Welcome to the jungle: Algal turf negatively affects recruitment of a Caribbean octocoral

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ABSTRACT

1. Algal cover has increased and scleractinian coral cover has steadily declined over the past 40 years on Caribbean coral reefs. In contrast, octocoral abundance has increased at those sites where octocoral abundances have been monitored. The effects of algal cover on recruitment may be a key component in these patterns, as upright octocoral recruits have the potential to escape competition with algae by growing above the ubiquitous algal turfs. However, the impacts of algal turf on octocorals have not been tested.
2. We used laboratory and field recruitment experiments to examine impacts of algal turf on settlement and then survival of newly-settled octocorals. Tiles were preconditioned on a Caribbean reef, allowing algae to settle and grow. Tiles were then partitioned into three treatments: lightly scrubbed (0% turf cover), left alone (19% turf cover), or kept for 15 days in a sea table without fish or large invertebrate herbivores (50% turf cover). Planulae of the common Caribbean octocoral *Plexaura homomalla* were allowed to settle and metamorphose on the tiles for six days. Tiles were then deployed onto a reef and survival of those recruits was monitored for seven weeks. Settlers that recruited to the tiles after deployment to the reef were also monitored.
3. Laboratory recruitment rate was significantly higher in lower turf cover treatments. Field survival was significantly reduced by increased turf cover; for every 1% increase in turf cover, polyps died 1.3% faster. In a model parameterized by the observed field survival, polyps exposed to 100% turf cover had a 2% survival rate over 51 days, while polyps exposed to no turf cover had a 32% survival rate over the same time.
4. *Synthesis.* We found that high densities of turf algae can significantly inhibit recruitment of octocorals. Octocoral survival rates were similar to those published for scleractinians, but field settlement rates were much higher, which likely contributes to the higher resilience of octocorals to disturbances. The factors that influence recruitment are critical in understanding the dynamics of octocorals on Caribbean reefs as continuing declines in scleractinian cover may lead to more octocoral-dominated communities in the Caribbean.

Keywords: Cnidaria, Cox mixed effects model, epilithic algal matrix, gorgonian, herbivory, mesofaunal predators, Octocorallia, Scleractinia

INTRODUCTION

Recruitment dynamics play a critical role in structuring and maintaining diversity in communities, and in the resilience of populations to disturbances (Warner and Chesson, 1985; Caley *et al.*, 1996; Wright, 2002). This is especially evident for sessile organisms, such as plants and benthic invertebrates, where variation in recruitment success is essential to recovery from disturbance and impacts adult population dynamics and spatial distributions and (Gaines and Roughgarden, 1985; McGuinness, 1996; Crawley, 2000; Price *et al.*, 2019). On Caribbean coral reefs the abundance of scleractinian corals has been decreasing for decades as a consequence of reduced recruitment in concert with bleaching events, hurricanes, and disease outbreaks (Goreau *et al.*, 1998; Gardner *et al.*, 2005; McWilliams *et al.*, 2005; Price *et al.*, 2019). Just as the decline in scleractinians is an inevitable consequence of failed recruitment, successful recruitment must have been essential to the increased prevalence of other taxa such as sponges and octocorals (Norström *et al.*, 2009; Ruzicka *et al.*, 2013; Lenz *et al.*, 2015; Edmunds and Lasker, 2016; Sánchez *et al.*, 2019).

Caribbean octocorals have always been a major constituent of contemporary Caribbean reef faunas (Kinzie, 1973). Coincident with the decline in scleractinian cover on some reefs, octocorals have increased in abundance (Ruzicka *et al.*, 2013; Lenz *et al.*, 2015; Edmunds and Lasker, 2016; Sánchez *et al.*, 2019). Octocorals have demonstrated greater resilience (ability to return to their previous population levels, *sensu* Gunderson, 2000) to disturbances than scleractinian corals (Edmunds and Lasker, 2016; Tsounis and Edmunds, 2017), but the basis of that resilience is still unknown. Reduced direct competition with scleractinians, higher fecundity, and greater juvenile survivorship and recruitment success have been suggested as potential reasons for their success in the Caribbean (Ruzicka *et al.*, 2013; Lenz *et al.*, 2015; Bartlett *et al.*, 2018). The lack of research concerning the mechanisms of resilience of octocorals is surprising, considering that octocoral forests are ecologically important (Kinzie, 1973; Williams *et al.*, 2015), provide some of the ecosystem functions that scleractinian reefs provide (e.g. Privitera-Johnson *et al.*, 2015; Tsounis *et al.*, 2016), and continue to maintain populations despite the increased prevalence of macroalgae.

Although recruitment is vital to maintaining coral populations (Yoshioka, 1996; Coles and Brown, 2007; McManus *et al.*, 2019), the interactions between benthic algae and octocoral recruitment are strikingly understudied, partly because of the difficulty in finding and repeatedly measuring newly-settled polyps (e.g., Linares *et al.*, 2007). The known effects of algae on the recruitment of octocorals are mixed; Alcolado *et al.* (2008) found no effect from macroalgae, while Linares *et al.* (2012) found a negative effect. Crusts from the family Corallinales promote settlement of octocorals (Lasker and Kim, 1996; Slattery *et al.*, 1999) while cyanobacteria may inhibit settlement (Kuffner *et al.*, 2006).

We differentiate between the two components of recruitment success: settlement and post-settlement survival. The distinction is important, as the two processes are often independent of each other. For example, while settlement patterns are critical to understanding the zonation of intertidal barnacles (Grosberg, 1982; Connell, 1985; Raimondi, 1988), post-settlement survival, not settlement, is the key factor in the establishment of distributional patterns in other systems (Grigg, 1988; Lasker *et al.*, 1998). Determining these differences has played an important role in understanding the ecology of recruitment and response to disturbance in many benthic taxa.

In this study, we used laboratory and field experiments to quantify the impacts of turf algae on the recruitment of newly-settled polyps of the octocoral *Plexaura homomalla* (Esper, 1792) by

using tiles of differing levels of turf cover. Algal turf communities are a multispecies community of filamentous algae shorter than one centimeter (*sensu* Steneck and Dethier, 1994). They are highly diverse and productive and can have significant impacts on recruitment of sessile invertebrates (Adey and Steneck, 1985; Arnold *et al.*, 2010; Kramer *et al.*, 2012). We define recruitment as the addition of individuals to a population following settlement (*sensu* Caley *et al.*, 1996). We hypothesize that recruitment will be negatively affected by algal turf cover. This work sheds light onto the interactions between newly-settled octocorals and the omnipresent turf algae that dominate Caribbean reefs (Hay, 1981; Birrell *et al.*, 2008). Understanding these processes will be important as further declines in scleractinian cover where they are still abundant could lead to more octocoral-dominated communities in the Caribbean (Tsounis and Edmunds, 2017).

METHODS

Collection, Spawning, and Larval Rearing

Female and male branches of *Plexaura homomalla* were collected from an octocoral-dominated reef in Round Bay, St. John, U.S. Virgin Islands (18.345 °N, 64.681 °W) on July 14-15, 2019 between 3.0 and 6.0 m depth. Colonies were determined to be gravid in the field by cutting a 5 cm piece diagonally and then looking for spermaries or eggs. Fragments of colonies were collected and transported to the Virgin Islands Environmental Resource Station and maintained in a sea table (i.e., flow-through, open-topped aquarium) with unfiltered running seawater pumped from Great Lameshur Bay (18.318 °N, 64.724 °W) from a depth of 1.5 m. Exchange rate in the sea table was approximately 200 L/h (60% of the volume hourly). Two EcoPlus 1/10 HP water chillers (Hawthorne Gardening Company, Vancouver, WA) were run in series to reduce the variability in temperature between day and night set to a temperature of 27°C. This reduced water temperature 0.5°C during the day (daily temperature range: 27.0-29.4°C) and maintained temperature at 27°C at night. Water temperature above 29°C is stressful to many Caribbean octocorals and can lead to bleaching (Prada *et al.*, 2010). Two submersible circulation pumps (Maxi-Jet 900 and Mini-Jet 404 [Marineland Spectrum Brands Pet LLC, Blacksburg, VA]) were placed within the tank to create a circular flow within the sea table.

Approximately two hours after sunset on the evenings of July 19-22, 2019 (3-6 days after full moon), both male and female *P. homomalla* colonies spawned in the tanks. Eggs from July 20 and 21 were used for the experiments. Pumps and water input were shut off at the start of spawning. Eggs were collected at least 30 minutes after spawning began to allow newly released eggs time to be fertilized. Eggs were collected and deposited into containers with 1 L of 10 µm filtered seawater (1500-2500 eggs/container). Shortly after collection, the gametes were diluted in 5 L polycarbonate containers with 3 L of 10 µm filtered seawater then reduced to 1 L through a 125 µm filter, which allowed the passage of sperm, but not eggs. This dilution was performed three times, leaving approximately 0.4% of the original seawater. This method reduces polyspermy, a potential source of early mortality in octocorals (Coelho and Lasker, 2016), and also removes decaying sperm that might promote bacterial growth in the cultures. During each of the subsequent four days, embryos were transferred to clean containers with minimal culture water to separate them from decaying gametes and embryos. These containers were filled to 5 L with 10 µm filtered seawater. After four days, embryos had developed into competent planulae.

Laboratory Recruitment Experiment

Prior to the laboratory experiment, custom-fired stoneware clay tiles ($n = 24$, $14 \times 14 \times 1$ cm) were deployed and conditioned on an octocoral-dominated reef in Grootpan Bay, St. John, U.S. Virgin Islands (18.309°N , 64.719°W) for 116 days. This site is also known as East Cabritte in other studies (e.g., Tsounis *et al.*, 2018; Lasker *et al.*, 2020). As refugia on tiles can improve recruitment rate of scleractinian larvae (Nozawa, 2008; Nozawa *et al.*, 2011), tiles were created with 0.5 cm deep and 1 cm wide pits and channels on one side. These substratum refugia were designed to examine the settlement preferences of octocoral and scleractinian larvae and post-settlement survival of octocoral larvae (Martínez-Quintana *et al.*, in prep). Before the experiments, one of three treatments was applied to each tile ($n = 8$ per treatment): a control, herein referred to as “Reef”; scrubbed with a soft nylon bristle brush, herein referred to as “Scrubbed”; or removed from the reef and maintained in a sea table for 15 days, herein referred to as “Protected”. Reef tiles represented substrata subject to the natural grazing of fishes and invertebrates, Scrubbed tiles represented substrata that have been grazed more heavily, and Protected tiles represented substrata protected from grazing by macrofauna.

One day prior to introducing planulae, tiles were placed into $41 \times 29 \times 17$ cm plastic containers (volume: 14 L, Sterilite Corporation, Townsend, MA). Containers were filled with 12 L of 10 μm filtered seawater. Two tiles from the same treatment were placed in each container on top of 1 cm square plastic mesh, rolled into 5 cm tall cylinders so that tiles were lifted off the bottom of the container to provide water circulation underneath. Pits and channels of the tiles were facing downwards. Water circulation in each container was provided by one glass Pasteur pipette attached to a Hydrofarm ActiveAQUA Air Pump Model PU110L (Hydrofarm LLC, Petaluma, CA). Water movement was slow but kept water moving throughout the container. Ambient sunlight was provided and temperature was held at 28°C .

Competent planulae ($n = 150$) were added to each container and allowed to settle for eight days and then polyps were counted. Planulae were competent when they readily attached to surfaces and were difficult to remove from the side of a glass pipette without forceful flushing of the water (Wells *et al.*, 2020). On day eight, no planulae were visible in the water and had either metamorphosed into polyps or died. 40% water changes were performed twice daily for the first two days and then daily afterwards, carefully checking for suspended planulae. Replacement seawater was 10- μm filtered for the first 6 days, after which seawater was 50- μm filtered. Motile invertebrates on the tiles were noted and identified to class or order. These tiles and associated polyps were used in the subsequent field survival and recruitment experiment.

Field Recruitment Experiment

Nine days after adding planulae, the tiles were deployed onto the reef at Grootpan Bay, where the tiles were initially conditioned. Sampling was designed to span the early recruitment phase (first several weeks) and then resample at the end of two months. To do this, we counted the number of polyps on the undersides of the tiles on the day of deployment (day 0) and 2, 5, 9, 14, 19, and 57 days after deployment. Settlement of planulae from octocorals in the field occurred and often led to an increase in number of polyps over time, which confounded calculation of mortality rates of the original polyps. Polyps on nine of the 24 tiles (three from each treatment) were mapped on days 6, 9, 11, 14, 16, 19, and 57 in order to assess polyp survival and quantify settlement in the field. Distances between each polyp and its nearest-neighboring polyp were measured to the nearest millimeter for every individual on the nine mapped tiles to assess if settlement was aggregative, random, or dispersed.

Percent cover of living cover was determined using digital images of each tile taken on days 0, 19, and 57 taken with an Olympus Tough TG-5 or TG-6 12-megapixel waterproof digital camera (Olympus Corporation of the Americas, Center Valley, PA) and two Sola Dive Pro 2000 lights (Light & Motion, Marina, CA). Living cover groupings were broad to characterize large shifts in communities and were ascidians, bivalves, bryozoans, crustose coralline algae, chlorophytes, non-coralline crustose rhodophytes, sponges, turf algae, calcareous worm tubes, and the coral-overgrowing *Ramirusta textilis* Pueschel & G.W. Saunders 2009. Images were analyzed with manual annotation using the online program CoralNet (Beijbom, 2015) with 100 randomly-generated points. This allowed us to quantify the differences in cover between the treatments and determine how the treatments changed after tiles were returned to the reef.

Statistical Analyses

All statistical analyses were performed in R version 3.6.2 with the packages boot 1.3-23, coxme 2.2-16, lme4 1.1-21, survival 3.1-8, and vegan 2.5-6 (Bates *et al.*, 2015; Therneau, 2015; Canty and Ripley, 2017; Oksanen *et al.*, 2019; R Core Team, 2019; Therneau, 2020). Where confidence intervals were calculated, 95% bias-corrected and accelerated bootstrap confidence intervals with 10,000 replicates were used.

Effects of the algal cover treatments in the laboratory settlement experiment were analyzed using a generalized linear mixed effects model (GLMM) with a Poisson family distribution (Nelder and Wedderburn, 1972). The effects were modeled with treatment as a fixed effect and container as a random effect.

Analyses of polyp counts on the tiles after they were transferred to the reef can be divided into those based on settlement and survival on the nine mapped tiles and those based on the total number of polyps present on all 24 tiles. Survival data from the mapped tiles were analyzed based on the number of days each mapped polyp was alive related to algal turf cover. A mixed effect Cox proportional hazard model (CPH, Cox, 1972) was used to predict the effect of turf cover on survival of polyps on the mapped tiles. The model incorporated turf cover as a time-dependent and fixed covariate and tiles and polyps nested within tiles as random effects. CPH regression assumes that the relative effect of the hazard is proportional and consistent over time (Cox, 1972). Hence, the proportional hazards assumption was tested prior to the analysis. The analysis generates hazard ratios which depict the effects of varying turf cover on the probability of mortality relative to the probability of mortality at the median turf cover. Higher hazard ratios indicate a faster rate of mortality while a lower ratio indicates a reduced rate of mortality. Kaplan-Meier survival curves were used to visualize differences in polyp survival over time when exposed at different turf cover (i.e. turf covers of 0%, 25%, 50%, 75%, and 100%) from the hazard ratios calculated in the CPH.

Analyses of total numbers of polyps on the tiles after they were deployed in the field incorporates the effects of both mortality and field settlement. Field counts were first tested for normality with the Shapiro-Wilks W-test (Shapiro and Wilk, 1965). As data were not normal (Shapiro-Wilks, $p < 0.05$), counts were square root transformed and then a two-way repeated-measures analysis of variance (rANOVA) was performed with treatment and time as fixed factors and tile as a random factor.

Field settlement rates were calculated from the appearance of new polyps on mapped tiles divided by the total number of days observed. The day 19 to day 57 interval was excluded as all other time intervals were two or three days and mortality would obfuscate settlement during this longer time period. A nearest neighbor index (NN, Clark and Evans, 1954) was calculated for each tile to determine if settlement was aggregative, random, or evenly distributed in the field. The nearest-neighbor index equation was as follows:

$$R_n = 2\bar{d}\sqrt{\frac{n}{a}}$$

R_n is the nearest-neighbor statistic, $\bar{d}$ is the mean observed nearest-neighbor distance for the tile in cm, n is the number of polyps on the tile, and a is the area in cm^2 . An R_n of 1.0 is consistent with random settlement; values less than 1.0 suggest aggregative settlement and values greater than 1.0 suggest a more uniform pattern of settlement. This approach assumes that polyps cannot crawl across the benthos, which has not been described in octocoral settlers.

Living cover on the tiles at the end of the laboratory experiments and over the course of the field deployment was assessed using non-metric multidimensional scaling ordination plot (nMDS) based on Bray-Curtis dissimilarities between tiles.

RESULTS

The amount and composition of cover on the tiles differed between treatments at the end of the laboratory experiment. Scrubbed tiles had low algal turf cover (0.1%), Reef tiles had middling turf cover (19%) and Protected tiles had high turf cover (50%). Turf was tallest in the Protected treatment (approximately 1 cm with some thalli almost 3.5 cm) and shortest in the Scrubbed treatment (no thalli above 0.5 cm). There were more motile invertebrates on the Protected tiles in the laboratory experiment, particularly amphipods, copepods, and small shrimp. Motile invertebrates were rarely observed on the Scrubbed tiles. Octocorals only recruited on tile surfaces. There was no recruitment on the chamber walls nor planulae in the water column at the end of the laboratory experiment. Recruitment was significantly different between tile treatments (GLMM, $n = 12$, $p < 0.001$). Protected tiles had low recruitment (11% of the initial planulae), Reef tiles had 38%, and Scrubbed tiles had 63% recruitment (Fig. 1).

Once tiles were deployed in the field, the differences in the community structure due to treatment became less apparent over time (Supp. Fig. 1). On day 57, treatments were indistinguishable. This was primarily driven by bare space being replaced by turf. Observation of the tiles in the laboratory and field indicated that small crustaceans, which made up the bulk of the mesofaunal community, qualitatively declined after deployment. In the field, the only visible animals were gastropods, hermit crabs, and urchins. Copepods, amphipods, and annelids were rare on the tiles. Two bearded fireworms *Hermodice carunculata* (Pallas, 1766) were observed on tiles: one on a Protected tile and one on a Scrubbed tile. Observations of fireworms were concurrent with 58 and 72% reductions in octocoral abundance. Grazing by herbivorous fish on the sides and tops of the tiles was heavy and newly-settled polyps on those surfaces died quickly.

Fig. 1. The effect of tile treatment on the proportion of octocoral polyps that recruited on the tiles in each container in the laboratory experiment. Treatments with reduced algal cover had greater numbers of recruits. Error bars are bootstrapped 95% confidence intervals of the means.

Analysis of the field data is complicated by two factors: settlement of naturally occurring planulae, which confounds estimates of mortality, and changes in the algal cover on the tiles, which affects the nature of the experimental treatments. When tiles were transferred to the field, they had a median of 21.5 polyps tile⁻¹ (95% CI [11.5, 32.0]) and after 57 days had 5.0 polyps tile⁻¹, (95% CI [3.0, 7.0]). However, counts on the tiles sometimes increased between observations due to settlement in the field. Multiple species appear to have contributed to the field settlement as the newly metamorphosed settlers had a range of colors and sizes. Therefore, survival rates of the polyps and the effects of turf on survival can only be determined for the polyps on the mapped tiles. Settlement and mortality on the mapped tiles are presented in Supp. Fig. 2. Among the mapped tiles, settlement was high, 8.7 polyps tile⁻¹ 19 days⁻¹ (95% CI [6.2, 11.3]), which can be extrapolated to 443 polyps m⁻² 19 day⁻¹ (95% CI [317, 577]) during this period of settlement. Positioning of new settlers on the tiles was random (NN, $R_n = 1.05$, 95% CI [0.94, 1.17], Supp. Fig. 3).

A total of 248 polyps were followed in assessing mortality rates on the mapped tiles. Mortality was 2.4% day⁻¹, 95% CI (1.7%, 3.8%). Every 1% increase in algal turf cover was associated with a 1.3% increase in the mortality rate (CPH, $p < 0.01$, regression coefficient = 0.013, Fig. 2). When turf cover was modeled at 0%, 32% of octocoral polyps survived to 51 days. At modeled levels of 50% and 100% turf cover, survival dropped to 14% and 2%, respectively (Fig. 3). There was no relationship between turf cover and settlement rate on the mapped tiles (linear regression, $F_{1,41} = 3.5$, $p = 0.66$). Comparisons of the net change in numbers of polyps across all tiles identified a significant effect of treatment by time on the number of polyps (rANOVA, $F_{2,161} = 3.5$, $p = 0.03$, Fig. 4). Early in the experiment (day 0 to 5), Protected tiles had the same number or gained polyps, counts on Reef tiles stayed the same, and Scrubbed tiles lost polyps (Fig. 5A). Between days 5 and 14, mortality was offset by settlement on tiles across all treatments (Fig. 5B). By day 57, all but two tiles had lost polyps (Fig. 4) indicating that either settlement rates had declined and/or mortality had increased between days 19 and 57. Both tiles that gained polyps were initially Protected tiles. Changes in mortality rates in Scrubbed tiles disappeared when changes were evaluated as per capita rates. In that case, Reef and Scrubbed tiles had near-zero per capita rates (1.4% day⁻¹, 95% CI [-1.2%, 8.1%] and -1.4% day⁻¹, 95% CI [-4.4%, 0.8%], respectively). As settlement was random and therefore independent of density, and mortality was proportional to density, tiles with initially higher densities (Scrubbed tiles) were less likely to have settlement overcome mortality of polyps.

DISCUSSION

While ecosystems naturally undergo changes in community composition, the prevalence and rates of change in modern communities are both high and accelerating (Dirzo *et al.*, 2014; Edmunds *et al.*, 2014; Ceballos *et al.*, 2015; Dornelas *et al.*, 2019). On Caribbean reefs, the past 4 decades have

Fig. 2. The relationship between algal turf cover and hazard ratio (i.e., ratio of the probability of mortality relative to the probability of mortality at the median turf cover [39%]). For every 1% increase in turf cover, octocorals polyps died 1.3% faster. The grey filled area is the 95% confidence interval.

Fig. 3. The modeled effect of constant algal turf cover on survival of octocoral polyps over time. Survival probability is significantly reduced with increased turf cover (Cox Mixed Effects Model, $p = 0.03$). The model does not interpolate survival between time points, creating the stepwise drops in survivorship. At the end of 51 days, survival probability was 16 times higher for individuals in 0% turf cover than in 100%. The endpoint of each model is indicated by a circle.

witness to the precipitous decline in the abundance of scleractinian corals, one of the most abundant ecosystem engineers of the community (Gardner *et al.*, 2003; McWilliams *et al.*, 2005). At some sites these decadal declines have been stepwise, related to bleaching events and hurricanes, while other declines have been less episodic but no less dramatic (Gardner *et al.*, 2005). The decline in the abundance of sessile organisms, such as corals, is inevitably a consequence of the death of older individuals without replacement by new colonies (i.e. without successful recruitment). The decline in scleractinians has also been associated with dramatically greater bottom cover by algae (Hughes, 1994), and the effects of algal cover on recruitment have been cited as cause of the failed recovery of scleractinians (Birrell *et al.*, 2008). In contrast, the success of octocorals (Ruzicka *et al.*, 2013; Lenz *et al.*, 2015), including their recovery following disturbance events (Tsounis and Edmunds, 2017; Lasker *et al.*, 2020), suggests that recruitment of these species has continued regardless of the high cover of algae on most reefs. However, we discovered that octocorals, or at least *P. homomalla*, are not immune to the negative effects of algal turf.

High densities of turf algae significantly inhibited settlement and survival of juvenile octocorals. In the laboratory experiment there were striking differences in the number of planulae that successfully settled on the tiles in the different treatments (Fig. 1). As we did not observe settlement on the container walls, the differences in the numbers that settled reflects some combination of survival of planulae, successful settlement on the tile, and survival of polyps. In the field, higher algal cover was associated with increasing recruit mortality and had no relationship with settlement during the first two months following spawning (Fig 2).

Multiple hypotheses can account for the lower recruitment on tiles with higher algal cover. These include: 1) algae released toxic chemicals that affect local survival (i.e., allelopathy); 2) algae promoted the presence of pathogenic microbial populations; 3) algal and/or algal-associated bacterial respiration decreased oxygen to hypoxic or anoxic levels locally; 4) algal abrasion caused more frequent polyp retraction or damage; and 5) algae provided habitat for invertebrates that prey upon planulae and newly-settled polyps. These processes apply to settlement and survival in both our laboratory and field experiments. However, the relative magnitude of the effects in our laboratory setting was likely to have differed from field settings.

Allelopathy has been observed in interactions between algae and scleractinian corals, and has been proposed as a major barrier to scleractinian recovery following transitions to macroalgal dominance (Kuffner *et al.*, 2006; Rasher *et al.*, 2011; Bonaldo and Hay, 2014). Additionally, some algae can act as a reservoir for virulent scleractinian diseases (Nugues *et al.*, 2004; Casey *et al.*, 2014). In our experiments, allelopathic chemicals and/or pathogenic bacteria on the algae may have accumulated within the turf understory.

Fig. 4. Change in median number of octocoral polyps over time by tile treatment. Scrubbed and Reef tiles decrease over time, while Protected tiles maintain a population of polyps. Data are median number of polyps. The last counts were performed on day 57. Error bars are bootstrapped 95% confidence intervals of the medians. Values have been offset on the x-axis to reduce overlap.

Fig. 5. Daily change in number of polyps between (A) day 0 and day 5 and (B) day 5 and day 14. Early in the deployment, Protected tile mortality was overwhelmed by settlement of field-spawned octocorals, while Scrubbed tiles had lost polyps. Between days 5 and 14, mortality was offset by settlement on tiles across all treatments. Error bars are bootstrapped 95% confidence intervals of the means.

Algal turfs also have significant impacts on the diffusive boundary layer depending on canopy height and microscale substratum topography (Carpenter and Williams, 1993) and can drive oxygen levels down to hypoxic conditions at night (Brown and Carpenter, 2013). Extended anoxic and hypoxic conditions, such as what may be experienced by an octocoral polyp within turf algae, can lead to tissue necrosis in adult scleractinians (Smith *et al.*, 2006) and likely death in recruits. While flow was provided during the laboratory experiment and waves provided mixing in the field, algal respiration could have reduced oxygen to hypoxic levels within the diffusive boundary layer. In addition, algal turfs can also lead to hyperoxia during the day, which can stress the relationship between corals and their endosymbionts (reviewed in Lesser, 2011). This latter effect was unlikely in both our experiments as most recruits were on the underside of the tiles and light levels in the laboratory were low (indirect, ambient light from windows and ceiling mounted fluorescent lights).

Although it was an unlikely source of mortality in the laboratory, algal cover also leads to physical interactions between polyps and upright algae. These interactions can reduce growth by continually disturbing the colony, keeping the polyps closed for more time (River and Edmunds, 2001; Box and Mumby, 2007). When polyps are closed, colonies have less time to both capture prey and expose their endosymbionts to sunlight, and thus have lower growth. River and Edmunds (2001) found that abrasion-mediated polyp retraction led to an 80% reduction in growth rate. Flow rates were low within the settlement containers, but we frequently observed algae on tiles moving with the waves and this abrasion and disturbance could have increased mortality on the reef, especially in the denser turf mats.

An indirect and striking difference among the tiles in the laboratory experiments was the presence of mesofauna (amphipods, copepods, and small shrimps) in higher turf cover treatments. The abundance of mesofauna on the Protected treatment tiles was assumedly due to the elevated turf levels (50% cover vs. 19% and 0% in the other treatments) and the exclusion of grazing fishes and macroinvertebrates for 15 days prior to the start of the settlement experiment. The effect of mesofauna on the recruitment of octocorals is unknown, although some groups, such as cyclopoid and siphonostomatoid copepods, can be parasites of scleractinian corals (Cheng *et al.*, 2016) and can inhibit settlement of invertebrates through predation (Dahms *et al.*, 2004). Mesofaunal populations were lower in the field experiment, although shelled invertebrates (e.g., hermit crabs and snails), sea cucumbers, sea urchins, and worms were more abundant in the field, especially on the undersides of the tiles. On the two tiles with fireworms (Amphinomidae), polyp abundances were reduced by 58 and 72%. Fireworms are voracious predators of invertebrates including octocorals (Witman, 1988; Vreeland and Lasker, 1989) and likely had significant impacts in the field.

Despite the negative impacts of turf algae on octocoral recruitment, the survival rates in our experiments were greater than those reported for other Caribbean octocorals (Lasker *et al.*, 1998; Evans *et al.*, 2013). This was surprising given that we deployed younger polyps in the field, which are likely at a higher risk of mortality as octocorals generally follow a type III survival curve (Linares *et al.*, 2007). The higher survival in our experiments was likely due to refuge provided by the tiles. Both Lasker *et al.* (1998) and Evans *et al.* (2013) followed the fates of polyps on the upper side of settlement plates. In our study those polyps died quickly, likely through incidental predation by grazing herbivorous fish, and the field survivorship that we report was based on polyps on the underside of the tiles.

The combination of high settlement and low early mortality may be a major contributor to the high resilience to disturbance seen in octocorals, but not scleractinians. In this study, observed

settlement rates for octocorals were higher than settlement rates of Caribbean scleractinian corals on tiles (e.g., Tomascik, 1991; Carlon, 2001; Green and Edmunds, 2011). For example, Green and Edmunds (2011) found an average scleractinian settlement rate of 76 polyps m⁻² 6 months⁻¹ on nearby reefs by counting skeletal remains on tiles after bleaching. In contrast, we observed settlement in the field more than five times as great in less than a month. Many octocoral species spawn for several months every year (Kahng *et al.*, 2011) and therefore settlement could be an order of magnitude greater than that of scleractinians. However, it is also important to recognize that recruitment rates may have been dramatically greater when scleractinians were far more abundant on Caribbean reefs (*cf.*, Sammarco, 1980, but also see Bak and Engel, 1979). Survival rates of octocorals fell within the range of survival rates published for scleractinians on tiles (Davies *et al.*, 2013; Trapon *et al.*, 2013; Doropoulos *et al.*, 2016). Davies *et al.* (2013) found that between 36 and 50% of *Agaricia* and *Porites* settlers survived the first 14 months, a higher survival rate than the 2 month survival of 33% that we observed for the octocoral polyps on our tiles. Doropoulos *et al.* (2016) found survival rates for scleractinian recruits between 13 and 47% after 50 days in the Pacific, and Trapon *et al.* (2013) found 42% survival after a month, similar to what we observed. Due to the difficulty of locating newly-settled corals on tiles, there are few studies looking at recruitment at the time scale of our observations. Simultaneous comparisons of octocoral and scleractinian settlement and survival are needed to determine if differences in recruitment can explain the differing trajectories of octocorals and scleractinians on many Caribbean Reefs. Future studies should include species-specific data with a particular emphasis on the survival within the first few months after settlement.

Our results suggest several directions where research should be productive. First, further research is required to understand the relationship between fish predators, mesofauna, and newly-settled octocorals. In this study, abundance of mesofauna seemed to be closely related to turf cover in the laboratory, suggesting that while fishes that prey on polyps will reduce survival, other fishes that consume mesofauna may have indirect positive effects on octocoral survival. Furthermore, the effects of the structural complexity of reef surfaces on survival must be further characterized. We observed differences in settlement and survival on the upper and lower surfaces of tiles. Lasker *et al.* (1998) reported differential settlement/survival of an octocoral on different structural elements of settlement plates and similar results have been reported for scleractinian recruitment rates (Edmunds *et al.*, 2014; Doropoulos *et al.*, 2016). However, the processes by which spatial complexity mediates facilitation, competition and/or predation is unknown. Finally, the effects of phenomena such as allelopathy, microbial load, and physiologically driven changes in water chemistry at the interface between the substratum and the water column are all poorly understood. Directed experiments looking at the effect of algal turfs on water quality within the benthic boundary layer may help explain distribution patterns of adult octocorals.

Caribbean reefs are undergoing a long-term increase in the abundance of octocorals while experiencing a reduction in scleractinian corals (Ruzicka *et al.*, 2013; Lenz *et al.*, 2015; Sánchez *et al.*, 2019). Those changes also affect the physical structure and ecosystem services provided by reef systems. In this study, we found that newly-settled octocorals do not survive as long in the presence of turfs, as has been reported for scleractinian corals (Birrell *et al.*, 2008; Penin *et al.*, 2011). However, on modern reefs octocorals may have greater settlement rates while maintaining a similar post-settlement survival, which suggests that octocorals might have higher early recruitment rates than scleractinians and that this process may be key in shaping the contemporary octocoral-dominated reef assemblages in the Caribbean.

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