

Do epibenthic algae induce species-specific settlement of coral larvae?

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Effect of epibenthic algae as species-specific coral settlement inducers was examined by laboratory experiments using six Acropora species. When epibenthic algae grew on artificial plates at three depths (shallow, middle and deep) on a reef slope over a period of two months, there was no effect as species-specific inducers. However, when the growth period was prolonged to five months, the larvae of Acropora digitifera which dominates on the shallow reef slope mainly settled on the plates that were conditioned at the shallow depth, while the larvae of A. muricata which dominates on the middle slope concentrated on the plates that were conditioned at the middle depth. These results indicate that epibenthic algae may act as a cue for the habitat selection of Acropora corals as a settlement inducer. However, the fact that there was no preference for specific plates in other species suggested that epibenthic algae do not act as a sole indicator in selecting a suitable settlement place for Acropora larvae.

Keywords: vertical zonation, *Acropora* corals, recruitment, reef slope

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INTRODUCTION

Supply-side ecology (Lewin, 1986) has an important role in determining the distribution of sessile organisms (Underwood & Keough, 2001). In most tropical shallow waters, reef corals show a clear zonation structure (Goreau, 1959; Dollar, 1982; Done, 1982). In particular, *Acropora* corals, one of the most dominant groups in the Indo-Pacific Ocean, show zonation at the species level on reef slopes; tabular and corymbose species dominate the shallow slope and branching species dominate in deeper slope areas (e.g. Suzuki *et al.*, 2008). In the last decade, the importance of the initial life stage on limiting the coral distribution has been focused on (Babcock & Mundy, 1996; Mundy & Babcock, 1998; Carlon, 2002; Suzuki *et al.*, 2008, 2009). Assuming that larval selection of settlement place is species specific, two hypotheses on pre-settlement behaviour could explain the cause of this depth-related selectivity. One is inter-specific habitat segregation in swimming larvae, and the other is the existence of species-specific inducers at settlement. In this study, the latter hypothesis was tested.

If all *Acropora* larvae swim in the water column at random, the epibenthic community would be the primary determinant for establishment of the zonation. Alternatively, physical factors such as light intensity or current speed could also affect larval settlement, but these factors are not sufficiently stable to reliably guide them to a suitable habitat. For example, luminance changes with time, and current speed differs with weather and wind direction (e.g. Yamano *et al.*, 1998). The lack of stability of these variables may increase the risk of larvae to fail to make an appropriate selection. In

contrast, biological factors could be a more stable guide for larval settlement because these organisms always exist irrespective of the physical environmental change (at least in an ecological time scale). In reef corals, several studies have reported the important role of epibenthic algae such as crustose coralline algae (CCA) (Morse & Morse, 1991; Morse *et al.*, 1996; Iwao, 1997; Heyward & Negri, 1999) or bacteria collected from CCA (Negri *et al.*, 2001) not only on settlement and metamorphosis, but also post-settlement survival (Harrington *et al.*, 2004), whereas the microorganisms not associated with CCA also induced coral metamorphosis (Webster *et al.*, 2004). Beside, macroalgae and cyanobacteria inhibited coral settlement and increased mortality rates of the recruits (Kuffner *et al.*, 2006). In other sessile organisms, larval settlement was influenced by the presence of conspecific (Jeffery, 2002) and microbial community (Thiyagarajan *et al.*, 2006) in intertidal barnacles, by biofilms in mussels (Bao *et al.*, 2006). Considering these results, biological factors, especially epibenthic algae, can affect larval behaviours of corals at settlement in suitable place. Indeed, the habitat specific epibenthos sampled from areas where adults of the same coral species dominated have been shown to induce the settlement of certain coral larvae (Baird *et al.*, 2003). As such a selectivity mechanism was suggested from the comparison among distantly related taxa (i.e. *Goniastrea* and *Fungia*), the biological factor is likely to act on the selective settlement of closely related species within the genus *Acropora* as an environmental signal. To examine whether *Acropora* corals utilize epibenthic algae as a cue for maintaining the vertical zonation, the larval selectivity on artificial plates which were conditioned at different depth habitats was compared between *Acropora* species which dominate in each habitat. Considering that the length of the conditioning period affects the algal community structure, the settlement experiments were conducted twice under different conditioning periods.

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MATERIALS AND METHODS

Collection of larvae

Study sites were located on the north shoreline of Ishigaki Island (24°27'N 124°12'E), Japan. In this area, four genera and 69 species of acroporid corals have been reported, particularly, *Acropora* is the most abundant group (Fujioka, 1998). Three depth points (2.5 m, 5.5 m and 11 m) were selected on the reef slope (Tomino Reef) and one was set on the inner reef (Urasoko Bay, depth 1.5 m) (Figure 1; Suzuki *et al.*, 2008). From the survey of the degree of cover (Suzuki *et al.*, 2008), six dominant species (*Acropora digitifera*, *A. hyacinthus*, *A. muricata*, *A. intermedia*, *A. tenuis* and *A. selago*) were selected and used for the settlement experiment. The experiment was performed twice (2004 and 2005), only four species (*A. digitifera*, *A. hyacinthus*, *A. muricata* and *A. tenuis*) were used in 2005. The corymbose colony species *A. digitifera* and the tabular colony species *A. hyacinthus* are abundant on the shallow slopes (2.5 m), whereas two branching species *A. muricata* and *A. intermedia* and the corymbose species *A. tenuis* dominate in the middle (5.5 m) and deep (11 m) slopes. A corymbose species *A. selago* is commonly observed in the inner reef habitat. In each year, three to six mature colonies per species were collected and induced to spawn in the aquarium around the night of full moon in May. To obtain the larvae simultaneously, the spawning induction technique using H₂O₂ (Hayashibara *et al.*, 2004) was adopted. The larvae were reared in 100 l tanks with filtered seawater and used for the experiment when four days old. Water temperature in the tanks was kept at the same temperature as natural seawater (26–27°C) by an air conditioner.

Analysis of the algal coverage on natural substratum

To describe then vertical distributions of encrusting algae on the reef slope, the algal coverage within a 5 cm quadrat was

calculated at 16 different depths (1.1, 1.7, 1.9, 2.3, 2.7, 3.5, 4.3, 4.6, 5.4, 6.2, 6.8, 7.5, 8.2, 9.3, 11 and 13.3 m). Photographs were taken randomly in three quadrats at each depth in May 2006. Algal coverage of each major taxon on the digital image was specified using the function of selecting a particular colour area in the software Photoshop 7.0.1 (Adobe Systems) and calculated using Scion Image 4.0.3 (Scion Corporation). To determine if the algal coverage of each taxon varies along depth, a simple regression analysis between the coverage and depth was conducted.

Conditioning of the settlement substratum

To make the habitat specific benthic community, settlement plates (4.5 cm² with 0.5 cm thickness unglazed tile) was submerged in each depth for 2 months (from 12 March to 12 May) by being fixed on a concrete block in 2004. Because the community structure differs according to the orientation of the plate, sunny (upward-facing) and shaded (downward-facing) plates were prepared by back-to-back setting as paired plates. Eighteen pairs of plates were fixed on a block and three blocks were established in each depth tying them with base rocks by a nylon tube. In the shallow depth (2.5 m), as the effect of wave is strong, the establishment of these blocks was reinforced with bolts and underwater bond. In 2005, the conditioning period was extended for a total of 5 months (from 18 December 2004 to 23 May 2005) in order to more reflect the habitat specificity on the plate community. The site of inner reef was excluded from the experiment and only the upward-facing (sunny) plate was prepared in this year in order to focus on depth difference within a reef slope and protect from wave pressure during winter (the plates were easy to lose if they were setting as paired plates).

Settlement experiment

In 2004, eight plates (four sites × two sides, i.e. paired plates) were randomly apposed in a polypropylene container (210 ×

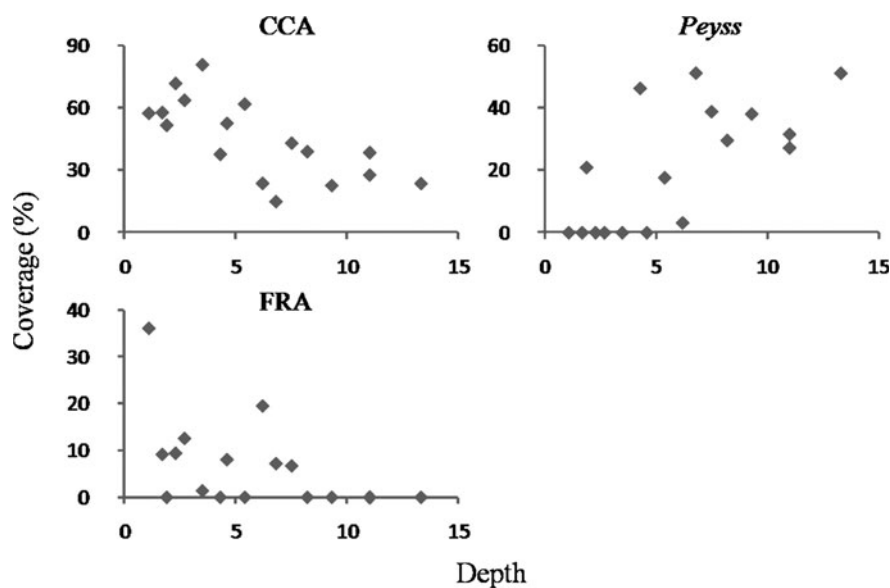


Fig. 1. Relationships between the algal coverage on natural substratum per 25 cm² quadrat and the depth in Tomino Reef. Algal taxa. CCA, crustose coralline algae; Peyss, *Peyssonnelia* spp.; FRA, filamentous red algae.

350 × 150 mm), and 1200 larvae were released into the container. Six replicates per species were prepared (total 36 containers), and these were bathed in running seawater to maintain a temperature of natural seawater. To avoid the effect of light penetration from the window on a certain container group consisted of a single species, all containers was randomly arranged in the room. After the larval release, they were reared in calm water with gentle aeration for six days and then the number of settled specimens was counted. At this time, the kind of sessile organism was recorded when a coral juvenile settled on it. Photographs of all plates were taken, and the algal coverage was calculated as stated above. Coverage of each algal taxon was compared among different conditioned plates with the Kruskal–Wallis test because the variance was not homogeneous and statistical significance ($P < 0.05$) was further examined by Scheffé's test for multiple comparison. To compare the larval selectivity on habitat specific sessile organisms among species, the settlement rate (the number of settlers on a plate/all settlers in a container) in each plate was calculated. This is because the comparison of the number of settlers was difficult due to the difference of the total number of settlers among species. The settlement rate between differently conditioned plates was compared for each species with a two-way ANOVA. The main effects were 'conditioned depth' with 3 levels (shallow, middle and deep) and 'location of plate' with 2 levels (upward- and downward-facing). Scheffé's test was performed for multiple comparisons. In 2005, the number of plates in a container was three; from shallow, middle, deep sites on the reef slope. Because many plates were lost probably due to storm waves during the conditioning period, four replicates per species (only three in *A. digitifera*) were prepared (total 15 containers). The number of released larvae per container was 450 in 2005. The settlement rate between differently conditioned plates was compared for each species with a one-way ANOVA, and Scheffé's multiple comparison tests were performed.

RESULTS

Relationship between depth and algal community on natural substratum

Algae on the natural substratum in the study area were classified into three major taxa; crustose coralline red algae (CCA), *Peyssonnelia* spp. and filamentous red algae (FRA). The coverage of CCA and depth were negatively correlated ($R = 0.70$, $P < 0.01$), whereas the coverage of *Peyssonnelia* spp. and depth were positively correlated ($R = 0.66$, $P < 0.01$) (Figure 1). No correlation was found between the coverage of FRA and depth ($R = 0.40$, $P = 0.126$).

Epibenthic algae on the plates

EXPERIMENT IN 2004

Filamentous red algae were most dominant in most plates, but CCA was abundant in the upward-facing plates, collected from 2.5 m and 10 m of Tomino Reef (Figure 2). Blue-green algae (Cyanophyta) were dotted only on the upward-facing plates. The algal coverage on the downward-facing plates of 5 m and 10 m was relatively small. The coverage of CCA

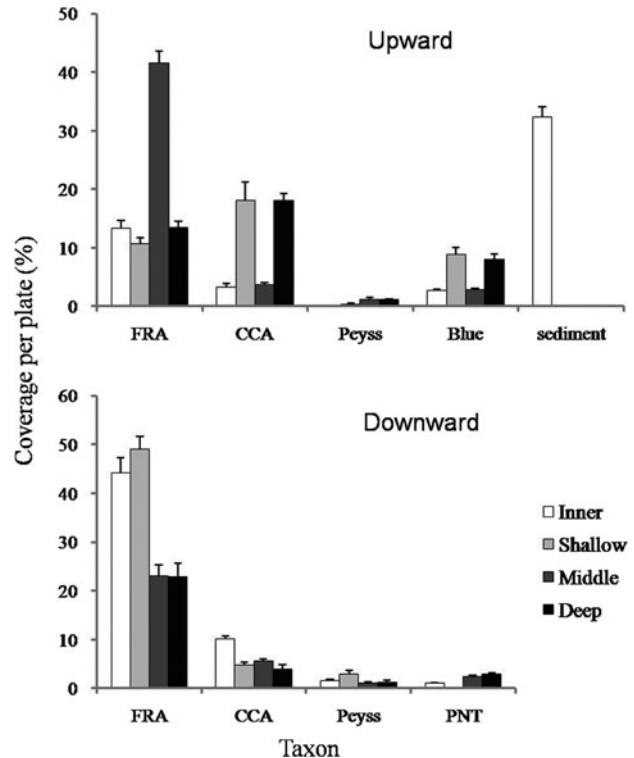


Fig. 2. Coverage of the algal community on the plates used in the 2004 experiment. Upper and lower graph shows the results of 'upward-' and 'downward-' facing conditioned plate, respectively. Algal taxa: blue, blue-green algae (the others are the same as in Figure 1). Sediment and polychaete nesting tube (PNT) were added as taxon because these were outstanding on specific plates. Conditioned depth of plates is shown on the right side of the lower graph. Inner, shallow, middle and deep indicates the place where the plates were conditioned in Urasoko Bay (1.5 m), 2.5 m, 5.5 m and 11 m on Tomino Reef, respectively. Error bars mean standard deviations.

was higher in the upward-facing plates than that in the downward-facing plates not only in surface area but also in thickness (Kruskal–Wallis test, $P < 0.01$). The algal composition on the plates was similar between the upward-facing plates of 2.5 m and 10 m, and also between the downward-facing plates of 5 m and 10 m.

EXPERIMENT IN 2005

In which only upward-facing plates were prepared, the coverage of all algal taxa was significantly different among the plates from different depths (Kruskal–Wallis test, $P < 0.01$) (Figure 3). The CCA coverage was highest in the shallow and lowest in the middle. Colonies of *Peyssonnelia* spp. were fewer in the middle depth plates. Dominance of FRA was observed only on the plates of the middle depth. Although blue-green algae occupied only a small part of the plate, the coverage was slightly higher in the deep.

Larval settlement rate on the plates

EXPERIMENT IN 2004

The total number of settlers per container was more than one-third of released larvae in *A. tenuis*, *A. muricata*, *A. intermedia* and *A. digitifera* (549, 428, 419 and 379 settlers on average, respectively), and less than one-fifth of released larvae in *A. selago* and *A. hyacinthus* (146 and 202 settlers

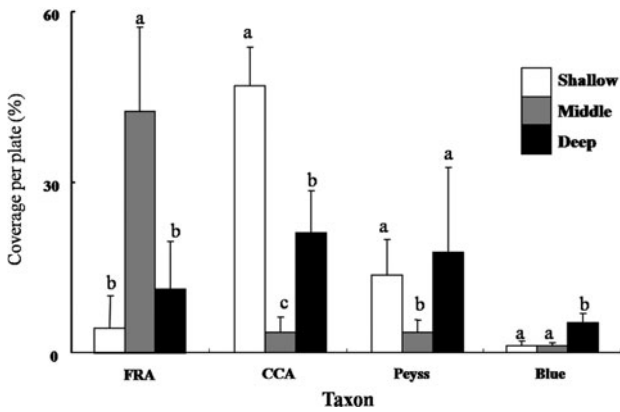


Fig. 3. Coverage of the encrusting algae on the plates used in the 2005 experiment. Open, grey and filled bars mean the conditioned place of plates on shallow (2.5 m), middle (5.5 m) and deep (11 m) on Tomino Reef. Abbreviations of algal taxa are the same as in Figures 1 & 2. Error bars mean standard deviations. Lower-case letters below the site name indicate groupings of the same level in algal coverage by the Scheffé's multiple comparison test ($P < 0.05$).

on average). The settlement rates of the all species except for *A. tenuis* were higher on the upward-facing conditioned plates than those on the downward-facing conditioned plates (Figure 4; Table 1). The number of the settlers on the plates conditioned in the 1.5 m depth of Urasoko Bay (UB plates) was lowest among all depths in all species probably because of a large amount of sediment (Figure 2). In four of six species (*A. digitifera*, *A. muricata*, *A. selago* and *A. tenuis*), the selective settlement rates were significantly

lower on the UB and 2.5 m plates than the 5 m and 10 m plates. The larvae of *A. selago* significantly preferred the deep plates to the middle plates.

Details of the settlement locations on the plates were recorded (Figure 5A). The settlement rate on the bare area where no visible sessile organisms were observed varied from 11% in *A. hyacinthus* to 32% in *A. digitifera*. Nearly half of the all larvae settled on CCA regardless of species. FRA was also preferred by the larvae. Low settlement rates were observed on the *Peyssonnelia* spp., blue-green algae colonies and polychaete tubes. There was no significant difference in larval preference on a certain algae among species.

EXPERIMENT IN 2005

The total number of settlers per container was high in *A. digitifera* and *A. hyacinthus* (217 and 147 settlers in average), and was low in *A. tenuis* and *A. muricata* (26 and 76 settlers in average). Significant larval preference on a particular plate was observed in two out of four species; a shallow dominant species with corymbose colony *A. digitifera* and a middle and deep dominant species with branching colony *A. muricata* (ANOVA, $P < 0.05$; Figure 6). Approximately half of *A. digitifera* larvae settled on the plates conditioned at the shallow reef than on the other plates. In *A. muricata*, 54% of the larvae settled on the plates conditioned at the middle depth. The larvae of other two species *A. hyacinthus* (shallow dominant) and *A. tenuis* (middle dominant) did not show a preference for any plates.

More than half of the larvae of the four species settled on CCA colonies (Figure 5B). FRA were not preferred by the

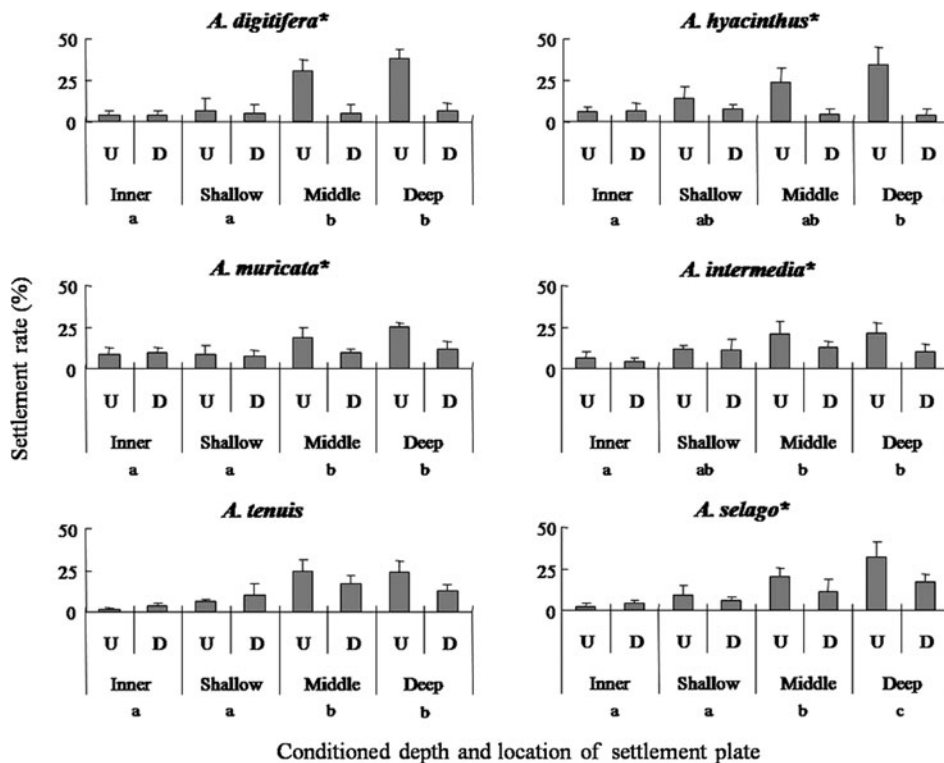


Fig. 4. Settlement rates of *Acropora* larvae in the 2004 experiment. U and D indicate 'upward-' and 'downward-' facing conditioned plate, respectively. Conditioned depths are the same as in Figure 2. Error bars mean standard deviations. Asterisks after the species name represent significant difference of selective settlement rate between the upward- and the downward-facing plates ($P < 0.01$, two-way ANOVA). Lower-case letters below the site name indicate groupings of the same level in settlement rate by the Scheffé's multiple comparison test ($P < 0.05$).

Table 1. Results of two-way ANOVA in the 2004 experiment.

		Depth	Location	Depth*location
<i>Acropora digitifera</i>	F	12.028	32.471	27.340
	P	0.000	0.000	0.000
<i>Acropora hyacinthus</i>	F	4.630	31.569	15.327
	P	0.007	0.000	0.000
<i>Acropora tenuis</i>	F	26.054	3.297	7.382
	P	0.000	0.076	0.000
<i>Acropora selago</i>	F	26.002	11.532	5.098
	P	0.000	0.002	0.004
<i>Acropora muricata</i>	F	12.224	17.395	7.916
	P	0.000	0.000	0.000
<i>Acropora intermedia</i>	F	11.606	13.795	3.291
	P	0.000	0.001	0.030

larvae in any species. The differences of the algal preference in settlement were not significant among species.

DISCUSSION

In this study, the hypothesis that *Acropora* coral larvae have species-specific settlement preferences for epibenthic algae was tested for clarification of the role of initial life stage in maintaining vertical zonation. To estimate the larval settlement selectivity on epibenthic algae in a laboratory experiment, it is essential to prepare settlement plates that provide the organisms which actually inhabit on the natural substratum. On the natural reef slope, the amount of CCA decreased with

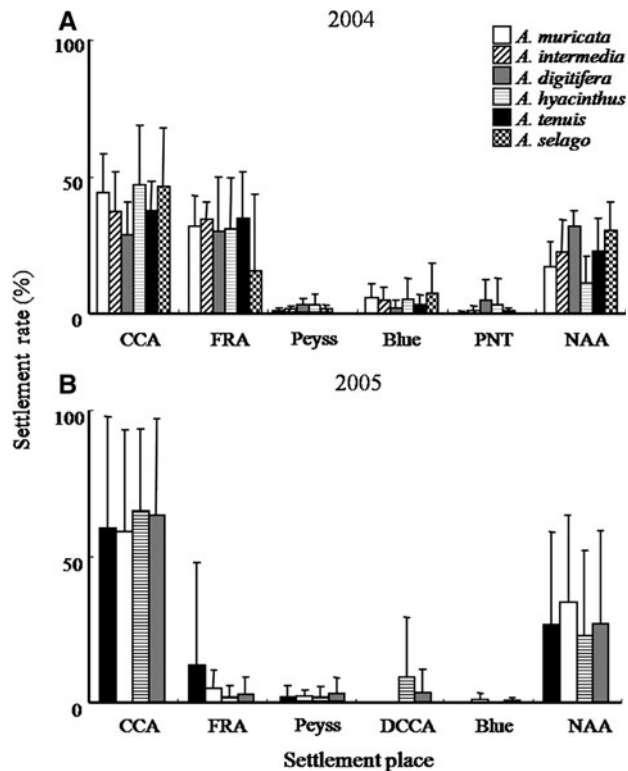


Fig. 5. Settlement rates on each algal taxon per plate by *Acropora* larvae. (A) 2004 and (B) 2005 experiment. DCCA, dead crustose coralline algae; NAA, no algal area; other abbreviations are the same as in Figures 1 & 2. Error bars mean standard deviations.

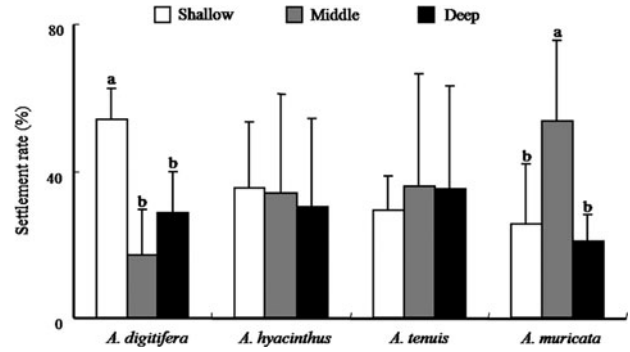


Fig. 6. Settlement rates of *Acropora* larvae in the 2005 experiment. Open, grey and filled bars mean the conditioned place of plates on shallow (2.5 m), middle (5.5 m) and deep (11 m) on Tomino Reef. Error bars mean standard deviations. Meaning of lower-case letters above bars is the same as in Figure 4.

depth, in contrast, the number of *Peyssonnelia* spp. colonies increased (Figure 1). Although it was unable to make the perfect copy of the algal communities on the natural substrata, the coverage of CCA on the plates conditioned in the shallow depth (2.5 m) was very high as well as the ambient CCA distributional pattern in the case when the conditioning period was long (approximately a half year). The remarkable difference of taxonomic composition between the plates and natural substratum was the dominance of FRA on the plates conditioned at the middle depth, whereas the abundance of FRA did not show a depth-related distribution on the natural substratum. However, because the concentrated distribution of FRA is commonly observed within the territory of damselfish which randomly distribute in branching coral area (i.e. middle depth in Tomino Reef), the occurrence of FRA on the settlement plates conditioned at the middle depth is worth using for the assessment of the larval preference. As a result, the encrusting algae on the plates would properly fulfil their roles and aims in the experiment. Although the bacteria communities on the substrata might have affected the coral settlement (Negri *et al.*, 2001), the experiments were conducted under the hypothesis that the bacterial composition also reoccurred on the plate.

In the 2004 experiment, a species-specific preference for a particular plate was not detected, although most species preferred the plates upward-facing conditioned on the middle and lower slopes (Figure 4). These preferred plates were covered mainly by CCA and FRA. This settlement preference for settlement on CCA has been reported previously in other *Acropora* corals (Morse *et al.*, 1996). Although *Acropora* larvae avoid the upside of settlement plates in field (e.g. Maida *et al.*, 1994), they preferred the biota formed in upward-facing condition in this experiment (i.e. under same light condition). This means that coral larvae possess independent preferences for light environment and epibenthic algae, respectively. Because the surface of natural substratum is complex and diverse in any spatial scales, multiple environmental indicators should be required to search for a suitable place for coral settlement.

When the degree of settlement preference to upward-facing plates was compared among six *Acropora* species, it seemed to be higher in the dominants in shallow waters, *A. digitifera* and *A. hyacinthus*, than the other four species (Figure 4). That is, in the selective settlement mechanism of *Acropora* corals, the kind of favourite algae is not different but strength of the favour to algae might be different among species. The conditioning period of settlement plate was approximately two

months in the 2004 experiment, and this period might have been too short to reproduce the ambient biota on the plate.

When the conditioning period was prolonged to five months (i.e. 2005 experiment), two species (*A. digitifera* and *A. muricata*) showed a species-specific preference (Figure 6). The algal species composition on the plates was significantly different between 'shallow' and 'middle' plates; the dominant algae was CCA on the shallow plates and FRA on the middle plates (Figure 2), while the former plates were preferred by *A. digitifera* and the latter were preferred by *A. muricata*. This result indicates that the epibenthic algae may play a role as a cue for the species-specific habitat selection of *Acropora* corals as a settlement inducer. However, even the *A. muricata* larvae intensively settled on CCA and no algal area (Figure 5B), which suggested that FRA were not selected as actual settlement place in touching directly but emitted water-soluble attractants for *A. muricata* larvae, otherwise CCA were strongly preferred by *A. digitifera* larvae regardless of the existence of FRA.

A natural inducer (bromotyrosine derivative) and two enhancers (carotenoids) were identified from CCA, and they had a synergistic effect in the metamorphosis of coral (*Pseudosiderastrea tayamai*) larvae (Kitamura *et al.*, 2007). Such a synergistic effect could enhance the species-specific settlement selectivity in *Acropora* corals. However, the fact that the other two species (*A. hyacinthus* and *A. tenuis*) settled equally on each plate conditioned at different depths implies that epibenthic algae do not act as a sole factor in maintaining the vertical zonation of *Acropora* corals. The conditioning period of five months from winter to early summer in the 2005 experiment may not have been long enough for algal communities to fully develop on the plates; natural algal communities on natural substrata should be used for the settlement experiment to clarify the degree of the contribution of epibenthic algae to the selective settlement mechanism of *Acropora* corals.

Although the interspecific difference in post-settlement survival is also an important factor for regulating the coral distribution, there were no differences of post-settlement survival among four dominant species in Tomino Reef at least during half a year from settlement (Suzuki *et al.*, 2009). Presumably, pre-settlement behaviours such as vertical distribution during swimming may contribute to maintain the zonation, although the effect of other settlement indicators such as light intensity should be examined.

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