esa ECOSPHERE

Macroalgal feedbacks and substrate properties maintain a coral reef regime shift

KERRYN A. JOHNS,[1],† MICHAEL J. EMSLIE,[1] ANDREW S. HOEY,[2] KATE OSBORNE,[1]
MICHELLE J. JONKER,[1] AND ALISTAIR J. CHEAL[1]

[1]*Australian Institute of Marine Science, PMB 3, Townsville MC, Townsville, 4810 Queensland, Australia*
[2]*ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, 4811 Queensland, Australia*

Citation: Johns, K. A., M. J. Emslie, A. S. Hoey, K. Osborne, M. J. Jonker, and A. J. Cheal. 2018. Macroalgal feedbacks and substrate properties maintain a coral reef regime shift. Ecosphere 9(7):e02349. 10.1002/ecs2.2349

Abstract. Coral reefs are among the world's most diverse and productive ecosystems, yet they are also one of the most threatened. The combined effects of local human activities and climate change have led to corals being replaced by macroalgae in various tropical settings, lessening the ecological, social, and economic value of these reefs. Once established, macroalgal regimes are maintained by a range of physical, chemical, and biological feedback mechanisms that suppress the settlement, survival, growth, and hence recovery of coral populations. Our understanding of these feedbacks has come largely from small-scale experimental studies, but their relative importance in sustaining a regime shift has rarely been examined in situ. We investigated the role of macroalgae in limiting coral recovery on an inshore reef on Australia's Great Barrier Reef that shifted to macroalgal dominance in 2001. Coral recruitment on terracotta tiles in habitats with low cover of macroalgae at the regime-shifted reef and at comparable habitats at an adjacent coral-dominated reef was similar, suggesting that neither larval supply nor reef-wide "avoidance" by coral larvae was contributing to the lack of coral recovery at the regime-shifted reef. However, within the regime-shifted reef, recruitment of corals on tiles, and their survival in the first two months post-settlement, was substantially lower in habitats characterized by dense beds of the brown macroalga *Lobophora* than in habitats just meters away that were relatively free of macroalgae. Despite the negative effects of *Lobophora* on recruitment and early recruit survival, there was no effect of *Lobophora* on the persistence of juvenile corals (1–50 mm diameter). Juvenile coral persistence in beds of *Lobophora* (50%) was comparable to that in neighboring habitats free of *Lobophora* (60%) over nine months. Rather, the persistence of juvenile corals was lowest (10%) in unconsolidated rubble habitat, where photographs of fixed quadrats showed that, over nine months, rubble substrate had been redistributed. Our results highlight two bottlenecks to coral recovery; inhibition of coral recruitment and recruit survival by macroalgae, and reduced juvenile coral persistence in patches of loose rubble substrate. Importantly, these processes appear to be habitat-specific and are unlikely to constrain coral recovery at a reef-wide scale.

Key words: coral recruitment; coral reef; feedback; Great Barrier Reef; juvenile coral; macroalgae; recovery; recruit survival; regime shift.

Received 24 May 2018; accepted 29 May 2018. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2018 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** k.crossman@aims.gov.au

INTRODUCTION

Many of the world's ecosystems are in decline with shifts between the dominant habitat-forming species becoming increasingly common (Jackson et al. 2001, Scheffer et al. 2001). These regime shifts are often triggered by a major external shock and represent a fundamental change in the structure and functioning of these systems (Scheffer and Carpenter 2003, Folke et al. 2004).

Once established, these shifts are difficult to reverse, with conceptual models suggesting that positive feedbacks serve to reinforce the new state (Mumby and Steneck 2008, van de Leemput et al. 2016). While causes of regime shifts and feedbacks that sustain them have been identified in a range of terrestrial and aquatic environments (Folke et al. 2004), a better understanding of the strength of feedbacks, how they interact and their spatial scale of effect is still necessary for the most successful management of vulnerable systems (Nyström et al. 2012).

Coral reefs are one of the world's most biodiverse and productive ecosystems, yet they are also one of the most threatened (Walther et al. 2002, Pandolfi et al. 2003). Detrimental effects of local human activities are being greatly compounded by climate change, shifting the balance from feedbacks that promote coral-dominated states toward those that promote macroalgal-dominated states. This replacement of hard corals by macroalgae (macroalgal regime shift) reduces the ecological, social, and economic value of affected reefs (Moberg and Folke 1999, Hughes et al. 2010). Macroalgal regime shifts have been particularly prevalent in the Caribbean (e.g., Hughes 1994, Shulman and Robertson 1996, McClanahan and Muthiga 1998) but have also occurred in the Indian (Cuet et al. 1988, Graham et al. 2015) and Pacific Oceans (Smith et al. 1981, Done et al. 1991, Cheal et al. 2010). The likelihood of macroalgal regime shifts is predicted to increase globally as reefs are increasingly exposed to more frequent and/or more severe stressors (Knowlton 1992, McManus and Polsenberg 2004, Cheal et al. 2017, Hughes et al. 2017). While the drivers of macroalgal regime shifts on coral reefs are relatively well established, the interacting mechanisms that sustain these shifts deserve more attention (Nyström et al. 2012).

Macroalgal regime shifts may be reinforced through mechanisms that promote the growth of the macroalgae itself and/or suppress the recovery of coral populations (Mumby and Steneck 2008, van de Leemput et al. 2016). For example, high biomass of *Sargassum polycystum* promoted the growth and survival of con-specifics (Dell et al. 2016), and herbivorous fishes avoided feeding in high-density patches of *Sargassum* (Hoey and Bellwood 2011), reinforcing macroalgal overgrowth. Macroalgae have been shown to inhibit the recruitment of corals (Baird and Morse 2004, Kuffner et al. 2006), and suppress their growth, survival, and fecundity (Tanner 1995, Jompa and McCook 2002, Foster et al. 2008, Rasher and Hay 2010), and thus the replenishment of coral populations.

The effects of macroalgae on the recruitment of coral larvae and early survival of recruits are particularly critical, because successful recruitment of sexually reproduced larvae is the primary mechanism of recovery for coral populations following disturbances (Connell et al. 1997). Coral recruitment is highly variable in both space and time (Hughes et al. 1999), and early survival rates of both pelagically dispersed larvae and settled coral recruits are very low (Connell 1973, Vermeij and Sandin 2008). Macroalgae can further limit coral recruitment by physically excluding coral larvae from accessing the substrate, releasing waterborne chemicals that act as negative cues to coral larvae, abrading coral recruits or by inducing changes to water flow, sediment regimes, water chemistry, and microbial communities of the microhabitat that are detrimental to recruit survival (Birrell et al. 2008*a*, Ritson-Williams et al. 2009).

Our understanding of the effects of macroalgae on coral recruitment and early survival of recruits has mostly been gained from small-scale experimental studies that have manipulated interactions between individual macroalgae and corals (Kuffner et al. 2006, Nugues and Szmant 2006, Rasher and Hay 2010, Morrow et al. 2017). However, inferring what happens on a regime-shifted reef from such studies is potentially problematic, because those studies cannot include all the ecological processes that occur in the "natural" setting. A rare study in a regime shift setting examined variation in reef-scale recruitment of corals and found that recruitment did not differ between adjacent coral- and macroalgal- dominated reefs (Chong-Seng et al. 2014). Conversely, another study comparing coral recruitment between coral- and macroalgal-dominated reefs coupled field manipulations with aquarium experiments to suggest that coral larvae use olfactory cues to actively avoid macroalgal-dominated reefs (Dixson et al. 2014). However, we are unaware of any studies that have examined how coral recruitment and recruit survival varies across smaller (i.e., within reef) spatial scales in natural macroalgal regime shift settings. This is critical as coral larvae are poor swimmers and ultimately make settlement choices on fine spatial scales (Hata et al. 2017).

Australia's Great Barrier Reef (GBR) is a well-managed ecosystem, and its coral communities have generally shown relatively rapid recovery (<10 yr) following disturbances (Halford et al. 2004, Johns et al. 2014). Despite this, macroalgal regime shifts have occurred on inshore reefs of the GBR (Done 1992, Cheal et al. 2010), where decreasing water quality from coastal land practices potentially shifts the balance of environmental conditions in favor of macroalgae over corals (Fabricius 2005). This has fueled speculation that many GBR inshore reefs currently dominated by macroalgae (Wismer et al. 2009) were once dominated by corals (Hughes et al. 2010). The best-documented macroalgal regime shift on the GBR is that of Havannah Reef, an inshore reef in the central GBR. Havannah Reef shifted to a macroalgal-dominated regime in 2001 and macroalgae cover generally persisted at high levels in the 15 yr that followed, with no evidence of coral recovery (Cheal et al. 2010). This presents an ideal system in which to examine the mechanisms that are limiting the recovery of coral populations. We use a combination of ecological surveys and in situ experiments at Havannah Reef and at an adjacent coral-dominated reef to investigate factors that have limited coral recruitment and early recruit survival, and the recovery of coral populations at Havannah Reef, and the spatial scales over which these processes operate.

METHODS

Data collection

Long-term trends in the cover of hard coral and macroalgae at Havannah Reef.—Havannah Reef is an island fringing reef in the central GBR, 13 nautical miles from the mainland Queensland coast (Fig. 1a). As part of the Australian Institute of Marine Science (AIMS) Long Term Monitoring Program, benthic communities at Havannah Reef were surveyed annually from 1997 until 2005, and biennially thereafter. Benthic communities were surveyed along five permanent 50-m transects set at a depth between 6 and 9 m in each of three sites in a standard reef slope habitat on the northeast flank of Havannah Reef (n = 15 transects per year). Digital imagery was used to quantify benthic community composition. Forty still frames were randomly selected from the images taken during transects (Jonker et al. 2008). Benthic organisms were identified to the finest taxonomic resolution possible (typically genus) under five points per frame (n = 200 points per transect). Macroalgae are defined as algae at least 2 cm long that have distinguishable structures such as fronds, stalks, and holdfasts.

Coral recruitment and recruit survival.—Coral recruitment was recorded on terracotta tiles that provide an attractive settlement surface for coral larvae. Corals were considered recruits if their skeletons (whether polyps were alive or dead) were visible on tiles at the time of counting. Recruits that were still alive were considered survivors.

The current substrata at the long-term study site at Havannah Reef is predominantly rubble, formed by remnants of the previous coral community that was destroyed by disturbances (bleaching then cyclone damage) from 1998 to 2000. Patches of consolidated substrate (hereafter bommies), typically over 10 m in circumference and 2–3 m high, are scattered sparsely throughout the rubble beds. To assess the influence of habitat on coral recruitment, eleven tiles (11 × 11 × 1 cm) were placed haphazardly into each of three habitats (i.e., *Lobophora,* Rubble, and Bommie) within the long-term study sites (7–8 m deep) on Havannah Reef (Fig. 1b). Havannah *Lobophora* is the most extensive habitat and consisted of rubble beds covered by dense macroalgae, predominantly *Lobophora,* with variable amounts of *Sargassum*, *Asparagopsis*, and *Padina.* Havannah Rubble habitat consisted of patches of rubble that were relatively free of macroalgae and mostly covered in turf algae, while Havannah Bommie habitat consisted of bommies that hosted a mix of corals and turf algae but had low cover of macroalgae.

To investigate whether the dense beds of macroalgae on the reef slope had broader influences on coral recruitment, we also deployed tiles on the adjacent shallow reef slope (~3 m deep) habitat on Havannah Reef that was largely free of macroalgae (Havannah Shallow; Fig. 1b).

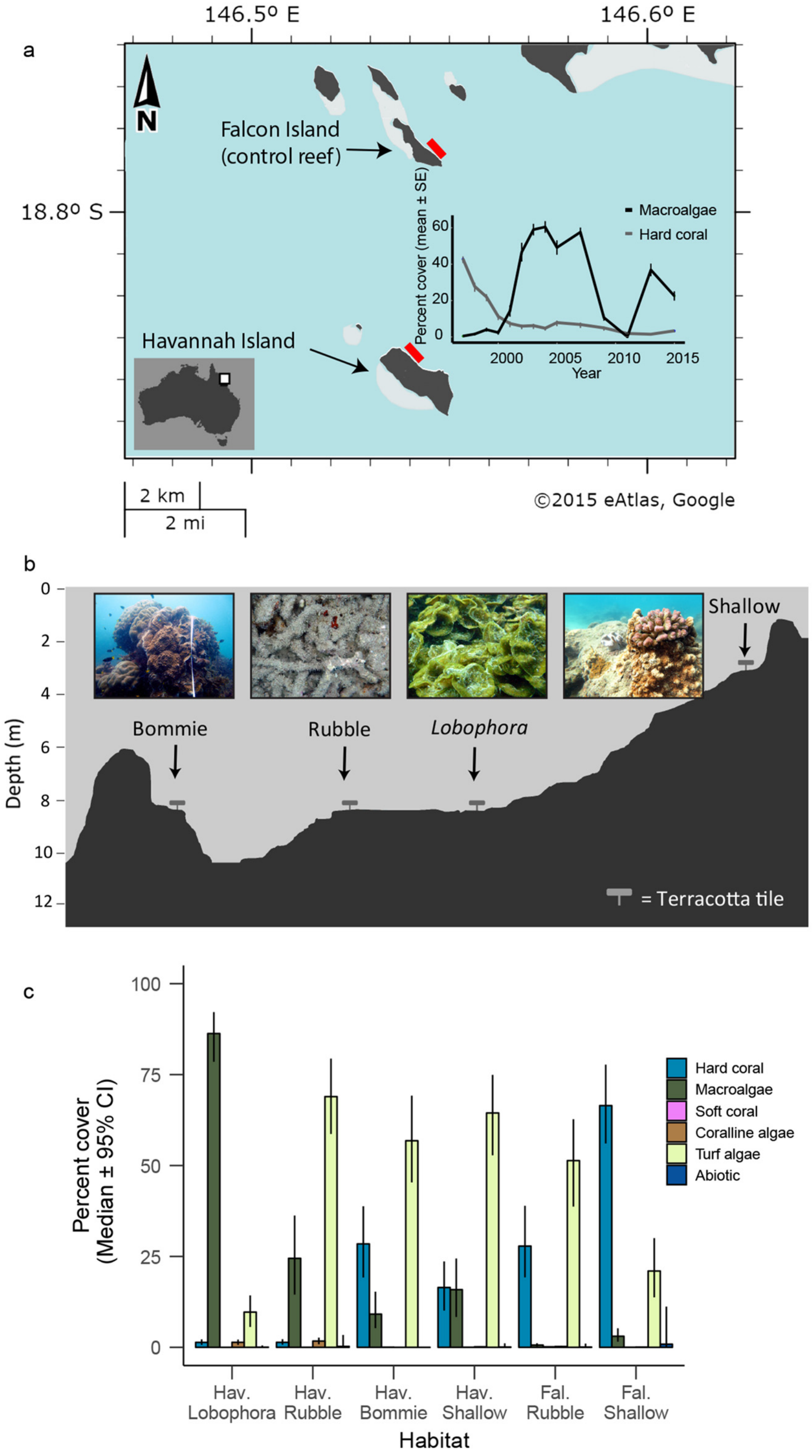

Fig. 1. (a) Sampling locations at Havannah Reef and the coral-dominated control reef (Falcon Island) are

(Fig. 1. *Continued*)
marked in red. Temporal trends of hard coral cover and macroalgae cover from a long-term data set are presented for Havannah Reef. (b) A depiction of the habitats at Havannah Reef used in the tile experiment and juvenile coral surveys. At Falcon Reef, only Rubble and Shallow habitats were included in the study. (c) The benthic community composition in the habitats at Havannah Reef (Hav.) and at the control reef (Fal.).

Further, to understand whether recruitment at Havannah Reef was comparable to other reefs in the region, tiles were also deployed at a neighboring control reef surrounding Falcon Island (Fig. 1a) in comparable shallow and deep reef slope habitats (Falcon Shallow, Falcon Rubble) with a similar aspect and substrate, but with low macroalgae cover. Macroalgae and bommies were rare or absent at the control reef, and were therefore not included in the experimental design. This meant that 66 tiles were deployed in total: 11 in each of the six habitats.

Tiles were deployed in October 2014 and allowed to condition for at least 1 month prior to the predicted split mass spawning of corals in November and December (Baird et al. 2009). At each habitat, 11 tiles were deployed separately on short sections of threaded rods with fasteners used as spacers to keep each tile 10 mm above, and parallel to, the substrate or algal bed (in the *Lobophora* habitat only). In *Lobophora* habitat, the tiles were set up where the algal growth form was prostrate or encrusting the rubble substrate, meaning that the tiles were elevated only slightly higher above the true substrate than in other habitat types.

To assess the influence of habitat on early recruit survival, tiles were collected in February 2015, carefully placed on narrow poles with spacers to avoid abrasion (up to 5 tiles per pole) and transported in bins of seawater (refreshed half-hourly during transit) to laboratory flow through tanks. To quantify live coral recruits, tiles were transferred to a shallow bowl of seawater and the sides and underside of the tiles were thoroughly and systematically examined under a stereo dissecting microscope. The upper surface of tiles was not examined as they were heavily fouled with silt and sand trapped in assemblages of turf algae. Tiles were subsequently soaked in a weak bleach solution (5%) for 24 h and dried, and then, all surfaces (including the upper surface) were examined for coral recruit skeletons. Coral recruitment was expressed as the total number of recruit skeletons on all tile surfaces. Survival was expressed as the proportion of the total number of recruits (counted after bleaching) on the underside and sides of tiles that were alive (prior to bleaching). Coral recruits were identified to the finest taxonomic resolution possible, typically family level (Babcock et al. 2003).

Characterizing habitats.—We quantified benthic communities in each of the six habitats using line intercept transects. Length and replication of transects were stratified according to the area of each habitat. Havannah *Lobophora*, Havannah Shallow, Falcon Rubble, and Falcon Shallow were surveyed using four replicate 10-m transects; however, Havannah Rubble and Havannah Bommie habitats were smaller in area so were surveyed using six replicate 5-m transects. The length of tape intersected by each benthic organism, identified to the finest taxonomic resolution possible, was recorded. The longest diameter of each hard coral colony was also recorded.

Juvenile coral persistence.—To determine whether the persistence of juvenile corals (1–50 mm diameter) on natural substrata differed among habitat types at Havannah Reef, we surveyed five replicate permanent quadrats in each of the four habitats (*Lobophora,* Rubble, Bommie, and Shallow) in November 2014, and again in August 2015. We use persistence rather than survival as we were uncertain about the fate of juvenile corals that could not be relocated. To test whether clearing the substratum of macroalgae would increase recruitment of coral larvae following the 2014 mass coral spawning event and result in higher juvenile counts months later than in plots left uncleared, we had also established six quadrats in Havannah *Lobophora* habitat in October 2014 (one month prior to establishment of other quadrats), in which we removed as much macroalgae as possible from the substratum (Havannah *Lobophora*; prior removal). Counts of juvenile corals in these plots in the following November and August were compared with juvenile counts from plots that were not cleared prior to spawning.

For the first census in November 2014, steel-framed 0.25 × 0.25 m quadrats were haphazardly placed within each habitat such that no adult coral colonies (>50 mm diameter) were within the quadrat, and two diagonally opposite corners of the quadrat were marked with small steel rods hammered into the substratum. One rod was tagged and the quadrat photographed. Quadrats were divided in to 5 × 5 cm squares using string, and each square was systematically searched in situ by a diver with a dive mask with a yellow barrier filter and a flashing blue light (NightSea) that induces auto-fluorescence of juvenile corals (Piniak et al. 2005). Juvenile corals were identified to the finest taxonomic resolution possible (typically genus), measured to the longest diameter, and mapped within the quadrat for tracking over time. In the Havannah *Lobophora* habitat, large macroalgae fronds were carefully removed to facilitate an effective search of the rubble substratum, but only after an initial search of the quadrat for juveniles to ensure none were removed along with the macroalgae. The steel-framed quadrats were removed after the surveys but the marking rods left in place.

The quadrat plots were revisited 9 months later (August 2015) and resurveyed for juvenile corals as described above. Individual juvenile corals were categorized as "persisting" if they were recorded in both November and subsequent August surveys. During these August surveys, it was clear that water movement had redistributed rubble substrate, along with any attached juvenile corals, in some quadrats. To account for this, we used size thresholds based on maximum increases in diameter measured in this study (Appendix S1) to distinguish newly arrived juvenile corals that were small and had potentially recruited from the preceding spawning event from those that were large and, rather, had arrived via a mobile piece of rubble (transient).

Data analysis

All analyses were performed in R (R Core Team 2015), using Bayesian hierarchical linear models fitted in STAN (Carpenter et al. 2017) via the brms package. All plots were produced using the package ggplot2 (Wickham 2009). Inferences for all response variables were based on 95% Bayesian Credibility Intervals (CIs) for modeled higher posterior density median effects. Our aims were to (1) compare benthic community composition among habitats at both Havannah Reef and Falcon Reef, (2) assess whether coral recruitment was similar among habitats at both Havannah Reef and Falcon Reef, and (3) compare recruit survival and juvenile coral persistence among habitats at Havannah Reef.

*Characterizing habitats.—*The benthic community composition of habitats at Havannah Reef and Falcon Reef was quantified by modeling the percent cover of hard coral, soft coral, macroalgae, coralline algae, and turf algae within each habitat against a binomial distribution with a logit link function, with the fixed factor of Habitat and transect as a random term. Models were fitted with three Markov chains of 2000 iterations (including a warm-up of 250 iterations), a thinning interval of two and uninformative priors on the fixed effects and residual variance.

*Coral recruitment and recruit survival.—*For the recruitment analysis, the total number of recruit skeletons was modeled against a negative binomial error distribution with a log link function and included a fixed factor of Habitat (Havannah *Lobophora*, Havannah Rubble, Havannah Bommie, Havannah Shallow, Falcon Rubble, and Falcon Shallow). Models included three Markov chains of 2000 iterations (including a warm-up of 250 iterations), a thinning interval of two and uninformative priors on the fixed effects and residual variance. Specific post-hoc contrasts were set up to examine the differences among Habitats using a Tukey's contrast matrix applied to the fitted parameter estimates. For the recruit survival analysis, Bayesian hierarchical linear models and post-hoc contrasts used in the recruitment analysis were repeated for Havannah Reef habitats. Statistical significance of differences in recruitment and recruit survival among habitats can be inferred from effect size plots when 95% CIs do not overlap an effect size of zero.

*Juvenile coral persistence.—*Juvenile coral abundance in established quadrats was low and variation was high, which precluded an effective analysis of variation in juvenile density among habitats. To assess variation in juvenile persistence among habitats, we modeled differences in proportion of juvenile persistence using poisson models in a Bayesian framework, comparing the habitat mean to the overall mean. We summarize other aspects of the juvenile coral data as totals (and associated proportions) pooled across quadrats for each habitat in the supporting information (Appendix S1: Table S1). Though our initial objectives were not all achieved, our tracking data provided other useful insights that we present in the results and discussion.

RESULTS

Long-term trends of hard coral cover and macroalgae cover at Havannah Reef

In 1997, average hard coral cover at Havannah Reef was 43% and the cover of macroalgae was <1% (Fig. 1a). Between 1997 and 2002, hard coral cover declined to 6% due to a combination of disturbances. Hard coral cover remained below 8% for the following 14 yr, reaching its nadir at 2% in 2013. Cover of macroalgae first exceeded hard coral cover in 2001 and continued to climb, peaking at 60% in 2004 (Fig. 1a). Despite a dramatic drop in macroalgae cover between 2007 (58%) and 2011 (<1%), due in part to an intense cyclone (Cyclone Yasi in 2011), macroalgae rapidly returned to 37% cover in 2013. *Lobophora* has dominated the macroalgae community composition since at least 2007 (Appendix S2: Table S1).

Characterizing habitats

Hard coral and macroalgal cover averaged 1.4% and 86.0%, respectively, in the Havannah *Lobophora* habitat (Fig. 1c). In contrast, cover of macroalgae did not exceed 25% in any other habitat. The macroalgal assemblage within the Havannah *Lobophora* habitat was primarily comprised of *Lobophora* sp. (60%, Appendix S2: Fig. S1), with lesser amounts of *Sargassum* (16%) and turf algae (9%). Turf algae comprised the majority of the benthic community (median range 51–69%, Fig. 1c) in Havannah Rubble, Havannah Bommie, Havannah Shallow, and Falcon Rubble habitats, while hard coral cover ranged between 1.5% and 29% (Fig. 1c) in these habitats. Hard coral cover was substantially higher in the Falcon Shallow habitat at 66%. Cover of coralline algae that may act as a cue for settlement of coral larvae was very low in all habitats (Fig. 1c).

Coral recruitment and recruit survival

Coral recruitment varied considerably among habitats, with the median number of recruits ranging from 20 per tile to 70 per tile (Fig. 2a). There was strong evidence that total recruitment was lower in the Havannah *Lobophora* habitat

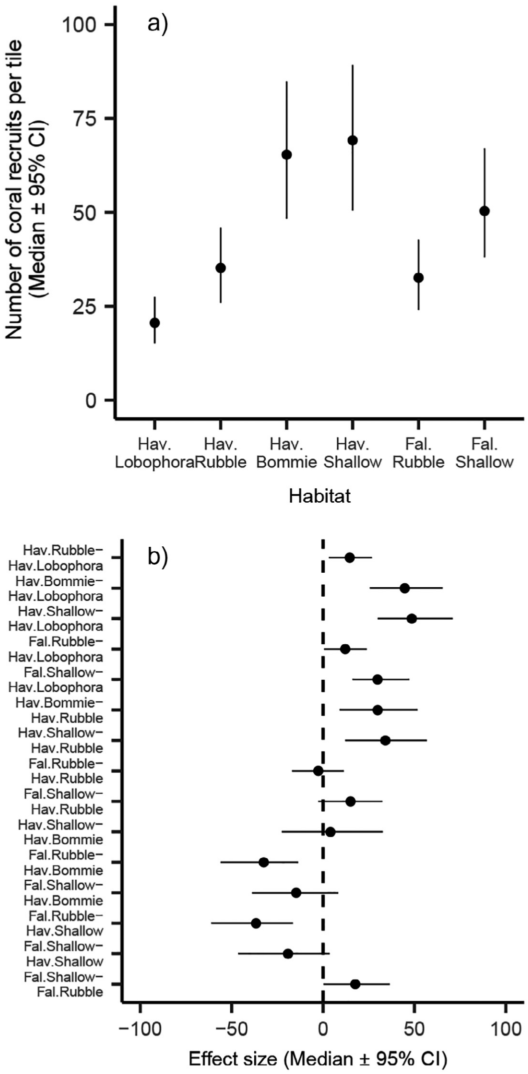

Fig. 2. (a) Total number of coral recruits on experimental tiles in each habitat at Havannah Reef (Hav.) and at the control reef (Fal.). (b) The effect sizes for pairwise comparisons of recruit numbers for each habitat. When 95% Bayesian credibility intervals (CI) do not overlap the vertical dotted line, there is strong evidence that the number of recruits is greater in the habitat that is first listed (to the right of the line) or second listed (to the left of the line).

compared to all other habitats (Fig. 2b). Recruitment was almost double in both Havannah Rubble and Falcon Rubble habitats, and triple in Havannah Bommie and Havannah Shallow habitat, compared to Havannah *Lobophora* habitat (Fig. 2a). The median recruit survival on tiles at Havannah Reef ranged from 27% to 44% in the *Lobophora* and Bommie habitats, respectively (Fig. 3a). There was strong evidence that median survival in *Lobophora* habitat was lower than in adjacent Rubble and Bommie habitats, but was similar to that in Shallow habitat (Fig. 3b).

Juvenile coral persistence

A total of 89 juvenile corals from 17 hard coral genera were recorded across 26 quadrats at Havannah Reef in November 2014. Of these, 31 were relocated within fixed quadrats nine months later in August 2015, along with 40 juvenile corals that had not been recorded in the initial census (November 2014). Juvenile corals were found in all habitats at Havannah Reef and median persistence of the 89 corals that were initially recorded in November ranged from 10% to 60% among habitats (Fig. 4). Persistence of juvenile corals in *Lobophora* habitat (57%) differed little to that recorded in Shallow and Bommie habitat. Persistence in *Lobophora* (prior removal) was less at 28%, but still within expected bounds based on pooled data (Fig. 4). However, persistence in Rubble habitat was much lower (10%) and below the expected range (Fig. 4).

During the August 2015 census, it was apparent from photographs that the substrate within some quadrats had changed substantially since November 2014 (Fig. 5), and some new juvenile corals attached to small pieces of unconsolidated rubble had arrived in quadrats. In total, there were 8 (or 1/5) of these transient juvenile corals among the 40 newly arrived individuals at Havannah Reef. These transients only occurred in habitats that had a rubble-based substratum (*Lobophora* [prior removal], *Lobophora,* and Rubble) rather than a solid substratum (Bommie, Shallow; Appendix S1: Table S1).

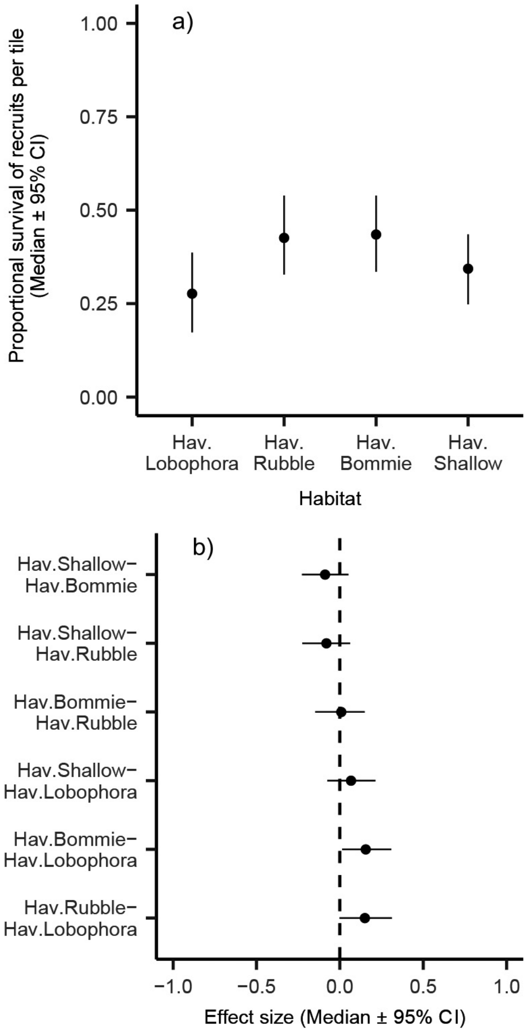

Fig. 3. (a) Proportional survival of coral recruits on experimental tiles in habitats at Havannah Reef. (b) The effect sizes for pairwise comparisons of recruit survival for each habitat. When 95% Bayesian credibility intervals (CI) do not overlap the vertical dotted line, there is strong evidence that proportional survival is greater in the habitat that is first listed (to the right of the line) or second listed (to the left of the line).

DISCUSSION

The causes of macroalgae regime shifts on coral reefs are well established; however, a deeper understanding of feedback mechanisms that inhibit the recovery of coral populations is still required (Nyström et al. 2012). Here we show that coral recruitment rates at a regime-shifted reef and at an adjacent coral-dominated reef were similar in comparable habitats that were largely free of macroalgae. While we cannot assume that these recruitment patterns directly reflect patterns established at settlement (see

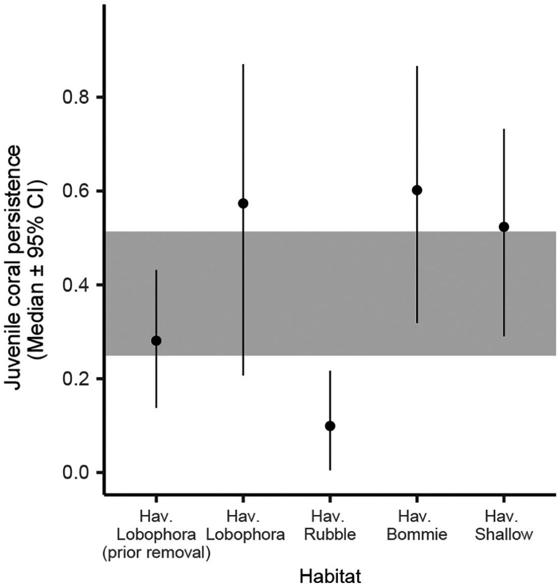

Fig. 4. Proportion of the total number of juvenile corals that persisted in quadrats from November 2014 to August 2015 in habitats at Havannah Reef. The gray band spans the upper and lower 95% Bayesian credibility intervals (CI) of median persistence of juvenile corals pooled across habitats. For each habitat, if CIs do not overlap with the gray band, then persistence is outside of the range expected based on the pooled data.

Keough and Downes 1982), they do suggest that the presence of extensive beds of macroalgae neither influenced larval supply or behavior to settle at the spatial scale of reefs. Rather, processes at finer spatial scales within the regime-shifted reef (i.e., among habitats) must be inhibiting coral recovery. Comparing neighboring but differing habitats within the regime-shifted reef, we show that coral recruitment and early (2 months) recruit survival was markedly reduced in the vicinity of dense macroalgae beds dominated by the brown macroalga *Lobophora,* compared with habitats relatively free of macroalgae just meters away. Surprisingly, beds of *Lobophora* did not appear to have similar negative impacts on juvenile corals, with juvenile coral persistence in this habitat similar to that in neighboring habitats. Rather, juvenile coral persistence was lowest in rubble habitat, presumably due to the observed movement of the unconsolidated substrata. The suppressed rates of coral recruitment and recruit survival for the first months on the reef coupled with the instability of the substratum are likely to have created dual bottlenecks to the recovery of coral populations on Havannah Reef.

Coral recruitment and recruit survival

Similar coral recruitment rates to tiles in comparable habitats at Havannah Reef and Falcon Reef suggest that larval supply was not a contributing factor to the lack of coral recovery at Havannah Reef. Naturally poor connectivity among reefs or reductions in coral brood stock (Hughes 1994, Hughes et al. 2000) or fecundity (Baird and Marshall 2002) following disturbances

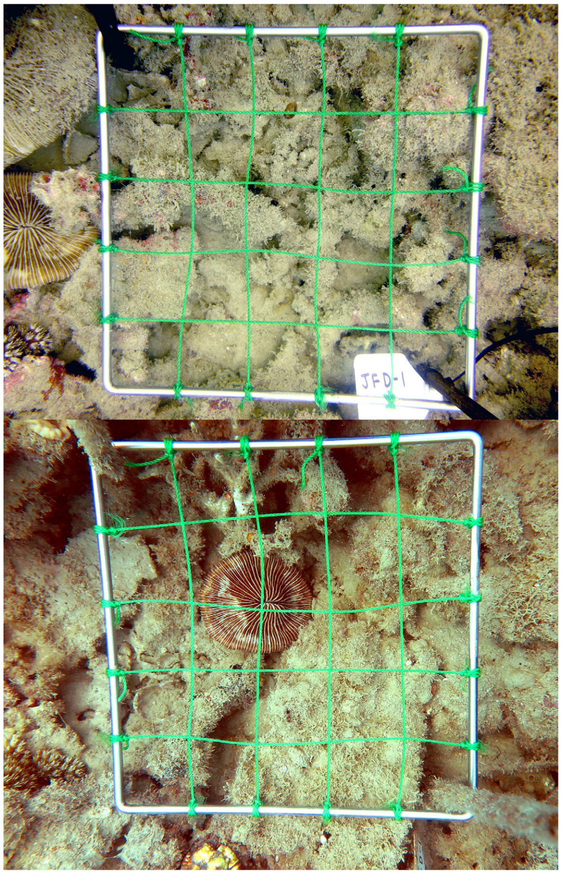

Fig. 5. Substrate in a juvenile coral quadrat in Rubble habitat in November 2014 (top) and in the same quadrat in August 2015 (bottom). The size and shape of the rubble substrate has clearly changed. The *Fungia* corals have also moved; this may be due to water movement, but these free-living corals can also move themselves. In the bottom left corner is a colony of *Galaxea* sp. that remained in its place.

can limit larval supply and hence the recovery potential of reefs. In 2014, the number of coral recruits on tiles within Rubble and Shallow habitats on Havannah Reef was greater than on tiles in comparable habitats on Falcon reef. Further, numbers of coral recruits on tiles in Shallow and Bommie habitats at Havannah Reef (~70 recruits per tile) were relatively high for the wider GBR (Hughes et al. 1999). It is possible that poor larval supply limited coral recovery potential in the early part of the time series, with sequential disturbances over five years (coral bleaching, 1998; Cyclone Tessi, 2000; coral bleaching, 2002) compromising regional coral health and brood stock abundance. Specifically, hard coral cover on nearby reefs (Palm Island Group and Rattlesnake reef) was reduced to low levels following the 1998 bleaching event in particular, with little recovery evident up until 2007 (Sweatman et al. 2007). Also, the magnitude of coral recruitment we recorded is unlikely to represent patterns over longer temporal scales. However, neighboring habitats at Havannah Reef (Bommie and Shallow) and habitats at the adjacent Falcon Reef (Rubble and Shallow) supported coral communities of moderate to high hard coral cover for GBR reefs (Miller et al. 2009) with a wide range of colony sizes (Appendix S2: Fig. S2). This suggests that coral recruitment and growth have been occurring in favorable habitats and limited larval supply has not been a regionally widespread constraint for coral recovery over the entire temporal series.

Despite the similarities in coral recruitment between reefs, there were substantial differences in recruitment and recruit survival among habitats on Havannah Reef. Coral recruitment in *Lobophora* habitat was approximately half of that in Rubble habitat, and less than a third of that in Bommie and Shallow habitats on Havannah Reef. Further, the survival of coral recruits in *Lobophora* habitat was just over half of that in adjacent Rubble and Bommie habitats, such that the number of coral recruits surviving up to 2 months post-settlement was approximately 3–5 times greater in Rubble and Bommie habitats than in the adjacent *Lobophora* habitat. These highly localized effects suggest that the dense beds of *Lobophora* on Havannah Reef are not deterring larvae from settling on the scale of the entire reef, as has been hypothesized for macroalgal-dominated reefs elsewhere (Dixson et al. 2014).

The effects of macroalgae on larval recruitment and recruit survival are highly variable and are dependent on both the identity of the algae and coral species (see reviews by Birrell et al. 2008*a*, Ritson-Williams et al. 2009). For example, *Lobophora* sp. induced recruitment of *Acropora millepora* larvae (Birrell et al. 2008*b*), but inhibited recruitment and/or killed *Stylophora pistillata* and *Acropora* spp. larvae (Baird and Morse 2004, Kuffner et al. 2006). These differences among studies are difficult to reconcile but may relate to variation in interactions depending on the coral species, or the experimental techniques (Birrell et al. 2008*a*). Even when direct negative effects of *Lobophora* on coral recruitment and survival are not evident, sub-lethal impacts on coral condition and growth can suppress the recovery of coral populations (Box and Mumby 2007, Birrell et al. 2008*b*). Critically, *Lobophora* may not only impact the early life stages of corals, but has also been shown to negatively impact adult corals (Jompa and McCook 2002), particularly through allelopathy (Rasher and Hay 2010, Morrow et al. 2017).

Macroalgae have been hypothesized to influence the recruitment and survival of corals through a variety of physical, chemical, and indirect mechanisms, including the pre-emption of space, canopy exclusion, abrasion, production of secondary metabolites, altered water flow and sediment regimes, and altered microbial communities (Birrell et al. 2008*a*, Ritson-Williams et al. 2009). Our study design does not allow us to differentiate the relative importance of these mechanisms on coral recruitment and survival; a number are likely to be contributing. However, we suggest that the lower recruitment of corals on tiles in *Lobophora* habitat is more likely related to chemical or indirect effects as tiles were set 10 mm above the algal canopy for consistency in experimental design among habitats, so limiting any potential physical effects. Also, even with physical interference by macroalgae removed as a potential driver of coral recruitment patterns, recruitment was highest on the upper surface of the tile in *Lobophora* habitat (Appendix S3: Fig. S1), which is contrary to typical patterns of recruitment on tiles (Raimondi and Morse 2000, Doropoulos et al. 2016). Considering that physical interactions between macroalgae and coral recruits would certainly occur on natural substrate in *Lobophora* habitat, it is likely that our coral recruitment and survival results in this habitat are overestimates. While our results show strong evidence of negative impacts of macroalgae on coral recruitment and recruit survival, they would have been strengthened if more regime-shifted reefs were available to allow replication at the spatial scale of reef. Additionally, our results argue for a closer evaluation of supply and settlement to examine how they influenced the patterns of coral recruitment in this study.

Juvenile coral persistence

The replenishment of coral populations is not only dependent on the successful settlement of coral larvae and their early survival, but the survival of juvenile corals until they enter the adult population. Juvenile corals in *Lobophora* habitat were able to persist as well as those in neighboring Bommie and Shallow habitats, and similar rates of survival (50–60%, equating to 5–7% mortality per month) have been observed in other settings that were also relatively free of macroalgae (e.g., GBR: Trapon et al. 2013, Florida: Cameron et al. 2016). In *Lobophora* habitat, possible reasons why these comparable persistence rates were not reflected in adult coral cover, as they were in Bommie and Shallow habitats, where hard coral cover was moderate, include the following: (1) very low initial abundance of juvenile corals in *Lobophora* habitat (which we were unable to adequately assess due to small sample sizes), (2) high mortality rates at larger colony sizes, and (3) incomplete progression of juvenile mortality processes in the nine-month experimental time frame, for example, where *Lobophora* may reduce juvenile coral growth rates, exposing them to size-dependent mortality for longer (e.g., Box and Mumby 2007). We cannot assess whether the initial clearing of quadrat plots in *Lobophora* habitat to enable identification of juveniles altered their persistence relative to juveniles that remained covered. However, given that one month after algal removal *Lobophora* had largely re-invaded plots cleared prior to spawning and that all plots were mostly indistinguishable from the general Lobophora habitat after nine months, we expect that persistence results are unlikely to have been unduly influenced by the initial clearing.

Persistence of juvenile corals was extremely low (10% over nine months) in Rubble habitat, most likely due to the mobilization of the rubble substrate. Over nine months, the substrate was turned over in rubble-based habitats (Havannah *Lobophora*, Havannah *Lobophora* (prior removal), and Havannah Rubble) and at least one quarter of newly arrived juvenile corals in these habitats appeared to be transient, having rolled in to the quadrat on a piece of rubble. Such evidence of rubble mobilization was a surprise, as we had assumed the rubble would be bound and stable so that rubble movement mostly occurred during cyclonic conditions that were not experienced during our study period. Mobilization of rubble causes smothering and abrasion of small corals and has resulted in juvenile coral killing fields in Indonesia after blast fishing (Fox et al. 2003). It has also been implicated in the lack of coral recovery in the Seychelles (Chong-Seng et al. 2014), Florida (Cameron et al. 2016), and the Lakshadweep archipelago (Yadav et al. 2016).

Prior to disturbance, the hard coral community at Havannah Reef was dominated by corals with arborescent and foliose growth forms (Appendix S2: Fig. S3), which are particularly vulnerable to structural breakdown following disturbances (Marshall 2000), causing the formation of rubble beds. A suite of physical and biological processes are involved in binding rubble (Rasser and Riegl 2002), which makes the substrate more conducive to successful recruitment, growth, and survival of corals. For binding processes to take place, the rubble must initially stabilize (Rasser and Riegl 2002). While we cannot speculate about the influence of various rubble binding processes at Havannah Reef, initial stabilization of rubble in sheltered substrate depressions may be prevented by the combination of low underlying substrate rugosity (Wilson et al. 2009) and regular exposure to wind-driven swells, precluding binding processes and further stifling coral recovery. Our serendipitous results provided unequivocal evidence that rubble redistribution in non-cyclonic conditions can impact young corals on the GBR and suggest that the factors determining rubble stability and its influence on system recovery deserve greater attention.

Summary and implications

The suppression of coral recruitment and early survival of recruits by *Lobophora*, and mobilization of rubble, reducing persistence of small corals, appear to be hindering the recovery of coral populations and reinforcing high macroalgal abundance at Havannah Reef. Further, the relative influence of these bottlenecks on coral recovery varies at small spatial scales (among adjacent habitats); that is, rubble mobilization is most influential in Rubble habitat, while detrimental effects of macroalgae on larval recruitment and recruit survival are most influential in *Lobophora* habitat. Unless these positive feedbacks are broken, it appears unlikely that coral populations at the monitored sites on Havannah Reef will recover. Reefs with similar characteristics such as high abundance of corals with high susceptibility to mechanical breakage, low substrate rugosity, and depauperate herbivore populations (Cheal et al. 2010) may be particularly subject to poor recovery rates, especially following physically destructive disturbances. As exposure of reefs to disturbances is increasing globally, recognition of reefs at risk of a similar fate is critical so that management strategies can be directed accordingly.

ACKNOWLEDGMENTS

This manuscript was greatly improved with constructive feedback from Dr. Mark Carr and two anonymous reviewers. We thank all past and present members of the Long-term Monitoring Program (LTMP) at the Australian Institute of Marine Science (AIMS) who helped to gather the data used in this study. Thanks to the staff of the AIMS Marine Monitoring Program, AIMS National Sea Simulator, Orpheus Island Research Station, AIMS Data Centre, and AIMS Marine Operations for the use of their facilities and their assistance. The Long-Term Monitoring Program is supported by AIMS and has been funded in part by the Australian Government's National Environmental Research Program and National Environmental Science Program.

LITERATURE CITED

Babcock, R. C., A. H. Baird, S. Piromvaragorn, D. P. Thomson, and B. L. Willis. 2003. Identification of scleractinian coral recruits from Indo-Pacific reefs. Zoological Studies 42:211–226.

Baird, A. H., J. R. Guest, and B. L. Willis. 2009. Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. The Annual Review of Ecology, Evolution, and Systematics 40:551–571.

Baird, A. H., and P. A. Marshall. 2002. Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Marine Ecology Progress Series 237:133–141.

Baird, A. H., and A. N. C. Morse. 2004. Induction of metamorphosis in larvae of the brooding corals *Acropora palifera* and *Stylophora pistillata*. Marine and Freshwater Research 55:469–472.

Birrell, C. L., L. J. McCook, B. L. Willis, and G. A. Diaz-Pulido. 2008*a*. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. Oceanography Marine Biology: an Annual Review 46:25–63.

Birrell, C. L., L. J. McCook, and B. L. Willis. 2008*b*. Chemical effects of macroalgae on larval settlement of the broadcast spawning coral *Acropora millepora*. Marine Ecology Progress Series 362: 129–137.

Box, S. J., and P. J. Mumby. 2007. Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. Marine Ecology Progress Series 342:139–149.

Cameron, C., R. Pausch, and M. W. Miller. 2016. Coral recruitment dynamics and substrate mobility in a rubble-dominated back reef habitat. Bulletin of Marine Science 92:123–136.

Carpenter, B., A. Gelman, M. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. A. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan: a probabilistic programming language. Journal of Statistical Software 76:1–31.

Cheal, A. J., M. A. MacNeil, E. Cripps, M. J. Emslie, M. Jonker, B. Schaffelke, and H. Sweatman. 2010. Coral–macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. Coral Reefs 29:1005–1015.

Cheal, A. J., A. M. MacNeil, M. J. Emslie, and H. Sweatman. 2017. The threat to coral reefs from more intense cyclones under climate change. Global Change Biology 23:1511–1524.

Chong-Seng, K. M., N. A. J. Graham, and M. S. Pratchett. 2014. Bottlenecks to coral recovery in the Seychelles. Coral Reefs 33:449–461.

Connell, J. H. 1973. Population ecology of reef-building corals. Pages 205–245 in O. A. Jones and R. Endean, editors. Biology and geology of coral reefs. Academic Press, New York, New York, USA.

Connell, J. H., T. P. Hughes, and C. C. Wallace. 1997. A 30 year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecological Monographs 67:461–488.

Cuet, P., O. Naim, G. F. Faure, and J.-Y. Conan. 1988. Nutrient-rich groundwater impact on benthic communities of La Saline fringing reef (Reunion Island, Indian Ocean): preliminary results. Proceedings of the 6th International Coral Reef Symposium 2:207–212.

Dell, C., G. O. Longo, and M. E. Hay. 2016. Positive feedbacks enhance macroalgal resilience on degraded coral reefs. PLoS ONE 11:e0155049.

Dixson, D., D. Abrego, and M. Hay. 2014. Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. Science 345:892–897.

Done, T. J. 1992. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121–132.

Done, T. J., P. K. Dayton, A. E. Dayton, and R. Steger. 1991. Regional and local variability in recovery of shallow coral communities: Moorea, French Polynesia and central Great Barrier Reef. Coral Reefs 9:183–192.

Doropoulos, C., G. Roff, Y. M. Bozec, and M. Zupan. 2016. Characterizing the ecological trade-offs throughout the early ontogeny of coral recruitment. Ecological Monographs 86:20–44.

Fabricius, K. E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin 50:125–146.

Folke, C., S. Carpenter, B. Walker, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. The Annual Review of Ecology, Evolution and Systematics. 35:557–581.

Foster, N. L., S. J. Box, and P. J. Mumby. 2008. Competitive effects of macroalgae on the fecundity of the reef-building coral *Montastraea annularis*. Marine Ecology Progress Series 367:143–152.

Fox, H. E., J. S. Pet, R. Dahuri, and R. L. Caldwell. 2003. Recovery in rubble fields: long-term impacts of blast fishing. Marine Pollution Bulletin 46:1024–1031.

Graham, N. A. J., S. Jennings, M. A. MacNeil, D. Mouillot, and S. K. Wilson. 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:94–97.

Halford, A., A. J. Cheal, D. Ryan, and D. Mc. B. Williams. 2004. Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. Ecology 85:1892–1905.

Hata, T., J. S. Madin, V. R. Cumbo, M. Denny, J. Figueiredo, S. Harii, C. J. Thomas, and A. H. Baird. 2017. Coral larvae are poor swimmers and require fine-scale reef structure to settle. Scientific Reports 7:1–9.

Hoey, A. S., and D. R. Bellwood. 2011. Suppression of herbivory by macroalgal density: A critical feedback on coral reefs? Ecology Letters 14:267–273.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551.

Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschaniwskyj, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 1999. Patterns of recruitment and abundance of corals along the Great Barrier Reef. Nature 397:59–63.

Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschaniwskyj, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 2000. Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. Ecology 81:2241–2249.

Hughes, T. P., N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, and R. S. Steneck. 2010. Rising to the challenge of sustaining coral reef resilience. Trends in Ecology & Evolution 25:633–642.

Hughes, T. P., et al. 2017. Global warming and recurrent mass bleaching of corals. Nature 543:373–377.

Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637.

Johns, K. A., K. Osborne, and M. Logan. 2014. Contrasting rates of coral recovery and reassembly in coral communities on the Great Barrier Reef. Coral Reefs 33:553–563.

Jompa, J., and L. J. McCook. 2002. The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*). Limnology and Oceanography 47:527–534.

Jonker, M., K. A. Johns, and K. Osborne. 2008. Surveys of benthic reef communities using underwater digital photography and counts of juvenile corals. Long-term Monitoring of the Great Barrier Reef. Standard Operational Procedure No. 10. Australian Institute of Marine Science, Townsville, Queensland, Australia.

Keough, M. J., and B. J. Downes. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia 54:348–352.

Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. American Zoologist 32:674–682.

Kuffner, I. B., L. J. Walters, M. A. Becerro, V. J. Paul, R. Ritson-Williams, and K. S. Beach. 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. Marine Ecology Progress Series 323:107–117.

Marshall, P. A. 2000. Skeletal damage in reef corals: relating resistance to colony morphology. Marine Ecology Progress Series 200:177–189.

McClanahan, T., and N. Muthiga. 1998. An ecological shift in a remote coral atoll of Belize over 25 years. Environmental conservation 25:122–130.

McManus, J. W., and J. F. Polsenberg. 2004. Coral–algal phase shifts on coral reefs: ecological and environmental aspects. Progress in Oceanography 60:263–279.

Miller, I., M. Jonker, and G. Coleman. 2009. Crown-of-thorns starfish and coral surveys using the manta tow and SCUBA search techniques. Standard Operational Procedure No. 9. Australian Institute of Marine Science, Townsville, Queensland, Australia.

Moberg, F., and C. Folke. 1999. Ecological goods and services of coral reef ecosystems. Ecological Economics 29:215–233.

Morrow, K. M., K. Bromhall, C. A. Motti, C. B. Munn, and D. G. Bourne. 2017. Allelochemicals produced by brown macroalgae of the *Lobophora* genus are active against coral larvae and associated bacteria, supporting pathogenic shifts to *Vibrio*-dominance. Applied and Environmental Microbiology 83: e02391–16.

Mumby, P. J., and R. S. Steneck. 2008. Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends in Ecology & Evolution 23:555–563.

Nugues, M. M., and A. M. Szmant. 2006. Coral settlement onto *Halimeda opuntia*: A fatal attraction to an ephemeral substrate? Coral Reefs 25:585–591.

Nyström, M., A. V. Norström, T. Blenckner, M. de la Torre-Castro, J. S. Eklöf, C. Folke, H. Osterblom, R. S. Steneck, M. Thyresson, and M. Troell. 2012. Confronting feedbacks of degraded marine ecosystems. Ecosystems 15:695–710.

Pandolfi, J. M., et al. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955–958.

Piniak, G. A., N. D. Fogarty, C. M. Addison, and W. J. Kenworthy. 2005. Fluorescence census techniques for coral recruits. Coral Reefs 24:496–500.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raimondi, P. T., and A. Morse. 2000. The consequences of complex larval behavior in a coral. Ecology 81:3193–3211.

Rasher, D. B., and M. E. Hay. 2010. Chemically rich seaweeds poison corals when not controlled by herbivores. Proceedings of the National Academy of Sciences of the United States of America 107:9683–9688.

Rasser, M., and B. Riegl. 2002. Holocene coral reef rubble and its binding agents. Coral Reefs 21:57–72.

Ritson-Williams, R., S. N. Arnold, N. D. Fogarty, R. S. Steneck, M. J. A. Vermeij, and V. J. Paul. 2009. New perspectives on ecological mechanisms affecting coral recruitment on reefs. Smithsonian Contributions to the Marine Sciences 38:437–457.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology & Evolution 18:648–656.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

Shulman, M. J., and D. R. Robertson. 1996. Changes in the coral reefs of San Blas, Caribbean Panama: 1983 to 1990. Coral Reefs 15:231–236.

Smith, S. V., W. J. Kimmerer, E. A. Laws, R. E. Brock, and T. W. Walsh. 1981. Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. Pacific Science 35:279–395.

Sweatman, H., A. Thompson, J. Delean, J. Davidson, and S. Neale. 2007. Status of near-shore reefs of the Great Barrier Reef 2004. Marine and Tropical Sciences Research Facility Research Report Series. Reef and Rainforest Research Centre Limited, Cairns, Queensland, Australia.

Tanner, J. E. 1995. Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. Journal of Experimental Marine Biology and Ecology 190:151–168.

Trapon, M. L., M. S. Pratchett, M. Adjeroud, A. S. Hoey, and A. H. Baird. 2013. Post-settlement growth and mortality rates of juvenile scleractinian corals in Moorea, French Polynesia versus Trunk Reef, Australia. Marine Ecology Progress Series 488:157–170.

van de Leemput, I. A., T. P. Hughes, E. H. van Nes, and M. Scheffer. 2016. Multiple feedbacks and the prevalence of alternate stable states on coral reefs. Coral Reefs 35:857–865.

Vermeij, M. J. A., and S. A. Sandin. 2008. Density-dependent settlement and mortality structure the earliest life phases of a coral population. Ecology 89:1994–2004.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer, New York, New York, USA.

Wilson, S. K., A. M. Dolman, A. J. Cheal, M. J. Emslie, M. S. Pratchett, and H. P. A. Sweatman. 2009. Maintenance of fish diversity on disturbed coral reefs. Coral Reefs 28:3–14.

Wismer, S., A. S. Hoey, and D. R. Bellwood. 2009. Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. Marine Ecology Progress Series 376:45–54.

Yadav, S., P. Rathod, T. Alcoverro, and R. Arthur. 2016. Choice and destiny: The substrate composition and mechanical stability of settlement structures can mediate coral recruit fate in post-bleached reefs. Coral Reefs 35:211–222.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2349/full