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REPORT

Larval settlement preferences of *Acropora palmata* and *Montastraea faveolata* in response to diverse red algae

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Abstract Settlement specificity can regulate recruitment but remains poorly understood for coral larvae. We studied larvae of the corals, *Acropora palmata* and *Montastraea faveolata*, to determine their rates of settlement and metamorphosis in the presence of ten species of red algae, including eight species of crustose coralline algae, one geniculated coralline and one encrusting peyssonnelid. Twenty to forty percent of larvae of *A. palmata* settled on coralline surfaces of *Hydrolithon boergesenii*, *Lithoporella atlantica*, *Neogoniolithon affine*, and *Titanoderma prototypum*, whereas none settled and metamorphosed on *Neogoniolithon mamillare*. Larvae of *M. faveolata* had 13–25 % settlement onto the surface of *Amphiroa tribulus*, *H. boergesenii*, *N. affine*, *N. munitum*, and *T. prototypum*, but had no settlement on the surface of *N. mamillare*, *Porolithon pachydermum*, and a noncoralline crust *Peyssonnelia* sp. Some of these algal species were common on Belizean reefs, but the species that induced the highest rates of larval settlement and metamorphosis tended to be rare and primarily found in low-light environments. The shallow coral, *A. palmata*, and the deeper coral, *M. faveolata*, both had increased larval settlement rates in the presence of only a few species of red algae found at deeper depths suggesting that patterns of coral distribution can only sometimes be related to the distribution of red algae species.

Keywords Larval ecology · Supply-side ecology · Coralline algae · Coral reefs · Recruitment

Introduction

Recruitment of new individuals is a critical process for the maintenance and recovery of marine benthic communities (Gaines and Roughgarden 1985; Underwood and Fairweather 1989). Reef corals and coral reef ecosystems are declining on a global scale (Bruno and Selig 2007; Halpern et al. 2008), and coral recruitment is necessary for the recovery and resilience of these ecosystems (Mumby and Steneck 2008). However, the ecological interactions driving coral recruitment are still poorly understood, especially those factors that determine successful settlement and metamorphosis.

For many sessile marine invertebrates, larval settlement is the stage where mobile larvae select the benthic habitat into which they settle, metamorphose, and ultimately recruit. Therefore, larval behavior influences where adults will live. Many cues can induce invertebrate larvae to stop their pelagic phase, undergo settlement by attaching to the benthos, and metamorphose into new recruits (Pawlik 1992; Hadfield and Paul 2001; Hadfield 2011). Reef corals may require a sequence of cues for their settlement (Raimondi and Morse 2000). Coral larvae descend in the water

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column in the presence of water from reefs (Gleason et al. 2009) and when exposed to natural reef sounds (Vermeij et al. 2010). Once delivered to the benthos, there is a hierarchy of settlement substrata on which larvae in the field settle and metamorphose (Arnold et al. 2010; Arnold and Steneck 2011; Price 2010). Some coral larvae settle on or near crustose coralline algae (Morse et al. 1988; Heyward and Negri 1999; Harrington et al. 2004) while others respond to microbial biofilms in the benthic microhabitat (Golbuu and Richmond 2007; Tran and Hadfield 2011). In the laboratory, some larvae of *Acropora* spp. select among different species of coralline algae for their settlement substrata (Harrington et al. 2004; Ritson-Williams et al. 2010; Doropoulis et al. 2012). It may be that selective settlement drives depth-distribution patterns of coral species (Carlon 2002; Baird et al. 2003). However, the diversity of coralline algae that facilitate coral larval settlement has not been tested for the majority of Caribbean CCA or coral species.

We studied the larval behavior of two major reef-building corals in the Caribbean, *Acropora palmata* and *Montastraea faveolata*; these two coral species now or once dominated shallow and mid-depth zones, respectively (Pandolfi and Jackson 2006). Among the benthic substrata onto which corals can recruit are the diverse crustose coralline algae (CCA). We tested eight CCA species and two other red algae for their effects on the settlement and metamorphosis of larvae of *A. palmata* and *M. faveolata*. Further, we quantified the diversity and zonation of these algae to determine whether coralline species from specific zones trigger coral settlement by species occupying those zones. Thus, we might expect more of a response from larvae from the shallow-water-dwelling coral *A. palmata* to shallow-water algae than from the deeper-water-dwelling coral *M. faveolata*. For our study, we selected a broad suite of algal species found in various habitats to test the hypothesis that different species of red algae induce different rates of settlement and metamorphosis of coral larvae.

Materials and methods

Species studied

Both *A. palmata* and *M. faveolata* are reef-building corals that spawn their gametes for external fertilization. Both of these corals have experienced increased mortality in recent decades, prompting a need to better understand their recruitment ecology. In 2006, *A. palmata* was listed as a threatened species under the US Endangered Species Act (NMFS 2006). *M. faveolata* has also been experiencing elevated mortality due to bleaching and disease (Brandt and McManus 2009; Miller et al. 2009a).

Different species of CCA are currently under revision, and there is little taxonomic literature relevant for the Caribbean taxa (Taylor 1960). Littler and Littler (2000) is a good field guide with excellent photographs, but it does not use the diagnostic taxonomic characters necessary to reliably determine coralline species. To better distinguish the taxa that we used in the larval settlement experiments, we define taxa on multiple independent characters that relate to regionally relevant described species. We provide descriptions of key anatomical and morphological characteristics of these CCA species in the electronic supplementary material (ESM).

Benthic transects

Line-intercept transects were conducted in front of South Water Cay (approximately 300 m north of Carrie Bow Cay) in Belize during July 22–25, 2010. There were three linear, replicate 10-m transects at each depth, 2.5, 5, 10, and 20 m. Twenty meters separated each replicate transect at each depth. Sessile invertebrates, corals, and algae were identified to species along each transect. The CCA were tentatively identified in the field and a voucher specimen of each species was brought back to the laboratory for microscopic confirmation of the identification. Percent cover for each group at each depth was calculated as a mean from the three replicate transects. Relative percent cover of each CCA species was calculated by dividing the total centimeter cover of each species found on a transect by the total centimeter cover of all CCA for that transect.

Coral larval collection and rearing

For both coral species, the coral colonies were monitored and gametes were collected in situ 2–4 h after sunset at the fringing reef just south of Carrie Bow Cay (CBC), Belize. Gametes of *A. palmata* were collected the night of August 12, 2006 (3 days after the full moon), and gametes of *M. faveolata* were collected the night of August 16, 2006 (7 days after the full moon). To collect coral gametes, any colony that was observed to “set” (when the gamete bundles are held in the mouth of a coral polyp) was covered with nylon net. During spawning, the nets concentrated the gamete bundles into small plastic jars at the top of the nets. At the end of spawning, the jars were removed from the net and returned to the laboratory where the eggs and sperm were separated from individual coral colonies and then were crossed with different conspecific individuals to ensure a high rate of fertilization. After an hour, the sperm were rinsed from the eggs, and the fertilized eggs were then placed in 4.7-L buckets with 180-µm (100 µm for *M. faveolata*) mesh on the bottom. These buckets were held in another slightly larger container, so that water could drip into the larval bucket, through the mesh on the bottom and overflow from the outside container without spilling the embryos. All of the larval buckets had fresh seawater dripped into them to ensure that developing embryos were constantly exposed to fresh natural seawater.

Developing embryos from each species were held in 6–10 larval buckets in the seawater system at CBC until the larvae reached metamorphic competency. The buckets were checked multiple times a day, and any dead larvae or debris were removed using pipettes or forceps. After 2–3 days, the larval buckets were exchanged for clean buckets, and the used buckets were rinsed thoroughly with fresh water to clean the mesh at the bottom of the buckets. Larvae of *A. palmata* were raised for 5 days after fertilization, and larvae of *M. faveolata* were maintained for 6 days before they were used in experiments. Previous experience had shown that larvae were competent once they began to elongate and swim toward the bottom of the bucket, which was observed at least one full day before these larvae were used in experiments.

Settlement experiments

To test larval settlement in response to different species of crustose and coralline algae, larvae were placed in individual wells of a 12 well plate (Costar #3513) with 3 ml of 0.2-µm-filtered seawater (FSW). All of the algae were tested simultaneously with the same batch of larvae. Ten larvae of *A. palmata* were added to individual wells, and 20 larvae of *M. faveolata* were used in a well. A small chip (approximately 1 × 1 cm) of algae attached to rock was added to each well and left with the larvae for 24 h. Small chips were generated from multiple individuals of the crustose and coralline algal species. In each well, there were three potential settlement substrata; the algal surface on top of the chip, the bare rock on which the encrusting alga was growing (except for *Amphiroa tribulus* for which the broken thallus where the plant was removed from the benthos was considered the rock substratum), and the plastic well that contained the larvae. FSW was used as a negative control for metamorphosis in the dish without settlement substrata, and a fragment of biofilmed *A. palmata* skeleton (approximately 1 × 1 cm) was used as a control for the presence of biofilmed substrata without algae. After 24 h, the numbers of larvae that had settled (attached to one of the substrata) and metamorphosed (the physiological and morphological change from a planula to an individual polyp) were counted on each available substratum. Only the larvae that had settled and metamorphosed were scored in these experiments as settlement alone can be a reversible process (see Hadfield and Paul (2001) for a review of chemical cues for settlement and metamorphosis—two distinct processes critical to larval recruitment to benthic marine habitats).

The percentage of settlement and metamorphosis was calculated for each replicate ($n = 6$ for *A. palmata* and $n = 7$ for *M. faveolata*), and the mean and standard error were calculated for total settlement and metamorphosis (the sum of all three potential settlement substrata) and for each potential settlement substratum within a treatment. In all cases, the FSW treatment was excluded from statistical analysis since this was often zero and served as the negative control. For the comparison among coralline algal surfaces, the biofilmed rock was also excluded from analysis to test whether there was a difference in the percent settlement and metamorphosis directly onto algal surfaces. The variances were homogenous (Bartlett's test) but the means were never normally distributed even after arc sine square-root transformation, so the data were rank transformed and analyzed with a one-way ANOVA. If the treatments were significantly different, a post hoc comparison of means using Tukey HSD was performed to determine significant groupings among the treatments. These experiments used all of the larvae that were available, and even though the power is low for an analysis of experiments with this many treatments, our goal was to compare as many coralline algae species as possible at the same time to eliminate potential sources of variation across batches of larvae from different years.

Results

Coral cover ranged between 13.8 and 19.3 % across all four depths (Fig. 1). *A. palmata* was found at 2.5 and 5 m but not on any of the transects below 5m. *M. faveolata* was most abundant at 10 and 20 m, rare at 2.5 m and not found at 5 m. Macroalgae were least abundant at 2.5 m and increased with depth to the highest percent cover (51.3 %) at 20 m. Crustose coralline algae declined in abundance from a high of 39.81 % at 2.5 m to a low between 10 and 20 m, which only had 6.98 and 6.96 % CCA cover, respectively. Of the 11 species identified on transects, *Neogoniolithon mamillare* and *Paragoniolithon solubile* together accounted for over 50 % of CCA cover on every transect, except at 20 m (43.5 %).

Individuals of *P. pachydermum* were found at 2.5 and 5 m and were 11.9 and 6.1 % of the CCA cover at those depths, respectively. *N. affine* was only found on the 2.5-m transect, which was one individual that covered 0.03 m of the total 120 m surveyed. At depths greater than 10 m, several melobesiod algae increased in abundance, including *Sporolithon dimotum*, *S. episporum*, and *Mesophyllum syntrophicum* (Fig. 1). *Hydrolithon boergesenii* was observed at the deeper depths but only had a relative abundance of 2.2 % at 10 m and 4.9 % at 20 m. In total, three individuals of *H. boergesenii* were found that covered

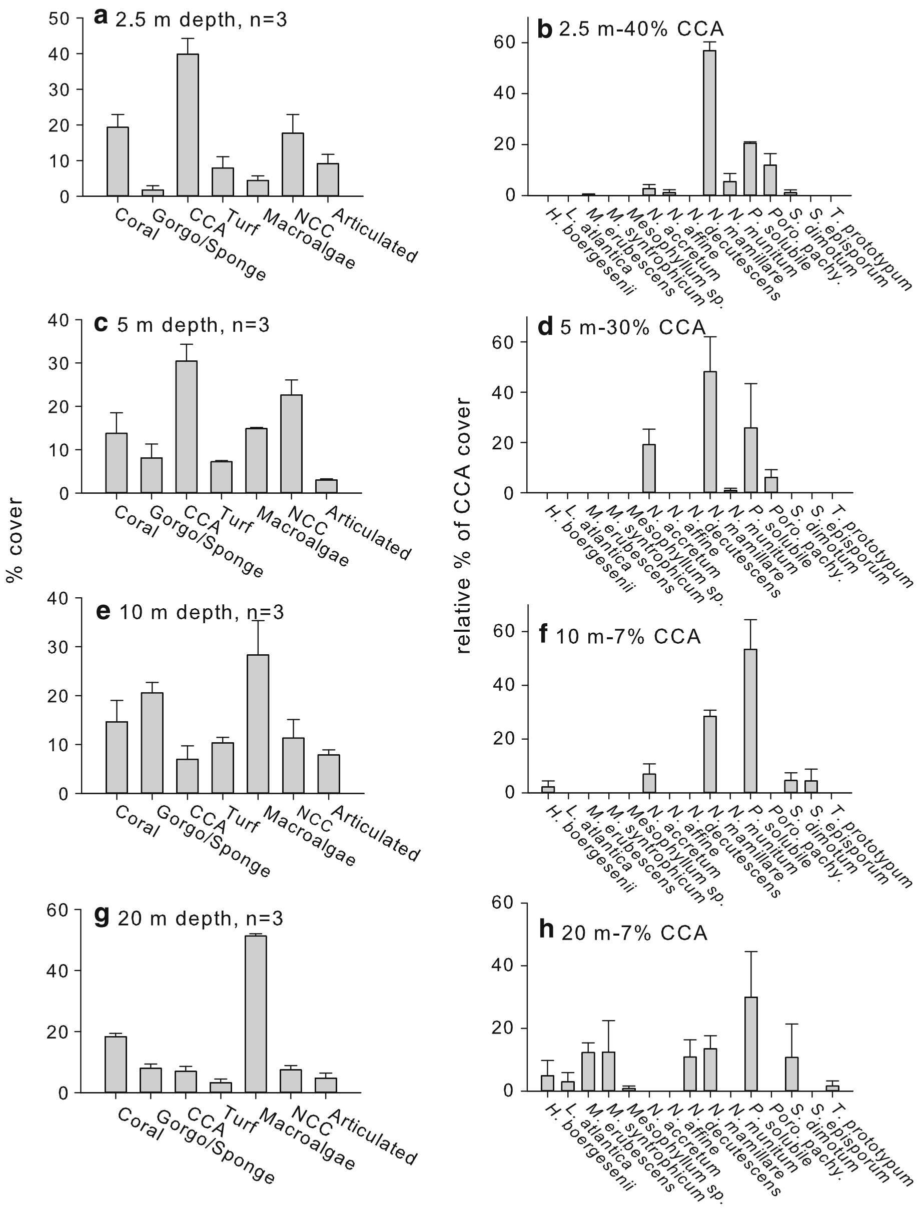

Fig. 1 The percent cover of benthic organisms (*left column*) and the relative abundance of crustose coralline algae species (*right column*) in the benthic community in Belize. *Bars* are means, and *error bars* are +1 SE. Functional groups of benthic algae were separated into the following categories: crustose coralline algae (CCA), filamentous turf algae, macroalgae, noncoralline crustose algae (NCC), and articulated algae which included *Amphiroa* spp. and *Halimeda* spp

0.09 m out of the 120 m surveyed. Only one individual of *Titanoderma prototypum* was observed at 20 m, which covered 0.02 m of the total 120 m surveyed. However, cryptic flora (those individuals living on the undersides of rocks or in cracks and crevices) would not be readily detected with the line-intercept method that was used to quantify benthic % cover.

Larvae of *A. palmata* had significantly different rates of total settlement and metamorphosis in response to different species of crustose and coralline algae (Fig. 2a; one-way ANOVA, $F = 6.09$, $p < 0.001$). There was more larval settlement and metamorphosis in the presence of *H. boergesenii* and *Porolithon pachydermum* than in response to the *A. palmata* fragment, *A. tribulus*, *N. mamillare*, and *N. munitum* (Tukey's post hoc test). These larvae also had different rates of settlement and metamorphosis onto the surface of the coralline algae (Fig. 2b; one-way ANOVA, $F = 6.36$, $p < 0.001$). Rates of larval settlement and metamorphosis were the same on *H. boergesenii*, *Lithoporella atlantica*, *Neogoniolithon affine*, and *T. prototypum*. All four of these CCA species induced greater rates of larval settlement and metamorphosis than *N. mamillare* (Tukey's post hoc test). There were no differences in the amount of larval settlement and metamorphosis on the rock substrata among the treatments (Fig. 2c; one-way ANOVA, $F = 1.17$, $p = 0.33$).

Larvae of *M. faveolata* also had different rates of total settlement and metamorphosis among the different species of coralline algae (Fig. 3a; one-way ANOVA, $F = 4.09$, $p < 0.001$). Larvae in the presence of *N. affine* had higher rates of settlement and metamorphosis than that of the *A. palmata* fragment, *A. tribulus*, and *N. munitum* (Tukey's post hoc test). There were also different rates of larval settlement and metamorphosis on the surfaces of the coralline algae (Fig. 3b; one-way ANOVA, $F = 7.74$, $p < 0.001$). *A. tribulus*, *H. boergesenii*, *N. affine*, *N. munitum,* and *T. prototypum* had similar rates of larval settlement and metamorphosis, and all of these species induced greater larval settlement and metamorphosis than *N. mamillare*, *Peyssonnelia* sp. and *P. pachydermum* (Tukey's post hoc test). Larvae of *M. faveolata* had different rates of settlement and metamorphosis on the rock substrata (Fig. 3c; one-way ANOVA, $F = 6.57$, $p < 0.001$). There were equal rates of settlement and metamorphosis on the rock under *P. solubile*, *Peyssonnelia* sp., and *P. pachydermum*, all of which were greater than the settlement and metamorphosis on the rock under the *A. palmata* fragment, *N. munitum*, *T. prototypum* and the broken thallus of *A. tribulus* (Tukey's post hoc test).

Discussion

Different crustose and coralline algae species induced different rates of settlement and metamorphosis in coral larvae of *A. palmata* and *M. faveolata*. For both of these coral species, some of the coralline algae species that were rare in abundance induced relatively high rates of larval settlement and metamorphosis on their surfaces, such as *H. boergesenii*, *N. affine*, and *T. prototypum*. Conversely, the

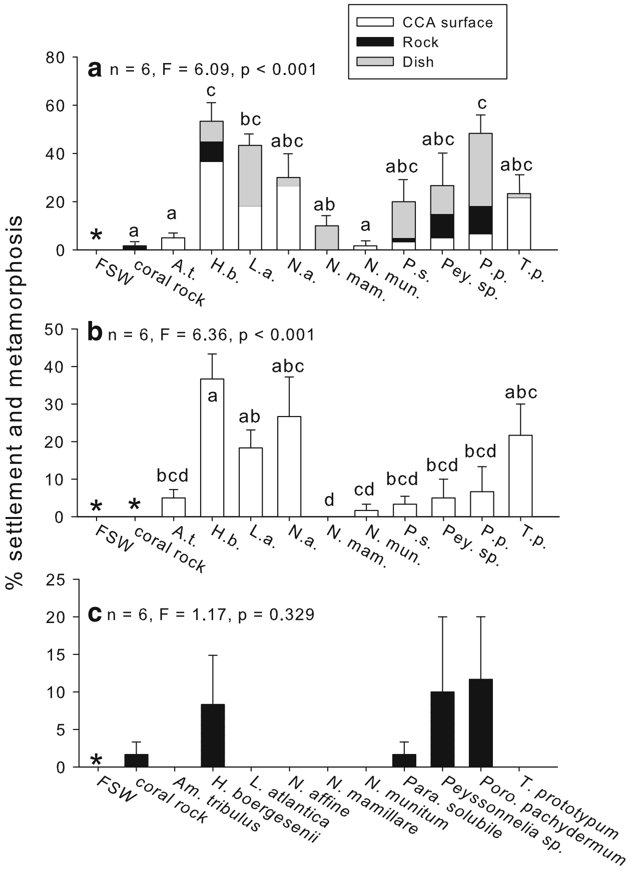

Fig. 2 The larval settlement and metamorphosis of *Acropora palmata* in response to different red algae species. Algal abbreviations correspond to species spelled out at the *bottom* of the figure and described in the methods. *Bars* represent mean for each treatment, and *error bars* are +1 SE. *Letters* above the *bars* indicate significant groupings, and *asterisk* indicates a treatment that was excluded from statistical analysis. **a** The total settlement and metamorphosis of the coral larvae in each treatment. **b** The settlement and metamorphosis of coral larvae onto the surface of the red algae species tested. **c** The settlement and metamorphosis of coral larvae onto the limestone rock on the underside of the alga

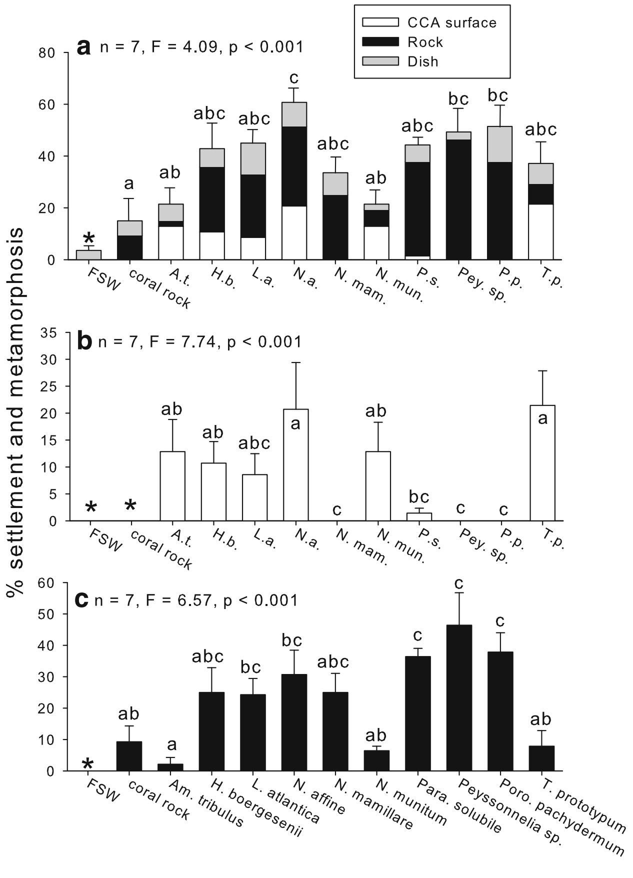

Fig. 3 The larval settlement and metamorphosis of *Montastraea faveolata* in response to different red algae species. Algal abbreviations correspond to species spelled out at the bottom of the figure and described in the methods. *Bars* represent mean for each treatment, and *error bars* are +1 SE. *Letters* above the *bars* indicate significant groupings, and *asterisk* indicates a treatment that was excluded from statistical analysis. **a** The total settlement and metamorphosis of the coral larvae in each treatment. **b** The settlement and metamorphosis of coral larvae onto the surface of the red algae species tested. **c** The settlement and metamorphosis of coral larvae onto the limestone rock on the underside of the alga

coralline algae species that were the most abundant on the benthic transects had low rates of settlement on their surfaces, including *N. mamillare*, *P. solubile*, and *P. pachydermum*. Larvae from both of these coral species had some settlement and metamorphosis in the biofilm control and both had the highest rates of settlement and metamorphosis in response to crustose coralline algae that were found on the 10- and 20-m transects.

These results are consistent with the preferences previously found for larvae of the *Acropora* spp., with *H. boergesenii* and *T. prototypum* inducing more settlement and metamorphosis than *P. pachydermum* (Ritson-Williams et al. 2010). In addition, here we show that *N. affine* and to a lesser extent *L. atlantica* can also induce settlement and metamorphosis on their surfaces. Among the three species of *Neogoniolithon* tested, there were a range of responses with relatively high rates of settlement and metamorphosis on the surface of *N. affine* (only one individual found on transects) and low rates on *N. mamillare* (common) and *N. munitum* (observed on the two shallow transects but uncommon). Some crustose and coralline algae species facilitated larval settlement and metamorphosis of *A. palmata* more than other species, even within one genus.

There are no previous records of the settlement behavior of larvae of *M. faveolata* in response to different species of coralline algae. A previous experiment showed that settlement of larvae of *M. faveolata* onto natural reef rubble was inhibited in the presence of water soluble compounds from macroalgae and cyanobacteria (Miller et al. 2009b). In normal salinity seawater, larvae of *M. faveolata* preferred to settle on coralline algae or terracotta chips more than the plastic petri dish (Vermeij et al. 2006). There were high rates of total settlement and metamorphosis among most of the species of coralline algae tested (Fig. 3a). Both *N. affine* and *T. prototypum* had higher rates of larval settlement and metamorphosis on their surface than *N. mamillare*, *P. solubile*, *Peyssonnelia* sp., and *P. pachydermum* (Fig. 3b). Even though there was little settlement on the surface of these crustose and coralline algae species, there were still high rates of settlement and metamorphosis on the rock under them. For larvae of *M. faveolata,* there was typically 15–40 % settlement on the rock adjacent to the CCA species. This may indicate that these larvae will settle on clean substrata over CCA surfaces, or that they prefer to settle on substrata that are orientated down, which has been found for most of coral larval settlement on field substrata (Birkeland 1977; Raimondi and Morse 2000; Price 2010; Arnold and Steneck 2011). Much like *Acropora* spp., larvae of *M. faveolata* had different rates of settlement and metamorphosis on the surface of different coralline algae species, but contrary to *A. palmata* larvae of *M. faveolata* also had relatively high settlement on bare substrata.

Recent research has shown that benthic habitat quality is important for successful coral settlement and metamorphosis (O'Leary and McClanahan 2010; O'Leary et al. 2012). Benthic competitors such as macroalgae and cyanobacteria can inhibit coral settlement and post-settlement survival (Kuffner and Paul 2004; Kuffner et al. 2006; Birrell et al. 2008; Miller et al. 2009b; Paul et al. 2011). Clean tile, *H. reinboldii* and *T. prototypum* were previously identified as facilitating larval settlement for *Acropora* spp. in the Pacific (Harrington et al. 2004). Note, however, that the *Titanoderma* species called *T. prototypum* is likely an undescribed sibling species and not the Caribbean coralline. In field experiments, bare substrata and *T. prototypum* were important components of the benthos that increase coral larval recruitment, but only a few species of coral larvae settled on these tiles (Arnold et al. 2010; Price 2010; Arnold and Steneck 2011). In Bonaire, 89 % of the settlers were *Agaricia* spp. (Arnold et al. 2010), and in Belize, 74 % of the settlers were *Agaricia* spp. (Arnold and Steneck 2011). In the Pacific, 90 % of the observed settlers were *Pocillopora* spp. (Price 2010). These field studies are consistent with our laboratory experiments showing that *T. prototypum* is a facilitating species of coralline algae for coral larval settlement. Most coralline algae slough their outer tissue layer as an antifouling mechanism, and species such as *P. pachydermum* have high rates of growth and probably slough their outer tissue layer frequently (RS, pers obs). If a coral recruit was to select the surface of these species for settlement, it would be removed as the outer tissue layer was shed (Harrington et al. 2004). Both *T. prototypum* and *L. atlantica* do not slough their tissue (RS, pers obs). As was shown in the laboratory, both bare substrata and *T. prototypum* had the highest rates of post-settlement survival for the coral *Acropora tenuis* (Harrington et al. 2004). It is important to note that *Hydrolithon reinboldii* also facilitated coral larval settlement (Harrington et al. 2004), and in the Caribbean, *H. boergesenii* had the same effect on post-settlement survival as *T. prototypum* for *A. palmata* (Ritson-Williams et al. 2010). This species also sloughs its outer tissue layer, but it does so in relatively small flakes. It is probable that coral larvae have evolved to distinguish among these CCA species as some will promote post-settlement survival more than others. There is a range of interactions among CCA species and coral larvae; some CCA species facilitate settlement, some inhibit it and others have little or no effect. Further research on the ecology (Steneck 1986, 1997), pigments (Mason et al. 2011), biofilms (Negri et al. 2001; Webster et al. 2004; Golbuu and Richmond 2007; Tran and Hadfield 2011; Hadfield 2011), and chemical compounds (Morse and Morse 1991; Morse et al. 1994; Heyward and Negri 1999; Harrington et al. 2004) in red algae is necessary to elucidate which characteristics are most influencing coral settlement.

Coral recruitment is known to be variable at different depths (Rogers et al. 1984; Wallace 1985; Baird and Hughes

1997). Some authors have attributed patterns of coral settlement at specific depths to physical parameters such as light and pressure (Mundy and Babcock 1998; Stake and Sammarco 2003). Other research has shown that some coral larvae can distinguish substrata conditioned at different depths offered at constant environmental parameters (Carlon 2002; Baird et al. 2003). This suggests that the organisms growing on these settlement substrata are distinct among depths. Our field survey data does show that there is a greater diversity of CCA species at deeper depths in Belize (Fig. 1). However, our methods did not quantify cryptic species that could have been in the interstices of the reef. At the site surveyed, there was a difference in the depth distribution of adults of the two corals species studied, *A. palmata* and *M. faveolata*. However, the shallow coral *A. palmata* preferred CCA species that were only found on the deepest transect. Larvae of *M. faveolata* also preferred CCA species found on the deepest transect. While the depth distribution of CCA species might be driving patterns of adult distribution of *M. faveolata*, other factors such as abiotic parameters or larval delivery could be driving observed adult distribution patterns of *A. palmata* (Mundy and Babcock 2000; Penin et al. 2010). For all corals, their successful recruitment relies on survival through a variety of larval and post-settlement processes (Ritson-Williams et al. 2009). However, it is also important to consider that coral distribution on modern reefs is the result of recruitment processes that occurred tens to hundreds of years previously. It is difficult to know whether the distribution patterns of CCA species that were observed on these transects remain constant or whether algal communities have shifted as a consequence of modern stressors.

The experiments presented here show that some crustose and coralline algae facilitate coral larval settlement and metamorphosis more than other species. By quantifying coralline algae species distribution, we have shown that many of the common species found on modern Caribbean reefs do not increase rates of coral larval settlement and metamorphosis. This is an important distinction because often researchers cite the presence of coralline algae as an indicator of good substrata for coral recruitment, but our data show that the species composition of coralline algae on a reef is critical to understanding its potential for coral settlement.

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