Persistent macroalgal beds in the warming waters of southwest Japan: a trophic cascade in a marine protected area with artificial reefs

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Introduction

The importance of predation in the maintenance of macroalgal beds through trophic cascades has been increasingly recognized worldwide [1, 2] except in Japan and some other countries. The disappearance of macroalgal beds owing to overgrazing by sea urchins is well known in Japan, but no studies have been conducted on why sea urchin populations have increased. Numerous studies comparing no-take marine reserves and adjacent fished areas indicated that the populations and behaviors of sea urchins are controlled by predators, and thus, overfishing the predators may lead to outbreaks of sea urchins, resulting in "urchin barrens" [1].

Japan has traditionally employed unique systems to manage coastal fisheries resources: almost all coastal waters within several kilometers from shores are areas in which common fishing rights have been exclusively provided to local fisheries cooperative associations (FCAs). This community-based fishery management system might have partially contributed to a reduction in competition for resources; however, it makes it impossible to assign large areas as no-take reserves.

In this paper, we describe a small bay in which macroalgal beds have thrived extensively through a trophic cascade involving spiny lobsters (*Panulirus japonicus*), sea urchins, and macroalgae in the warming waters of southwest Japan. Although laboratory experiments showed that *P. japonicus* preys on sea urchins[3], nothing is known about the influence of its predation in the field.

Materials and methods

The study areas included a small (about 0.3 km^2) bay area entirely designated by Ikenoura Branch, Kochi Prefecture FCA as a marine protected area (MPA) since about 1932 to enhance a stock of spiny lobsters, as well as its adjacent areas. Kelp and fucoid beds largely disappeared along the Kochi coast in the period 1997–2000, after which urchin barrens became common. However, upright macroalgae (primarily *Sargassum* spp.) have thrived extensively within the MPA in the period March–July every year. *Panulirus japonicus* is nocturnal and always hides in shelters during the daytime. The MPA contained only a few natural shelters suitable for lobsters, such as well-developed coral patch reefs. Quarry-rock artificial reefs (ARs; amounting to 1.3 ha) were thus constructed in the inner part of the MPA to enhance lobster stocks.

Two different samplings were conducted to assess benthic community structures in Ikenoura MPA and the adjacent unprotected areas. First, sea urchin densities and size distributions were compared in July and November 2013 between urchin's preferred habitats, boulder beds (pBB1 and uBB2, where the first letter 'p' and 'u' indicate a site in the MPA and unprotected areas, respectively) and coral reefs (pCR1 and uCR3) in the MPA and an adjoining unprotected bay area similar in shape and size. Two dominant urchin species (*Echinometra* sp. A and *Heliocidaris crassispina*) were counted in 30 successive quadrats of 1 m^2, and test

diameters (TDs) of haphazardly collected urchins were measured at each location. In addition, the variation in community structure based on the distance from lobster shelters in the MPA was assessed by sampling 10 successive quadrats at 0–50 m distances from the AR closest to the west coast (AR2) along a depth contour of 5–6 m on August 4, 2015 and further (53–88 m) distances from a slightly offshore AR (AR1) on July 18–20, 2017.

To compare the potential predation on sea urchins among sites that differed in distance from lobster shelters, tethering experiments were performed in coral reefs (pCR1 and uCR3) in and out of the MPA, as well as a cobble bed about 3 m offshore from pCR1 and urchin-dominated pBC1, which was about 100 m away from the nearest lobster shelter AR1. Thirty *Echinometra* urchins (30.9–49.7 mm test size) per site were tethered to 1 kg lead weights on August 27–28, 2014 and were monitored to determine survival rates. Remaining urchin tests were also examined to obtain information on the sources of predation. Test intact with a large opening around the Aristotle's lantern is characterized by lobster predation but does not occur when large-sized lobsters consumed small or mid-sized *Echinometra* urchins because the lobsters eat urchins entirely[3].

The lobsters were counted in five successive quadrats (5 × 5 m) at the above four tethering sites on September 15, 2014. Lobster densities and size distributions were quantified at AR1 and AR2 in mid-July to early-August (closed fishing season) or in November (mostly, immediately after fishing), 2015–2017. Lobsters were counted in 5 or 6 successive 5 × 5 m quadrats placed over quarry rocks and the carapace lengths (CL) were estimated by the method described by Kawamata and Taino[4] using stereo cameras.
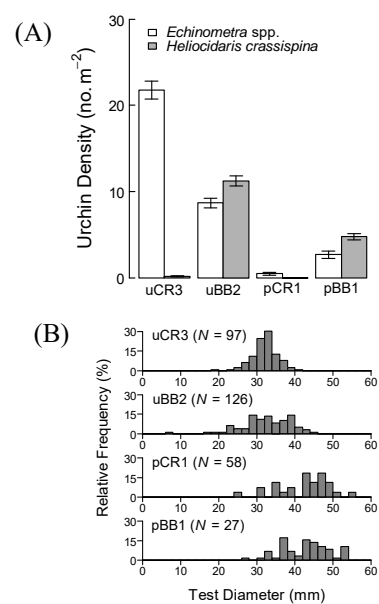
Results

Fig. 1. (A) Sea urchin densities (mean ± SE) and (B) the size distribution of the most abundant urchin *Echinometra* in coral reefs and boulder beds both in the MPA and in an adjacent unprotected bay with similar shape and size.
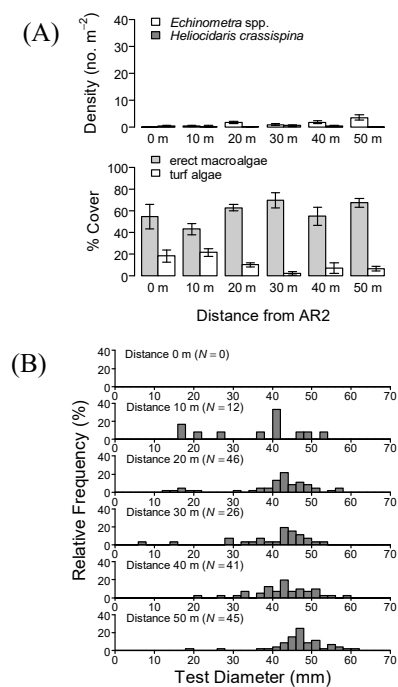

Fig. 2. Variations in (A) sea urchin densities (mean ± SE) and (B) the size distribution of the most abundant urchin *Echinometra* with the distance from AR2.

Comparison between the MPA and the adjoining bay area with similar shape and size showed that sea urchins were less abundant in the MPA than in the unprotected
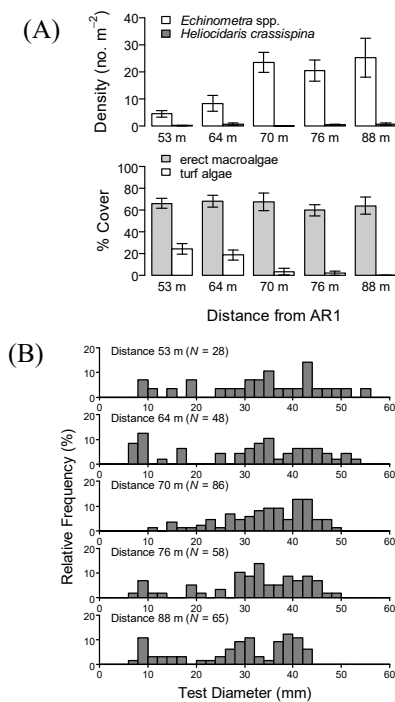
(A)

(B)

Fig. 3. Variations in (A) sea urchin densities (mean ± SE) and (B) the size distribution of the most abundant urchin *Echinometra* with the distance from AR1.

Fig. 4. Lobster densities in ARs. Asterisks indicate dates after once-a-year fishing.
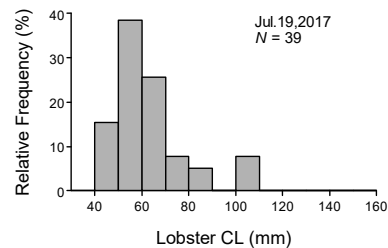
Fig. 5. Frequency distribution of CLs of lobsters at AR1.

areas (Fig. 1A). In particular extremely high density of *Echinometra* occurred in an unprotected coral reef but was scarce in a protected one, which were inhabited by lobsters. The urchins in protected sites were larger than those in unprotected sites (Fig. 1B).

Variations in sea urchin densities and size distributions with the distance from AR2 showed that the density of sea urchins remained very low within the distance of 50 m, with a slight increase with the increasing distance (Fig. 2). Most of these urchins were large compared to urchins in unprotected barrens (e.g., uCR3 and uBB2 shown in Fig. 1B). Sampling at further distant locations from AR1 showed that the area with reduced urchin densities ranged up to about 65 m from the nearest lobster shelter (Fig. 3A). Interestingly, however, relative cover of erect macroalgae (primarily *Sargassum* spp. and *Padina arborescens*) remained high beyond this limit of the area with few urchins (Fig. 3B).

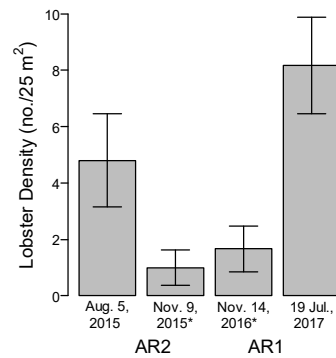A tethering experiment showed that the mortality of

tethered urchins both within and 3 m away from pCR1 were similarly much higher than those in uCR3 and pBB3. Only 20% of tethered urchins survived in and around pCR1 after 5 d, while 20% or more tethered urchins survived at uCR3 and pBB3 even after 82 d. 89% of 120 tethered urchins were missing or left only with intact or broken test after 82–83 d. Test intact with an enlarged peristomial opening remained in 20% and 13% of tethered urchins in uCR3 and pBB3, respectively, whereas no such tests were observed in and near pCR1.

At the tethering experiment sites, no lobsters were found except at pCR1 with a mean (± SE) density of 1.4 (± 1.0) lobsters/25 m². In the MPA, before once-a-year fishing (usually done from late October to early November), lobsters were more abundant in ARs (Fig. 4) than in the coral reefs pCR1 and pCR2 (mean densities = 1.4–3.0 lobsters/25 m²). Although the densities might be reduced considerably by once-a-year fishing in the MPA, lobster densities could be recovered by next summer. Stereo-camera observations showed that more than 20%

of lobsters in ARs were larger than 70 mm CL (Fig. 5).

Discussion

Our results supported the hypothesis that the maintenance of extensive macroalgae-dominated communities only within the Ikenoura MPA might primarily be attributed to predation by *Panulirus japonicus* lobsters on sea urchins in and around their daytime shelters. *P. japonicus* is nocturnal and strongly requires shelters. Ikenoura MPA has quarry-rock ARs, allowing a large lobster population to inhabit the small bay. Although the lobster population was reduced considerably by once-a-year fishing in the MPA, it recovered by next summer. It also should be noted that more than 20% of lobsters were large (CL > 70 mm), suggesting that a strict restriction of fishing may lead to a balance between landing and net immigration, with preserving large-sized lobsters. A laboratory experiment (Kawamata et al., unpublished data) showed that only lobsters of CL > 70 mm were capable of preying on large-sized *Echinometra* sp. A (TD > 45 mm) and *Heliocidaris crassispina* (TD > 40 mm) urchins. Despite high mortalities observed in tethered urchins, no test with an enlarged peristomial opening was left only around lobster shelters, suggesting that predation on sea urchins might be primarily owing to large lobsters around lobster shelters in the MPA. This was consistent with results of time-lapsed photography with tethered urchins (Kawamata et al., unpublished data) in the Ikenoura MPA showing that only lobsters with CL > 80 mm preyed on tethered *H. crassispina* urchins of ~ 36 mm TD.

The nearshore rocky reefs in adjacent unprotected areas were dominated by small to mid-sized sea urchins, while in contrast only a few large-sized urchins with fewer recruits occurred in and around lobster shelters, indicating that predation by lobsters was spatially limited to their shelters. With respect to major lobster shelters,

i.e., ARs in the Ikenoura MPA, the limit of high predation was estimated to be about 60–70 m from spatial variation in sea urchin densities. It is noteworthy that with marked increase in urchin densities beyond this limit, macroalgal cover remained almost constant up to at least about 90 m. Possible mechanisms responsible for extending macroalgal beds are (1) the supply of drift algae and propagules from central macroalgal beds and (2) lobster-induced restriction of urchin feeding activity.

References

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