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Microhabitats enhance recruitment and survival, but inhibit growth of propagules of the tropical macroalga *Sargassum swartzii*

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Abstract

For organisms with discrete life-histories, any mechanism that enhances growth and/or survival at critical life-history transitions may significantly influence adult population size. On coral reefs, structurally complex microhabitats have been shown to enhance the early post-settlement growth and/or survival of fishes and corals, however, the importance of such microhabitats to the early life stages of tropical macroalgae is largely unknown. Here, we investigate the effect of crevices on the recruitment, growth and survival of propagules of a common coral reef macroalga, *Sargassum swartzii*. We settled *S. swartzii* propagules onto terracotta settlement tiles that had a series of 3 mm deep crevices evenly spaced on their top (exposed) surface. Recruitment of *S. swartzii* was 21% greater, but propagules were 18% shorter, 18-days post-settlement within crevices than on adjacent exposed surfaces. Exposing tiles to local fish assemblages for five days showed that survival of propagules was 90% greater in crevices than on exposed areas of the tiles on the reef crest, but not on the reef flat. Underwater video footage revealed that few fishes fed from within the crevices (18% of all bites) with the majority of feeding being concentrated on the exposed surface of tiles. Interestingly, small-bodied fishes from the family Blenniidae (predominantly *Ecsenius* spp.) accounted for the majority of the feeding activity on the tiles, and likely contributed to the mortality of propagules. Structurally complex microhabitats, such as crevices, that shelter vulnerable early post-settlement propagules from herbivory may therefore be important for the persistence of macroalgae on coral reefs.

Key words: Herbivory, coral reef, refuge, early post-settlement, Blenniidae

1. Introduction

For organisms with discrete life history stages, processes affecting dispersal, settlement and early post-settlement survival can have a large influence on adult population size (Connell 1985, Vadas et al. 1992). Indeed, for many marine organisms, the first few days following settlement have been identified as a critical period shaping adult populations, as recently-settled individuals are typically small (Vadas et al. 1992, Hunt & Scheibling 1997), undergo a range of physiological changes (McCormick et al. 2002), and are exposed to a diverse suite of predators for the first time (Vadas et al. 1992, Almany & Webster 2006, Scheibling & Robinson 2008). For example, mortality in the first days to weeks after settlement has been estimated to be as high as 58 % for coral recruits (Vermeij & Sandin 2008, Trapon et al. 2013), up to 75 % for coral reef fishes (Hoey & McCormick 2004, Almany & Webster 2006), greater than 90 % for many marine invertebrates (Gosselin & Qian 1997, Hunt & Scheibling 1997) and up to 99 % for temperate marine algae (Vadas et al. 1992, Kendrick & Walker 1994). Factors that mediate rates of mortality at this critical life history transition include the size of an individual (i.e., ‘bigger-is-better’ hypothesis; (Miller et al. 1988, Bailey & Houde 1989)), growth rate (i.e., ‘stage duration’ hypothesis; (Leggett & Deblois 1994)), physiological condition (e.g., Hoey and McCormick 2004), inter- and intra-specific competition (Menge & Sutherland 1976, Bonin et al. 2009), and the structural complexity and suitability of the settlement habitat (Diaz-Pulido et al. 2010, Yadav et al. 2016, Doropoulos et al. 2017, Mallela 2018). Of these, structural complexity of the settlement habitat is thought to be a major driver of rates of survival (Tupper & Boutilier 1997, Nozawa 2008, Brandl & Bellwood 2016, Mallela 2018).

The structural complexity of a habitat (i.e., its three-dimensional structure, composed of living and dead organisms and abiotic substrata) can mediate rates of mortality through the provision of refugia (Crowder & Cooper 1982, Graham & Nash 2013). The value of structural complexity in providing refugia is dependent on the relative size of available refuges: large enough to allow prey to access, but small enough to exclude predators (Menge & Lubchenco 1981). Therefore, small-scale structural complexity, such as small cracks and crevices, may allow recently settled organisms to avoid the predation pressure of adjacent open or exposed surfaces (Menge & Lubchenco 1981, Brandl et al. 2014, Franco et al. 2015).

On coral reefs, early post-settlement mortality is high (>50 %) for both fish and corals (Almany & Webster 2006, Nozawa 2008), and has led to this being viewed as a critical period in the life history of these organisms. Importantly, however, specific microhabitats can enhance the early post-settlement survival of corals and reef fish several-fold, presumably through the provision of refugia (Nozawa 2008, Bonin et al. 2009, Brandl et al. 2014). For example, Nozawa (2008) reported the complete mortality of corals that had settled on exposed surfaces within four months, while up to 12 % of corals that had settled in crevices survived the first year post-settlement. Similarly, the early post-settlement survival of coral reef fishes is also enhanced when fishes settle on patch reefs with higher structural complexity (Bonin et al. 2009). Whilst the importance of microhabitats to the settlement and survival of corals and fishes has been relatively well-studied on coral reefs (Nozawa 2008, Bonin et al. 2009, Trapon et al. 2013, Doropoulos et al. 2016), the importance of microhabitats for early life stages of macroalgae has received less attention (Brandl et al. 2014, Poray & Carpenter 2014).

To date, studies investigating spatial and temporal variation in rates of herbivory on coral reef macroalgae have primarily focused on the consumption of adult thalli (Hay 1981, Lewis 1986, Loffler et al. 2015), yet it is often assumed that macroalgal biomass is largely controlled through the grazing of early life stages of macroalgae (Done 1992, Diaz-Pulido & McCook 2003, Bellwood et al. 2004). Spatial and temporal refuges may facilitate the early post-settlement survival of macroalgae by providing a refuge from herbivory through reductions in grazing pressure (Brandl et al. 2014, Brandl & Bellwood 2016), potentially allowing propagules to grow to a size more resistant to grazing (Lubchenco 1983, Stiger et al. 2004, Briggs et al. 2018). In this study, therefore, we investigate how reef microtopography (i.e., crevices) influences the recruitment, growth and survival of propagules of the common tropical macroalga *Sargassum swartzii*.

2. Materials and methods

2.1 Study organism

Sargassum is a genus of tall (up to 3 m), leathery, brown macroalgae common on many coastal and/or degraded coral reefs (Done 1992, Chong-Seng et al. 2014). *Sargassum* reproduces through the release of tens of thousands of zoospores per plant (Diaz-Pulido & McCook 2003), with mortality of settled propagules in temperate *Sargassum* near absolute (ca. 99.9999 % after one year (Kendrick & Walker 1995)). Any reduction in early post-settlement mortality may, therefore, result in a higher rate of survival to adulthood (Vadas et al. 1992). The species *Sargassum swartzii* was used to investigate the value of microtopographic refuges for the recruitment and survival of *Sargassum* propagules, as this species occurs in high abundance on inshore reefs in the northern Great Barrier Reef (GBR) (Wismer et al. 2009).

2.2 Study sites

This study was conducted between October-November 2017 at Lizard Island, a granitic mid-shelf island in the northern Great Barrier Reef (GBR), Australia (14°40’S, 145°28’E;

Supplement Fig. S1). To examine the effect of microtopography on the recruitment, growth and survival of macroalgae propagules, we settled *Sargassum swartzii* propagules to tiles with regular crevices, and exposed these tiles to local herbivore assemblages on the exposed reef flat and reef crest (Supplement Fig. S1b). These two reef zones were selected as they differ in depth, benthic composition, herbivore abundance and/or biomass and rates of herbivory. Reef flat zones are generally characterised by lower rates of herbivory, lower structural complexity and a higher abundance of macroalgae (especially on inshore reefs) than reef crest zones (Fox & Bellwood 2007, Wismer et al. 2009, Hoey & Bellwood 2010a). Depth differs across the two reef zones, with the reef flat experiencing diel tidal changes resulting in water depths between 0.5 m to 2.5 m, and the reef crest experiencing water depths between 1.5 to 3.5 m.

2.3 Collection of adult *Sargassum swartzii* and seeding of propagules

Forty-eight terracotta settlement tiles (110 x 110 x 10 mm), each with four crevices (4 mm wide, 3 mm deep, 110 mm long) spaced evenly across the top surface of the tile (Supplement Fig. S2), were placed on the bottom of a 1000 L aquarium. Twenty-four hours later, 50 adult, reproductively mature *S. swartzii* thalli were collected by hand from the inshore reefs of the Turtle Group (14°43’S, 145°12’E), approximately 11 km west of Lizard Island (Supplement Fig. S1a). Thalli were kept in 80 L plastic aquaria (L x W x H: 60 x 37 x 38 cm) filled with seawater and returned to Lizard Island within 3 h of collection. Thalli were stressed within five hours of collection using cold-shock to stimulate propagule release. Briefly, thalli were placed in an 80 L plastic aquaria filled with cold seawater (9 °C) for 10 minutes (following Carl et al. (2014)), and then transferred to the 1000 L aquarium containing the tiles at ambient (26 °C) seawater temperature. The *S. swartzii* thalli were then agitated in the 1000 L aquarium by hand twice per day to further encourage release of the propagules and were left in this aquarium with static water and supplemental aeration for three days. After three days, the adult *S. swartzii* were removed from the tank and the water remaining in the aquarium filtered through 20-micron mesh. Propagules were first seen on the tiles two days after the adult *Sargassum* were removed from the tanks. The tiles with attached propagules were then cultured in the aquarium with supplemental aeration and unfiltered flow-through seawater for a further 18 days. This period allowed turf algal assemblages to establish on the upper surface of the tiles.

To determine if recruitment (i.e., settlement and any mortality during the first 18 days) was higher in crevices than on the upper, exposed microhabitat (i.e., the flat surface of the tiles between crevices; Supplement Fig. S2) of the tiles, the density of propagules within crevices and on the exposed microhabitat of the tiles was quantified after 18 days by haphazardly placing a quadrat (L x W: 25 x 4 mm; area: 1 cm^2) either over a crevice, matching the width of the quadrat to the width of the crevice (8 quadrats/tile) or on the exposed microhabitat (10 quadrats/tile) of the tile. All measurements were conducted using dissecting microscopes to ensure accurate quantification of the small propagules within the quadrats. The resulting dataset included 864 data points across 48 tiles and two treatments (crevice vs. exposed microhabitat) describing the density of propagules on the tiles. To quantify any differences in the growth of propagules that had settled in the crevices versus the exposed microhabitats of the tiles, the height of ten propagules (per microhabitat per tile), on a subset of six haphazardly chosen tiles, were measured to the nearest 0.1 mm with callipers, resulting in 120 data points.

2.4 Herbivore exposure

Tiles seeded with propagules were deployed on the reef for five days to determine the susceptibility of propagules within crevices versus those on adjacent exposed microhabitats to herbivory. Each tile was secured to the reef by passing a bolt attached to a stainless-steel base plate through a 5 mm hole in the centre of the tile and fastening with a wingnut; push mounts were used to secure the base plate into drilled holes in the reef (following Mundy (2000)). Twelve tiles were deployed at each of two reef crest and two reef flat sites, with at least 3 m between adjacent tiles within a site. Within each site, six tiles were left exposed to local herbivore assemblages, and six tiles were placed within exclusion cages (L x W x H: 150 x 150 x 40 mm; 5 mm square plastic mesh) to control for the effects of handling and translocation. After five days, the tiles were collected, placed onto a stainless-steel bar with 10 mm plastic spacers between each tile to prevent contact between tiles and transported back to the research station in small aquaria with 30 min of collection. Tiles were placed back into the 1000 L aquarium with flow-through seawater and supplemental aeration and the density of propagules within crevices and on the exposed microhabitat of each tile was re-quantified as previously described. This resulted in 1728 data points across the 48 tiles, collected before and after deployment, across two sites, two habitats and the two microhabitats per tile.

2.5 Video observations

At each site, four of the six tiles exposed to herbivores were haphazardly chosen to record feeding activity using stationary underwater video cameras. A small video camera (GoPro HERO3 or HERO4) attached to a dive weight was placed adjacent (30 – 40 cm) to each of the four selected tiles at each of the four sites (16 cameras per day). Each camera started recording between 08:00-09:00 and recorded continuously for three hours. This process was repeated each day for the 5-day experimental period, resulting in ~240 h of video footage. The entire video footage was viewed and for each fish observed taking bites on the tile, the species and total length of each fish, number of bites, and bite location (exposed or crevice) was recorded. For those fishes that were too small to accurately identify to species, they were recorded to the lowest taxonomic level possible (typically genus). Any bites taken on the sides of the tiles were not included in counts, as propagule densities were only quantified on the upper microhabitat of the tiles. To account for differences in the availability of crevices versus adjacent exposed areas, the number of bites recorded on each microhabitat was standardised by the area of that microhabitat (i.e., crevice: 17.6 cm^2; exposed microhabitat: 103.4 cm^2).

2.6 Statistical analysis

Bayesian linear mixed models were used to analyse differences in the recruitment, growth, and mortality of *S. swartzii* propagules between crevices and exposed surfaces. Analyses were conducted in R version 3.3.2 (R Development Core Team 2016) and the models fitted in STAN with Markov chain Monte Carlo sampling (Stan Development Team 2016b, Carpenter et al. 2017) using the rstanarm package version 2.13.1 (Stan Development Team 2016a). The broom (version 0.4.4; Robinson 2017) and CODA (version 0.19.1; Plummer et al. 2006) packages were used to summarise model outputs using highest posterior density intervals with a probability level of 0.95. Plots were produced using ggplot2 version 2.2.1 (Wickham & Chang 2008).

To analyse differences in propagule density and height between crevices and flat microhabitats of tiles before deployment, generalized linear mixed models were used. The models included microhabitat (i.e. crevice vs. exposed) as a fixed factor and microhabitat nested within tile as a random intercept, to account for the variation between quadrats within each microhabitat and tile. Both models used a Gamma error distribution with a log-link transformation. Weakly informative priors were used on slope coefficients (density: normal(0,10), height: normal(0,10)), intercept coefficients (density: normal(0,10), height: normal(0,10)), and the error standard deviation (density and height: cauchy(0,5)), with 6000 iterations, a warmup of 3000, three chains and a thinning factor of four for both models.

To quantify changes to propagule density after exposure to herbivores, we used the proportion of propagules remaining (i.e., the post-deployment average density divided by the initial average density for the crevice and exposed areas on each tile) as the response variable. This model had the fixed factors of microhabitat (either exposed or crevice), reef zone (either reef flat or reef crest) and treatment (either caged or uncaged). Tile identity was included as a random intercept to account for any variation in propagule densities among tiles and the non-independence of the flat and crevice microhabitats on the same tile. Estimating mean propagule density through haphazard quadrat placement on the tiles at two time points meant that there were some instances where the mean propagule density recorded post-deployment was greater than the mean density recorded pre-deployment, and hence the estimate of proportion survival was >1. As such, neither a beta nor a binomial distribution was appropriate for this data; a Gamma error distribution with a log link transformation best fit the data. Weakly informative priors were used on slope coefficients (normal(0,5)), intercept coefficients (normal(0,5)) and error standard deviation (cauchy(0,5)), with 5000 iterations, a warmup of 2500, three chains and a thinning factor of four.

For all models, diagnostic plots were visually examined to ensure there was convergence of chains and no evidence of heteroscedasticity or autocorrelation. Medians and central intervals from prior and posterior distributions were compared to ensure that the chosen priors were sufficiently wide so as to not dictate any trends, without being flat (non-informative). All Rhat values were <1.05 and the ratio of effective samples to total sample size >0.6.

Planned contrasts comparing the difference in the proportion of propagules remaining between the crevice and exposed microhabitats of each tile were performed for each reef zone and treatment combination. When calculating planned contrasts, the generated model matrix was queried to estimate the probability of the difference by summing the number of slopes >0 if the estimate of the parameter was >0 (and vice versa), dividing this number by the total number of observations, and multiplying by 100 to get a percentage:

$$If\ y > 0,\ \frac{\sum a{>}0}{n}\times 100,\ else\ if\ y < 0,\ \frac{\sum a{<}0}{n}\times 100$$

where *y* = the estimated value of the slope produced by the model, *a* = all predicted values of the slope and *n* = the total number of estimated values of the slope.

3. Results

3.1 Effect of microhabitat on recruitment and growth of propagules

Prior to deploying the tiles on the reef (i.e., 18-days post-settlement), model estimates indicated that the density of propagules within crevices was 21 % higher than the density on the exposed microhabitat of the tiles (mean [95 % credible intervals]; crevices: 29.7 [26.9, 32.9] propagules cm^{-2}; exposed microhabitat: 23.4 [21.0, 25.6] propagules cm^{-2}; Fig 1a). Propagules within crevices were, however, 18 % shorter than those on the exposed microhabitat (1.05 [0.95, 1.13] vs 1.27 [1.18, 1.36] mm, respectively; Fig 1b).

3.2 Effect of microhabitat on propagule survival

Microhabitats enhance propagule survival

There were differences in the survival of propagules between microhabitats on the reef crest, but not on the reef flat (Fig. 2a; Supplement Table S2). Modelled survival of propagules on the exposed surface of uncaged tiles on the reef crest was (mean [95% credible intervals]) 0.42 [0.34, 0.50] (i.e. 42 % of the initial number of propagules remained), whereas survival in the crevices of the same tiles was 0.80 [0.66, 0.97] (Fig. 2a; Supplement Table S2). In contrast, survival of propagules within cages on the reef crest was similar between microhabitats: 0.68 [0.55, 0.82] on the exposed surface vs. 0.68 [0.55, 0.81] in crevices. There was strong evidence (>99 % probability) of a difference between the proportion of propagules remaining (i.e., surviving) in crevices compared to the exposed microhabitat of uncaged tiles on the reef crest, but no effect for caged tiles on the reef crest (Fig. 2b and Supplement Table S3).

There was less evidence of an effect of microhabitat on propagule survival for uncaged tiles on the reef flat. Model estimates of survival of propagules on the exposed surface of uncaged tiles deployed on the reef flat was 0.70 [0.58, 0.85], compared to 0.80 [0.65, 0.96] in the crevices. There was an 88.5 % probability of having more propagules remaining in the crevices than on the exposed microhabitat of the uncaged tiles on the reef flat (Fig. 2b and Supplement Table S3). For caged tiles on the reef flat, survival of propagules was 0.71 [0.57, 0.86] on the exposed surface and 0.63 [0.50, 0.76] in crevices (Fig. 2a).

Overall mean bite rates on the tiles were over 150 % greater on the reef crest (1.67 ± 0.49 bites hr^{-1} cm^{-2}) compared to the reef flat (1.02 ± 0.45 bites hr^{-1} cm^{-2}). For both reef zones the majority of bites (standardised by the area of each microhabitat) were taken from the exposed microhabitat of the tile (reef crest: 79 %; reef flat: 87 %) rather than in crevices. The majority of bites in both reef zones were taken by blennies of the genus *Ecsenius,* averaging 1.19 ± 0.20 bites hr^{-1} cm^{-2} on the exposed microhabitat and 0.27 ± 0.10 bites hr^{-1} cm^{-2} in crevices of tiles on the reef crest and 0.61 ± 0.22 bites hr^{-1} cm^{-2} on the exposed microhabitat and 0.09 ± 0.04 bites hr^{-1} cm^{-2} in the crevices of tiles on the reef flat (Fig. 3). The only other species that took a substantial number of bites was *Salarias fasciatus* (f. Blenniidae) which took an average of 0.21 ± 0.11 bites hr^{-1} cm^{-2} on the exposed microhabitat and 0.03 ± 0.02 hr^{-1} cm^{-2} in crevices on the reef flat, but wasn't recorded to take any bites from tiles on the reef crest.

4. Discussion

Our results demonstrate that in areas of high herbivory, microtopographic refuges (crevices) afforded *Sargassum* propagules a survival advantage through the provision of a refuge from herbivory. Such a survival advantage may come at a cost, however, as propagules were 18 % shorter in crevices compared to those on the exposed surface of the tiles, indicating that crevices may be less favourable for early post-settlement growth. Furthermore, contrary to previous suggestions that feeding by larger-bodied grazing fishes is a major source of mortality for macroalgal propagules on coral reefs (Diaz-Pulido & McCook 2003, Bellwood et al. 2006), our results suggest that small-bodied blennies, specifically of the genus *Ecsenius*, are likely to have been the primary removers of early post-settlement stage *S. swartzii*.

The refuge afforded to propagules within crevices may be particularly important for the survival of juvenile *S. swartzii,* as *Sargassum* propagules have few chemical or morphological defences (Stiger et al. 2004). On the reef crest, where herbivory is generally high (Fox & Bellwood 2007), survival of *S. swartzii* propagules on the exposed microhabitats of the tiles after 5-day exposure to local herbivore assemblages was only 42 %, compared to 80 % survival within crevices. Our findings add to the growing literature from a range of ecosystems emphasising the importance of refugia to the early post-settlement survival of organisms. Microtopographic refuges have been identified as important early post-settlement refuges for sessile organisms such as bryozoans (Keough & Downes 1982), encrusting sponges (Maldonado & Uriz 1998) and corals (Nozawa 2008). Indeed, Franco et al. (2015) reported that rates of herbivory on temperate reefs in Portugal structured the distribution of *Laminaria* (kelp) recruits; in areas where herbivory was high, most recruits occurred in crevices, whereas in areas where herbivory was low, the majority of recruits were found in exposed, or open, habitats. This is consistent with our findings that crevices were important for the survival of *Sargassum* propagules in areas where herbivory was high (i.e., the reef crest) but were not as important to survival in areas with lower levels of herbivory (i.e., the reef flat), at least over the 5-day temporal scale of this study.

Microtopographic refuges may be extremely important in mediating benthic community assemblages on coral reefs through the provision of grazing refuges, promoting the survival of benthic taxa otherwise vulnerable to consumption by grazers (Brandl & Bellwood 2016). Microtopographic refuges have been shown to support diverse groups of algal turfs, in contrast to exposed surfaces that are predominantly composed of fast-growing, filamentous green algae (Brandl & Bellwood 2016). The present study provides direct evidence of the lower grazing rates, and hence higher survival of macroalgal propagules, within crevices. Such enhanced survival is likely to result in higher algal species diversity within crevices, as demonstrated for other grazing refugia (Menge & Lubchenco 1981, Hoey & Bellwood 2010b, Brandl & Bellwood 2016). Further, crevices may also enhance diversity of the benthic assemblage by not only reducing overall rates of herbivory, but also by affecting the components of the algae available to grazers. Grazing fishes generally can only access and crop the apical portions of algae growing within crevices, leaving the holdfast, or basal cells, of the algae intact within the crevice (Hixon & Brostoff 1996). Many algae, including *Sargassum*, can regrow from the holdfast (Loffler et al. 2018), and, consequently, consumption of the apical portions is unlikely cause mortality of the individual. This reduction in grazing pressure is likely to facilitate the survival of a diverse suite of algae, including *Sargassum*, within crevices in areas of high grazing intensity.

Although settling within crevices appears to confer a survival advantage for *S. swartzii* propagules, it may come at a cost. Eighteen days after settlement, the height of *Sargassum* propagules within crevices was 18 % lower than propagules that had settled to the exposed microhabitats of the tiles. This lower growth within crevices could be related to different light and water flow regimes within crevices compared to exposed microhabitats, and/or density-dependent factors. Unlike other algal species (Christie 1973), *Sargassum* propagules are non-motile, and it is therefore likely that the higher initial density in crevices was a result of the negatively buoyant propagules being ‘trapped’ in a crevice and settling rather than actively choosing to settle in this microhabitat (Norton & Fetter 1981). Kendrick (1994) reported that the growth of temperate *Sargassum* recruits was negatively related to density, indicating that there may be a trade-off between survival and growth within crevices and on exposed surfaces (Amsler et al. 1992, Bergey 1999, Bergey 2005, Brandl et al. 2014). Our results suggest that the benefits of settling in a crevice may only outweigh the disadvantages when rates of herbivory are high, by enhancing propagules’ survival at a stage characterised by high mortality (Kendrick & Walker 1995, Brandl et al. 2014, Franco et al. 2015). However, the slower growth of propagules within crevices may mean that they are subject to consumption by grazing organisms for longer (i.e., the stage-duration hypothesis (Leggett & Deblois 1994)) which could partially or completely negate any protective value of the crevices.

Rapid increases in algal biomass following the exclusion of large herbivores has led to the widely-held assumption that large-bodied grazing fishes, such as surgeonfishes and parrotfishes, are primarily responsible for the removal of macroalgal propagules in the epilithic algal matrix (EAM: a conglomerate of turf algae, macroalgal propagules, detritus, sediment and microbes) (Diaz-Pulido & McCook 2003, Bellwood et al. 2004). Our results question this assumption, as few large-bodied grazing fishes fed on the tiles, and none of the fishes previously identified as ‘crevice feeders’, including *Siganus* spp. and *Zebrasomas* spp. (Fox & Bellwood 2013, Brandl et al. 2015), were observed performing this function within the crevices of our experimental tiles. This lack of feeding by *Siganus* and *Zebrasoma* may be related to the size of the crevices, with the 3 mm-deep, 4 mm-wide crevices being too small for these larger-bodied specialised crevice-feeding fishes to access (Fox & Bellwood 2013, Brandl et al. 2014). Small crevices may, therefore, represent an important refuge for the recruitment of benthic marine organisms such as macroalgae.

Small-bodied cryptobenthic blennies (*Ecsenius* spp.) may play an important role in the early post-settlement mortality of macroalgal propagules, as these fishes took a disproportionately higher number of bites on uncaged tiles than any other grazing fishes. Grazing by the combtooth blenny *Salarias fasciatus* has been demonstrated to reduce the survival of early-post settlement coral recruits (Christiansen et al. 2009, Doropoulos et al. 2012), even though *S. fasciatus* are thought to primarily consume detrital aggregates within the EAM (Wilson 2000). *Ecsenius* spp. may similarly reduce propagule survival through grazing of the EAM even though detrital aggregates may be the primary dietary target (Wilson 2000, Brandl et al. 2018). Although our results suggest that cryptobenthic blennies contribute to the mortality of small *Sargassum* propagules (<2 mm, and up to 25 days post-settlement), it is likely that

Sargassum and other macroalgal propagules will quickly reach a size refuge from blennies as they grow (Lubchenco 1983, Briggs et al. 2018). It is yet to be determined if propagule removal by blennies at this early post-settlement stage could translate to lower densities of adult macroalgae, or if other species of grazing fishes consume larger macroalgal propagules.

Our findings also suggest that the importance of microtopographic refuges for the survival of macroalgal propagules varies among reef zones. On the reef flat, where conditions for *Sargassum* growth are favourable (McCook 1996) and herbivory is generally low (Hay 1981, Fox & Bellwood 2007), the survival of *Sargassum* propagules did not differ between caged and uncaged tiles. This result is consistent with the findings of previous studies that have shown the density and/or biomass of herbivorous fishes (Lewis & Wainwright 1985, Wismer et al. 2009) and rates of herbivory (Hay 1981, Fox & Bellwood 2007), are lower on the reef flat than the reef crest, and have led to suggestions that the reef flat is a spatial refuge from herbivory (Hay et al. 1983, Lewis & Wainwright 1985). In areas of lower herbivory, refuges may be less critical for the survival of *Sargassum* propagules (Franco et al. 2015).

The results of our study highlight the potential importance of crevices for the early post-settlement survival and growth of *S. swartzii,* however, further research is needed to investigate how the size of refugia and the potential agents of mortality (i.e., herbivores) change with macroalgae size and vary among macroalgal taxa. Whilst crevices were of uniform size in the present study, the size and depth of crevices relative to propagule size is likely to have a large influence on the degree of protection afforded to propagules (Lubchenco 1983, Bergey 1999). Furthermore, the fish species responsible for the removal of propagules are likely to change as the juvenile *Sargassum* grows. We do not know which fishes remove these larger (0.5 – 5 cm) juveniles, if the phenolic content of *S. swartzii* increases ontogenetically, as in *Sargassum mangarevense* (Stiger et al. 2004), possibly decreasing susceptibility to herbivores with age, nor if the protective value of the crevices for early post-settlement propagules significantly affects rates of survival to maturity.

The results of the present study provide a useful insight into the value of microtopographic refuges for the recruitment, growth and survival of newly-settled *Sargassum* propagules, and is one of the first to highlight the potential role of blennies in consuming newly-settled macroalgal propagules on coral reefs. Microtopographic refuges on coral reefs can provide newly-settled propagules a refuge from grazing in this vulnerable early post-settlement stage. Higher early-post settlement survival of propagules within refuges may facilitate the persistence of *Sargassum* communities on coral reefs, particularly in areas where herbivory pressure is high.

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Ethical approval

This research was conducted under JCU Ethics A2459. All applicable institutional and national guidelines for the care and use of animals were followed.

Conflict of interest

The authors declare that they have no conflict of interest.

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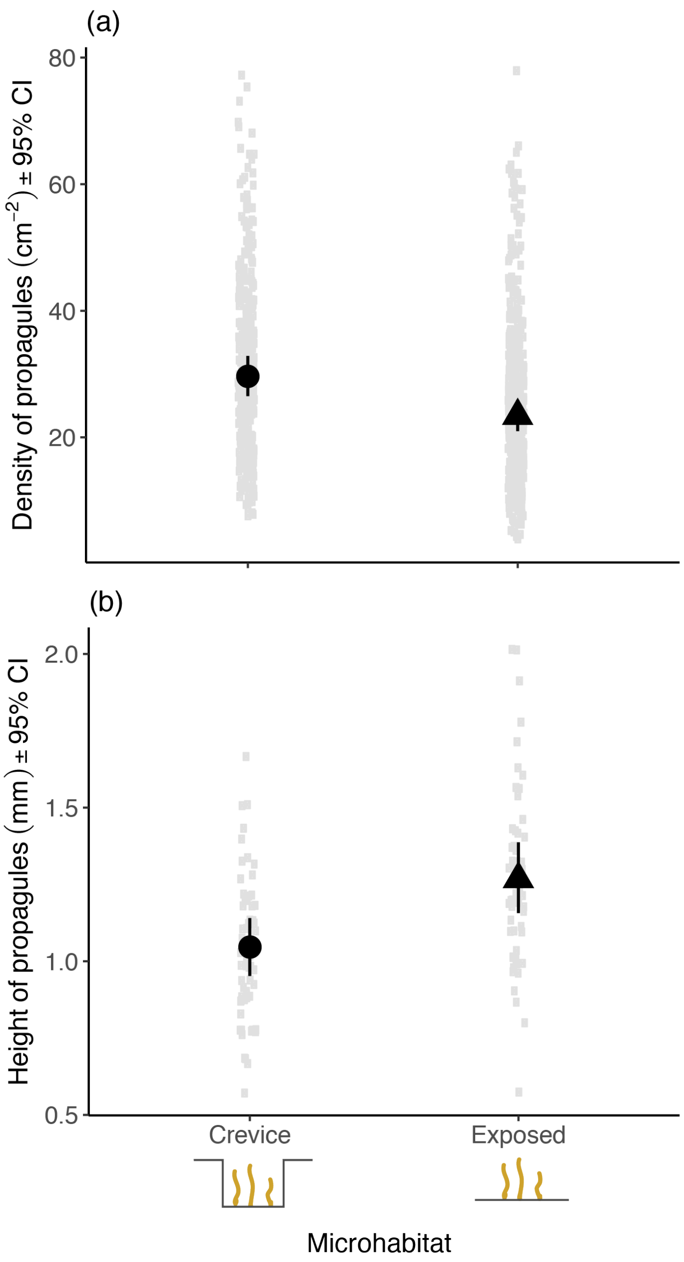


Figure 1: Model estimates of the influence of microhabitat on the recruitment and growth of *Sargassum swartzii* propagules (black points and intervals), and violin plots showing the distribution of raw data (grey outline): (a) Density of propagules in crevices and exposed surface of experimental tiles 18 days post-settlement; (b) Height of propagules in crevices and on flat microhabitat of tiles 18 days post-settlement. Error bars show ± 95 % Credible Intervals

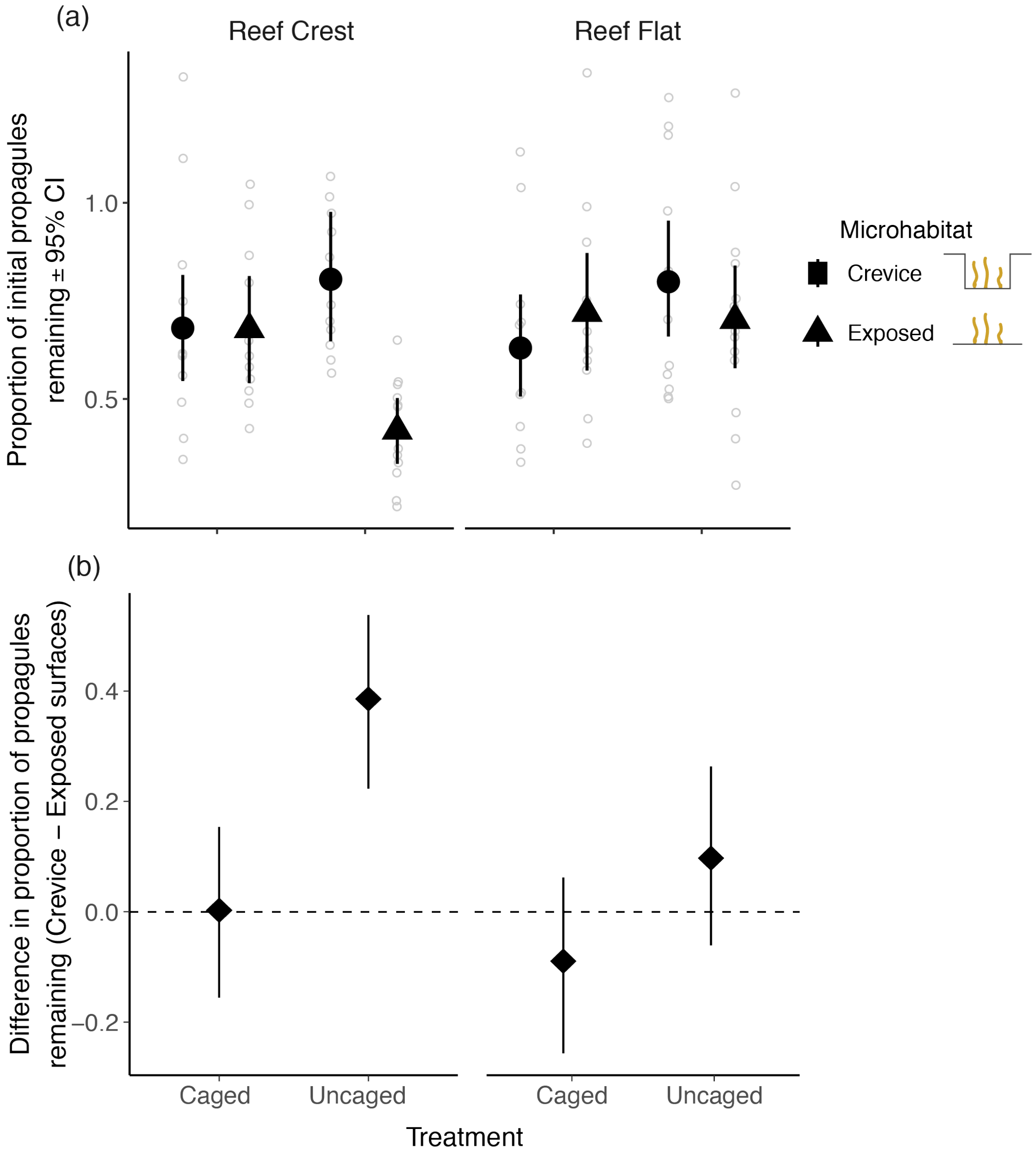
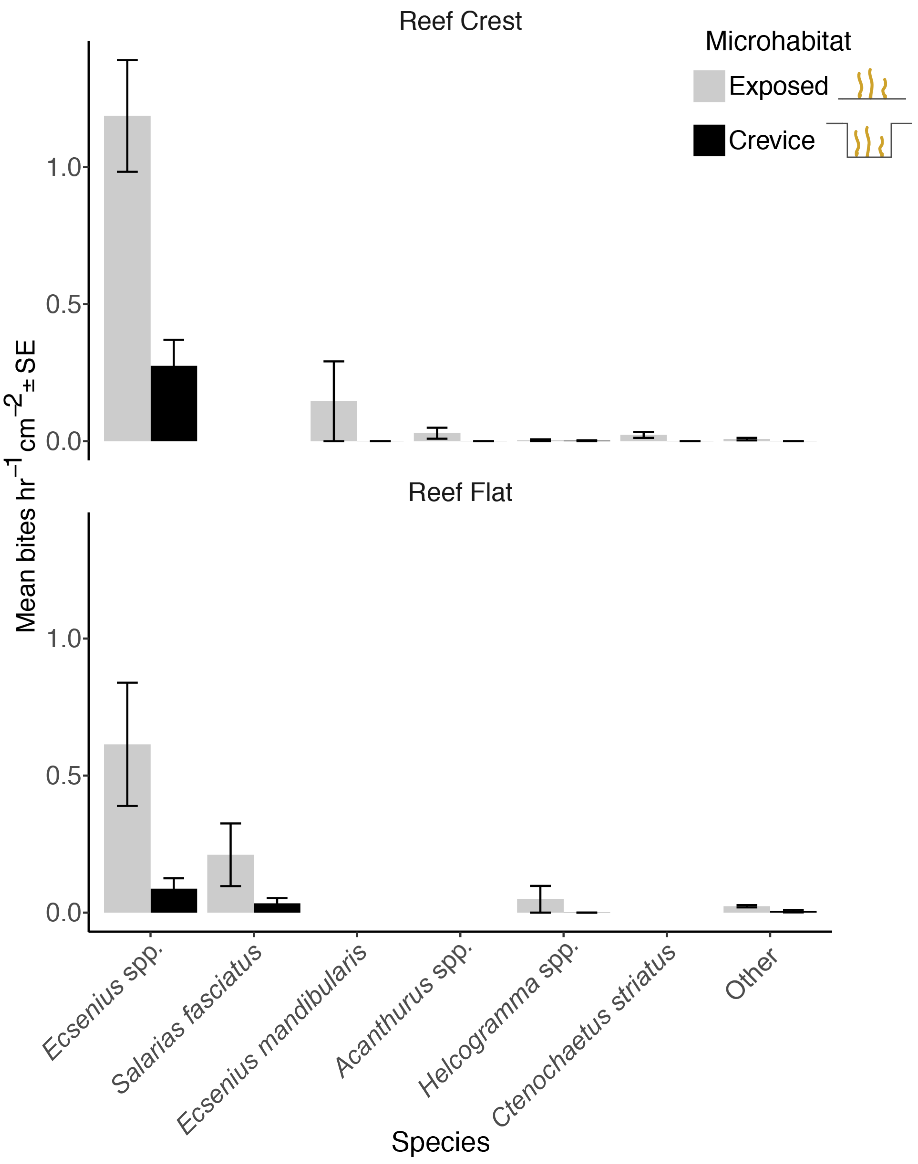


Figure 2: (a) Model estimates of the survival of *Sargassum swartzii* propagules between reef zones (reef crest or reef flat), microhabitat (exposed or crevice) and treatments (caged or uncaged) after 5-day deployment ± 95 % Credible Intervals. Grey open circles indicate the spread of the raw data; (b) Planned contrasts comparing the survival of *Sargassum swartzii* propagules in crevices vs. exposed microhabitats of tiles, in each reef zone and treatment combination. Lines indicate 95 % credible intervals calculated using highest posterior density. Estimates (black diamonds) to the right of the dashed line indicate that there were,

on average, more propagules in the crevices than on the exposed microhabitat of the tiles. Black diamonds to the left of the line would indicate that there was a higher proportion of propagules on the exposed microhabitat of the tiles than in the crevices.



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628 Figure 3: Average bite rate by fishes on exposed tiles hr^{-1} cm^{-2} (mean ± SE) between reef

629 zones and microhabitats.

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