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FEATURE ARTICLE

Species-specific effects of herbivorous fishes on the establishment of the macroalga *Lobophora* on coral reefs

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ABSTRACT: Herbivory is a key ecosystem function that influences ecosystem trajectories. However, interactions between plants and herbivores are species-specific and change throughout the plants' lifetime. On coral reefs, herbivorous fishes reduce competition between corals and macroalgae through their grazing activity, thereby regulating the ecosystem state. Grazing vulnerability of marine algae generally decreases with increasing algal size. Therefore, the removal of newly settled recruits by herbivorous fish is likely important in preventing macroalgal blooms and reducing competition with corals. We studied the grazing susceptibility of recruits of the brown macroalga *Lobophora* to multiple fish species through a combination of feeding observations and manipulative *in situ* and *ex situ* experiments. Further, we recorded short-term *Lobophora* growth patterns and adult survival over 9 wk. *Lobophora* recruits were more susceptible to herbivory than adults, likely owing to their smaller size. However, recruit mortality was driven by only 3 of the studied species: *Acanthurus nigrofuscus*, *Scarus niger* and *Chlorurus spilurus,* whereas other common herbivores did not remove any *Lobophora* recruits. Our data also suggest variable growth and recruitment among months. These findings point to a possible increase in grazing resistance with age for *Lobophora*. As such, a decrease in grazing pressure by key fish species controlling *Lobophora* recruits could permit *Lobophora* to establish more grazing-tolerant adult populations.

The parrotfish *Chlorurus spilurus* feeding on coral reef substrate covered with turf and macroalgae.
Photo: Peter J. Mumby

KEY WORDS: Ontogeny · Algae · Herbivory · Phase shift · Seaweed · Diversity · Propagule

1. INTRODUCTION

Herbivory can exert strong impacts on plant community structure, but the effect varies depending on the plant and herbivore species involved (Gruner et al. 2008, Barton & Koricheva 2010). Plants regulate their grazing susceptibility through a variety of defence mechanisms, such as physical defences, for

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example through the development of tough leaves (Gilbert 1971, Kearsley & Whitham 1989, Loney et al. 2006), or chemical defences such as secondary metabolites that deter herbivores (Feeny 1970, Whittaker & Feeny 1971, McConnell et al. 1982). Grazing susceptibility can change throughout ontogeny (e.g. Cipollini & Redman 1999, Fritz et al. 2001, Goodger et al. 2006), often decreasing with age, as predicted by the 'growth-differentiation balance' (Herms & Mattson 1992). In contrast, the 'plant-age hypothesis' predicts higher levels of defence in the most vulnerable stages, such as juvenile plants (Bryant et al. 1992, sensu Spiegel & Price 1996). Numerous studies have provided supporting evidence for both hypotheses (e.g. Lubchenco 1983, Cipollini & Redman 1999, Fritz et al. 2001, Goodger et al. 2006), but a meta-analysis of these patterns found little support for decreasing defences in plants as they mature (Barton & Koricheva 2010). Instead, increased consumption of older plants was driven by herbivore species-specific preferences without an associated decrease in plant defences (Barton & Koricheva 2010), highlighting the fact that ontogenetic changes in grazing susceptibility of plants depend on the herbivore species involved.

In tropical marine systems, herbivory is intense and herbivorous fishes play an important role in regulating algae (Carpenter 1986, Polunin & Klumpp 1992). On coral reefs, macroalgae often compete with reef-building corals for space, a major limiting resource (Connell et al. 1997, Miller et al. 1999). Reefs dominated by corals provide habitat to numerous species and deliver ecosystem services to millions of people living close to tropical coastlines (Moberg & Folke 1999). However, increasing anthropogenic impacts have shifted the balance in favour of algae, which has caused an increase in macroalgae on many of the world's reefs (Hughes 1994, McClanahan & Muthiga 1998). While macroalgae can have a variety of negative influences on corals (e.g. Jompa & McCook 2002a,b, Nyström et al. 2008, Rasher & Hay 2010), upright macroalgae can also provide habitat to fish, especially juveniles (Dahlgren & Eggleston 2000, Evans et al. 2014). It is therefore important to understand the role herbivorous coral reef fishes play in preventing macroalgal proliferation. While some notionally herbivorous fishes acquire their nutrition from other organisms, here, we will refer to 'herbivores' from an ecological perspective, i.e. if they cause biologically mediated disturbance to algae (sensu Steneck et al. 2017).

The removal and digestion of adult brown macroalgae, a common macroalgal group involved in phase shifts on coral reefs (e.g. Bellwood et al. 2006, Ledlie et al. 2007, Roff et al. 2015), is difficult and therefore confined to specialised herbivorous fish species ('browsers'; Green & Bellwood 2009). Brown macroalgae store their energy in mannitol and laminarin, polysaccharides that are difficult to digest by vertebrates (Saunders & Wiggins 1981, Painter 1983). There is no evidence of fish being able to produce proteins that would enable them to break down these macroalgal polysaccharides (Clements & Choat 1997). In order to derive nutrition from brown macroalgae, common 'browsing' fish species, such as unicornfishes (nasids) and rudderfishes (kyphosids; Puk et al. 2016), have a hindgut caecum which harbours microorganisms (Horn 1989, Seeto et al. 1996). These microorganisms are capable of fermenting mannitol and laminarin and convert them into short-chained fatty acids (SCFAs), which are digestible by fish (Clements et al. 1994, Seeto et al. 1996). However, herbivores first need to deal with the physical removal of macroalgae. Several algal species are readily removed (Mantyka & Bellwood 2007, Fox & Bellwood 2008), while others may present a more challenging resource because of their calcified or encrusting morphology (Paul & Hay 1986, Coen & Tanner 1989). Some fish species, such as parrotfishes, are better equipped than others to remove tough or encrusting algae because of their strong jaws and scraping or excavating feeding habit, which allows them to remove parts of the reef substrate, including the endolithic organisms growing within it (Bellwood & Choat 1990). Many brown macroalgae also have high levels of polyphenolics, which can hinder the herbivores' protein assimilation by forming hydrogen bonds (Stern et al. 1996). Still, some fish species, such as parrotfishes, may be unaffected by these polyphenolics because they have a basic gut environment that inhibits hydrogen bonding (Horn 1989, Appel 1993). However, parrotfishes have been identified as microphages, which target microorganisms, including cyanobacteria (Clements et al. 2017). Therefore, while parrotfishes may incidentally remove macroalgae when foraging for epiphytic microorganisms, they are not expected to target macroalgae (although the genus *Sparisoma* in the Atlantic is an exception; Targett et al. 1995). Other groups, such as nasids and kyphosids, which can acquire nutrition from macroalgae with the help of microorganisms (Horn 1989), will target macroalgae as their main source of nutrition but may be restricted in their ability to remove encrusting species.

It is commonly assumed that a large number of grazing fishes which target smaller turf algae incidentally ingest macroalgal recruits while foraging

(Green & Bellwood 2009). While macroalgal recruits are readily removed *in situ* (Diaz-Pulido & McCook 2003), limited empirical evidence identifies the fish species involved in this removal. Recruits of the brown macroalga *Sargassum* sp. were consumed by all roving herbivorous species tested (Marshell 2014), indicating that some macroalgal species are readily consumed by most herbivorous fishes on coral reefs. However, other macroalgae may differ in their defences against herbivorous fishes.

A common macroalga that has multiple detrimental effects on corals is the genus *Lobophora* (e.g. Jompa & McCook 2002a,b, Nyström et al. 2008, Rasher & Hay 2010). *Lobophora* impacts multiple life history stages of corals because it decreases coral fecundity (Foster et al. 2008), inhibits coral larval settlement (Kuffner et al. 2006, Evensen et al. 2019) and growth (Box & Mumby 2007), and can even overgrow some live corals (Ferrari et al. 2012, Vieira et al. 2015). *Lobophora* is a brown alga with an encrusting to foliose morphology (Vieira et al. 2014). The alga has reproductive thalli year-round (de Ruyter van Steveninck & Breeman 1987a) and is believed to reproduce monthly (C. Vieira pers. comm.), but its dispersal range is limited (de Ruyter van Steveninck & Breeman 1987b). Turnover rates of individual *Lobophora* thalli are high, with blades exhibiting half-lives of 15 to 39 d (de Ruyter van Steveninck & Breeman 1987b). In contrast to upright macroalgae (Dahlgren & Eggleston 2000, Evans et al. 2014), its encrusting growth form likely provides little refuge to larger species such as fish.

Reports of effective herbivory on the alga vary (e.g. Hay 1981, de Ruyter van Steveninck & Breeman 1987b, Jompa & McCook 2002a), possibly driven by different morphologies (Coen & Tanner 1989), chemical defences (Paul & Hay 1986, Arnold et al. 1995), induced defences (Weidner et al. 2004) and a large cryptic diversity (Sun et al. 2012, Vieira et al. 2014) where different species, albeit morphologically similar, may vary in their susceptibility to herbivores. However, a recent study demonstrated a limited role of chemistry and morphology on grazing susceptibility of *Lobophora* (Vieira et al. 2019). Herbivorous fishes and sea urchins are known to graze on *Lobophora* (Vieira et al. 2019), with *Diadema* sea urchins shown to have a considerable influence on *Lobophora* cover (de Ruyter van Steveninck & Breeman 1987a, Hernández et al. 2008). Like many other macroalgae, *Lobophora* may exhibit a strong ontogenetic shift in its susceptibility to grazing, as recruits were removed readily, whereas adult algal control was limited (Diaz-Pulido & McCook 2003). However, which herbivores are able to remove *Lobophora* recruits is unknown.

Here, we examined the role of several common fish 'herbivores' in the control of the common brown macroalgal genus *Lobophora.* We used a series of field and tank experiments to examine whether *Lobophora* is primarily controlled at its recruit or adult stage and identified the fish species able to remove *Lobophora* recruits, which may inform efforts to protect key species that help prevent algal blooms.

2. MATERIALS AND METHODS

2.1. Study site

The field experiments were conducted on Lighthouse Reef in the Pacific island nation of Palau (07° 16′ 27.9″ N, 134° 27′ 31.0″ E). Lighthouse Reef lies on the eastern coast of Palau and experiences medium wave exposure. This reef used to have high coral cover (77 %) until typhoon Bopha destroyed nearly all corals in December 2012 (Roff et al. 2015). Consequently, the reef experienced a bloom of the red alga *Liagora* sp., which disappeared 6 mo later (Roff et al. 2015) but left in its wake a *Lobophora* sp. bloom which reached a maximum cover of 40 % and persisted for over 2 yr (Bozec et al. 2019). Most of the *Lobophora* specimens at the study site were dark brown in colour and had an encrusting to decumbent morphology.

2.2. Experimental design

2.2.1. Adult *Lobophora* dynamics and impact of fish herbivory

Three sites, >100 m apart, were chosen on Lighthouse Reef (Site 1: 07° 16′ 30.3″ N, 134° 27′ 32.6″ E; Site 2: 07° 16′ 27.9″ N, 134° 27′ 31.0″ E; Site 3: 07° 16′ 26.3″ N, 134° 27′ 29.0″ E). At each site, 3 full cages, 3 partial cages and 3 open plots without cages (all 50 cm long, 50 cm wide, 20 cm high) were set up at a depth of 4 to 6 m, yielding a total of 27 plots. Plots were fixed to the benthos between 20 and 25 February 2017 and were left for 9 wk. Pictures were taken weekly throughout the 9 wk on 6 or 8 March, 12 March, 19 March, 27 March, 4 April, 10 April and 27 April 2017. Fifty cells of 1 cm diameter were placed randomly on each plot and their *Lobophora* occupancy tracked throughout the study period to analyse *Lobophora* mortality.

GoPro cameras (GoPro Hero 3+) were deployed on the 9 open (uncaged) plots used in the 9 wk observational experiment described above, and feeding behaviour was recorded for 4 h each. Cameras were replaced after about 2 h due to battery and storage limitations. The cameras were deployed on 3 consecutive days (10 to 12 March 2017). All cameras were deployed around noon and recorded throughout the afternoon to coincide with the highest grazing rates of herbivorous fishes.

2.2.2. *Lobophora* recruitment and influence of fish herbivory

To investigate recruitment in the presence and absence of fish herbivory, 2 sets of caged and uncaged tiles were deployed. The first set comprised 10 caged and 3 uncaged flat cement tiles that were deployed at each of the 3 sites in Lighthouse Reef between 27 September and 3 October 2017. The second set comprised 27 caged and 27 uncaged 'microhabitat' cement tiles that were installed on the reef on 23 March 2018. Both sets of tiles were removed after 3 wk when macroalgal recruits became visible and the number of recruits was counted under a microscope (12× magnification). While there were differences between sets in tile morphology (the microhabitat tiles consisted of easily accessible crowns and concealed crevices; see Doropoulos et al. 2016 for details), in both cases *Lobophora* recruits were only counted on surfaces easily accessible to herbivores, i.e. the whole surface on the flat tiles and the crowns on the microhabitat tiles. The recruits in the concealed crevices of the microhabitat tiles were not included, as herbivorous fish may have limited access to these areas and could therefore not be compared to easily accessible areas. The number of recruits counted on each tile was standardized by unit area to permit comparison among sets of tiles.

2.2.3. Species-specific removal of *Lobophora* recruits

Although we documented the feeding behaviour of reef fishes on *Lobophora* as part of the experimental study (described above), such observations do not indicate which species (if any) were responsible for algal mortality. We therefore ran 2 additional experiments to examine the species-specific removal of *Lobophora* recruits: a controlled tank experiment and an *in situ* experiment to verify that the findings from the controlled experiment are applicable on a reef.

Tank experiment. A tank experiment was conducted to evaluate the ability of different fish species to remove *Lobophora* recruits. Forty flat cement tiles (100 cm^2) were deployed on 22 September 2018 in cages at 4 to 6 m depth on Lighthouse Reef and retrieved once *Lobophora* recruits became visible on 13 October 2018, after ~3 wk. Tiles were transported back to the research station and kept in a tank with flow-through seawater until they were used in the experiment (15–27 October 2018). Tiles were mapped under a microscope at 12× magnification. A grid of 2.5 × 2.5 cm was used to map the location of *Lobophora* recruits on each tile. All recruits were flush against the tile, thereby not reaching a height of more than 2–3 mm above the substrate. The blade size of the recruits was estimated to be up to 5 mm.

Ten individuals of *Acanthurus nigrofuscus*, 12 individuals of *Ctenochaetus striatus*, 10 initial phase (IP) *Chlorurus spilurus* and 10 *Zebrasoma scopas* were caught on the inshore reefs of Palau. These fish species are common on Palau's coral reefs and were chosen for the following reasons: *A. nigrofuscus* is a common grazing surgeonfish with intermediate SCFA levels (Clements & Choat 1995), meaning it may be able to achieve some nutrition from macroalgae. *C. striatus* is not expected to have a strong impact on macroalgal recruits due to its feeding ecology and low SCFA levels (Clements & Choat 1995), but is the most common fish feeding from the benthos in Palau. *C. spilurus* can be expected to remove *Lobophora* because of its scraping feeding habit, even though it is unlikely to achieve nutrition directly from macroalgae. *Z. scopas* may also be able to achieve some nutrition from macroalgal recruits, as it has high SCFA levels and its SCFA profiles are more similar to browsing fishes than most other grazing surgeonfishes (Clements & Choat 1995, Clements et al. 2017). The fish were transported to the station, where 2 individuals of the same species were moved into a tank (235 cm length × 95 cm width × 70 cm depth) and left to acclimatise for 2 d before the experiments were run. One of the *Z. scopas* pairs displayed highly aggressive behaviour towards one another, so they had to be separated and only 9 *Z. scopas* individuals participated in the experiment. Each fish was measured before being released into the tank. The average size of *A. nigrofuscus* was 10.2 cm, *C. striatus* was 13.6 cm, *C. spilurus* IP was 13.9 cm, and *Z. scopas* was 10.3 cm. While *A. nigrofuscus* can grow up to a maximum of 21 cm (fishbase.org), few large individuals were observed, and the average size of *A. nigrofuscus* on Palauan reefs is closer to those used in the study.

The fish were not starved and had access to turf algae and detritus associated with rubble at all times except during the experimental trials. A tile with turf algae was left in the tank so fish could get used to the presence of a tile in their tank, as we previously observed avoidance behaviour of the fish towards new tiles. The fish often started feeding from tiles after they were in the tank for 2–3 h and were seen taking regular bites from the tiles that were left in the tank. During the experiment, the tile was replaced with 1 experimental tile in each tank on which feeding behaviour was recorded (GoPro Hero 3+) for 2.5 h. Macroalgal recruits (including *Lobophora*) and turf algae were present on the experimental tiles. During the trial, all other food sources (e.g. rubble) were removed in order to obtain a sufficient number of bites on the experimental tile. At the beginning of each set-up, the grid used for mapping the tiles was held into the frame on top of the tile to allow mapping of bites later (i.e. the grid was removed before the experiment). After the experiment, tiles were remapped as described earlier by counting *Lobophora* recruits. For each fish species, 5 replicates (with 2 individuals each) were run except for *C. striatus*, for which we ran 6 replicates. A total of 5 controls were run using the same procedure except that fish were unable to feed on the tiles because a cage was added.

In situ experiment. A similar experiment was conducted *in situ* on the reef using the microhabitat tiles deployed in March 2018 (see description in Section 2.2.2). For the following analyses, only the flat crowns were used because they were readily accessible to all species. To relate fish feeding behaviour to recruit removal, the *Lobophora* recruits on 15 of these tiles, which had previously been caged, were mapped. Nine of these tiles were deployed on the reef at Site 3 on 8 April 2018 in sets of 3. GoPro Hero 3+ cameras were set up to observe feeding behaviour of herbivorous fish on the tiles for 4 h in the absence of divers. Cameras were replaced after about 2 h due to battery and storage limitations. The other 6 tiles were caged to act as controls. Tiles were retrieved after 4 h and remapped. All observed bites taken on the flat crowns were counted, the species taking the bite was identified, and the fish length was recorded. Data were only included in the following analysis if only a single species fed at a location.

2.2.4. Sea urchin density survey

A survey of sea urchin abundance was conducted on 6 November 2019 at the study site. A total of 80 quadrats (50 × 50 cm) were placed randomly on hard reef substrate, and the density and size of sea urchins were recorded. Surveys were conducted during the day, so all crevices and overhanging spaces were extensively searched, as sea urchins often display nocturnality. All individuals were identified to genus level.

2.3. Statistical analysis

All statistical analysis was conducted using the program R (version 3.5.0, www.r-project.org), and all generalized linear mixed-effects (GLME) models were computed using the 'lme4' (Bates et al. 2015) package or the 'glmmTMB' package (Brooks et al. 2017).

2.3.1. Adult *Lobophora* dynamics and impact of fish herbivory on adult *Lobophora*

Second-order polynomial GLME models with binomial error distribution were fitted to the 50 random cells after visual examination of the cover over time. The response variable was presence/absence of *Lobophora* within a cell, Treatment and Days were set as interacting fixed factors, and Cell was nested within Plot, which was in turn nested within Site as random factors.

A GLME model with beta distribution was fitted to test for differences in *Lobophora* cover between the first and the last observation of permanent plots. Treatment and Timepoint were included as interacting fixed factors, and Plot was included as a random factor. A pairwise Tukey post hoc comparison was run using the R package 'emmeans'.

To analyse differences in adult *Lobophora* survival in response to whether they were caged or exposed to fish herbivory, a Kaplan-Meier curve was created and a survival coxme model was fitted. Coxme survival models allow observations to be censored if the observation period ends before an individual died, i.e. the fate of the individual is unknown after the observational period. Treatment was set as the predictor variable and Plot was nested within Site as a random effect.

Whether fish avoid or target *Lobophora* was investigated visually by plotting the % of bites on *Lobophora* over the % *Lobophora* cover. Chi-squared was calculated after averaging % *Lobophora* cover, sum of bites observed on *Lobophora* and expected bites on *Lobophora* for each of the following fish groups: *Acanthurus* spp., *Chlorurus* spp., *Ctenochaetus* spp., *Naso* spp., *Scarus* spp. and *Zebrasoma* spp. To confirm that the bites were correctly identified as being taken on *Lobophora* or on another substrate type in areas further away from the camera, bites taken in the closer half of the plot to the camera were compared to bites taken in the half further away using separate linear models for parrotfishes and surgeonfishes. Percent bites taken on *Lobophora* was set as the response variable, whereas *Lobophora* cover and Plot position (front vs. back) were set as interacting predictor variables.

2.3.2. *Lobophora* recruitment and influence of fish herbivory

The number of *Lobophora* recruits observed on tiles in September/October 2017 was compared to the recruits counted on the crowns of tiles in March/April 2018. We fitted a negative binomial generalized linear model, with Time and Treatment as fixed factors and included an offset of the tile area to account for the different areas included. Post hoc multiple comparisons were conducted using the 'multcomp' package in R (Hothorn et al. 2008).

2.3.3. Species-specific removal of *Lobophora* recruits

Tank experiment. For the following analyses, only locations where feeding activity occurred were included. Further, *Z. scopas* consumed some *Lobophora* recruits only partially. Since partially removed recruits may be able to recover, they were regarded as having 'survived'.

To determine if a fish species was able to remove significantly more recruits than were lost on a control tile, we used a binomial model (see Eqs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m637p001_supp.pdf) following Harborne et al. (2009), since quasi-complete separation prohibited the use of a GLME model.

A GLME model with binomial distribution was fitted to compare the species' abilities to remove *Lobophora* recruits. The number of successes and the number of failures of *Lobophora* removal were bound and set as the response variable, Species was set as a fixed factor and Tile nested within Set-up were set as random factors. Post hoc multiple comparisons were conducted using the 'multcomp' package in R (Hothorn et al. 2008).

In situ experiment. To investigate which species can remove *Lobophora* recruits *in situ*, we used the video observations and recruit removal data obtained on the reef. Only locations that originally had *Lobophora* recruits were included in the analysis. Additionally, locations were only included if a bite was made by a single fish species to avoid confounding results due to multiple species taking bites. This limited the bite data per location and we thus fitted a GLME model with binomial error distribution, setting the probability of a *Lobophora* mortality event (1 vs. 0) as the response variable. Species (including control) was set as the predictor variable, with a species being recorded if any bites were taken at that location.

3. RESULTS

3.1. Adult *Lobophora* dynamics and impact of fish herbivory on adult *Lobophora*

When herbivorous fishes were excluded in caged plots, *Lobophora* cover increased throughout the experiment with a slight levelling off after ~40 d. Both the first- and second-order polynomial terms were significant ($p < 0.001$ for both; Fig. 1A). In contrast, when herbivores had access in partially caged and open plots, *Lobophora* cover increased in March but started to decrease again in April (Fig. 1A). Correspondingly, there was evidence for a second-order polynomial relationship (not different from second-order polynomial relationship in caged plots; $p > 0.05$), but no evidence for a first-order polynomial relationship (significantly different from the linear increase in caged plots; $p < 0.001$). Interestingly, there was no change in cover in partial cages and open plots from the first to last time point 9 wk later (open: $p = 0.15$, partial: $p = 0.53$), but there was a significant increase in cover in fully caged plots ($p < 0.05$; Fig. 1B).

Lobophora survival did not differ among treatments ($p > 0.05$, Fig. 2). The mean ± SD age was 2.5 ± 3.0 wk in caged treatments, 2.6 ± 3.8 wk in partially caged treatments and 2.9 ± 3.3 wk in open treatments.

The percentage of bites taken on *Lobophora* by both surgeonfishes and parrotfishes increased positively with the cover of *Lobophora* (Fig. 3). The number of bites taken by parrotfishes on *Lobophora* was proportionate to the alga's cover (chi-squared: 0.4 and 1.1 for *Scarus* spp. and *Chlorurus* spp., respectively). All surgeonfishes, including *Acanthurus* spp.,

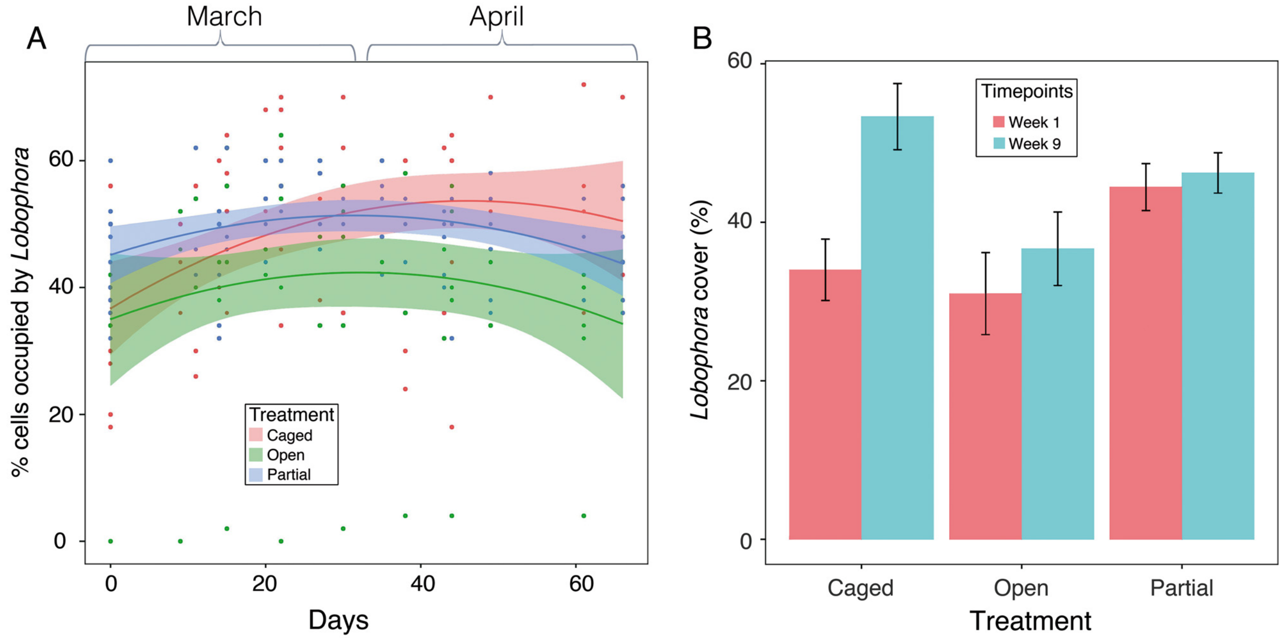

Fig. 1. (A) Percentage *Lobophora* cover observed over a 9 wk period. Data were obtained through 50 random cells which were followed throughout the experiment. Individual observations and polynomial regressions are displayed. Error margins show 95% confidence intervals. Treatments are described in Section 2. (B) Percentage of *Lobophora* cover (mean ± SE) at the first and last time-point measured

Ctenochaetus spp., *Zebrasoma* spp. and *Naso* spp., took more bites on *Lobophora* than expected (chi-squared: 37.7, 83.2, 47.1 and 7.2, respectively; Fig. 3). Identification of the substrate bitten was consistent between the front and the back half of the plot for both surgeonfishes and parrotfishes ($p > 0.05$ both), implying that bites taken further away from the camera were recorded correctly.

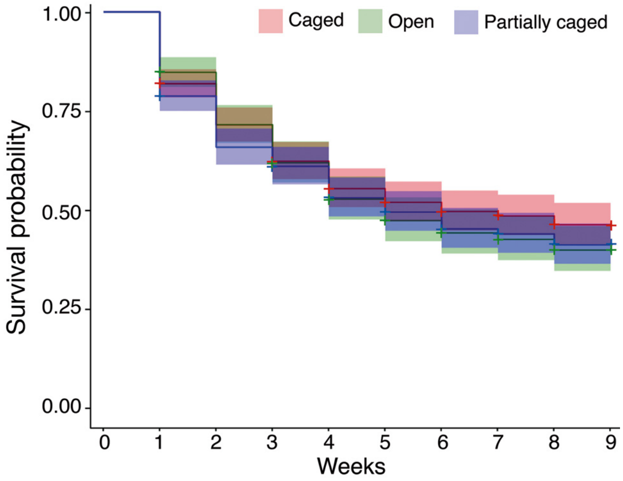

Fig. 2. Kaplan-Meier survival curve using 50 random cells within each plot type (described in Section 2) of which cells occupied by *Lobophora* were followed throughout a 9 wk period. + symbols show that some cells did not 'die' at that timepoint, but disappeared from observations, which happens when a cell was still alive at the end of the experimental period and its fate is therefore unknown

3.2. *Lobophora* recruitment and fish species-specific recruit mortality

3.2.1. Recruitment dynamics

When herbivorous fishes were excluded from tiles in caged treatments, more *Lobophora* recruits established compared to tiles which allowed access by fish to the algal recruits ($p < 0.001$; Fig. 4). This held true in March/April 2018 and in September/October 2017 ($p < 0.001$ for both).

More *Lobophora* recruits were observed in March/April 2018 compared to September/October 2017. This was the case for caged treatments ($p < 0.05$; Fig. 4) and for uncaged treatments ($p < 0.05$).

3.2.2. Species-specific removal of *Lobophora* recruits

In the tank experiment, only 2 fish species showed a clear impact on recruit mortality. *A. nigrofuscus* ($p < 0.05$) and *C. spilurus* ($p < 0.01$) removed more *Lobophora* recruits than were lost in control treat-

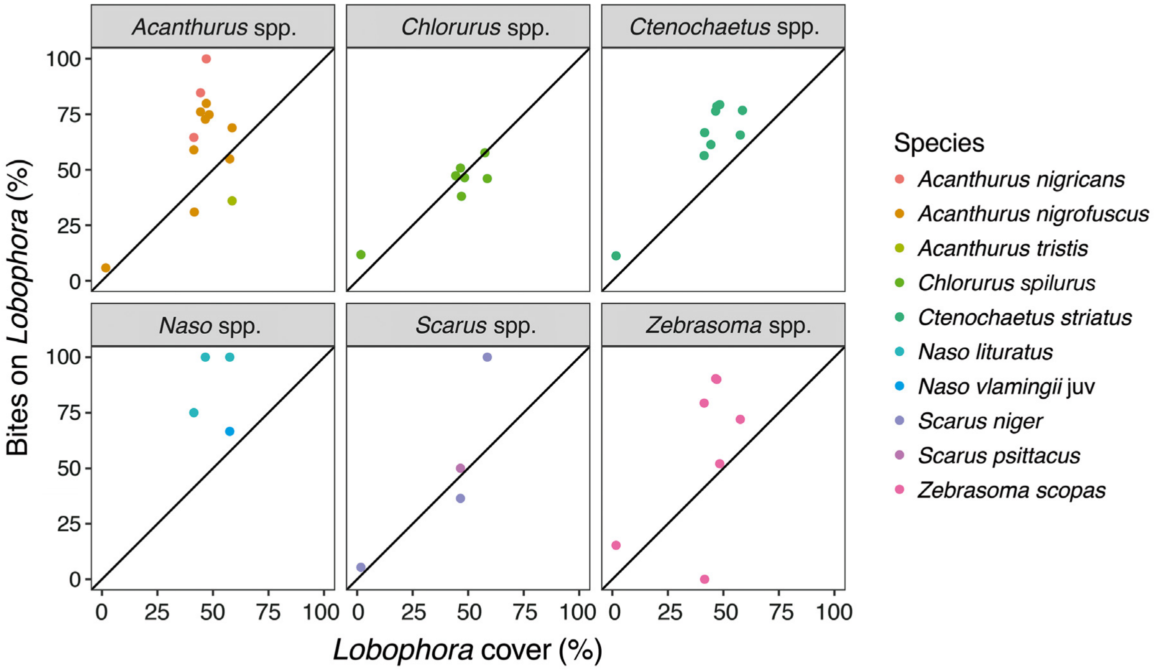

Fig. 3. Percentage of bites taken by surgeonfish and parrotfish on *Lobophora* in a monitored plot of 50 × 50 cm graphed over the percentage *Lobophora* cover within that plot (as percentage of available area). Dots are individual observations, colours show species identity, and line shows a ratio of 1:1. Dots above the line indicate that more than proportionate amounts of bites were taken, dots below the line indicate fewer bites than expected

ments, whereas *C. striatus* ($p > 0.05$) and *Z. scopas* ($p > 0.05$) did not. *A. nigrofuscus* and *C. spilurus* did not differ in their ability to remove *Lobophora* recruits ($p > 0.05$). *C. striatus* was also not significantly different from *A. nigrofuscus* or *C. spilurus*, but this observation was based on a single recruit removal. Only *A. nigrofuscus* and *Z. scopas* differed significantly, with *A. nigrofuscus* removing more *Lobophora* recruits than *Z. scopas* ($p < 0.05$; Fig. 5A).

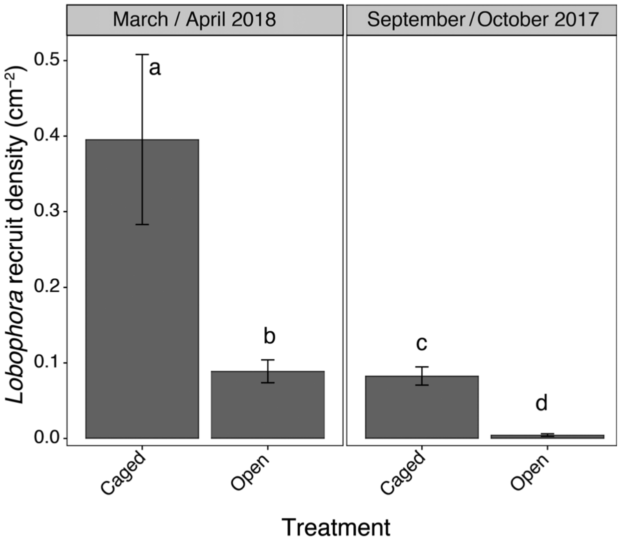

Fig. 4. Comparison of *Lobophora* recruits on easily accessible crowns of tiles in March 2018 and flat tiles deployed in September 2017. Letters symbolize significantly different results. Mean ± SE are displayed

During the *in situ* experiment where observations of feeding could be linked to a single species at a time, 7 nominally herbivorous fish species visited the tiles. Only *A. nigrofuscus* and *S. niger* caused significantly higher *Lobophora* recruit mortality compared to controls ($p < 0.01$ and $p < 0.05$, respectively; Fig. 5B). *Z. scopas* was marginally insignificant ($p = 0.06$), and neither *C. spilurus*, nor *Ctenochaetus binotatus*, *C. striatus* or *N. lituratus* caused *Lobophora* recruit mortality (all $p > 0.05$). The maximum number of bites per location, and therefore the likelihood that a recruit may have been removed during non-targeted feeding, varied among species. *A. nigrofuscus* took a maximum of 2 bites per location, *C. spilurus* and *S. niger* took a maximum of 3 bites, *C. binotatus* took a maximum of 4 bites, and *Z. scopas* and *N. lituratus* each took a maximum of 5 bites. *C. striatus* took the most bites with a maximum of 12 bites per location (Fig. 5B).

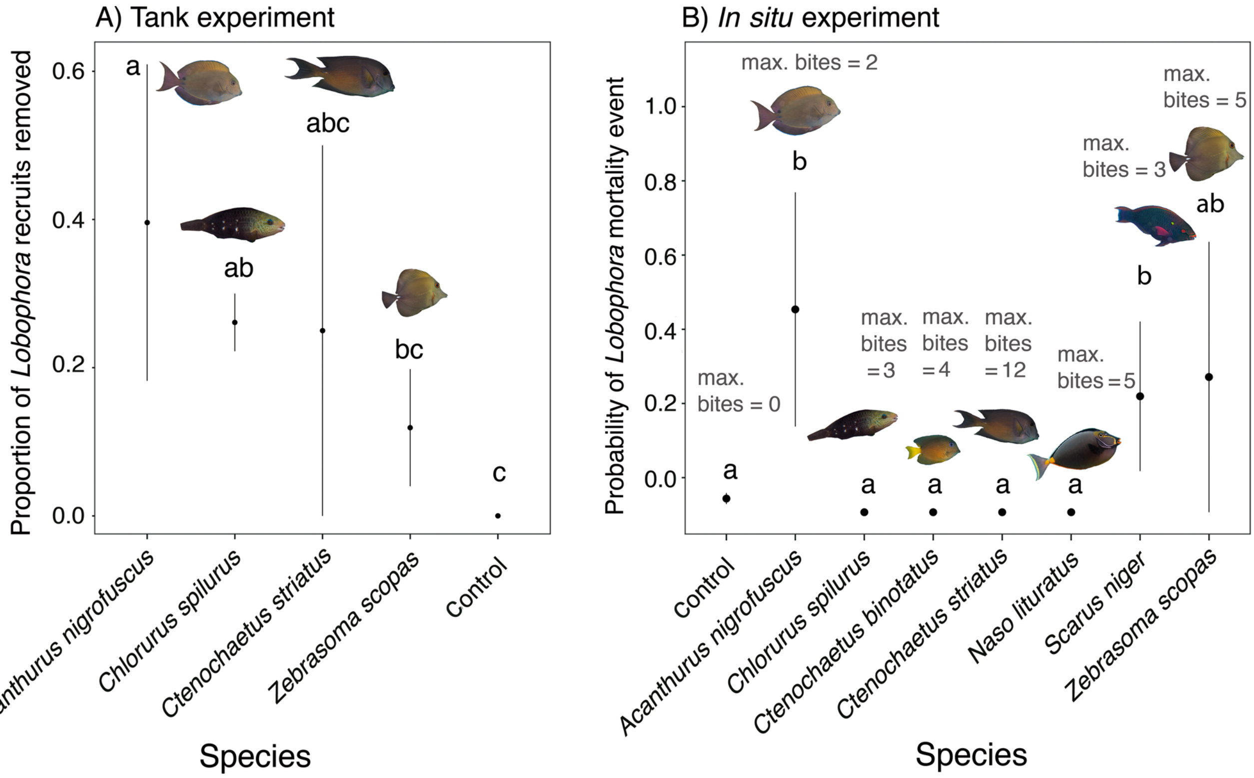

Fig. 5. (A) Mean proportion of *Lobophora* recruits removed by different fish species during the controlled tank experiment. Letters symbolize significantly different results. Error bars show standard error. (B) Probability of *Lobophora* recruits being removed when a fish species visited a tile during *in situ* feeding observations and took bites on locations with *Lobophora* recruits present. Locations were included when only 1 species took bites on them to avoid confounding feeding by multiple species on the same recruit location. Letters symbolize significantly different results. max. bites: maximum number of bites taken at 1 location

3.3. Sea urchin density

The density of sea urchins at Lighthouse Reef was low, with a mean ± SE of 0.3 ± 0.1 ind. m^{-2}. All sea urchins found belonged to the genera *Echinostrephus* and *Echinometra* in the family Echinometridae. The size (diameter) of the echinometrids ranged from 10 to 22 mm. The mean ± SD size of *Echinostrephus* was 11.3 ± 1.2 mm, while *Echinometra* was 20.7 ± 2.3 mm. No diadematids were found at our study site.

4. DISCUSSION

While grazing activity severely reduced recruit establishment, control of adult algae was limited. However, the ability of fish species to remove recruits varied considerably. Out of 7 species observed, only *Acanthurus nigrofuscus*, *Chlorurus spilurus* and *Scarus niger* removed *Lobophora* recruits. These species-specific algal–fish interactions highlight the need to consider species-level behaviours driving or preventing shifts to macroalgal dominance.

Fish herbivory had a stronger influence on *Lobophora* recruit establishment and mortality compared to adult *Lobophora* mortality. During the 2.5 h tank experiment, up to 40% of recruits were removed depending on the fish species involved. During the 4 h *in situ* observations, fish caused a mortality event with up to 50% probability. Additionally, over 3 wk, 78 to 95% fewer recruits became established when they were exposed to herbivores. These values are similar to the herbivore-driven spore and growth reductions of other algal species (Lotze et al. 1999).

In contrast, we found much less impact of herbivory on adult *Lobophora*. The trajectory of *Lobophora* cover differed between caged vs. open plots and partially caged treatments, which implies that herbivores did influence *Lobophora* trajectories in some way. While caged plots showed a linear increase in cover, the cover in open and partial cages increased for about 4 wk before decreasing again to a similar *Lobophora* cover as recorded at the beginning of the experiment. Indeed, when herbivores had access to the adult algal patches, overall *Lobophora* cover did not change from the first timepoint to 9 wk later (Fig. 1B). However, cover did increase by 19.3% in cages. This indicates that there is an equilibrium between herbivory and *Lobophora* growth when herbivores have access to the alga, but when herbivory is reduced, the alga can increase its cover. Interestingly, adult *Lobophora* survival was independent of herbivore access, indicating that the observed change in cover may be driven by the establishment of new algae rather than the consumption of established *Lobophora* thalli. Given the low number of fish species that can be expected to derive nutrition from adult *Lobophora* (Horn 1989, Choat et al. 2002), this pattern is not surprising. These findings indicate that adult *Lobophora* may be less susceptible to grazing by herbivorous fishes than recruits, but further research is necessary to explore this hypothesis specifically by investigating the removal of an equivalent amount of adult and recruit biomass.

While we did not test whether the lower removal of adult algae was driven by chemical (e.g. secondary metabolites) or morphological (e.g. size) changes in the alga, there is some support for both concepts. Apart from differences in their sizes, recruits are relatively flush against the substrate (which also sets them apart from other macroalgal recruits), but are only attached by 1 holdfast, whereas adult encrusting or decumbent *Lobophora* of the same species are well attached to large areas of the substrate (L. D. Puk pers. obs.). Along with larger sizes, these morphological differences would make the removal of adult *Lobophora* much more difficult than the removal of recruits. Phlorotannins, secondary metabolites of brown macroalgae, polymerize and increase in size as they age (Targett & Arnold 2001), which makes them more likely to interfere with the digestion of other macromolecules (Boettcher & Targett 1993). However, the aging process is quite rapid and has been observed over a few hours (Targett & Arnold 2001). It is therefore unclear whether this mechanism would act over weeks or months as would be required to explain differences between adult and recruit chemical defences. Whichever mechanism dominates, our findings suggest decreased herbivory on adult algae compared to recent recruits as predicted by the growth-differentiation balance (Herms & Mattson 1992). This ontogenetic decrease in grazing may be more pronounced in *Lobophora* than in other macroalgae, because recruit removal rates were similar to other algae (Lotze et al. 1999), whereas *Lobophora* adult removal was low compared to the consumption of other macroalgal species (Hoey & Bellwood 2010, Bennett & Bellwood 2011).

The ability of herbivorous fishes to control *Lobophora* recruits is species-specific. The grazing surgeonfish *A. nigrofuscus* removed *Lobophora* recruits in both the controlled tank experiment and the feeding observations on the reef, whereas the grazing/detritivorous surgeonfish *Ctenochaetus striatus* did not remove recruits in either of the 2 experiments. While *C. striatus* was not significantly different from *A. nigrofuscus* and *C. spilurus* in tank experiments (likely an artefact of the high variance observed for *C. striatus*), the ability of this species to control *Lobophora* seems very limited. The lack of recruit removal *in situ*, where *C. striatus* took by far the highest number of bites without causing *Lobophora* mortality, corroborates its likely minimal impact on *Lobophora*. This is an important difference between *A. nigrofuscus* and *C. striatus*, as *C. striatus* is one of the most abundant herbivorous fishes on Indo-Pacific reefs (Russ 1984, Cheal et al. 2012), but our study indicates that it is unable to control outbreaks of macroalgae like *Lobophora*.

The grazing tang *Zebrasoma scopas* did not remove *Lobophora* recruits in either the tank experiment or the *in situ* experiment. However, we found multiple *Lobophora* that had been partially removed by *Z. scopas*. It therefore seems that *Z. scopas* does feed on *Lobophora* recruits, but whether its feeding activity has any impact on the survival of *Lobophora* recruits is unknown and would require longer-term monitoring of recruit growth and survival when exposed to *Z. scopas.*

The fourth species observed both *in situ* and in the tank was the parrotfish *C. spilurus,* which removed recruits in the tank experiment but did not remove any recruits *in situ*. It is possible that *C. spilurus* avoided *Lobophora* recruits *in situ*, because parrotfish have been identified as microphages, which target microorganisms such as cyanobacteria (Clements et al. 2017). However, while foraging for microorganisms in the reef substrate, *C. spilurus* ingests algae because of its excavating feeding mode (Bellwood & Choat 1990). Further, the morphological adaptations of *C. spilurus* for excavating reef substrate while feeding means they remove more substrate than the scraping parrotfish *S. niger* (Bellwood & Choat 1990), which removed recruits *in situ*. It is therefore likely that *C. spilurus* does remove *Lobophora* recruits during its foraging, and the lack of evidence from the field is due to the low number of bites observed. While *Naso lituratus*, a common browser adapted to removing macroalgae (Choat et al. 2004, Rasher et al. 2013, Plass-Johnson et al. 2015), did not remove any recruits in our *in situ* study, we have only limited data on *N. lituratus* (2 forages) and cannot draw conclusions about its ability to remove *Lobophora* recruits on a reef scale. Overall, our experiments show important differences in the ability of fish species to remove *Lobophora* recruits.

While *Lobophora* recruits are readily removed by multiple species, adult *Lobophora* are often persistent though time (Van den Hoek et al. 1978, de Ruyter van Steveninck & Breeman 1987a, Roff et al. 2015), and only a few herbivore species are expected to control the alga (Horn 1989, Choat & Clements 1998). Two groups of herbivorous fishes reported to remove adult *Lobophora* are rabbitfishes (Pillans et al. 2004, Bennett et al. 2010, Vieira et al. 2019), which were rare at our study site, and parrotfishes (Roff et al. 2015). Parrotfish took a proportionate number of bites on *Lobophora* during our study, indicating that they neither target it nor do they avoid the alga, which is in line with their feeding ecology (Clements et al. 2017). Because of the lack of *Lobophora* avoidance and the ability of parrotfish to scrape the reef substratum clean of algae, parrotfish have incidental impacts on *Lobophora*. In contrast to parrotfish, unicornfish *Naso* spp., which are able to digest macroalgae (Choat et al. 2004), consistently took disproportionately many bites on the alga. Other surgeonfish species are highly unlikely to remove adult *Lobophora*, especially the encrusting morphology dominating in Palau (L. D. Puk pers. obs.), because of their jaw morphology (Purcell & Bellwood 1993) and gut physiology, which is unsuitable for macroalgal digestion (Horn 1989, Choat et al. 2004). It is more probable that surgeonfish target either the turf algae, epiphytes or detritus growing on the surface of *Lobophora* (Fricke et al. 2011, Eich et al. 2019) and therefore have little direct influence on *Lobophora*. It is interesting to note that no avoidance behaviour of adult *Lobophora* patches was observed, a behaviour previously shown in other adult macroalgal patches (McClanahan et al. 1999, Hoey & Bellwood 2011). While the reason for this is unknown, it is possible that the lack of physical structure of the mostly encrusting *Lobophora* cover could lead to less avoidance behaviour than observed, for example, for *Sargassum* (Hoey & Bellwood 2011). Generally, it seems that the removal of adult *Lobophora* is limited to few fish species, including parrotfish and potentially browsing herbivores.

The density of sea urchins at our study site was low, with a mean ± SE of 0.3 ± 0.1 ind. m^{-2} and a mean size (diameter) of 16 ± 2.2 mm. Sea urchins can be major grazing agents on *Lobophora*, as shown for *Diadema* in the Caribbean and Canary Islands, but namely at high population densities (>2 ind. m^{-2}) (de Ruyter van Steveninck & Breeman 1987a, Tuya et al. 2001, Hernández et al. 2008). Only 2 genera of small (10 to 22 mm diameter) echinometrids were found at our study site (*Echinostrephus* and *Echinometra*), with no observations of larger-bodied *Diadema*. Predators tend to restrict echinometrids to crevices, which reduces their influence on exposed fleshy algae, including *Lobophora* (McClanahan 1999). Furthermore, *Echinometra* show food preferences for turf macroalgae (e.g. *Acanthophora*) while avoiding *Lobophora* (Sangil & Guzman 2016). While feeding behaviour on *Lobophora* adults and recruits was only recorded during the day (and sea urchin activity tends to be greatest at night), the species composition, low density and small size of sea urchins at our site suggest that their influence on *Lobophora* cover would be minimal.

Variable *Lobophora* growth and recruitment was observed at different times of the year. Independent of whether herbivores had access to *Lobophora*, the alga's cover increased over 4 wk, indicating that herbivory did not control its growth sufficiently. After 4 wk, *Lobophora* in caged treatments without herbivore access kept growing until it plateaued after around 6 wk, which could have been driven by a reduction in growth during the second half of the experiment. In contrast, *Lobophora* in partial and open treatments, which allowed herbivore access, declined again after Week 4 until the end of the experiment. This decline in *Lobophora* cover shows that herbivory during the second half of the experiment was able to reverse *Lobophora* growth, possibly because of reduced growth rates. Similar to *Lobophora* cover, *Lobophora* recruitment showed variability throughout time, with 4 times higher recruitment rates in March 2018 compared to September 2017. While our data do not allow us to conclude that this variability is driven by seasonality, *Lobophora* has previously been found to be highly seasonal in the Indo-Pacific (Diaz-Pulido et al. 2009), and maximum *Lobophora* cover was observed in April in Palau (Roff et al. 2015). Repeated multi-year observations would be necessary to assess seasonality of *Lobophora*. Temporally variable growth has implications at the scale of entire reefs. If reductions in grazing pressure, for example through fishing or increases in grazable area after mass coral mortality, co-occur with peak growth and recruitment, it may have a much more substantial ecological impact than grazing reductions during low growth and recruitment times. The timing of disturbances may therefore play a role in the formation of *Lobophora* blooms, which can subsequently persist for several years (Roff et al. 2015, Bozec et al. 2019).

Overall, we found that herbivorous fishes readily removed *Lobophora* recruits, but this removal was driven by only a few species. In contrast, removal of adult *Lobophora* was comparably low. In a world of increasing macroalgal proliferation on coral reefs, fish species able to remove macroalgal recruits and thereby prohibit the establishment of more resistant adult populations, such as *A. nigrofuscus* and parrotfishes, are important for the resilience of coral reefs. The abundance of these key species should thus be monitored, and fishing regulations should be considered by managers.

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