

## NOTE

## Habitat selection by larvae influences the depth distribution of six common coral species

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**ABSTRACT:** The depth range of coral species has often been attributed to post-settlement mortality reflecting different physiological tolerances of species along physical gradients, such as light and water movement. Consequently, the potential of habitat selection by larvae to contribute to these patterns has been largely ignored. To test whether larvae prefer substratum conditioned in the parental habitat, the larvae of 6 common coral species, with contrasting depth distributions, were introduced to aquaria containing settlement tiles conditioned at 2 and 12 m (shallow and deep), plus unconditioned tiles. *Goniastrea aspera* and *G. retiformis*, reef-flat species, settled on shallow tiles in densities 4 times greater than on deep tiles. *Fungia horrida*, a species locally restricted to deeper water, was 6 times more abundant on deep tiles. *F. repanda*, with a similar distribution, settled exclusively on deep tiles. *Platygyra daedalea*, a species with a wide depth range, settled preferentially on shallow tiles; however, this preference was much less pronounced than in *G. aspera* or *G. retiformis*. *Leptoria phrygia*, another species with a wide depth range, was equally abundant on deep and shallow substrata. We conclude that the depth distribution of these species is influenced, in part, by substrate preferences of larvae at settlement.

**KEY WORDS:** Coral reef · Settlement · Recruitment · Substratum cues · Larval choice

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The zonation of coral assemblages is one of the most prominent features of coral reefs worldwide (e.g. Goreau 1959, Stoddart 1969). Predictable coral assemblages are found in particular reef habitats, with patterns consistent over a wide geographical area (e.g. Done 1982). Community characteristics, such as relative abundance and species diversity, vary predictably among these zones (e.g. Loya 1972, Sheppard 1982).

Zonation in coral assemblages has traditionally been attributed to different physiological tolerances of species to physical factors, such as light or water movement that change predictably with increasing depth

(e.g. Rosen 1975, van den Hoek et al. 1978, Done 1983). Biological interactions between organisms, such as competition (e.g. Sheppard 1979, Huston 1985) and predation (e.g. Glynn 1976, Neudecker 1979), have also been recognized as contributing to coral zonation.

Implicit in these explanations of coral zonation is the assumption that larvae settle relatively uniformly over a wide depth range and that the depth distribution of adult corals emerges as a result of differential patterns of post-settlement mortality. While habitat selection by larvae or limited dispersal may influence the spatial distribution of adults within reef zones (e.g. Lewis 1974, Morse et al. 1988, Carlon & Olson 1993, Baird & Hughes 2000), the potential contribution of larval habitat selection to the vertical zonation of adults has largely been ignored, despite evidence that the depth distribution of juveniles is often similar to that of adults (e.g. Bak & Engel 1979, Harriott 1985, Colgan 1987).

Kawaguti (1941) was the first to suggest that differences in the degree of photo taxis between coral larvae might influence the depth distribution of adults. Similarly, Mundy & Babcock (1998) demonstrated that light intensity and spectral quality affected the settlement density of larvae from zone-specific coral species. Furthermore, when 11 d old juveniles of these zone-specific species were transplanted outside the adult habitat, they survived equally as well as juveniles located within the adult habitat, indicating that differential patterns of mortality were not sufficient to explain the depth distribution of these species (Mundy & Babcock 2000). These results strongly suggest that larval response to cues during dispersal or at settlement may influence the depth distribution of these species. Nevertheless, a direct link between habitat selection by coral larvae and depth distribution of adults remains to be established.

The aim of this study was to investigate the effect of habitat-specific substratum cues on larval settlement, as a factor influencing the observed depth distribution of adults. More specifically, we tested the hypothesis that larvae will settle preferentially on substratum conditioned in the parental habitat.

**Materials and methods.** The study was conducted on the fringing reef on the south-east side of Pelorus Island (18° 46' S, 146° 15' E) in the central Great Barrier Reef (GBR). Pelorus Island is a continental island, 18 km from the mainland of Australia, supporting extensive fringing reefs typical of moderately exposed, offshore mid-shelf reefs on the GBR. The reef is relatively shallow (<15 m) and highly turbid, with underwater visibility rarely exceeding 8 to 10 m and relatively sheltered from oceanic conditions by the expanse of the GBR lagoon. Six species of scleractinian corals were chosen on the basis of their depth distribution at this location. *Goniastrea aspera* and *G. retiformis* are generally found only on the reef flat. *Fungia horrida* and *F. repanda* are locally restricted to unconsolidated substrata at the base of the reef slope. *Platygyra daedalea* and *Leptoria phrygia* are common over a broad depth range. All species are broadcast spawners and the larvae have a similar minimum planktonic period of 2 to 4 d. The depth distributions of these species was confirmed using 6 replicate 15 × 0.5 m belt transects laid at each of 3 depths: the reef flat (2 m), the mid-slope (6 m) and at the base of the reef slope (12 m). The number of colonies of each species in each transect was counted (Table 1).

Larvae were cultured as described in Babcock et al. (2003). Adult colonies for spawning were collected from the same site where transects to determine depth zonation of the 6 species were run (see above) and where the settlement tiles for the experiment were conditioned (see below). The larvae were maintained until the majority were motile, a period of between 32 and 48 h depending on the species. To test whether larvae could recognize tiles conditioned in the parental habitat, motile larvae were introduced into 2 replicate tanks

per species, i.e. only 1 species of larvae in each tank making 12 tanks in total. The number of larvae introduced into replicate tanks was determined by availability: *Goniastrea retiformis*, 400; *G. aspera*, 300; *Leptoria phrygia*, 300; *Platygyra daedalea*, 2000; *Fungia horrida*, 800; *F. repanda*, 200. The tanks were bathed in large flow-through outdoor aquaria (to prevent heating) at Orpheus Island Research Station. The light environment in the tanks was similar to that at 1 to 2 m on the reef flat. An air stone was placed in each tank to oxygenate the water. Each tank contained 9 clay paving tiles (35 × 35 × 10 mm), 3 tiles from each of 3 treatments: (1) tiles conditioned at 2 m (shallow tiles); (2) tiles conditioned at 12 m (deep tiles); and (3) unconditioned tiles. The tiles were conditioned by bolting them to concrete blocks in a horizontal position for 8 wk at the site on Pelorus Island where the depth distribution of the adults was established. The larvae were given 10 d to allow the majority to metamorphose, after which the tiles were removed and censused in a water bath under stereo-dissector and finally, the number of metamorphosed larvae recorded. Metamorphosis was defined as the initiation of deposition of the basal plate, which is generally visible through the juvenile coral tissue within 24 h of settlement (Babcock et al. 2003). The total number of larvae metamorphosed in each aquarium was calculated and the mean proportion of larvae on differently treated tiles was compared for each species with a 1-way ANOVA. Difference between the treatments were examined using Tukey's honest significant difference (HSD) tests. Differences in the absolute number of larvae completing metamorphosis in the replicate aquaria required that a comparative measure of metamorphosis be obtained using log-transformed data (following Heyward & Negri 1999) according to the following equation:

$$Lp_i = \ln[(a + 0.5)/(n - a + 0.5)]$$

where  $Lp_i$  is logit transformed probability of metamorphosis,  $a$  is total number of larvae metamorphosed and  $n$  is total number of larvae (McHullagh & Nelder 1998).

To compare the fouling communities on conditioned tiles, 6 tiles from each depth were censused and the number of crustose red algae (CRA), bryozoans, polychaetes, worms, bivalves and foraminifera were recorded.

**Results and discussion.** Larval substratum preferences generally corresponded with those predicted on the basis of the depth distribution of the adults. Zone-specific species showed a clear and pronounced preference for tiles conditioned in the parental habitat. The reef flat species (Table 1), *Goniastrea aspera* and *G. retiformis*, settled on shallow tiles in densities 4 times greater than on deep tiles (Table 2, Fig. 1). *Fungia horrida*, which was locally restricted to the

Table 1. Depth distributions of the 6 coral species. Values are the total number of colonies found within six 15 × 0.5 m belt transects at each depth at Pelorus Island

Species	Depth (m)		
	2	6	12
<i>Goniastrea aspera</i>	67	4	0
<i>Goniastrea retiformis</i>	54	6	0
<i>Fungia horrida</i>	1	0	21
<i>Fungia repanda</i>	0	4	28
<i>Platygyra daedalea</i>	17	23	18
<i>Leptoria phrygia</i>	15	13	14

Table 2. ANOVA testing for differences among the mean proportion of larvae metamorphosed on tiles from each of 3 treatments. a: unconditioned tiles; b: tiles conditioned at 2 m; c: tiles conditioned at 12 m. No results are presented for *Fungia repanda* as these larvae metamorphosed exclusively on tiles conditioned at 12 m

Species	$F_{0.5}(2, 3)$	p	Tukey's HSD
<i>Goniastrea aspera</i>	157.30	0.001	a ≠ b ≠ c
<i>Goniastrea retiformis</i>	63.52	0.004	a ≠ b ≠ c
<i>Fungia horrida</i>	41.76	0.006	a = b ≠ c
<i>Platygyra daedalea</i>	331.90	0.0003	a ≠ b ≠ c
<i>Leptoria phrygia</i>	790.31	<0.0001	a ≠ b = c

base of the reef slope (Table 1), was 6 times more abundant on deep tiles (Table 2, Fig. 1) and *F. repanda* settled exclusively on deep tiles (Fig. 1). In contrast, *Leptoria phrygia* settled in equal densities on shallow and deep tiles (Table 2, Fig. 1), which is consistent with its broad depth distribution at this location (Table 1). While the larvae of *Platygyra daedalea* settled preferentially on shallow tiles (Table 2, Fig. 1), this preference was much less pronounced than in either of the reef flat species (Fig. 1). These results suggest that the

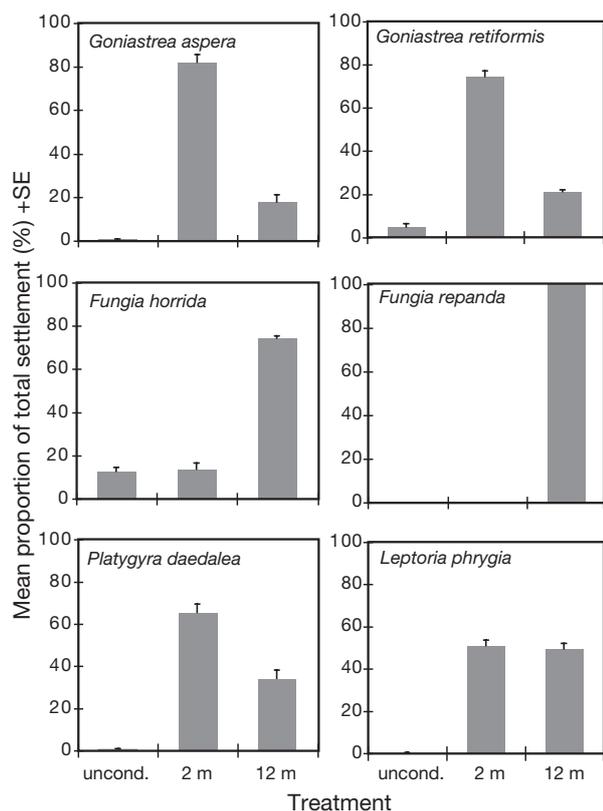


Fig. 1. Relative abundance of recruits of 6 coral species on 2 m, 12 m and unconditioned (uncond.) tiles expressed as the mean proportion + 1 SE of total settlement in 2 replicate aquaria

Table 3. Total number of various calcareous organisms on 2 and 12 m tiles

Higher taxa	Taxon	2 m	12 m
Foraminifera	Foraminiferan	176	100
Polychaete	Serpulid a	51	177
	Serpulid b	111	195
	Serpulid c	23	307
Bivalvia	Bivalvia	1	21
	Ascophora	0	2
Ascophora	Ascophora a	0	2
	Ascophora b	0	2
Tublioporata	Lichenoporidae a	0	11
	Lichenoporidae b	1	5
Anasca	<i>Thalamoporella</i>	23	25
	Articulata	0	6
Crustose red algae		455	78
Total Polychaeta		185	679
Total Ascophora		0	4
Total Tublioporata		1	16
Total Anasca		23	31
Total Bryozoa		24	51

depth distribution of these species is influenced, in part, by patterns established at settlement.

The observed patterns of settlement indicate that larval preference for tiles conditioned in the adult habitat is strong; however, it is not absolute. In all the zone-specific species, with the exception of *Fungia repanda*, some larvae settled on both deep and shallow tiles (Fig. 1) and although unconditioned tiles were generally avoided by larvae, in *F. horrida*, 13% (SE 1.7) of the larvae settled on unconditioned tiles (Fig. 1). This avoidance of unconditioned tiles is consistent with observations that surface contact with chemical cues associated with the substratum are necessary to induce metamorphosis in many invertebrate larvae (Pawlik 1992, Morse et al. 1996, Hadfield & Paul 2001). The variability in settlement behavior among species and its dependence on depth of substratum conditioning suggest that a range of substratum cues are being used by these larvae.

Ample depth-related variability in settlement tile fouling communities was observed to provide a range of biological cues for depth-specific settlement and metamorphosis. Most of the fouling organisms were abundant on tiles conditioned at either 2 or 12 m, but not at both depths. The only exception to this was *Thalamoporella*, which was equally abundant on deep and shallow tiles (Table 3). The difference in the density of settlement of the reef flat species between shallow and deep tiles was very similar to the difference in abundance of CRA on tiles at these 2 depths, with CRA being 4 times more abundant on the shallow tiles (Table 3). Other organisms (e.g. polychaetes, anascan bryozoans) were found in higher abundance or even exclusively (e.g. ascophoran bryozoans) on

the deep tiles (Table 3). Zone-specific CRA species or bacterial flora (Johnson et al. 1991, Negri et al. 2002) may also have been factors influencing settlement, although the taxonomic resolution of CRA used in this study did not allow this hypothesis to be examined. Similarly, bacterial and microalgae were not examined, but would have been part of the biofilms present on the plates.

Bacteria have been implicated in the induction of settlement of many marine organisms (e.g. Rodriguez et al. 1993, Johnson et al. 1997, Negri et al. 2002). Bacterial assemblages typically include microorganisms that may provide a chemical signature characteristic of a particular micro-habitat as well as ubiquitous microorganisms common to many micro-habitats (Johnson et al. 1997). Consequently, bacteria and other microbial organisms could provide characteristic and consistent cues to enable larvae with specific habitat requirements to distinguish between habitats. For larvae of generalist species, a proportion of the bacterial assemblage could also provide consistent cues in a wide range of habitats (Johnson et al. 1997). The settlement patterns of larvae from the generalist species used in this study support these suggestions.

Our data suggest that while settlement cues supplied by organisms characteristic of the parental habitats may induce metamorphosis, the cues are not 100% depth specific. However, settlement patterns in the field are likely to be affected by larval response to other features of the environment. For example, the ability of larvae to recognize depth-specific differences in light quality (Mundy & Babcock 1998) and intensity (Morse et al. 1988) is known to influence larval settlement in corals in ways that would tend to make settlement in the adult habitat more likely.

Larval habitat selection at the time of settlement is likely to be of key importance in determining coral distribution patterns. Nevertheless, processes operating at other phases of coral life histories are also likely to play a role. The sole use of depth-specific cues at the time of settlement as a means of determining the site of attachment is likely to entail substantial risks for larvae. For example, if a larva contacts the substratum outside the optimal depth/habitat it will not derive any information that will enable it to locate the optimal habitat. Depending on the likelihood of later encounters with the substratum, this could reduce the chances of larval survival. If coral larvae also use light as an orientation cue during their planktonic phase, few larvae may arrive at depths outside those of the adults. Consequently, more than 1 feature of the environment may be used by larvae to navigate to and select suitable settlement sites, and behavioral responses to cues may be required at multiple stages during larval dispersal (Raimondi & Morse 1991). Differential patterns

of post-settlement mortality in juvenile corals may also be involved in establishing the depth distribution of adults; however, there is no clear evidence for this despite several attempts to demonstrate it (Babcock & Mundy 1996, Mundy & Babcock 2000). Alternatively such differential mortality may occur in adult corals, but evidence for this is also lacking since depth-related zonation patterns are usually evident even in small or young colonies (Bak & Engel 1979, Rogers et al. 1984).

The substratum preferences reported in this study demonstrate that larvae of several zone-specific coral species respond to habitat-specific substratum cues at the time of settlement. More importantly, this study demonstrates that larvae of these species are capable of active choice when confronted with a range of settlement environments. This suggests that the depth distribution of the adults is influenced by patterns established at settlement. Furthermore, the contrasting choice exhibited by larvae of different species further supports suggestions that settlement cues may be species-specific and more complex than had been previously suggested.

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