal coverage in the 0 ind. m⁻² cage corroborate the findings of these previous studies. In our cage experiment, we found a negative relationship between algal coverage and the density of *D. setosum*. In the Canary Islands, a density of *D. africanaum* higher than 2 ind. m⁻² was found to drastically reduce non-crustose macroalgal coverage (Hernández et al. 2008). An earlier study of Haidaura Bay showed that algal coverage increased when *Diadema* spp. density decreased to 2 ind. m⁻² or lower by the removal of *Diadema* spp. (Kurashima et al. 2014). In the present study, algae were observed on blocks in cages with a *D. setosum* density of 2 ind. m⁻² or lower.

Based on these results, the threshold *Diadema* density at which algae can grow in barren grounds is approximately 2 ind. m⁻². This *Diadema* density demarcates the transition from barren grounds to seaweed beds. Although our study and that of Hernández et al. (2008) indicated a threshold *Diadema* density of approximately 2 ind. m⁻², Tuya et al. (2004) reported a much higher threshold in which net benthic primary production was approximately matched by consumption of about 10 *D. africanaum* m⁻². This higher threshold is due to Tuya et al. (2004) using mean net primary production measured in seaweed beds, while we used data from barren grounds. Discontinuous phase shifts between sea urchin-dominated barren grounds and seaweed beds have been reported. In discontinuous phase shifts, the threshold sea urchin biomass and density for forward (to barren ground) shifts is higher than for reverse (to seaweed beds) shifts (Filbee-Dexter & Scheibling 2014, Ling et al. 2015).

Dotsum et al. (2002) set the density of *D. setosum* at 5 ind. m⁻² in experimental cages set on top of boulders. The decrease in the number of algal species from 12 to 2 after 2 months was attributed to grazing by *D. setosum* (Dotsum et al. 2002). At the end of the present experiment, 11–14 algal species were observed in the cages with *D. setosum* density of 0, 1 or 2 ind. m⁻². Kurashima et al. (2014) found 11–19 algal species in an area near the present study site. Only *C. sinuosa* was observed in the 4 ind. m⁻² cage, and no algae were observed in the 8 ind. m⁻² cage. On the other hand, there was little difference in the number of algal species in cages with densities of 0, 1 and 2 ind. m⁻². These results indicate that grazing by *D. setosum* decreased the number of algal species when the density of *D. setosum* was higher than 2 ind. m⁻² but that the higher density did not have an effect on the number of algal species contributing to the algal coverage and biomass.

Small annual algae such as *P. arborescens* and *C. sinuosa* contributed to a large proportion of the algal biomass on blocks in the cages with densities of 0, 1, 2, and 4 ind. m⁻². Change in algal coverage on blocks in the 0, 1, 2, and 4 ind. m⁻² cages greatly depended on *C. sinuosa*. Coverage of *C. sinuosa* rapidly increased from December to April and decreased after April. At the coral reefs of Eilat, coverage of *C. sinuosa* rapidly increased from March to April and reached up to 60%, but this bloom lasted only a short time (Benayahu & Loya 1977).

In a preliminary study in Haidaura Bay, *P. arborescens* and *C. sinuosa* were opportunistic species and were observed in the early period of recovery from barren ground (Kurashima et al. 2014). Small annual algae growing rapidly push up the algal biomass during the transition from barren grounds to seaweed beds.

Seaweed beds consisting of *Sargassum* spp. exist in the inner part of Haidaura Bay (Kurashima et al. 2014). *S. alternato-pinnatum* grew on blocks in all cages where *Sargassum* spp. were observed. A colony of *S. alternato-pin- natum* was observed on the rocky substrate near the study site, and the *S. alternato-pinnatum* found on experimental blocks originated from this colony. In the early part of the experiment, the densities of *Sargassum* spp. on blocks in cages with *D. setosum* was lower than in the cage without *D. setosum*. *D. setosum* decreased the density of *Sargassum* spp. in a short period by grazing on juveniles. At the end of the experiment, *Sargassum* spp. were observed in cages with *D. setosum* densities of 0, 1, and 2 ind. m⁻². This suggests that *Sargassum* spp. can grow in the presence of *D. setosum* at a density of 2 ind. m⁻² or lower.

Grazing activities of *D. setosum* changes with water temperature (Dotsum et al. 2002). Algal coverage and densities of *Sargassum* spp. on experimental blocks in cages with *D. setosum* were low during both summer and winter seasons when water temperatures were low. Therefore, grazing by *D. setosum* controls algal coverage and density of *Sargassum* spp. throughout the year.

In conclusion, our findings clearly indicate that algal biomass and species composition are strongly affected by the density of *D. setosum*. Understanding the ecological effects of *D. setosum* is the first step toward restoring seaweed beds from Diadema-dominated barren grounds. *D. setosum* density of 1 ind. m⁻² and higher drastically decreased algal coverage, biomass and density of *Sargassum*
spp. in barren grounds. On the other hand, *D. setosum* density of 2 ind. m\(^{-2}\) and lower did not have a great effect on algal species number. Experimentally, we revealed the threshold *D. setosum* density at which shifts from barren grounds to seaweed beds can occur. Grazing by *D. setosum* has a great effect on the seaweed bed ecosystems in the central Japan.

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