Estimation of the feeding pressure of a sea urchin (Diadema setosum) population on a barren ground in a temperate region of Japan

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Abstract: This study aimed to estimate the feeding pressure of a Diadema setosum population on a barren ground in Kata Bay, Mie Prefecture, Japan, which is a temperate region. We combined data of the feeding rate of D. setosum from tank experiments and of the D. setosum population dynamics obtained from monthly surveys. We conducted tank experiments to clarify the relationships between the feeding rate of D. setosum and the water temperature and test diameter of the sea urchins. The feeding rate and water temperature were positively correlated over the range of 15°C to 30°C. The test diameter composition of the D. setosum population in Kata Bay was stable throughout the study period (June 2014 to May 2015). The results revealed distinct seasonal changes in the feeding pressure of the D. setosum population owing to temperature variations.

Key words: Diadema setosum, sea urchin, barren ground, feeding pressure

Introduction

The feeding pressure of herbivorous animals is a major factor controlling the dynamics of seaweed communities (Steneck et al. 2002, Kuempel & Altieri 2017). Sea urchins often exert drastic feeding pressure on coastal oceans, and their activity results in very low seaweed density regions, known as barren grounds (Watanabe & Harrold 1991, Tegner et al. 1995). The decline and disappearance of seaweed beds have also been attributed to rising temperatures and the feeding pressure of herbivorous fish such as Siganus fuscescens and Calotomus japonicus (Kiriyama et al. 1999, Noda et al. 2014, 2016).

The feeding activities of members of the sea urchin genus Diadema have a direct impact on coral reefs and algal communities (Sammarco 1982, Muthiga & McClanahan 2013). From 1983 to 1984, Diadema antillarum suffered a mass mortality event over a stretch of more than 2000 km in the Caribbean Sea; this is the most extensive die-off of a marine invertebrate to date (Levitan 1988, Lessios 1988, Carpenter 1990). The dramatic 95%–99% reduction in the D. antillarum population density (Lessios 1988) resulted in a relief from feeding intensity; in turn, this brought about a 22%–439% increase in the algal biomass along with a decrease in the abundance and recruitment of scleractinian corals (Carpenter 1990, Muthiga & McClanahan 2013). Diadema setosum is widely distributed in the Indo-Pacific Ocean (Clark & Rowe 1971) and its presence has also been reported in the central and southern parts of the Japanese Archipelago (Lessios et al. 2001). Removal and cage experiments conducted off the coast of central Japan demonstrated that the removal of D. setosum from barren grounds decreased the feeding pressure and resulted in the rapid recovery of the seaweed community (Kurashima et al. 2014, Ishikawa et al. 2016, 2017).

To estimate the feeding pressure of a sea urchin population, it is important that we clarify the relationship of the sea urchin's feeding rate with water temperature and body size. The feeding rates of herbivorous animals, such as sea urchins and fishes, are affected by water temperature (Miller & Mann 1973, Asano et al. 1990, Scheibling & Anthony 2001, Noda et al. 2016) and body size (Barker et al. 1998).
There is a negative correlation between the test diameter (TD) of sea urchins and their population density (Carpenter 1981, Levitan 1989). The TD composition of a D. setosum population also varies depending on the habitat. Therefore, both the population density and the TD composition are important parameters in estimating the feeding pressure of sea urchin populations. However, many sea urchin studies have been conducted with a focus on density without taking into account the TD and the biomass (Alvarado 2016).

Tank experiments can eliminate the influence of other organisms and allow water temperature to be maintained at stable levels. In this study, we conducted tank experiments to clarify the relationship between the feeding rate of D. setosum and the water temperature and TD of the sea urchins. In addition, we conducted monthly field surveys to examine the population density and TD of D. setosum in a barren ground in Kata Bay. The objective of this study was to estimate the feeding pressure of the D. setosum population by combining feeding rate data from the tank experiment and population dynamics data from the monthly surveys.

**Materials and Methods**

**Tank experiments at different water temperatures**

Diadema setosum individuals were collected at a depth of 5 m from a barren ground in Haidaura Bay (33°59′N, 136°15′E), Mie Prefecture, Japan (Fig. 1). The collected sea urchins were placed in a cooler box filled with seawater that was quickly transported to the laboratory. The mean TD and wet weight of the sea urchins used in the experiment were 46.6±0.5 mm (mean±SE) and 55.5±2.2 g (mean±SE), respectively. An experimental tank (600×300×360 mm) was divided in half (300×300×360 mm on each side), filled with artificial seawater (Marine Art SF-1; Tomita Pharmaceutical Co., Ltd., Tokushima, Japan), and held at one of six water temperatures: 10 °C, 15°C, 20 °C, 25 °C, 30 °C, and 35 °C. One individual was placed in each compartment, and the individuals were acclimatized to each experimental water temperature for 2 weeks or longer. During the acclimatization period, the sea urchins were not fed. The water temperature was maintained using a water tank cooler (LX-110gx; IWAKI Co., Ltd., Tokyo, Japan) for the tanks maintained at 15°C, 20 °C, 25 °C, 30 °C, and 35°C. One individual was placed in each compartment, and the individuals were acclimatized to each experimental water temperature for 2 weeks or longer. During the acclimatization period, the sea urchins were not fed. The water temperature was maintained using a water tank cooler (LX-110gx; IWAKI Co., Ltd., Tokyo, Japan) for the tanks maintained at 15°C, 20 °C, 25 °C, 30 °C, and 35°C. Two tanks held at 10 °C and 35°C were kept in water baths controlled by a temperature controller (CL-150R; TAITEC, Saitama, Japan). The water in the experimental tanks was circulated through an external filter (2215; EHEIM, Deizisau, Germany). Light was provided by a 20 W fluorescent lamp with a 12:12 h light:dark cycle. Before the start of the experiment, frozen alga (Sargassum okamurae) was thawed in artificial seawater at about 20°C for 24 h or longer. Then, 1.01–4.28 g of the alga was clipped and fixed on a slide glass at its base (75 mm×25 mm). Individual sea urchins were treated with seaweed for 23–26 h at 25°C and 30°C and for 71–73 h at 15°C and 20°C. The experimental period at lower temperatures was extended because the feeding rate in the preliminary experiment declined at these temperatures. At the start and end of the experiment, each alga piece was detached from the slide, wiped with a paper towel, and wet weighed. At the end of each experiment, all of the remaining algae pieces were collected and measured. Food consumption (FC) (g dw ind.−1 day−1) was calculated using the following formula:

\[ FC = 24(A_i - A_f)C_{wd}/ET; \]

where, \( A_i \) and \( A_f \) stand for the initial and final wet weights of the algae pieces, \( C_{wd} \) is the correction value to convert wet weight to dry weight, and ET is the experimental time (h). To obtain the \( C_{wd} \) 10 frozen algae pieces thawed using the same method described above were wet weighed and then dried at 65°C for 48 h to obtain the dry weight. The mean of the dry to wet weight ratios of these 10 algae pieces were used as the \( C_{wd} \).

Three D. setosum were observed at each water temperature, and the tank experiment was repeated three times with the same individuals. After each experiment, the TD and wet weight of each sea urchin were measured. The feeding rate was the FC divided by the wet weight of each sea urchin.
Tank experiments with different sized individuals

We used sea urchins of three different size ranges for this experiment. Small and large individuals were collected from Haidaura Bay and Kata Bay (33°58′N, 136°12′E), Mie Prefecture, Japan (Fig. 1), respectively. The data of medium-sized individuals were obtained from the experiment conducted at 25°C, which was described in the previous section. The mean TD and wet weight of the large, medium, and small individuals were 65.0±0.4 mm and 147.0±3.6 g, 46.5±0.4 mm and 56.2±1.2 g, and 20.5±1.0 mm and 5.9±0.8 g, respectively. The sea urchins were treated in the same manner as described in the previous section and maintained at 25°C before the experiment started. The wet weight of the thawed algae, with which each sea urchin was supplied, ranged from 1.45–6.1 g. The experimental period was 23–26 h for large individuals and 94–97 h for small individuals. The experimental period for the small individuals was extended because their feeding rate was observed to be lower in the preliminary experiment. Measurements were obtained as described in the previous section.

TD composition and density of the *D. setosum* population in the barren ground

Field surveys were conducted to determine the density and the TD composition of the *D. setosum* population at the study site in Kata Bay (Fig. 1). Kata Bay opens to the south and has three branches spreading to the east, west, and north. The bottom substratum of the study site consisted of boulders, and the water depth ranged between 2.8 m and 11.0 m. At the study site, the 6230 m² barren ground was dominated by *D. setosum*.

The TD composition of the *D. setosum* population was measured once per month from June 2014 to May 2015. Approximately 100 individuals were randomly selected from the population at the study site, placed on a whiteboard underwater, and photographed from above along with a ruler. This method is a nondestructive TD measurement strategy that allows the return of the sampled individuals after they have been measured. The photographs were processed with image processing software (Photoshop CS 5; Adobe, San Jose, CA, USA), and the TD data were obtained by comparing each individual against the ruler. In February 2014, 10 individuals were photographed underwater and were brought back to the laboratory, where their TDs were measured by direct methods using a caliper to correct any errors of the underwater photographing and image processing method. The TDs obtained by image processing were on average 3.48 mm larger than those measured with calipers. Therefore, 3.48 mm was subtracted from the processed images as a correction value.

The population density of *D. setosum* was surveyed in May 2015. Sixty-one 1 m² quadrats were randomly placed in the study site, and the number of *D. setosum* individuals in each quadrat was counted.

Estimation of the feeding pressure of the *D. setosum* population

The density and TD composition data of the *D. setosum* population were obtained from the field survey, and the food consumption data were obtained from the tank experiment. These data were used to estimate the feeding pressure of the *D. setosum* population on the study site.

*Diadema setosum* individuals from the study site population were divided into 5 mm classes (e.g., 10 mm<TD≤15 mm and 15 mm<TD≤20 mm). The intermediate values of each class (e.g., 12.5 mm for the 10 mm<TD≤15 mm class and 17.5 mm for the 15 mm<TD≤20 mm class) were used as the TDs for estimating the feeding pressure. For each TD class, the feeding pressure at 25°C was estimated by multiplying the number of individuals and the FC per individual.

The feeding pressure of each TD class was integrated over the TD to estimate the feeding pressure of the population on the study site. The feeding pressure was converted to unit area (1 m²) by dividing it by the area that the *D. setosum* population occupied at the study site (6230 m²). The feeding pressure per m² was corrected for the mean daily water temperature by multiplying it with the correction value (CV) for water temperature. The CV was estimated based on the relationship between the water temperatures and the feeding rates of the intermediate individuals in each size class.

The water temperature used for the CV was recorded every 30 min from June 2014 to May 2015 at a depth of 3 m at the study site using a data logger (UTBI-001; Onset Computer, Co., Bourne, MA, USA). The feeding pressure was estimated daily. In addition, we estimated the feeding pressure of the *D. setosum* population at the mean annual water temperatures, which were higher than the water temperatures used in this study.

Data analysis

The FC rates under the different water temperature conditions were analyzed by one-way ANOVA and Tukey’s HSD test. These statistical tests were performed with R software (version 3.1.0; The R Foundation for Statistical Computing, Vienna, Austria). The same analysis was carried out for the FC rates of individuals with different TDs.

Results

Tank experiments at different water temperatures

The mean FC and feeding rates of *D. setosum* at different water temperatures are shown in Fig. 2. At 10°C, all individuals died within the 14-day acclimatization period. Feeding experiments were not conducted at 35°C as an abnormality was detected on the surface of the epidermis where part of the shell was exposed. At 15–30°C, the FC and the feeding rates increased with the increas-
Diadema setosum feeding pressure

Diadema setosum feeding pressure

ing water temperature; these two rates were the highest at 30°C [0.48±0.4 g dw ind.−1 day−1 (mean±SE) and 9.28±0.5 mg dw g wt−1 day−1, respectively]. The ANOVA results indicated significant differences in the FC (ANOVA, df=3, F=26.407, p<0.001) and the feeding rate (ANOVA, df=3, F=47.678, p<0.001) of D. setosum at each water temperature.

Tank experiment with different sized individuals

The mean FC rates of D. setosum individuals of different TDs and the feeding rates at 25°C are shown in Fig. 3. The FC rates of the large-, medium-, and small-sized individuals at 25°C were 0.77±0.05, 0.26±0.05, and 0.05±0.01 g dw ind.−1 day−1, respectively. The FC differed significantly among the large, medium, and small individuals (ANOVA, df=2, F=74.354, p<0.001). The mean feeding rates of the large, medium, and small individuals were 5.25±0.42, 4.58±0.88, and 7.61±0.65 mg dw g−1 day−1, respectively. The ANOVA results indicated significant differences in the feeding rates (ANOVA, df=2, F=5.547, p<0.05). The results of Tukey’s HSD test indicated significant differences between the small and medium individuals (p<0.05) but not between the small and large (p=0.106) and the medium and large individuals (p=0.771).

TD composition and density of the D. setosum population in the barren ground

The TD composition of D. setosum at the study site is shown in Fig. 4. The smallest TD measured was 44.2±0.9 mm (mean±SE) in June and the largest was 49.6±0.9 mm in December. The TD composition of D. setosum was stable throughout the study, with medium-sized individuals (with a TD of 40–55 mm) dominating the population. In June 2014, small individuals appeared; these grew rapidly from July to September and were indistinguishable from the medium-sized individuals by October. The D. setosum population density at the study site in May 2016 was 10.1 ind. m−2.

Estimation of the feeding pressure of the D. setosum population

The relationship between the TD and the FC of D. setosum is shown in Fig. 5. The FC at 25°C (g dw ind.−1 day−1) was estimated as follows:

\[ \text{FC} = 0.0003 \text{TD}^{2.4298} \]

The relationship between the water temperatures and the feeding rates of the medium-sized D. setosum individuals is shown in Fig. 6. Based on this relationship, the CV of the feeding rate at 25°C was obtained using the following formula:
Fig. 4. Monthly changes in the test diameters of *Diadema setosum* at Kata Bay from June 2014 to May 2015.

Fig. 5. Relationship between the test diameter and the food consumption of *Diadema setosum* at 25°C.

Fig. 6. Relationship between water temperatures and the relative feeding rates when the mean feeding rate of the medium-sized *Diadema setosum* individuals at 25°C is 100%.
positively (Schebling & Anthony 2001) and negative effects
(Larson et al. 1980) on the feeding rates of Strongylocen-
trotus droebachiensis. Strongylocentrotus intermedius is
also negatively impacted by high temperature (Zhao et al.
2016). Based on the results of the present and previous
studies, water temperature likely has a positive effect on
the feeding rates of D. setosum in the range of 15°C to
30°C.

Barker et al. (1998) reported that the feeding rates of
sea urchins depend on their TDs. In the Indo-Pacific coral
reefs, the bioerosion rate of Diadema savignyi depends on
their TDs (Bak 1990). In the present study, a positive cor-
relation was found between the TD and the feeding rate of
D. setosum. Our results suggest that the large D. setosum
individuals exerted a greater feeding pressure on the sea-
weed community than the small and medium individuals.

The feeding rates of sea urchins differ depending on
the algal species; S. droebachiensis and M. nudus have
a strong feeding preference for kelp (Himmelman & Nédé-
lec 1990, Machiguchi et al. 1994, Scheibling & Anthony
2001), Diadema africanum and D. antillarum exhibit sig-
nificantly different feeding rates depending on the algal
species (Solandt & Campbell 2001, Rodríguez et al. 2017).
It should be noted that, in this study, we estimated the
feeding pressure of D. setosum by feeding it with only a
single algal species (S. okamurae).

The population density of members of the Diadema ge-
nus varies greatly depending on their location in the sea.
The density of Diadema mexicanum is 0.47±0.15 ind. m−2
in the coral reef area of California Bay (Alvarado et al.
2016), whereas that of D. antillarum is 0.013–1.553 ind.
 m−2 in the southeastern Cuban coral reefs (Blanco et al.
2011) and 14.38 ind. m−2 in the Virgin Islands (Levitan
1988). The density of Centrostephanus rodgersii in barren
grounds is higher than that in seaweed beds (Ling & John-
son 2009), and the density of D. antillarum at the same
depth is high in barren ground areas and low in seaweed
beds (Edmunds & Carpenter 2001). Based on these find-
nings, the sea urchin population density tends to be higher
in barren grounds than in seaweed beds. In the present
study, the population density of D. setosum was 10.1 ind.
 m−2, which was relatively higher than that reported in the
aforementioned studies. However, in this study, the pop-
ulation density was investigated only once, i.e., in May
2015. Agatsuma (2014) reported seasonal changes in the
densities of M. nudus and Hemicentrotus pulcherrimus in
northern Japan. We targeted a stable population with small
changes in its average TD composition throughout the
study period. For this reason, the feeding pressure of D.
setosum was estimated based on the assumption that there
was no seasonal variation in the population's density.

In the Canary Islands, D. africanum populations have
a higher proportion of smaller individuals owing to food
limitations as the population density is higher; moreover,
a negative correlation was observed between the TD and
the population density (Levitan 1989). Along the north-
ern coast of Kumano-nada, central Japan, the mean TD of the *D. setosum* population is 46.3 mm in Syuku-ura and 54.3 mm in Nie-ura (Oki & Okumura 2004). In the Caribbean coral reefs, the TD of *D. antillarum* is 57.0±3.6 mm on the reef slope and 56.9±0.7 mm on the reef edge (Blanco et al. 2010). The TD of *D. mexicanum* in the coral reef of California Bay is 43.8 mm±15.0 (Alvarado et al. 2016) and that of *D. setosum* around Pangkor Island, Malaysia, is 58.7±0.1 mm (Rahman et al. 2012). Therefore, the mean TD of *Diadema* populations is within a 40–60 mm range. In the present study, the mean monthly TD ranged from a minimum of 44.2±0.9 mm to a maximum of 49.6±0.9 mm; therefore, it was within the mean TD range of the *Diadema* populations examined in the aforementioned studies.

The TD composition of the *D. setosum* population at the study site was stable throughout the year. Although we investigated the TD composition for only 1 year, Rodríguez-Barreas (2015) noted that changes in the TD composition of sea urchin populations could be detected in the course of 1 year. In this study, medium-sized individuals with a 40–55-mm TD dominated throughout the study period and the proportion of small individuals was low. In the *D. antillarum* population of the Caribbean coral reefs, medium and large individuals with 51–70-mm TDs account for 48% of all individuals; small individuals with TDs of 40 mm or less account for only 16% of the population (Blanco et al. 2010). Around Okinoshima Island, located at the mouth of Tokyo Bay, medium-sized *D. setosum* individuals have been reported to be dominant, whereas small individuals (approximately 5 mm or less) are rare (Fujita et al. 2013). These findings suggest that, in stable *Diadema* populations, medium-sized individuals dominate and seasonal TD composition changes are small. Small-sized individuals that appeared in June 2014 and were included in this study seemed to grow up rapidly (Fig. 4). The growth of members of the *Diadema* genus may be very rapid in the first year after settlement, with another burst of rapid growth at 3–4 years of age until they reach their maximum size (Lewis 1966). In addition, size-dependent mortality has been reported in *D. africanum* with a 40-mm TD (Clemente et al. 2007). Owing to the high mortality rate and the rapid growth of small individuals, it can be suggested that there were few small individuals and that the medium-sized individuals dominated the *D. setosum* population in the barren ground examined.

The feeding pressure of sea urchins is generally high in the summer when the water temperature is high (Vadas 1977, Larson et al. 1980, Agatsuma et al. 1996). Okubo et al. (2003) measured the feeding pressure of *D. setosum* on the hermatypic coral *Acropora pruinosa* using cage experiments and observed seasonal changes, with low pressure in the winter and high pressure in the summer. In southwestern Hokkaido, Japan, the feeding activity of *M. nudus* declines in low water temperatures (Agatsuma et al. 1996); moreover, the feeding pressure could be estimated from the wave and water temperature characteristics; thus, this value was high in the summer when the flow rate decreases and the water temperature increases (Yamashita et al. 2012). In the present study, the feeding pressure of the *D. setosum* population also depended highly on water temperature, and distinct seasonal changes with high feeding pressure in the summer and low feeding pressure in the winter were confirmed.

The feeding rates of herbivorous fish, such as *S. fuscescens* and *K. bigibbus*, are influenced by water temperature (Kiriyama et al. 2001, Noda et al. 2016), and the feeding pressure of these species shows seasonal dependence (Noda et al. 2014). The feeding activity of herbivorous fish is higher during the summer, which coincides with the higher feeding pressure of *D. setosum*. The increased feeding pressures of herbivorous fish and *D. setosum* that coincide in the same season will likely have a high influence on the seaweed community.

In this study, we clarified the effects of water temperature and TD on the feeding rates of *D. setosum* based on tank experiments. We used data generated from the tank experiments in combination with data on *D. setosum* population dynamics to estimate the feeding pressure of *D. setosum* populations in barren grounds. The feeding pressure of *Diadema* populations in the temperate regions of Japan may have distinct seasonal changes. Further studies on *Diadema* populations in different temperate regions are required to support this assumption.

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