Spatial patchiness in change, recruitment, and recovery on coral reefs at Lizard Island following consecutive bleaching events

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Abstract

The world's coral reef ecosystems are steadily being reconfigured by climate change. Lizard Island, on Australia's Great Barrier Reef, offers an opportunity to examine coral reef reassembly following disturbance, as this location has been impacted by consecutive tropical cyclones and consecutive coral bleaching events. Based on repeatedly monitoring the same 349 photoquadrats around Lizard Island over a 5-year period (2016-2021) we revealed that bleaching in 2016 drove a ~50% reduction in hard coral cover, and a concomitant increase in algal turf cover. From 2018 to 2021, significant increases (>600%) in coral cover were detected on two semi-exposed reefs and were associated with substantial *Acropora* recruitment. By contrast, fourteen lagoonal and back reefs exhibited virtually no recovery nor *Acropora* recruitment. Given that the timeframe between disturbances is set to decrease, our results suggest that some recovery is possible immediately after severe cumulative disturbances, although this recovery may be highly spatially heterogenous.

Key words:

Acropora; Algal turf; Coral bleaching; Coral community; Coral recovery; Coral regeneration; Ecosystem function; Recruitment; Reassembly; Resilience

1.0 Introduction

Global warming now represents a substantial stressor for the world's ecosystems (Walther et al. 2002; Williams et al. 2003; Jiménez-Muñoz et al. 2016), with coral reefs providing a particular clear example of how this stressor can disturb ecosystems (Stuart-Smith et al. 2018; Sully et al. 2019; Dietzel et al. 2021). Indeed, the impacts of climate change manifest on reefs in the form of mass coral bleaching events (Hoegh-Guldberg 1999; Hughes et al. 2018a; Romero-Torres et al. 2020; Raj et al. 2021), as well as bringing the potential for more severe tropical cyclones/hurricanes (Cheal et al. 2017; Puotinen et al. 2020). As the future for coral reefs is set to be punctuated more frequently by such disturbances, understanding how reefs respond to, and recover/reassemble after, these disturbances is important (Graham et al. 2011; Bellwood et al. 2019; Bruno et al. 2019). In this regard, examining the trajectories that coral reef benthic communities take immediately following disturbance events, especially in terms of their capacity to recover, may be particularly informative.

One location that may yield particularly interesting insights into the trajectories of coral reef communities post-disturbance is Lizard Island in the northern Great Barrier Reef (GBR), Australia. This is because, in recent years, Lizard Island has been impacted by numerous, cumulative, large-scale disturbances. These disturbances at Lizard Island include severe tropical cyclones in 2014 and 2015 and coral bleaching events in 2016 and 2017 that severely damaged coral cover across a 1400 km expanse of the GBR (Hughes et al. 2019b). While we have a relatively clear understanding of how such disturbances impact coral reef benthic communities, principally through the mass mortality of many coral species (Hoegh-Guldberg 1999; Marshall and Baird 2000; Loya et al. 2001; Hughes et al. 2018b), our understanding of the trajectories coral reefs take immediately after such significant cumulative disturbances, especially in terms of coral recovery, is less clear and may vary substantially (e.g. Gilmour et al. 2013; Pisapia et al. 2016; Gouezo et al. 2019; McWilliam et al. 2020; Cannon et al. 2021; Moritz et al. 2021).

Previous studies have suggested that factors such as high herbivory (Mumby and Steneck 2008; Chong-Seng et al. 2014; Viviani et al. 2019), coral larval supply and recruitment (Holbrook et al. 2018; Gouezo et al. 2021), and survival of settled corals (Chong-Seng et al. 2014; Evans et al. 2020) may be important in the recovery trajectories of coral cover. However, our understanding of how these mechanisms operate and relate to the recovery of coral reefs following severe cumulative disturbances, such as those that have affected Lizard Island, remains limited. Indeed, the bleaching events in 2016 and 2017 were so severe that coral recruitment appeared to collapse along the GBR, with 89% fewer recruits than historical baselines (Hughes et al. 2019a). This led to the suggestion that the capacity for reefs to recovery around Lizard Island, at the centre of this recruitment failure, is highly uncertain (Hughes et al. 2019a). This uncertainty is further compounded by the fact that, in many cases, the data on coral reef benthic communities is not collected at a high spatial resolution (i.e. accurately at small scales with sampling across multiple sites) and often lacks adequate temporal replication, stymying our ability to assess ‘patchiness’ in post-disturbance benthic dynamics. We therefore have a surprisingly limited understanding of how and where benthic coral reef communities respond to, or recover/reassemble after, cumulative disturbances, especially when associated with collapses in coral recruitment across large spatial scales.

Understanding the capacity for corals to recover over short-term timeframes is becoming increasingly important as the expected ‘recovery window’ between disturbances on reefs is shrinking, principally because the effects of climate change are intensifying (Hughes et al. 2018a; Puotinen et al. 2020). However, given the extent of recent disturbances to Lizard Island, and the GBR in general, one may hypothesise that recruitment of corals and recovery of coral cover would be negligible over such short-term timeframes (i.e. 3-4 years post-disturbance). To explore this hypothesis the aims of this study were: a) to assess where and how coral reef benthic communities changed in response to large scale disturbances (consecutive coral bleaching), b) assess the spatial extent of coral cover recovery or regeneration over a short-term time frame, and c) assess the spatial extent of *Acropora* recruitment. To address these aims we tracked the benthic community composition dynamics of 349 spatially and temporally matched photo quadrats on shallow reefs around Lizard Island. In addressing these aims, this study will provide insights into how this location was disturbed by recent coral bleaching and then, specifically, it will allow us to explore the hypothesis of negligible coral recruitment and recovery at this location over the short-term.

2.0 Methods

2.1 Study site and disturbance history

Lizard Island is a granitic mid-shelf island located on the northern Great Barrier Reef (GBR), Australia, and is relatively remote in terms of direct human pressures (Figure 1). Lizard Island was impacted by two severe cyclones (Ita in 2014 and Nathan in 2015) which passed close to the island as Category 4 systems and reduced coral cover on the reefs on the exposed and semi-exposed sides of the island (Madin et al. 2018) (Figure 1b). Notably, these cyclones had little impact on the reefs on the sheltered leeward side of the island, or in the protected lagoon (Madin et al. 2018). Following these cyclones, this location was at the centre of the 2016 coral bleaching event that spanned the northern third of the GBR, and was, at the time, the most severe coral bleaching event recorded on the GBR (Hughes et al. 2019b). Subsequent coral beaching events that were less severe in the northern GBR also impacted this location in 2017 and 2020 (Hughes et al. 2021; Pratchett et al. 2021).

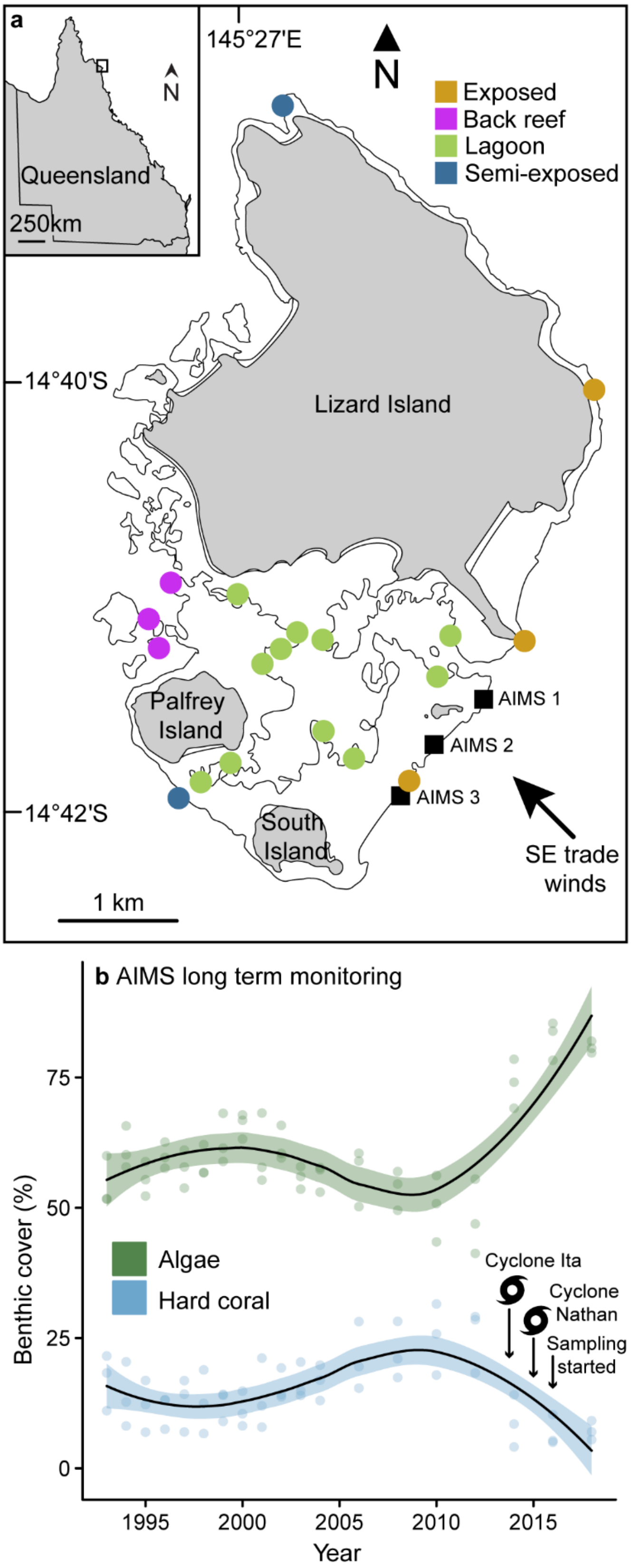

Figure 1 a) Map of Lizard Island showing the 19 sampling locations and their exposures, as well as the locations of the Australian Institute of Marine Science's (AIMS) long term

monitoring sites. The exposure categorisation was based on the position of locations relative to the prevailing south-east trade winds. The inset shows the location of Lizard Island relative to Queensland, Australia. b) The long-term trajectory of algae and hard coral cover at the AIMS long term monitoring sites. The coloured dots are the raw data points (sourced from Australian Institute of Marine Science [2015]), while a smoother and associated 95% confidence intervals were fitted based on a generalised additive model smoothing function to help visualise trends (Wickham 2016).

2.2 Sampling

In February 2016, immediately prior to the onset of major bleaching, 451 fixed quadrats (measuring 1 m^2) spread over 19 transects around Lizard Island were photographed. The quadrats were approximately 5 m apart along each transect, with transects varying in length from 12-38 quadrats depending on the nature of the reef. All quadrats were located on the reef crest/reef edge at a depth of 0 – 4 m below chart datum. Three transects were in exposed locations, two in semi-exposed locations, three in leeward back reef locations and eleven were spread across the protected lagoon (Figure 1a). These exposure categories were based on the position of transect locations relative to the prevailing south-east trade winds (Figure 1a) and follow the categories used in previous studies which have quantified water-flow speeds in some locations at Lizard Island (Fulton and Bellwood 2005; Johansen 2014). It should be noted that the first sampling period occurred after the two cyclones had impacted the island (Figure 1b), and as such, we are unable to determine the spatial extent of their impacts on coral cover at our specific sites using these data (although see the section on ‘coral loss’ in the discussion for further details of how the cyclones in 2014/2015 impacted coral cover around Lizard Island).

For each quadrat location a photograph of the reef with the quadrat in place was taken from a 'birds-eye' view for benthic cover analysis. Photoquadrats were subsequently taken in October 2016, January 2018, January/February 2020 and January/February 2021 (Figure 2). In all cases, photographs were taken with a Nikon Coolpix W300 camera. As the quadrats were not fixed in place, to minimise the impact on the location, we relocated quadrats using a second Nikon Coolpix camera, loaded with the previous sampling periods photographs, to act as a guide. While we could relocate most quadrats across the 5-year study period, some could not be re-located, or quadrat placement differed substantially from initial placement; these were excluded from the analyses. The final dataset, therefore, consisted of 349 quadrats in each of the five sampling periods. It should be noted that although there is a long-history of examining coral cover around Lizard Island (e.g. Done 1992; Pratchett 2010; Madin et al. 2018) this photo quadrat method was initially designed to investigate fish-coral interactions (see Wismer et al. 2019a, 2019b). However, the first sampling trip (February 2016) coincided exactly with the 2016 coral bleaching event (April 2016) on the GBR. Given the high-resolution nature of our sampling method, and the potential for it to provide insights into the benthic trajectories of specific sites post-disturbance, the value in continuing sampling until January 2021 was immediately apparent.

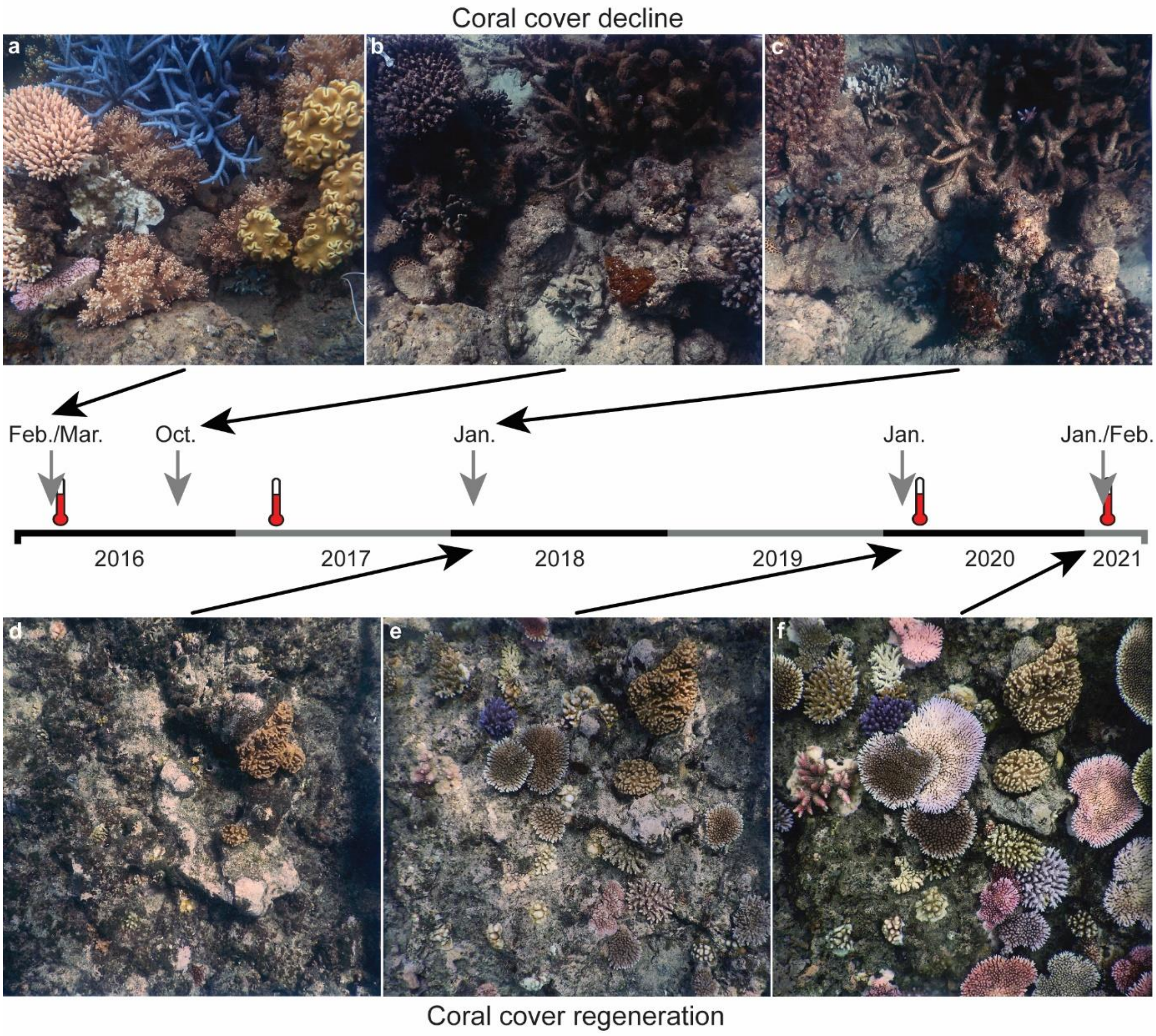

Figure 2 The loss of hard and soft corals between February 2016 and January 2018 at a reef site in the lagoon as a result of coral bleaching (a, b, c). The recovery of *Acropora* cover at a semi-exposed reef site from January 2018 to January 2021 (d, e, f). Note the onset of coral bleaching in (f) and the high cover of algal turfs in (b, c, d, e). Timeline of sampling (indicated by grey arrows) and coral bleaching events (thermometers).

2.3 *Photograph analysis*

From the photographs we quantified benthic cover under 40 randomly stratified placed dots in the software photoquad v_1_4 (Trygonis and Sini 2012). Under each dot we identified organisms to genera (where possible). Where taxonomy could not be applied, we used functional groupings based on the biotic covering and the substratum that category was on (e.g. algal turf on rubble, algal turf on dead coral). On the rare occasions where a dot fell on a benthic component that could not be identified, such as gaps in the reef, in holes or overhangs, these dots were excluded from the analyses. It is important to note that the use of random dot placement in each year factors out any effects of minor quadrat misplacement. This has previously been checked using a sensitivity analysis (see Wismer et al. 2019a). Furthermore, in the 2018, 2020 and 2021 photographs we counted the numbers of new *Acropora* recruits in each quadrat. A coral was considered a recruit if it was not visible in photographs of the previous sampling periods. The minimum size of recruits detected in our photographs were 3 cm^2 (~2 cm in diameter) (see Figure S1 for an example). Given that *Acropora* recruits are ~1 cm in diameter at one year of age (Babcock 1985; Baria-Rodriguez et al. 2019) and can then grow (change in diameter) at up to ~5 mm per month to reach sizes of ~6-7 cm in diameter at two years of age (Trapon et al. 2013; Baria-Rodriguez et al. 2019), the ‘recruit’ corals detected in our system were probably between one and two years of age. *Acropora* was chosen because this coral genus is numerically dominant on most GBR reefs and is critical in early-stage recovery (Johns et al. 2014; Hughes et al. 2019a; Roff 2021).

2.4 Statistical analyses

Initially, we visually explored variation in coral reef benthic community composition using multivariate ordination . Due to the high number of zeros in the data, we pooled benthic data into ten coarse categories based on biotic cover to facilitate analysis: *Acropora*, *Porites*, other hard scleractinian corals, soft corals, algal turfs, macroalgae, crustose coralline algae [CCA], cyanobacteria, sand and ‘other’ (please note that the other category was mainly composed of sessile invertebrates such as sponges and ascidians). Based on the percent cover of these categories in each quadrat we calculated a similarity matrix based on the Morisita-Horn index and fourth-root transformed data. The Morisita-Horn index was used as it is robust when sample sizes differ (Jost et al. 2011). To visualise variation in benthic composition, we used a CAP ordination, which was constrained by the factors year and exposure. 50% kernel density estimates were then calculated for each year and exposure combination to aid in the visualisation of the core areas of multivariate space occupied by the quadrats. Unlike convex hulls, which are traditionally used to visualise multivariate spaces, kernel density estimates show how multivariate space is occupied. They are less sensitive to outliers and, therefore, focus on key areas of multivariate space occupation, rather than how outlying data points influence the occupation of multivariate space (Blonder 2018). Kernel density estimates are becoming increasingly popular for examining space use with applications ranging from animal movement ecology (Worton 1989) to space use in multivariate analyses (Blonder 2018). In our case, we are examining the distribution of quadrats in multivariate space. It is important to note that the analysis was undertaken on the full dataset, however, only data from February 2016, January 2018 and January 2021 are shown on the plots for clarity.

Following the multivariate visualisations, we specifically examined the temporal dynamics in benthic cover of the two primary space holders on coral reefs in this location (hard scleractinian corals [all genera] and algal turfs). To do this we used generalised linear mixed effects models (GLMMs) fitted with a binomial distribution and logit-link function. We treated sampling trip and exposure as fixed categorical factors, while quadrat identity nested within transect identity were included as random effects, to account for the lack of independence due to the repeated sampling nature of this study. For both models, a full model was initially fitted which included an interaction term between the fixed factors. The models were then simplified, and the most parsimonious model was selected based on the corrected Akaike Information Criterion (AICc) (Table S1). Model fit and assumptions were examined via residuals using simulation-based model-checking. Where overdispersion was detected, an observation-level random effect was added to the model to account for this. Post-hoc pairwise means comparisons were performed with a Tukey's adjustment to examine key within factor differences.

To explore spatial patterns in *Acropora* recruitment we used a GLMM to compare the total number of new recruits (summed across 2018, 2020 and 2021 due to the nature of the data) in each quadrat among exposure regimes (categorical fixed effect). In this case transect identity was fitted as a random effect to account for the lack of spatial independence. Due to the high number of zeroes in the data (even when summed together) we fitted a zero-inflated model with a tweedie distribution and log-link function. Model fit and assumptions, as well as post-hoc pairwise tests, were performed as above. A detailed examination of how *Acropora* recruitment related to key explanatory variables was also performed and these details are provided in the supporting information (Text S1). All statistical analyses were conducted in the software R (R Core Team 2020), using the *glmmTMB* (Brooks et al. 2017), *vegan* (Oksanen et al. 2019), *emmeans* (Lenth 2020), *tidyverse* (Wickham et al. 2019), *adehabitatHR* (Calenge 2006) and *DHARMa* (Hartig 2020) packages.

3.0 Results

3.1 Benthic change and coral loss

The composition of the coral reef benthic community changed markedly across the study period, with clear differences in the trajectory of these changes among locations of differing exposures (Figures 3, S2, S3). Notably, following the coral bleaching events, the lagoonal sites lost a substantial amount of soft coral cover as the area of multivariate space typified by soft corals was completely lost, and this had not recovered by January 2021 (Figure 3d). Since January 2018, lagoonal sites were typified by high relative cover of *Porites*, sand, macroalgae and 'other' sessile benthic organisms (Figure 3d). By contrast, back reef sites were consistently typified by soft coral cover throughout the study period (Figure 3c). However, as for the lagoonal sites, the back reef sites also had relatively higher coverage of sand and *Porites* when compared to exposed and semi-exposed sites (Figure 3c, S3).

The dynamics of exposed and semi-exposed sites differ from those of lagoonal and back reef sites. Specifically, while exposed sites also lost soft corals during the bleaching event (Figure 3a), they subsequently occupied an area of space typified by crustose coralline algae (CCA) and to a lesser extent cover of algal turfs and 'other' hard corals (Figure 3a, S2). Semi-exposed sites also occupied the area of multivariate space typified by high CCA cover (especially in January 2018) (Figure 3b), although, from January 2018 to January 2021, there was a marked shift in semi-exposed sites towards the area of multivariate space typified by *Acropora* cover and to a lesser extent the cover of algal turfs and 'other' hard corals (Figure 3b). In this respect, the shift in position of semi-exposed locations in multivariate space from January 2018 to January 2021 (towards an area typified by higher *Acropora* cover) was particularly notable as all other exposure regimes have largely occupied the same area of multivariate space between January 2018 to January 2021 (Figure 3). This, therefore, suggestd that the benthic community composition of semi-exposed reefs may have changed since the disturbance events, while benthic dynamics at other reef locations may have remained constant.

Interestingly, algal turf cover was not a strong driver of separation in any exposure regime (as indicated by the length of the corresponding vector loading in Figure 3). However, bar plots of percent cover by these ten major benthic coverings suggested that algal turfs consistently covered >50% of the benthos across all sampling periods (Figure S2). Indeed, together with all hard corals (i.e. *Acropora*, *Porites* and other hard corals), these two benthic coverings, algal turfs and hard corals, have consistently dominated benthic dynamics at Lizard Island, invariably covering >75% of the total benthos (Figure S2). It is also notable that hard coral cover at Lizard Island is principally composed of *Acropora* and *Porites* corals, with fluctuations in *Acropora* cover being particularly notable (Figure S3). Indeed, bar plots of the percent cover of the fifteen most abundant hard coral genera revealed that the other genera made minimal contributions to total benthic cover at Lizard Island during the study period. Although the almost complete loss of some genera such as *Seriatopora* from this location is notable (Figure S3).

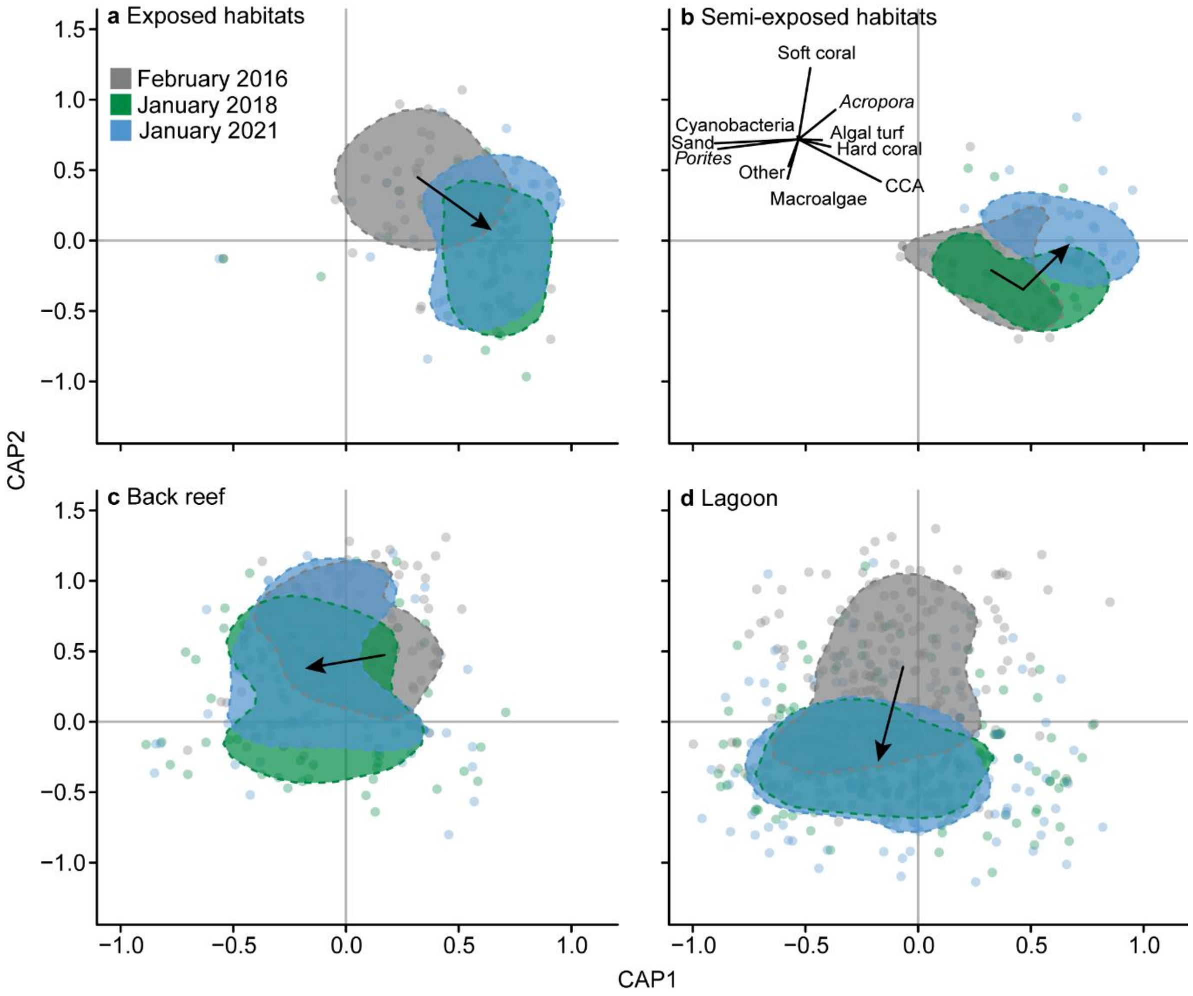

Figure 3 Constrained multivariate ordination plots of coral reef benthic composition based on the Morisita-Horn index in a) exposed, b) semi-exposed, c) back reef, and d) lagoonal habitats. The coloured dots are the positions of individual quadrats, while the coloured polygons denote 50% kernel density estimates which show where the quadrats are concentrated in multivariate space. The vectors (black lines) in b) show the relationship between the benthic categories and their contribution to the position of quadrats in multivariate space (indicated by their length). For clarity, only the benthic composition of quadrats in February 2016, January 2018 and January 2021 are shown. The black arrows in each panel highlight the direction of major shifts in benthic composition across years. CCA = crustose coralline algae, hard coral = hard corals other than *Acropora* and *Porites*. See Figures S2 and S3 for bar plots of benthic cover.

Due to the substantial contribution of algal turfs and hard corals (all genera) to the benthic composition at Lizard Island, a specific examination of how their respective cover varied among locations through time was warranted. In all habitats, the coral bleaching event in April 2016 resulted in a significant decrease in hard coral cover between February and October 2016 (Figures 2a, b, c, 4, S4; Tables S2, S3). Specifically, mean coral cover decreased by 50.2%, 52.6%, 50.3% and 41.8% across back reef, exposed, lagoonal, and semi-exposed habitats, respectively. However, as coral cover was initially higher in back reef and lagoonal sites, this correlated to an absolute decrease of 6.4%, 5.8%, 12.7%, and 2.8% across back reef, exposed, lagoonal, and semi-exposed habitats (to a mean cover of 6.4%, 5.2%, 12.6% and 3.9%), respectively. Importantly, the 2017 coral bleaching event did not appear to have any substantial effects on hard coral cover, as there was no significant change in hard coral cover between October 2016 and January 2018 in any habitat (Figure 4; Tables S2, S3). As coral was lost from February 2016 to October 2016, algal turf cover significantly increased in all habitats, apart from semi-exposed habitats (Figure 4; Tables S2, S3).

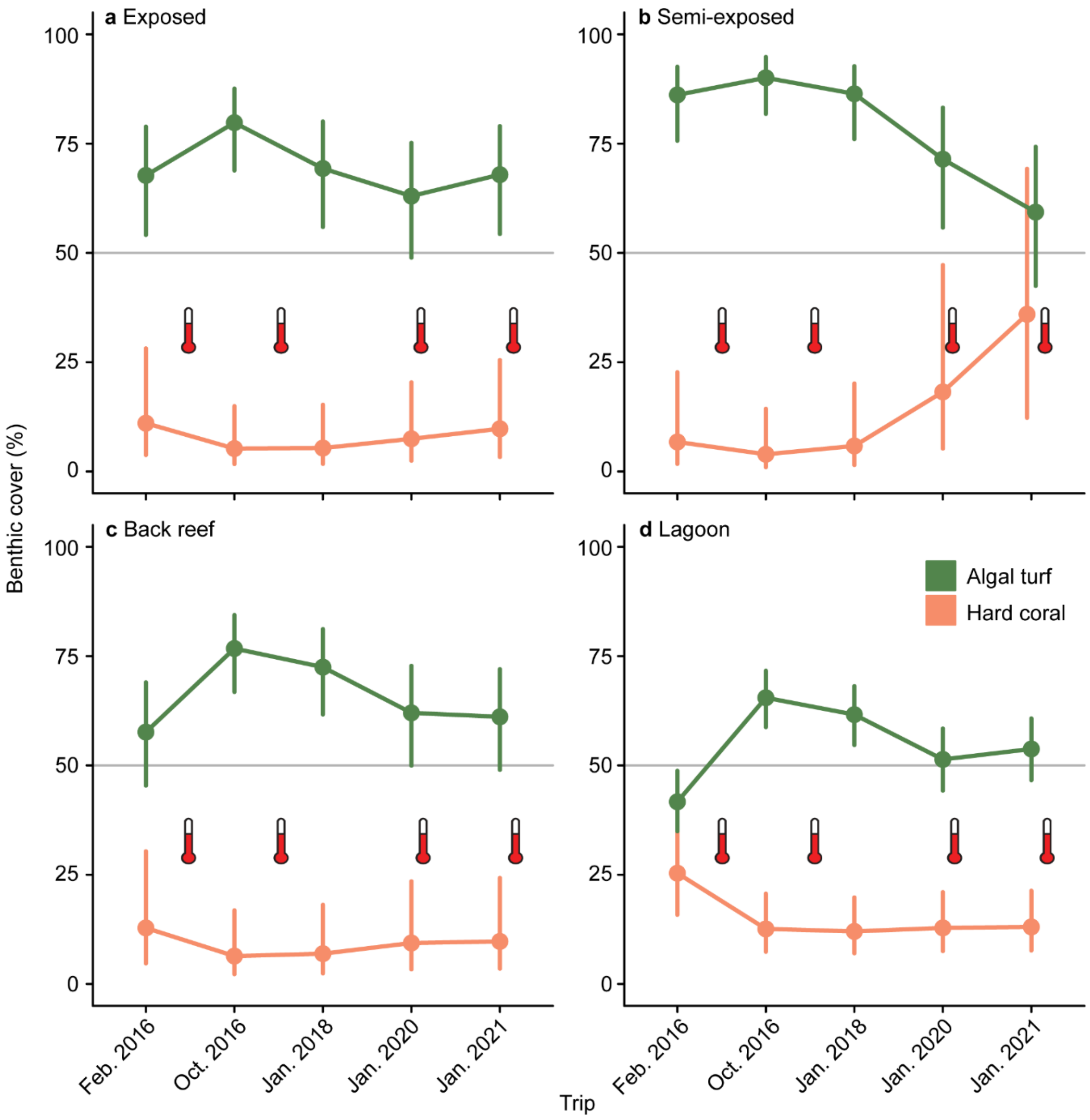

Figure 4 The temporal dynamics of algal turf cover and hard coral cover at a) exposed, b) semi-exposed, c) back reef and d) lagoonal reef sites. The coloured dots and ranges denote the mean predicted fit (± 95% confidence intervals) from generalised linear mixed effects models. Note the increase of algal turf cover from February 2016 to October 2016 due to coral bleaching and subsequent mortality, as well as the marked increase in coral cover from January 2018 to January 2021 at semi-exposed reef sites. The thermometer symbols denote coral bleaching. See Figure S4 for coral cover dynamics at the transect and quadrat scale.

3.2 Recruitment and coral recovery

Our examination of *Acropora* recruitment around Lizard Island from January 2018 to January 2021 revealed marked spatial patchiness in this process with distinct differences among locations of different exposures (Table S4) (Figure 5). Specifically, *Acropora* recruitment was significantly higher in semi-exposed locations compared to all other locations (Table S5) and, on average, was 88-fold, 18-fold, and 9-fold higher on semi-exposed reefs than lagoonal, back reef or exposed locations, respectively (Figure 5). Indeed, there was virtually no recruitment in lagoonal and back reef areas (zero recruits were recorded in 83.9% of lagoon and back reef quadrats) (Figure S5). By comparison, the GLMM suggested there was an average of 9.8 ± 5.78 (± SE) *Acropora* recruits m^{-2}, with up to 29 new *Acropora* recruits recorded in a single m^2 quadrat, on semi-exposed reefs over the 3-year period (Figure 5a).

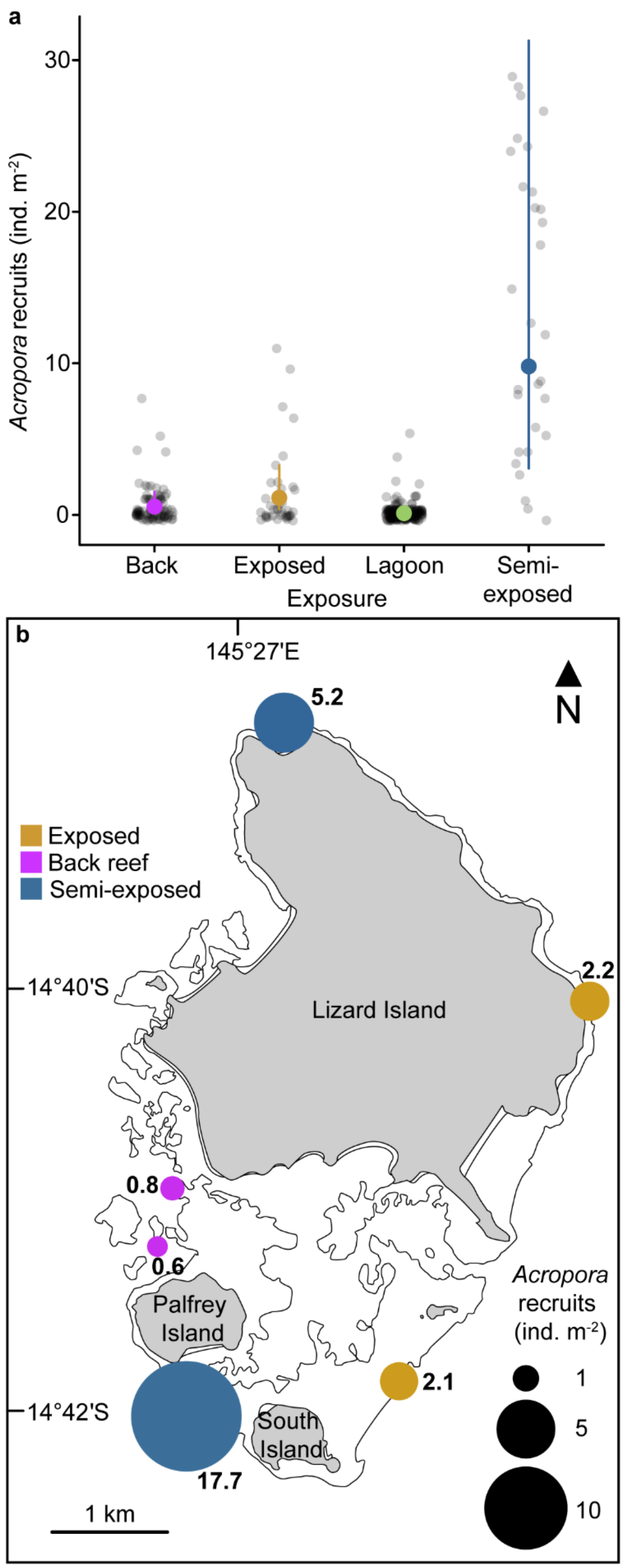

Figure 5 The spatial dynamics of *Acropora* recruitment around Lizard Island. a) The differences in *Acropora* recruitment among exposures revealed by a generalised linear mixed

effects model. The coloured dots and ranges denote the mean predicted fit (± 95% confidence intervals), while the grey dots denote the raw data points. b) Map of Lizard Island showing the distribution of *Acropora* recruits (the circles and adjacent numbers denote the mean density of recruits [individuals m^{-2}]). Only locations with mean recruit densities of >0.5 m^{-2} are shown. For the abundance of *Acropora* recruits in individual quadrats on each transect see Figure S5.

As for *Acropora* recruitment, the recovery of hard coral cover from January 2018 to January 2021 also diverged markedly among locations with different exposure regimes (Figure 4), as initially indicated by the multivariate ordinations (Figure 3). Specifically, there were significant increases in hard coral cover in back reef and exposed sites in the order of 40.6% and 82.4%, respectively (Figure 4; Tables S2, S3). However, this was negligible compared to hard coral cover dynamics on semi-exposed reefs, which increased by 616% from January 2018 to January 2021 (Figures 2d, e, f, 4; Tables S2, S3). By contrast, there was no significant change in hard coral cover in lagoonal sites (Figure 4; Tables S2, S3). These increases in coral cover from January 2018 to January 2021 equate to an annual change in absolute cover of 0.9%, 1.5%, 0.3%, and 10% (to a total hard coral cover of 9.7%, 9.8%, 13.1% and 36% in January 2021) for back reef, exposed, lagoonal, and semi-exposed sites, respectively. It is important to note that the trajectories of coral cover described were the same at the individual transect scale and, generally, at the quadrat scales (see Figure S4), with increases predominantly being driven by increasing *Acropora* cover (Figures S2, S3). Clearly, high *Acropora* recruitment occurred in the same exposure regime (semi-exposed reefs) where hard coral cover also increased the most from January 2018-January 2021 (Figures 4, 5).

4.0 Discussion

Coral reefs are facing a growing number and increasing intensity of disturbances, with stressors associated with climate change acting over the largest spatial scales (Bruno et al. 2019; Sully et al. 2019; McManus et al. 2020; Dietzel et al. 2021). Indeed, the extent to which coral bleaching has affected coral communities (Berkelmans et al. 2004; Frade et al. 2018; Stuart-Smith et al. 2018; Hughes et al. 2019b, 2021) and recruitment (Hughes et al. 2019a) along the GBR are particularly well-documented. By tracking benthic dynamics in 349 quadrats around Lizard Island, we documented the local impact of coral bleaching in 2016. Our findings on the effects of bleaching support previous studies from the GBR (e.g. Hughes et al. 2018b; Madin et al. 2018; Richardson et al. 2018; Stuart-Smith et al. 2018) and on many other coral reefs globally (e.g. Robinson et al. 2019; Contreras-Silva et al. 2020; Babcock et al. 2021; Raj et al. 2021). Importantly, given the cumulative nature of recent disturbances to the northern GBR this led to the hypothesis that coral cover recovery and recruitment would be negligible at Lizard Island in the years immediately following these recent disturbances. Contrary to these expectations, we revealed significant levels of *Acropora* recruitment, and increases in hard coral cover, on some semi-exposed reefs at Lizard Island since January 2018. However, this finding must be set in the context of limited levels of *Acropora* recruitment and hard coral cover recovery across the lagoon and back reef sites and low total coral cover across these sites. In most locations where coral cover has remained static, benthic dynamics have been typified by consistently high cover of algal turfs.

4.1 Coral loss

In 2016 the northern third of the GBR was impacted by the most severe coral bleaching event recorded to-date on the GBR (Hughes et al. 2021). In 2017 the area was impacted by an even more severe heating event, resulting in the first record of mass bleaching events in consecutive years on the GBR (Hughes et al. 2019b). Our results support previous studies in highlighting: a) the significant decline of live hard coral cover (an ~50% decrease) immediately post bleaching (Hughes et al. 2018b; Richardson et al. 2018; Stuart-Smith et al. 2018), and b) the minimal impacts of the 2017 bleaching event in the northern GBR despite more severe heating (Hughes et al. 2019b, 2021). It appears, the 2016 bleaching event was sufficiently severe to kill the majority of susceptible coral species, with negligible impacts of the second event on the few corals that remained. Notably, there was also bleaching at this location in 2020, however, the impacts again appear to have been minimal, potentially due to the fact that heating was more severe in the central and southern regions, rather than the northern region, of the GBR during 2020 (Hughes et al. 2021; Pratchett et al. 2021).

In terms of the spatial footprint of bleaching-mediated coral loss at our study locations, hard coral (and soft coral) loss was clearly highest, in absolute terms, in the lagoonal sites (Figures 3, 4, S2). This is probably a result of two principal factors. Firstly, reef morphology means that lagoons and other sheltered locations have restricted water circulation and longer water residency times (Lowe et al. 2009; Green et al. 2019). This morphology can afford a level of protection against disturbances such as tropical cyclones (depending on their trajectory) (Harmelin-Vivien 1994; Cuttler et al. 2018), but also it means that hot water can pool in these locations, potentially leading to more severe heating and coral bleaching (Jokiel and Brown 2004; Cowburn et al. 2019; Green et al. 2019; but see (McClanahan et al. 2005; Safaie et al. 2018). As such, reef morphology and its interaction with hydrodynamics can underpin spatial heterogeneity in disturbance impacts on reefs.

Secondly, previous disturbances, especially tropical cyclones Ita and Nathan, that impacted our study location immediately prior to the onset of the sampling regime need to be considered. A previous study showed that these cyclones drove declines in coral cover of up to 90% on the exposed/semi-exposed reefs around Lizard Island (Madin et al. 2018). This was supported by the Australian Institute of Marine Sciences long term monitoring data which showed a clear decline in coral cover in exposed locations following the cyclone events (Figure 1b). As such, there were few corals in these exposed and semi-exposed areas left to bleach by 2016 and this could explain why absolute coral loss in these locations was relatively low (although the bleaching event still reduced coral cover by a further 50% at these locations). By contrast, coral cover in the lagoon generally escaped the worst of the cyclone impacts (Madin et al. 2018), potentially leading to the higher absolute loss of coral cover in these locations in 2016.

It is important to note that these previous cyclone impacts could also explain why the extent to which bleaching in 2016 reduced coral cover at Lizard Island is relatively low (Figure 4) compared to the wider northern region of the GBR during the same period (see Hughes et al. 2018b). Cyclones generally have a far smaller spatial disturbance footprint compared to bleaching events, with cyclone disturbances also impacting reefs in a more heterogenous manner compared to bleaching events (Dietzel et al. 2021). This means that while coral cover at Lizard Island may already have been reduced by cyclones Ita and Nathan prior to the 2016 coral bleaching event, this situation was not the same across the entire northern GBR region, leading to the severe loss of coral at the regional level in 2016 due to coral bleaching (as documented in Hughes et al. 2018b). Overall, however, the cumulative nature of these disturbances clearly highlights the need to consider previous disturbance events when assessing the extent of coral loss on reefs (sensu Hughes et al. 2019b), including the widespread extent to which coral cover was reduced at Lizard Island from 2014 – 2017.

4.2 Coral recovery and recruitment dynamics

As for the loss of corals, there was a clear spatial footprint in short-term recovery of coral cover around Lizard Island, with a clear divergence in recovery capacity depending on the exposure of the reef locations. The substantial increase in absolute coral cover on semi-exposed reefs (10% year^{-1}), and negligible increase in the lagoon (0.3% year^{-1}) and back reefs (0.9% year^{-1}), is particularly notable as these values represent some of the highest and lowest rates, respectively, reported in the literature (Graham et al. 2011; Koester et al. 2020). Indeed, Graham et al. (2011) found that across 48 reef sites the global mean annual rate of change in absolute coral cover was 3.56% with a range of 0.13 - 12.49%. Similarly, the recruitment of *Acropora*, the genus of corals principally responsible for underpinning early coral recovery on Indo-Pacific reefs (Golbuu et al. 2007; Emslie et al. 2008; Linares et al. 2011; Johns et al. 2014; Roff 2021), also varied substantially, with individual 1 m^2 quadrats yielding from 0 up to 29 new *Acropora* colonies (Figure S5). Again, this recruitment was largely limited to semi-exposed locations with negligible *Acropora* recruitment in lagoons and back reefs (0 recruits in 83.9% of quadrats) despite surveying in January 2018, 2020 and 2021.

This divergence in recovery trajectories between locations in relatively close proximity (<100 m in some cases), is remarkable. While such habitat-dependent recovery has been documented previously (e.g. Connell et al. 1997; Golbuu et al. 2007; Gouezo et al. 2019; Moritz et al. 2021), other studies have found limited among-habitat differences in recovery (e.g. Morri et al. 2015; Koester et al. 2020), including the meta-analysis conducted by Graham et al. (2011). This variability in short-term recovery at Lizard Island, as well as in the existing literature, clearly highlights the context-dependent nature of coral recovery and has important implications for our understanding of the capacity for coral reefs to reassemble following cumulative disturbances.

From the patterns documented herein, it is clear that the greatest increases in coral cover occurred where the recruitment of *Acropora* was also highest (i.e. semi-exposed reefs). As in previous studies, this suggests that new coral recruits in this location are responsible for driving early recovery dynamics (Holbrook et al. 2018; Gouezo et al. 2019; Evans et al. 2020), rather than via regeneration and growth of existing corals (see Connell et al. 1997; Diaz-Pulido et al. 2009). A parsimonious explanation for these patterns, therefore, is that factors related to the supply of coral larvae, and subsequent settlement and survival of these larvae, probably underpinned the spatial patchiness in coral recovery dynamics (see Text S1 for further details). In this regard, the interaction between reef geomorphology and currents may be a key factor driving this among-exposure coral recovery heterogeneity. This is because currents bring new coral propagules to reefs (Wood et al. 2014; Gouezo et al. 2021) and as the currents predominantly interact with reefs around their windward perimeter at Lizard Island (Johansen 2014), this may maximise delivery of larvae to these areas. Furthermore, as currents frequently form eddies as they pass islands (Heywood et al. 1996; Wolanski et al. 2003), which concentrate coral larvae (Sammarco and Andrews 1988; Willis and Oliver 1990), it may be concluded that the semi-exposed sites are interacting with such eddies in a manner that facilitated high *Acropora* recruitment rates, as demonstrated in previous experiments on the GBR (Sammarco and Andrews 1988, 1989).

In addition to currents, other factors (beyond those considered in the supplemental examination see Text S1, Figure S6) may also have contributed to heterogenous *Acropora* recruitment around Lizard Island. For example, if corals settle soon after finding a suitable settlement area, and as semi-exposed/exposed reefs often have favourable settlement conditions (high CCA cover and low algal turf sediment loads [Harrington et al. 2004; Birrell et al. 2008; Speare et al. 2019]), it may be that the vast majority of corals settled in semi-exposed and exposed reef areas before the coral propagules ever filtered through to the more sheltered reef habitats. This factor may be particularly important in driving heterogeneity in this context considering that the number of *Acropora* propagules around Lizard Island was likely to be relatively low (Hughes et al. 2019a). It could also be that the numbers of coral propagules that make it through to lagoonal and back reef areas were further depleted by predation. Planktivorous fishes have been documented to feed on coral propagules (Pratchett et al. 2001), with prior evidence that such fishes can form a 'wall-of-mouths' that significantly depletes planktonic resources around reefs (Hamner et al. 1988). Even after the significant coral loss, many planktivorous fishes remained relatively abundant in the lagoons and back reef habitats around Lizard Island (Wismer et al. 2019a, 2019b), as well as on off-reef slopes (Morais and Bellwood 2019; Valenzuela et al. 2021). This may have been due to a greater propensity for behavioural flexibility than expected, as well as the fact that structures remained largely intact over short-term temporal scales (for details see Wismer et al. 2019a, 2019b). However, regardless of the exact mechanisms, although heterogenous, there has been a marked recovery of coral cover as well as relatively high *Acropora* recruitment at some locations around Lizard Island following cumulative disturbance by cyclones and bleaching events.

The fact that there has been a notable degree of coral recovery and *Acropora* recruitment at any location at all around Lizard Island is interesting given that coral recruitment following bleaching was previously reported to have collapsed along the GBR, especially around Lizard Island (Hughes et al. 2019a). Indeed, in 2017 and 2018 coral recruitment onto recruitment tiles at Lizard Island was reported to be just 1% and 3.2%, respectively, relative to pre-2016 bleaching recruitment rates (Hughes et al. 2019a). However, there are two primary reasons why our results differ from, and extend, those of Hughes et al. (2019a). Firstly, it is important to consider the temporal timing of the two studies. The most recent recruitment event quantified by Hughes et al. (2019a) was that which occurred across 2017/2018 (i.e. recruitment tiles were deployed in November 2017 and retrieved in January 2018). This aligns with the first year that we started recording *Acropora* recruits in our quadrats (i.e. January 2018). In this year we only documented 26 recruits across the entire 349 m^2 area censused. This supports the conclusions of Hughes et al. (2019a) as coral recruitment appeared to be extremely low at this location from 2016 to 2018. However, we also recorded recruits in January/February 2020 (466 new recruits documented) and 2021 (64 new recruits documented). As such, it appears that the major *Acropora* recruitment event at Lizard Island, in our dataset, occurred after the study by (Hughes et al. 2019a) ended. Probably in the austral summer months of 2018/2019 given the size of recruits when they could be detected in our study. This lack of temporal overlap between studies may therefore be a major factor explaining any differences in the findings between the two studies.

The second factor that could have contributed to any differences in conclusions between our study and that of Hughes et al. (2019a) is how ‘recruits’ were quantified. Hughes et al. (2019a) used artificial recruitment tiles to quantify the abundance of settling coral larvae. By contrast, we counted the number of new *Acropora* colonies that ‘recruited’ to our specific censused areas. Our recruits had successfully settled onto the reef substratum and survived the various immediate post-settlement bottlenecks, which can hinder coral survival at this life stage (Jones et al. 2015; Doropoulos et al. 2016). Importantly, a recent study by Evans et al. (2020), on reefs off Western Australia, revealed that there is little concordance between coral recruitment to tiles and juvenile coral densities on the substratum (i.e. our ‘recruits’). Indeed, Evans et al. (2020) found that coral recruitment to settlement tiles was not a good predictor of coral recovery. However, juvenile acroporid densities were found to be a good indicator of coral cover recovery in future years (Evans et al. 2020). This finding aligns remarkably well with our results from Lizard Island. This lack of a relationship between coral recruitment to tiles and recruitment to, and survival on, natural reef substrata may, therefore, have resulted in differences in the results of our study and those of Hughes et al. (2019a). This highlights the value, and complementary nature, of large scale macroecological studies and high-resolution examinations of individual reef systems.

It is also important to note that despite documenting some recovery and recruitment at specific locations around Lizard Island our results should be considered within the context of future disturbance regimes. Given that the frequency and severity of disturbances to coral reefs is set to increase in the future (Cheal et al. 2017; Hughes et al. 2018a; Sully et al. 2019) with the median return time between severe coral bleaching events on reefs now being just 6 years (Hughes et al. 2018a) then this is far shorter than the decade-long timeframe that previous studies have suggested is needed for the fastest growing coral assemblages to recover (Connell et al. 1997; Johns et al. 2014; Osborne et al. 2017; Romero-Torres et al. 2020). This point was highlighted by the fact that the ‘recovering’ corals in our quadrats were already exhibiting early stages of bleaching again in January 2021 during the last sampling period (Figure 2f). This means that in semi-exposed reef habitats at Lizard Island where we documented significant levels of recovery over very short timeframes there was also the potential for rapid repeat bleaching. This is likely to facilitate boom and bust coral cover dynamics in this habitat (cf. Wilson et al. 2019; Pratchett et al. 2020; Morais et al. 2021). By contrast, the lack of recovery and recruitment across the lagoon and back reefs may mean that these areas at Lizard Island have a limited capacity for regeneration before the next major disturbance and could remain dominated by the alternative benthic space holders that have succeeded following coral mortality. Boom and bust coral dynamics vs coverage by alternative space holders may represent spatially separated alternative conditions on future reefs (cf. Morais et al. 2021).

4.3 The constancy of algal turfs

Despite the different dynamics of coral loss and recovery between locations in the current study, there was one overwhelming constant across all locations; the abundance of algal turfs. At all sampling time points, coverage generally exceeded 50% (Figure 4). Importantly, this phenomenon is not just limited to Lizard Island, with similarly high levels of algal turf cover (>40-50%) reported from many other reef areas globally (Smith et al. 2016; Jouffray et al. 2019; Kennedy et al. 2020; Cannon et al. 2021), especially after coral bleaching events (Gilmour et al. 2013; Emslie et al. 2019; Koester et al. 2020). Moreover, this is not just a recent phenomenon, as the AIMS data highlighted that algal cover (principally composed of algal turfs in this area) already covered >50% of the benthos back to 1993 (Figure 1b). This notion is supported by previous studies on other reefs during the latter half of the 20th century (e.g. Marsh 1976; Adey and Steneck 1985; Klumpp and McKinnon 1989; Adey 1998). The data herein, and previous literature, therefore suggest that algal turfs can be the most abundant benthic covering on reefs, with this dominance potentially set to increase further as the loss of coral cover on reefs continues.

4.4 Conclusions

Lizard Island has endured consecutive cyclones and consecutive coral bleaching events in recent years. The latter resulted in widespread coral mortality and a collapse in coral recruitment across 1400 km of the GBR (Hughes et al. 2019a, 2019b). Yet Lizard Island, located at the centre of these disturbances, demonstrated that some recovery in hard corals was still possible over short time frames, even in the years immediately following disturbance. Indeed, we found that significant increases (>600%) in early successional coral cover occurred on semi-exposed reefs, driven primarily by recruitment of *Acropora*.

However, while we document that high rates of recovery are possible on a reef that has experienced consecutive severe cyclones and consecutive coral bleaching, it is important to note that this recovery was far from spatially homogenous. No detectable recovery in hard coral cover occurred across large expanses of reef area (in this case the entire lagoon at Lizard Island) reflecting an apparent failure of a chief recovery mechanism; *Acropora* recruitment. Recovery in these lagoonal areas may only occur on temporal scales exceeding those of the current study, or once local stock-recruitment dynamics recover. As such, the future of these lagoonal reefs is likely to be highly dependent on future disturbance regimes. Given that algal turfs already cover >50% of the benthos around Lizard Island, it appears likely that the future of these reefs could be one typified by high algal turf cover. In a world where the impacts of global climate change continue to operate, we may increasingly be working with algal turf-covered reefs with spatially patchy recovery of corals between disturbances.

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