Abstract Overharvesting of herbivorous fishes is assumed to be one of the causes for phase shift on coral reefs from coral- to macroalgal-dominated communities by reducing inhibitor of algal growth. In order to reveal the effect of herbivorous fishes on algae and juvenile acroporid corals, field experiment was conducted in Okinawa, southern Japan. Grazer-exclusion cages were established where small (≈2 cm in length) coral branchlets of Acropora tenuis were transplanted both inside and outside the cages. During the exclusion experiment, algal biomass, survival and growth of the transplanted corals were monitored. The cages effectively excluded herbivorous fishes that resulted in significantly greater algal biomass inside the cages than outside. While algal biomass continued to increase within the cages, algal species composition has changed drastically at the middle of the experimental period. During the first half period (3 months) when encrusting turf algae covered substrate adjacent to coral branchlets inside the cages, coral branchlets could not expand their attachment area on the substrata. In contrast, during the second half period (3 months) corals started rapid growth after turf algae disappeared and frondose macroalgae dominated. We conclude that turf algae may prevent the growth of juvenile acroporid corals especially in the early stages of horizontal expansion prior to the vertical growth.

Keywords Phase shift, Coral-algal competition, Acropora, Caging experiment

Introduction

Coral reefs around the world have undergone severe, multiple stresses over the last several decades. It is generally recognized that overfishing on herbivorous fishes or eutrophication of seawater, which change the local environment of coral reefs into those that are more suitable for macroalgae than for corals, may cause the phase shift from coral- to macroalgal-dominated communities (Hughes 1994; Bellwood et al. 2004). Since macroalgae are superior space competitors over corals by their rapid growth, macroalgae overgrow corals, and reduce survival or growth of corals, in reefs where environmental conditions are suitable for macroalgae (Tanner 1995; Jompa and McCook 2002; Box and Mumby 2007).

The coral genus Acropora Oken, 1815 is an abundant group of coral communities in the Indo-Pacific region, which is more sensitive to environmental change or stresses than other groups of corals (Loya et al. 2001; McClanahan et al. 2001). Although there have been a few studies that investigated the effect of algae on percent cover and number of recruits of naturally occurring acroporid corals (Tanner 1995; Hughes et al. 2007), informa-
tion about process of competition between acroporid corals and macroalgae is still limited. In this study, we intended to simulate the effect of algae on survival and growth of juvenile *Acropora*, which is indispensable for recovery of degraded coral communities in Indo-Pacific region, by transplanting small (∼2 cm long) branchlets of *Acropora tenuis* Dana 1846 to cage and open treatments. Our field experiment was conducted around Iriomote Island (24° 25.4′ N, 123° 48.2′ E), southern Japan, where local anthropogenic disturbance to coral reefs is almost negligible; human population density there was 8 km$^{-1}$ in 2006 (Okinawa Prefecture 2006; Geospatial Information Authority of Japan 2007). By conducting a caging experiment there, the effect of herbivorous fishes on algae and corals can be evaluated excluding the effect of eutrophication. The purpose of the present study is to examine the effect of herbivory on competition between small *Acropora* transplants and algae. Our hypotheses were: (1) reduced herbivory will cause increase in algal biomass, (2) high algal biomass will negatively affect survival and growth of small *Acropora*.

**Material and methods**

**Experimental Treatments**

To determine the effect of herbivorous fishes on algal biomass, and the effect of algae on coral survival and growth, we conducted a caging experiment on a reef flat of Iriomote Island. Two experimental alternative conditions, cage and open, were established. We assumed non-significant effect of reduced light level and water flow in the cages on survival and growth of corals and algae, since Hata and Kato (2003) concluded that the cages that they used for their caging experiment which were similar to the present experiment did not affect algal succession, even though they used much finer meshed net (2 mm openings) than the present study (13 mm openings).

Calcareous plates of different sizes (small, 12×8 cm in length and width, and 1.5 cm in height; large, 15×12×1.5 cm) were carved out from skeletons of dead massive poritid corals. The small plates were prepared for measurement of algal biomass, and the large plates were used for evaluation of survival and growth of *Acropora* branchlets. The surface of the small plates was almost flat. Five holes with 7 mm in diameter and 7 mm in depth were drilled at equal intervals for attaching the coral branchlets on the large plates; 1 hole at the center and 4 holes at the corners of the plates. Ten branchlets (∼2 cm long) including axial polyp were cut from each of 5 *Acropora tenuis* colonies around the study site. One branchlet from each of 5 donor colonies was put into the hole of the large plates. The branchlets were fixed in the holes with underwater epoxy glue (Konishi Underwater Bond); the lower side of the branchlets was put into the hole and the axial polyp of the branchlet was at upright position. The branchlets were placed randomly except the hole at center of the plate. In each treatment, a branchlet from each donor colony was placed at the center once, because the center and the corner position might have a different microenvironment.

Each 20 small and 5 large plates with the coral branchlets were deployed for cage and open treatments. The plates for cage treatment were enveloped with cuboids of 1.3 cm meshed net made with 2 mm width plastic lines. The bottom of the cuboids was open, and the net was bent beneath the plates (ca. 3 cm) to hold the net. The plates were randomly attached on a shallow reef flat (2 m depth at high tide) with the underwater epoxy glue at intervals of approximately 30 cm. The height of the cages for small and large plates was about 8 and 11 cm, respectively.

In order to exclude the effect of transplanting handlings from the results, transplanted branchlets were just observed for 2 weeks before starting the experiment for acclimatization; the cages were opened during the acclimatization period. Two branchlets, each 1 from both treatments, which died during this period, were removed from the results.

**Responses of macroalgae and coral**

Algal biomass was measured as wet weight. Each set of 5 small plates which was randomly selected from cage and open treatments was detached from the reef every month. All algae on the recovered plates were torn off, and sediments and other organisms than algae that were trapped or hidden in the algae were removed as much as possible under a stereoscopic microscope. The wet weight of the algae was measured after removing excess water with a paper towel.
In order to evaluate survival and growth of the transplanted branchlets, photographs were taken from just above the branchlets with a scale once in a month, and the mean diameter of live tissue was calculated on computer using Sigma Scan Pro (SPSS Inc.) as an average of major and minor diameters to the nearest mm. The height of corals with live tissue was measured directly in the field with a ruler to the nearest mm when photographs were taken. The experiment was conducted from June to October 2006.

**Number and size of fishes**

The abundance of fishes at the study site was recorded by remote video for all the open plates during spring tide in every month. Video recording was conducted for 15 minutes at each tide level; high tide, falling tide (at the middle between high and low tide), low tide, and rising tide (at the middle between low and high tide). We analyzed 10 out of 15 minutes of the video recordings; first 4 minutes and last 1 minute was excluded from data because observer’s action to set and manipulate the camcorder might have affected behavior of fishes. We counted the numbers of fishes that bit the plates or the coral branchlets during the 10 minutes as “visit”. The visited fishes were identified to acanthurids and scarids as herbivores, and to other fishes which eat coral polyps as coralivores based on Okamura and Amaoka (2001). The number of visits per plate on large plates was reduced to half, because area of the large plates was 2 times larger than that of the small ones. We also recorded approximate body length of herbivorous fishes as 2 or 3 size classes: small (\(<12\) cm Total Length, TL), medium (\(12 \leq <18\) cm TL), large (\(\geq 18\) cm TL) for acanthurids; medium (\(12 \leq <18\) cm TL), large (\(\geq 18\) cm TL) for scarids. Small scarids with less than 12 cm TL was not included in the results, because their foraging behavior was obscure and could not be recognized well. We did not survey sea urchins, because they were almost absent at the study site.

**Statistical analyses**

Algal biomass was compared between the treatments with repeated measures using ANOVA throughout the experimental period. Algal biomass was transformed to log (x+1) if necessary. The growth of coral branchlets was compared between the treatments with 3 way ANOVA by setting initial size of the branchlets as covariate, and donor colonies and treatments as main effects. When interaction terms were not significant, they were eliminated based-on the stepwise procedure (Sokal and Rohlf 1995). In the growth analyses, dead or disappeared branchlets were excluded from the data.

**Results**

**Temporal changes in algae**

Mean biomass of algae on the plates of open treatment was less than 0.2 g/plate during the whole experimental period (Fig. 1). In contrast, the mean biomass in cage treatment increased steadily throughout the period; it was 4.0±0.7 g/plate (N=5, ±SE) one month after the initiation of the experiment, and was 8.7±0.9 g/plate at the end.

While algal biomass continued to increase in cage treatment during the period, species composition of algae within cage treatment had changed drastically in August, which was at the middle of the period. Until August, turf algae (functional group after Littler and Littler 2007, species unidentified) dominated in cage treatment, but they disappeared and, thereafter, macroalgae (functional group after Littler and Littler 2007) Padina minor Yamada 1925 dominated until October (Fig. 2). Hence we divided the experiment period into two: the first (June to August)
In the first period, algal biomass was significantly higher in cage treatment than in open treatment (RM-ANOVA, p < 0.01, Table 1). In addition, interaction of treatment and time was also significant in this period, which means that the growth rate of algal biomass in cage treatment was significantly higher than that in open treatment. In the second half, the interaction term was not significant, but algal biomass was significantly higher in cage treatment than in open treatment (RM-ANOVA, p < 0.01, Table 2).

Number and size of fishes

The mean numbers of fishes in each size class that visited the open plates for each 10 minutes of video recordings are shown in Fig. 3. Herbivorous fishes were relatively abundant in both periods, whereas bites by corallivores on coral branchlets were not observed. Among three groups of fishes counted, visits by acanthurids were most frequent; the average number of acanthurids visited on one plate during 10 minutes was more than 0.6 individuals in both periods, which was about 36-fold and 3.6-fold of scarids’ visits in each first and second half, respectively. Acanthurids grazed on various kinds of substrate such as reef surface, experimental plates or plastic net of cages, whereas scarids showed preference to natural reef surface rather than to experimental plates. Scarids never grazed on plastic net.

Growth and survival of corals

Six coral branchlets out of 48 had died or been detached from the base during the experimental period (6 months). All 6 branchlets were found dead or detached in open treatment; 1 branchlet detached between August and September, 1 died (broken) and other 5 were detached between September and October. Two typhoons passed by Iriomote Island, one in August and one in September. Although the branchlets were dislodged during the typhoons, the cages were not affected.

Table 1  Repeated-measures ANOVA table for testing differences in algal biomass between two treatments (cage and open) for the first half period (from June to August).

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>1</td>
<td>1.68</td>
<td>475.59</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Time</td>
<td>2</td>
<td>1.21</td>
<td>170.88</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Treatment*Time</td>
<td>2</td>
<td>0.92</td>
<td>129.94</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Table 2  Repeated-measures ANOVA table for testing differences in algal biomass between two treatments (cage and open) for the second half period (from August to October).

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>p</th>
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</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>1</td>
<td>5.64</td>
<td>891.45</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Time</td>
<td>2</td>
<td>0.02</td>
<td>1.19</td>
<td>0.3221</td>
</tr>
<tr>
<td>Treatment*Time</td>
<td>2</td>
<td>0.03</td>
<td>2.06</td>
<td>0.1491</td>
</tr>
</tbody>
</table>
Temporal changes in coral growth rate of the branchlets in the mean diameter are shown in Fig. 4. The branchlets in open treatment grew almost constantly from June to September; their mean diameter increased by 17.5±4.0 % (N = 5, mean ± SE) from their initial size. In contrast, in cage treatment, the growth rate was negative until August due to partial death of branchlets and it drastically increased from August to September. The branchlets in open treatment decreased their mean diameter by 6.7±2.4% from the initial size from June to August, whereas they grew quickly (up to 20.7±9.0% from their initial size) from August to September. The growth rate in cage treatment between August and September was three times higher than that in open treatment. From September to October, mean diameter of the branchlets was almost same in both treatments.

In both experimental periods, the initial size of the branchlets was a significant covariate of the increment in mean diameter (Tables 3–4). Therefore, the growth of branchlets in mean diameter was evaluated with adjusted mean values, in which the effect of initial size was eliminated from the measured values. During the first half, the growth in open treatment was significantly larger than that in cage treatment (p < 0.01, Table 3, Fig. 5). On the other hand, the growth in cage treatment was significantly larger than that in open treatment during the second half (p < 0.01, Table 4, Fig. 5). The effect of donor colonies on the growth in mean diameter of branchlets was not significantly different in both periods (3way ANCOVA, p = 0.145 and p = 0.07 in first and second half, respectively, Table 3 and Table 4).
The height of the branchlets showed almost no increase in both treatments throughout the experimental period (Fig. 6). It decreased in the second half (p < 0.01, RM-ANOVA), but difference was not significant between the treatments (p = 0.50, RM-ANOVA), and the interaction of treatments and time was not significant (p = 0.49, RM-ANOVA).

**Discussion**

**Effect of herbivorous fishes on algal biomass**

Herbivorous fishes appeared to have kept algal biomass at almost zero in the open treatment of the present study during the whole experimental period, because other herbivores such as sea urchins were rarely observed at the study site. Acanthurids were considered to have most actively consumed turf and macroalgae (algal functional groups in Littler and Littler 2007) on the plates (Fig. 3).

However, this may not mean that scarids rarely contribute to algal reduction on natural reefs around the study site. Scarids frequently grazed on natural substrates around the experimental plates, but they did not on the plates. Scarids have round-shaped dental plates to excavate or scrape substrate with algae (Bellwood and Choat 1990). The structure of their mouth may not be suitable for grazing on flat surface like the experimental plates.

### Effect of algae on coral survival and growth

The results of the present study suggest that, even if tall macroalgae such as *Sargassum* do not bloom, increase in turf algae due to reduction of grazing pressure of herbivorous fishes may negatively affect growth and survival of small coral colonies. Although Littler and Littler (2007) pointed out that dense cover of turf algae would be an indicator of undesirable state of reef benthic communities with low herbivory, most studies have focused on the effect of macroalgae on corals (e.g. Hughes et al. 2007). Experimental studies on reefs showed that prolonged reduction of grazing pressure by herbivorous fishes induced macroalgal bloom, and overgrowth by macroalgae caused coral mortality (Lewis 1986; Burkepile and Hay 2006; Hughes et al. 2007). In this study, whole mortality of the branchlets which was induced by competition with algae did not occur, because tall macroalgae that may overgrow corals did not appear. Increased turf algae, how-

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**Table 3** Three way ANCOVA table for testing differences in mean diameter (mean of major and minor diameters in projected image) of branchlets among the two treatments (cage and open) and 5 donor colonies at the end of the first half period.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>1</td>
<td>6.45933</td>
<td>8.7048</td>
<td>0.0052</td>
</tr>
<tr>
<td>Donor colony¹</td>
<td>4</td>
<td>5.37859</td>
<td>1.8121</td>
<td>0.145</td>
</tr>
<tr>
<td>Initial size²</td>
<td>1</td>
<td>62.1408</td>
<td>83.7431</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

¹Random effect
²The initial mean diameter was included in the analysis as a covariate.

**Table 4** Three way ANCOVA table for testing differences in mean diameter (mean of major and minor diameters in projected image) of branchlets among the two treatments (cage and open) and 5 donor colonies at the end of the second half period.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>1</td>
<td>56.4954</td>
<td>14.9514</td>
<td>0.0005</td>
</tr>
<tr>
<td>Donor colony¹</td>
<td>4</td>
<td>36.1305</td>
<td>2.3905</td>
<td>0.07</td>
</tr>
<tr>
<td>Initial size²</td>
<td>1</td>
<td>118.281</td>
<td>31.3027</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

¹Random effect
²The initial mean diameter was included in the analysis as a covariate.

**Fig. 6** Temporal change in mean growth (±SE) of the branchlets in height. The growth rate was calculated as [value in each month − initial value] / [initial value] × 100 (%) for each month.
ever, prevented horizontal growth (expansion of attached area) of the Acropora branchlets in the cage treatment by forming encrustation on the experimental plates. Since the turf algae grew in an encrusting manner by covering almost all the surface of the plates around the bases of the branchlets, the branchlets could grow neither horizontally nor vertically; before upward growth of developing branchlets three-dimensionally, young and small colonies of branching Acropora spp. should expand their attachment bases (Loya et al. 2001). The branchlets in the cage treatment drastically increased their diameter after August when the turf algae disappeared in the cages and the space around their bases was unoccupied. The rapid growth of the branchlets in the diameter after disappearance of the turf algae clearly indicates that the turf algae prevented the growth of the branchlets; the branchlets would be able to grow vertically afterward. Although biomass of the macroalga Padina minor increased in the cage treatment, it did not prevent the growth of the branchlets during the study period, probably because P. minor grew upward with relatively small attached bases. Box and Mumby (2007) also showed that impact of macroalgae may not always be fatal for corals depending on algal species or physical interaction between corals and algae.

The results of this study imply that the effect of turf algae on small acroporids cannot be disregarded for coral recovery after disturbances even though phase shift from coral to macroalgae did not occur in reef benthic communities. Around Okinawa Island, coral communities were devastated by the mass coral bleaching in 1998 (Loya et al. 2001), and coral communities have not recovered well from bleaching event yet at some reefs, though blooms of macroalgae have not occurred on these reefs (K. Sakai and R. Tamai, pers. obs.). In Okinawa Island, turf algae might have caused the delay in recovery of coral communities by preventing growth of juvenile Acropora colonies. Thus, we suggest that prevalence of encrusting turf algae should be checked in addition to bloom of macroalgae in coral reef monitoring.

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Ⓒ Japanese Coral Reef Society