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REPORT

Algal turf negatively affects recruitment of a Caribbean octocoral

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Abstract Algal cover has increased and scleractinian coral cover has steadily declined over the past 40 years on Caribbean coral reefs, while octocoral abundance has increased at sites where abundances have been monitored. The effects of algal cover on recruitment may be a key component in these patterns, as upright octocoral recruits may escape competition with algae by growing above the ubiquitous algal turfs. We used laboratory and field recruitment experiments to examine impacts of algal turf on recruitment of the common, upright, and zooxanthellate Caribbean octocoral *Plexaura homomalla*. Laboratory recruitment rate was significantly higher in lower turf cover treatments. The survival of recruits in the field 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. We found that high densities of turf algae can significantly inhibit recruitment of octocorals. Experimentally obtained octocoral survival rates were higher than those published for Caribbean octocorals. 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.

Keywords Cox mixed effects model · Epilithic algal matrix · Gorgonian · Herbivory · Mesofaunal predators · Octocorallia

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, because their recruitment success is essential to the recovery of adult populations following disturbance events, and variation in recruitment success can drive adult population abundance and spatial distributions (Gaines and Roughgarden 1985; Crawley 2000; Price et al. 2019). The role of recruitment success in community dynamics is particularly striking on Caribbean reefs, where scleractinian coral populations have declined due to local human stressors (e.g., overfishing, pollution, poor water quality) and increasing global climatic events (e.g., bleaching and hurricanes). Those stresses have impacted critical ecological processes such as survivorship, growth, reproduction, settlement, and recruitment (Goreau et al. 1998; Gardner et al. 2005; McWilliams et al. 2005; Price et al. 2019). However, just as the decline in scleractinians is an inevitable consequence of failed recruitment, successful

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recruitment has 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).

Octocorals have always been a major constituent of contemporary Caribbean reef faunas (Kinzie 1973). Coincident with the decline in scleractinian cover, octocorals have increased in abundance on some reefs (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 in the Caribbean due to reduced direct competition, higher fecundity, and greater juvenile survivorship and recruitment success (Ruzicka et al. 2013; Lenz et al. 2015; Bartlett et al. 2018). Lasker et al. (2020) suggested that high recruitment following disturbance on reefs on St. John, U.S. Virgin Islands supports the ecological resilience of those octocoral communities. The lack of research concerning the mechanisms of resilience in octocorals is surprising, considering that octocoral forests are ecologically important (Kinzie 1973; Williams et al. 2015), provide some of the ecosystem functions provided by scleractinian reefs (e.g., Privitera-Johnson et al. 2015; Tsounis et al. 2020), 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. Research to date has identified a variety of interactions between algae and octocoral recruitment. Linares et al. (2012) found that macroalgae had a negative effect on the recruitment of octocorals in the Mediterranean Sea. 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).

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 upright and zooxanthellate octocoral *Plexaura homomalla* (Esper 1794) on tiles with differing levels of turf cover. 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 (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). We define recruitment as the addition of observable individuals to a population following settlement (sensu Caley et al. 1996). We hypothesized that recruitment would be negatively affected by algal turf cover. Algal turf communities are a multispecies community of filamentous algae shorter than two centimeters (sensu Tebbett and Bellwood 2019). 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). This work sheds light onto the interactions between newly settled octocorals and the omnipresent turf algae that now dominate Caribbean reefs (Hay 1981; Birrell et al. 2008). Understanding these processes is important, as further declines in scleractinian cover, where they are still abundant, may lead to more octocoral-dominated communities in the Caribbean (Tsounis and Edmunds 2017).

Methods

Collection, spawning, and larval rearing

Branches of *Plexaura homomalla* were collected from eleven females and four males in an octocoral-dominated reef in Round Bay, St. John, U.S. Virgin Islands (18.345° N, 64.681° W) on 14–15 July, 2019 between 3.0 and 6.0 m depths. Colonies were determined to be gravid in the field by cutting a 5-cm piece diagonally and then looking for spermaries or eggs. A 15-cm branch was collected from each colony and transported to the Virgin Islands Environmental Research 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° N) 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) set to a temperature of 27 °C were run in series to reduce the variability in temperature between day and night. 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 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 20 and 21 July were used for the experiments. Pumps and water input were shut off at the start of spawning. Eggs were collected at least 30 min after spawning began to provide time for newly released eggs to be fertilized. Eggs were deposited into containers with 1 L of 10-µm filtered seawater (1500–2500 eggs/container), further diluted with 3 L of 10-μm filtered seawater, and 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 procedure was followed to reduce polyspermy, a potential source of early mortality in octocorals (Coelho and Lasker 2016), and remove decaying sperm and debris from lysed eggs 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 × 14 × 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 allowing turf algae and invertebrates to recruit to the tiles. 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 larvae and post-settlement survival of octocoral polyps (Martínez-Quintana et al. unpublished data). 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 without macrograzers for 15 days, herein referred to as “Protected.” Reef tiles represented substrata subject to the natural grazing of fishes and invertebrates and had similar cover to the reef in Grootpan Bay, which had 23% turf cover in August 2019 (Lasker, unpublished data). Scrubbed tiles had nearly no algal turf and were a proxy for a heavily grazed substratum whereas algal turf cover on protected tiles was approximately 50% and represented substrata protected from grazing by macrofauna. Importantly, no octocoral polyps were present on the tiles prior to the experiment.

One day prior to introducing planulae, tiles were placed into 41 × 29 × 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 plastic mesh cylinders so that they 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 bubbling air from a glass Pasteur pipette attached to an air pump. Water movement was slow but circulation was observed throughout the container. Ambient sunlight was provided from large south facing windows and temperature of the room was held at 28 °C.

Competent planulae (*n* = 150) were added to each container and allowed to settle for eight days before being counted. Planulae were deemed metamorphically competent to settle (sensu Gleason and Hoffman 2011) when they readily attached to surfaces and were difficult to remove from the side of a glass pipette without forceful flushing of the water. 40% water changes were performed twice daily for the first two days and then daily afterward, carefully checking for suspended planulae. Replacement seawater was 10-μm filtered for the first 6 days, after which seawater was 50-μm filtered. We assumed all primary polyps were generated from one planula. Chimera formation has been observed in octocorals (Barki et al. 2002), but cases of fusion they reported initially generated a chimera of two or more polyps. On day eight, planulae had either metamorphosed into polyps or died, as no planulae were visible in the water. Motile invertebrates on the tiles were noted and identified to class or order to assess abundance of organisms that may graze on or otherwise interfere with octocoral recruits. These tiles and associated polyps were used in the subsequent field recruitment and survival experiment.

Field recruitment and survival experiment

Nine days after adding planulae (3 August, 2019), the tiles were deployed onto the reef at Grootpan Bay, where they were initially conditioned. Tiles were attached to the reef with 10-cm aluminum rods with the refugia-side 5 cm above the substratum. This likely reduced access of grazing fishes to the underside of the tile. We counted the number of polyps on the undersides of all 24 tiles on the day of deployment (day 0) and 2, 5, 9, 14, 19, and 57 days after deployment. Surveys were designed to span the early recruitment phase (first several weeks) with a final survey conducted at the end of two months. Settlement of planulae from unidentified 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 *P. homomalla* polyps. All 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 recruitment in the field (logistical considerations precluded mapping all polyps on all of the tiles). 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 recruitment was aggregative, random, or dispersed. Aggregative distributions have been observed in octocorals at small scales (1/64 m^2) in Puerto Rico (Yoshioka 1997, 2005).

Percent living cover on the tiles was determined using digital images of each tile taken on days 0, 19, and 57 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). To analyze percent cover in the digital images, living cover was identified and divided into the following categories: ascidians, bivalves, bryozoans, crustose coralline algae, chlorophytes, non-coralline crustose rhodophytes, sponges, turf algae, calcareous tubes of worms, or the coral-overgrowing *Ramicrusta textilis* Pueschel & G.W. Saunders. These broad categories were chosen to characterize general shifts in community composition on the tiles (e.g., increasing turf cover) without the destructive sampling that would be required to identify taxa at higher resolution. 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, 2020; Canty and Ripley 2017; Oksanen et al. 2019; R Core Team 2019). Where confidence intervals were calculated, 95% bias-corrected and accelerated bootstrap confidence intervals with 10,000 replicates were used. Generally, medians are reported, as the recruitment and mortality data were not normally distributed.

Effects of the algal cover treatments in the laboratory recruitment experiment were analyzed using a generalized linear mixed effects model (GLMM) with a negative binomial distribution (Nelder and Wedderburn 1972). The effects were modeled with container (random effect) nested within treatment (fixed effect) with tiles as independent replicate measurements for each container. In order to see if tiles within the same container were competing for settlers, the numbers of settlers on each tile in a container were compared using a Spearman's rank correlation (Spearman 1904).

Analyses of polyp counts on the tiles after they were transferred to the reef were divided into those based on recruitment 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. Tiles and polyps nested within tiles were modeled as random effects. CPH regression assumes that the relative effect of the hazard is proportional and consistent over time (Cox 1972) and that assumption was tested prior to the analysis. CPH 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. Hazard ratios greater than 1.0 indicates mortality greater than the median, while those less the 1.0 indicate reduced mortality rates. Kaplan–Meier survival curves (Kaplan and Meier 1958), based on the hazard ratios calculated in the CPH, were used to visualize differences in polyp survival over time when exposed to different levels of turf cover (i.e., turf covers of 0%, 25%, 50%, 75%, and 100%).

Analyses of total numbers of polyps on all 24 tiles after they were deployed in the field incorporates the effects of both mortality and field recruitment. 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 recruitment 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. A nearest neighbor index (NN, Clark and Evans 1954) was calculated for each tile to determine if recruitment was aggregative, random, or evenly distributed in the field. The nearest neighbor index equation was as follows:

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

R_n is the nearest neighbor statistic, 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 recruitment; values less than 1.0 suggest aggregative recruitment and values greater than 1.0 suggest a more uniform pattern of recruitment. 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

Laboratory recruitment experiment

Living cover and composition on the tiles differed among treatments; Scrubbed tiles had low algal turf cover (0.1%), Reef tiles had middling turf cover (19%) and Protected tiles had high turf cover (50%). We observed more motile invertebrates on the Protected tiles than the Scrubbed or Reef tiles in the laboratory experiment, particularly amphipods, copepods, and small shrimp. Motile invertebrates were rarely observed on the Scrubbed tiles. *Plexaura homomalla* only recruited to tile surfaces and there were no planulae in the water column at the end of the experiment. Recruitment was significantly different among tile treatments (GLMM, $n = 24$, $p \leq 0.05$, Fig. 1, Online Resource 1–2). Protected tiles had low recruitment with a median recruitment of 22 of the original 150 planulae within each container. A median of 64 recruits settled on Reef tiles and Scrubbed tiles had a median of 94 recruits.

Field recruitment and survival experiment

Settlement of new recruits on the mapped tiles was random with respect to other recruits (NN, $R_n = 1.05$, 95% CI [0.94, 1.17], Online Resource 3). All of the polyps that recruited to the upper surface of the tiles in the settlement experiment died within days of being transferred to the field. The upper sides of the tiles were heavily grazed by herbivorous fish; grazing marks produced by acanthurid and scarid fishes were apparent and abundant. Polyps on the upper sides were not included in the survival analyses. Two bearded fireworms *Hermodice carunculata* (Pallas 1766), predators of octocorals (Vreeland and Lasker 1989), 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.

Statistical analyses of the field data were complicated by two factors. First, recruitment of naturally occurring octocoral planulae in the field confounded estimates of mortality. Therefore, the effects of turf on mortality rates of the polyps could only be determined for the polyps on the mapped tiles. Second, tiles became increasingly dominated by turf algae over time, reducing differences in turf cover among the experimental treatments (Online Resource 4). Thus, the power of comparing the treatments was reduced, but comparisons based on the percent turf cover remain valid.

Mean recruitment on the underside of the mapped tiles was 8.7 polyps tile^{-1} 19-days^{-1} (95% CI [6.2, 11.3]). Assuming all reef surfaces are similarly suitable for recruitment, this can be extrapolated to 443 polyps m^{-2} of available reef 19-day^{-1} (95% CI [317, 577]). There was no relationship between recruitment rate and treatment (ANOVA, $F_{2,6} = 0.34$, $p = 0.73$) or turf cover (linear regression, $F_{1,41} = 3.5$, $p = 0.66$) on the mapped tiles.

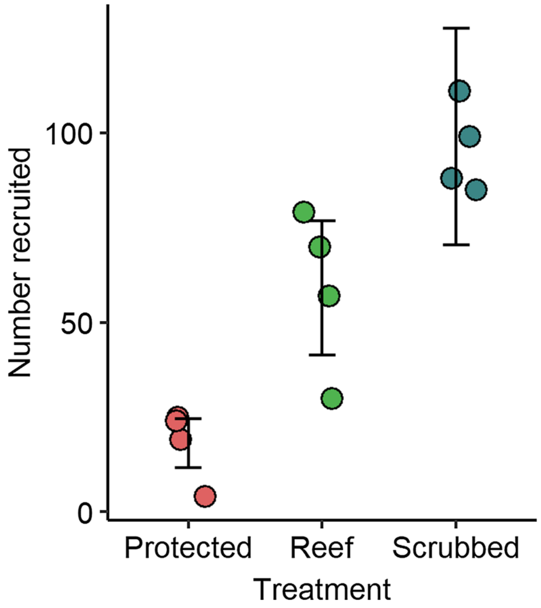


Fig. 1 Effect of tile treatment on the number of octocoral polyps that recruited on pairs of tiles in each container in the laboratory experiment. Error bars are bootstrapped 95% confidence intervals of the means

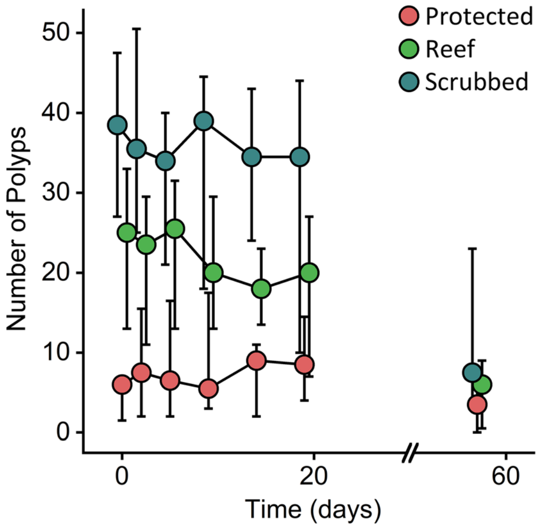
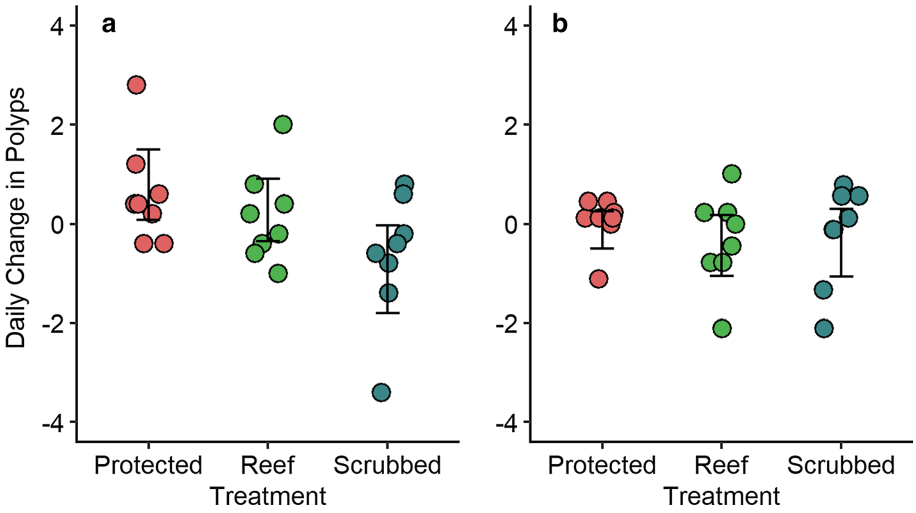


Fig. 2 Change in median number of octocoral polyps over time by tile treatment. The last counts were performed on day 57. Error bars are bootstrapped 95% confidence intervals of the medians. Values have been offset on the x-axis to reduce overlap

Fig. 3 Daily change in number of polyps between (**a**) day 0 and day 5 and (**b**) day 5 and day 14. Error bars are bootstrapped 95% confidence intervals of the means



Tiles had a median of 21.5 polyps tile^{-1} (95% CI [11.5, 32.0]) at the start of the field experiment and after 57 days had 5.0 polyps tile^{-1}, (95% CI [3.0, 7.0]). 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. 2). Early in the experiment (day 0–5), Protected tiles had the same number or gained polyps, counts on Reef tiles stayed the same, and Scrubbed tiles lost polyps (fig. 3a). Between days 5 and 14, mortality was offset by recruitment on tiles across all treatments (Fig. 3b). By day 57, all but two tiles had lost polyps (Fig. 2) indicating that either recruitment rates had declined and/or mortality had increased between days 19 and 57. Both tiles that gained polyps were initially Protected tiles.

A total of 248 *P. homomalla* recruits were followed in assessing polyp mortality rates on the mapped tiles (Online Resource 5). Mean polyp mortality on the tiles was 2.4% day^{-1} (95% CI [1.7%, 3.8%]) and the CPH analysis indicates that 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. 4). Based on the hazard ratios calculated in the CPH, octocoral recruits on tiles modeled with no turf cover had a 32% survival rate after 51 days. At modeled levels of 50% and 100% turf cover, survival dropped to 14% and 2%, respectively (Fig. 5).

Discussion

The increase of octocoral abundance on many reefs (Ruzicka et al. 2013; Lenz et al. 2015; Tsounis and Edmunds 2017; Sánchez et al. 2019) suggests that recruitment has continued regardless of the increasing cover of algae on most reefs. However, we found that *P. homomalla* recruitment and survival was negatively affected by algal turfs. In the laboratory experiment, there were striking reductions in the number of planulae that successfully recruited on the tiles with higher turf cover (Fig. 1), and even cover of 20% reduced successful settlement. In the field, higher algal cover on the tiles was associated with higher recruit mortality (Fig. 4).

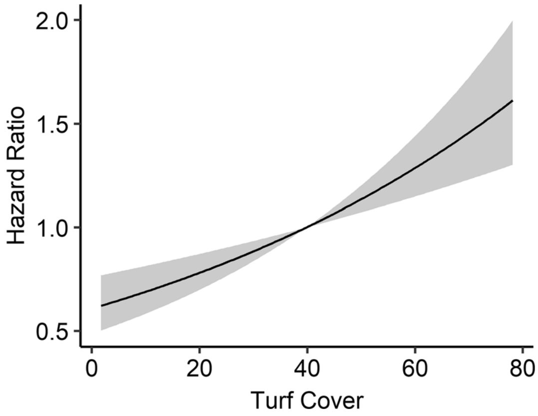


Fig. 4 Relationship between algal turf cover and hazard ratio (i.e., ratio of the probability of mortality relative to the probability of mortality at the median turf cover [39%]). The gray filled area is the 95% confidence interval

The mechanisms by which octocoral recruitment was negatively affected by the presence of algal turfs are unknown. Predation and indirect effects of grazing are likely sources of mortality for recruits. Polyps that settled on the upper surfaces of tiles rapidly died. Although less accessible to fishes, predation was also a likely source of mortality on the underside of the tiles. Additionally, we noted mortality associated with the presence of *H. carunculata*. We did not collect quantitative data on mesofauna abundances, but higher turf cover tiles had large numbers of mesofauna which were far more apparent than on low

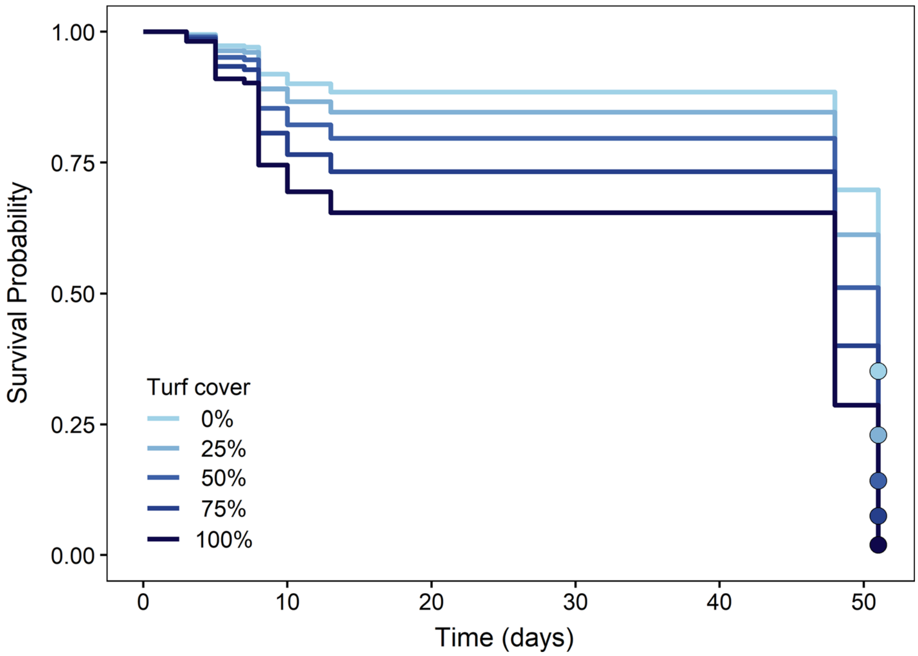


Fig. 5 Modeled effect of constant algal turf cover on survival of octocoral polyps over time. Survival probability is significantly reduced with increased turf cover (Cox Mixed Effects Model, $p = 0.03$). The model does not interpolate survival between time points, creating the stepwise drops in survivorship. The endpoint of each model is indicated by a circle

turf cover tiles. Other potential mechanisms for the negative effects of algal turfs on octocoral recruitment, which have been observed with scleractinian corals, include allelopathic competition (Kuffner et al. 2006; Rasher et al. 2011; Bonaldo and Hay 2014), algae providing a reservoir for virulent diseases (Nugues et al. 2004; Casey et al. 2014), microscale alterations of conditions in the benthic boundary layer (Carpenter and Williams 1993; Brown and Carpenter 2013), and physical interactions between polyps and upright algae (River and Edmunds 2001; Box and Mumby 2007).

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 since we deployed younger polyps than Lasker et al. (1998) and Evans et al. (2013), which are likely at a higher risk of mortality because octocorals generally follow a type III survival curve (Linares et al. 2007). The higher survival in our experiments was likely due to the 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 recruitment plates. In our study, those polyps died quickly, likely through predation by grazing herbivorous fish, and the field survivorship that we report was based on polyps on the underside of the tiles.

Our results suggest several directions where future research should be productive. Simultaneous comparisons of octocoral and scleractinian recruitment 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 recruitment. Further research is also required to understand the relationship between fish predators, mesofauna, and newly settled octocorals. In this study, the 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. Additionally, we treated algal turfs as a single category, but not all algal turfs equally affect ecosystem functions and services (Tebbett and Bellwood 2019). The processes by which spatial complexity mediates facilitation, competition, and/or predation affecting polyp survival are 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. We found that newly recruited octocorals do not survive as long in the presence of turfs. Similar results have been reported for scleractinian corals (Birrell et al. 2008; Penin et al. 2011). The extent to which octocorals recruitment and subsequent survival have changed relative to scleractinian corals may be the key in shaping the contemporary octocoral-dominated reef assemblages in the Caribbean.

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