

Confronting feedback processes on degraded coral reefs

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STATEMENT OF CONTRIBUTION OF OTHERS

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ABSTRACT

Coral reefs are degrading under global stressors that are increasing in frequency and severity as the Anthropocene accelerates. My thesis contributes to our scientific understanding of the dynamics that govern degraded coral reef states. More specifically, I contribute to our understanding of feedback processes on degraded coral reefs in conceptual and experimental ways by confronting both ecological and social-ecological feedbacks in ways that may have merit in triggering coral recovery.

My four presented studies (**Chapters 1-4**) pursue the following research questions: 1. Which habitat drivers best predict juvenile coral densities following bleaching? 2. Can macroalgae-reinforcing feedbacks be weakened through shading? 3. Can sea urchins effectively weaken macroalgal feedbacks given their current natural densities? 4. Can red and green loops uncover missing social-ecological feedbacks?

Juvenile corals are a critical life history stage representing survival and growth of new recruits into the population. **Chapter 1** compares juvenile coral densities from before the 2016 bleaching event with those after and identifies abiotic and biotic habitat drivers collected in the inner Seychelles that predict juvenile coral densities. Following the 2016 bleaching event, juvenile coral densities were significantly reduced by about 70 %, with a particularly severe decline in juvenile *Acropora* corals. Macroalgae present a major obstacle to survival of juvenile corals shortly following mass bleaching, but their influence varies as a function of herbivore biomass, reef structure, and reef type. In contrast, increasing structural complexity on granitic reefs is a strong positive predictor of juvenile coral density.

Macroalgae can maintain and increase their dominance with effective self-reinforcing feedback mechanisms and can significantly compromise ecosystem function. **Chapter 2** assesses shading as a management tool in an experimental confrontation of macroalgal feedbacks, aiming to maximise the benefit of habitat mosaic reefs in the inner Seychelles. Shading reduces the algae's ability to photosynthesise by 29 % to the point where macroalgal cover can be reduced by 51 % and turf algal growth can be reduced by 82 % within six weeks of shading. After removal of shading structures,

herbivore grazing rates decreased at shading plots, and algal beds recovered quickly, almost completely regrowing within three months.

Tropical sea urchins are often considered as macroalgal grazers, but this assumption relies heavily on geographically limited observations of select species. **Chapter 3** addresses these gaps for a common urchin species in the Seychelles, *Echinothrix calamaris*, using a combination of survey and experimental approaches in the inner Seychelles. Habitat driver models revealed patch-reef types as the best positive predictor and macroalgae as the best negative predictor of urchin densities. Experimentally penning urchin densities (maximum 4.44 urchins m⁻²) resulted in a reduction of macroalgal cover by only 13 %. Therefore *E. calamaris* at current densities in Seychelles (mean: 0.02 urchins m⁻², maximum: 0.16 urchins m⁻²) are unlikely to perform significant macroalgae controlling functions.

People use their local ecosystems and can retrieve signals about how their actions affect ecosystem health. Capturing, interpreting, and responding to signals that indicate changes in ecosystems is key for their sustainable management and breaks in this signal-response, called missing feedbacks, will allow ecosystem health to degrade unnoticed. **Chapter 4** applies an existing concept from sustainability science, the red-loop green-loop (RL-GL) model, to uncover missing feedbacks between reefs and people of Jamaica from the year 600 until now. This allowed the factors responsible for missing feedbacks to be identified – a main factor in Jamaica was seafood exports. An intervention to move Jamaica back to more sustainable dynamics between people and reefs could be to gradually move away from seafood exports and build ownership and management capacity in local seafoods.

Overall, my thesis emphasises the importance of habitat for coral recruitment following severe coral bleaching as well as for urchin density and function in Seychelles. Furthermore, I cover management approaches to confront reinforcing feedbacks of expanding macroalgal fields, especially for a mosaic reefscape setting. I test the first method to reduce macroalgal cover via the alteration of the light regime. My thesis also includes the first study to apply the RL-GL concept to a coral reef social-ecological system and I advocate for its practicality in uncovering missing feedbacks and in gaining an understanding of past, present, and future sustainability that can be of use in other systems.

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GENERAL INTRODUCTION

Coral reef degradation and regime shifts

Many coral reefs around the world are degrading (Pandolfi et al. 2003; Wilkinson 2008; Cinner et al. 2016). The habitat-forming hard corals (Order Scleractinia) are degrading under an array of stressors that extend from local to global scales. Stressors such as eutrophication from coastal run-off (Bell 1992; McCook 1999), overfishing (Hughes 1994), erosion (Schönberg et al. 2017) from ocean acidification or storms (De'ath et al. 2012), as well as mass bleaching from ocean warming (Graham et al. 2015) have led to major shifts in the structure and function of coral reef systems. Future projections of some of these stressors underpin an increasing frequency of shifts away from coral-dominated regimes (Mumby 2009). Mass bleaching of corals, for instance, is expected to increase in frequency over the coming decades (Hughes et al. 2018) and is one of the major stressors that caused significant losses in coral cover on global reefs (Goreau et al. 2000; Hughes et al. 2017b). When scleractinian corals are reduced in benthic dominance, shifts to alternative regimes, such as algae, sponges, or soft corals (Norström et al. 2009) are often reported. Even reef ecosystems where corals are still dominant or instances where they are recovering often show assemblages vastly different from historical baselines (Graham et al. 2014). For instance, on Indo-Pacific coral reefs, modern climate and anthropogenic disturbances appear to select stress-tolerant and 'weedy' (quick growth, short-lived, small size) traits within the coral community (McClanahan et al. 2014). Despite it still being a coral-dominated state, the new community composition can be very different in composition and function (Alvarez-Filip et al. 2013).

Coral reef recovery and juvenile coral density

Corals can recover from large scale losses in coral cover which requires the reassembly of the scleractinian community (Connell et al. 1997). Coral recovery often takes decades to accomplish (Gilmour et al. 2013; Graham et al. 2015), provided key factors such as anthropogenic climate change, water quality, and fishing are kept within safe operating spaces (Norström et al. 2016). Coral recruitment, the replenishment of the local population by new individuals from within or outside an

existing population (Hughes et al. 2010), is a key aspect of coral recovery. The coral recruit stage, the life stage immediately after coral larvae have settled from the water column onto the reef, is when benthic coral mortality is proportionately highest (Hughes et al. 2007; Doropoulos et al. 2016). Despite mortality rates still being higher than in other benthic coral life stages, the juvenile coral stage (0.5 – 5 cm; Roth and Knowlton 2009) marks the survival of the initial demographic mortality spike following recruit settlement (Doropoulos et al. 2016). The importance of this critical life stage to recovery dynamics paired with the relative ease of measurement (Doropoulos et al. 2016) make juvenile coral density a common measures of coral recovery potential (Doropoulos et al. 2015; Graham et al. 2015; Álvarez-Noriega et al. 2018; Jonker et al. 2019).

In their long-term study, Graham et al. (2015) found five positive predictors of whether a coral reef is able to rebound from mass-bleaching events, including herbivore biomass, nutrient concentration, initial structural complexity, depth, and juvenile coral density. However, which habitat drivers predict where juvenile coral densities are likely to be highest immediately after a mass-bleaching event, are poorly studied. Being able to predict in which areas juvenile corals are most likely to aggregate in light of more frequent bleaching events is an important research gap to coral recovery research and coral reef management alike.

Alternative stable states and feedback processes

Regime shifts are often initiated by press disturbances or external drivers (chronic events, e.g. climate change, pollution). These can trigger a new ecosystem trajectory, alter environmental conditions (e.g. high temperatures, eutrophication) and render the current state more susceptible to pulse disturbances (acute events, e.g. mass bleaching of corals, algal blooms), which can push the system into an alternative stable state (Sternberg 2001). When systems do not readily recover to their original state and instead become locked in an alternative stable state, the occurring lag is called ‘hysteresis’ (Scheffer et al. 2001). Alternative stable states can exist in similar environmental conditions as the original state and each can be stabilised or destabilised by internal processes. These are integral parts of any ecosystem and are referred to as ‘feedback processes’ (Nyström et al. 2012) – two-way (A affects B affects A) or more complex, circular interactions (A affects B affects C affects A) between various ecosystem components

(van de Leemput et al. 2016). The reduction of one component can lead to amplification of another and vice versa. Those that reduce fluctuations, create attractors, and can lock a system in a state are referred to as ‘reinforcing feedbacks’ (or ‘negative’ or ‘stabilising feedbacks’). Feedbacks that oppose this trajectory amplify changes and cause the system to destabilise, are therefore referred to as ‘destabilising feedbacks’ (or ‘positive’ or ‘amplifying feedbacks’; DeAngelis et al. 1986). Pulse and press disturbances can interact with feedbacks, weaken reinforcing ones, and cause destabilising ones to gain dominance. In summary, feedback processes can weaken or strengthen the stability of individual states in an alternative stable states model (Fig. 0.1).

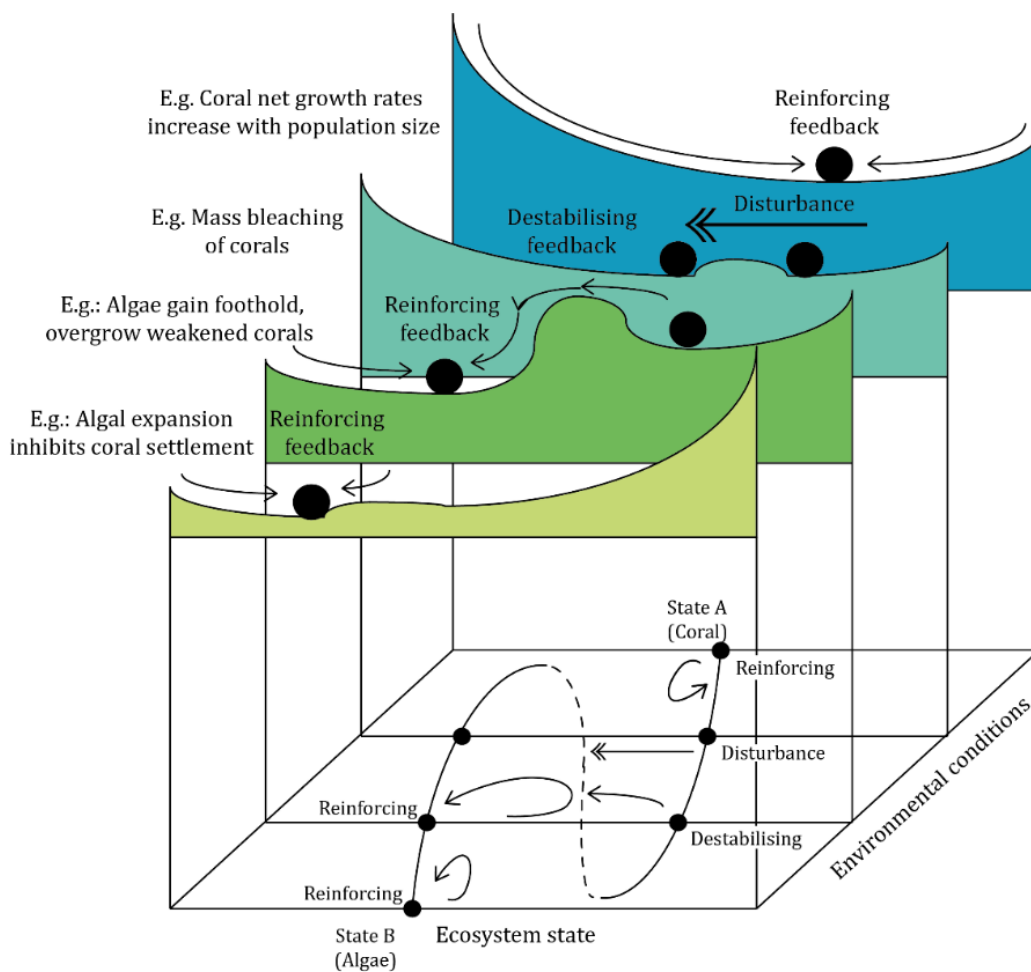


Figure 0.1 Ball-and-valley diagram (above) and feedback-threshold diagram (below) showing transition from ecosystem state A (e.g. coral) to degraded state B (e.g. macroalgae) through range of environmental conditions and with effect of feedback processes (single arrows) and disturbances (double arrow), two balls in one environmental condition point display alternative stable states, split by the feedback threshold (dotted line); modified from Scheffer et al. (2001).

Stability landscapes diagram

The nature of feedbacks can change depending on whether they are acting across or within a feedback threshold. Feedback thresholds or tipping points are often depicted by a hill peak in the ball-and-valley diagram and as a dotted line in the feedback-threshold diagram (Fig. 0.1). Destabilising feedbacks promote the ecosystem trajectory to an alternative attractor across the threshold or hill peak. Once the valley of the alternative attractor is reached, they act as reinforcing feedbacks to it (Mumby and Steneck 2008). The diagram is also referred to as a ‘stability landscapes diagram’ because it displays the stability of each attractor and state as a valley (Scheffer et al. 2001). The depth of each valley represents the state’s resilience and the strength of reinforcing feedbacks. Changes in environmental conditions, strength of disturbances and strength of destabilising feedbacks can alter the size and shape of the slopes even to the point where a valley disappears completely (Scheffer and Carpenter 2003). Often, more localised feedbacks act within the threshold boundaries and only become apparent once the system approaches the feedback threshold or tipping point between two attractors; i.e. once the ball approaches a downward slope. Since interactions between processes are the core of ecosystems, feedback processes are no exception (Scheffer et al. 2001). Multiple feedbacks can work in conjunction, alongside or opposing each other and vary in strength. Single feedbacks, if strong enough in relation to other ecosystem processes (including opposing feedbacks), can create an alternative attractor and push a system’s current state towards it, creating a hysteretic response to environmental condition (van de Leemput et al. 2016). Strong feedbacks can cause a threshold response (i.e. ball pushed up to a hill peak) while even stronger ones can cause a hysteresis and catastrophic shifts (i.e. ball pushed into alternative attractor valley; Scheffer et al. 2001; Nyström et al. 2012). Several weaker but interactive feedbacks can have a similar effect. Multiple weak feedbacks can act in conjunction and are most often the cause for unexpected and abrupt shifts between alternative stable states or dominant regimes (van de Leemput et al. 2016; Hughes et al. 2017a).

Coral-algal regime shifts and macroalgal feedbacks

Reef regime shifts from coral to algae are arguably among the most well-documented (Bellwood et al. 2004; Hughes et al. 2007; Mumby 2009; Graham et al. 2015) and are governed by the interplay of

external (e.g. chronic and acute disturbances) and internal drivers (e.g. reinforcing and destabilising feedbacks). The coral-dominated reef ecosystem state is becoming increasingly degraded by chronic stressors, i.e. the valley sidewalls are eroded away (Fig. 0.1). Communities of fleshy macroalgae can act as one alternative attractor to corals and current climatic drivers appear to often favour macroalgae-dominated ecosystem states (Bellwood et al. 2004). Macroalgal dominance is not determined by a clear quantitative cut-off. The term ‘macroalgal dominance’ is usually referring to the relative increase of macroalgal cover compared to historic baselines and other specific benthic settlers (Hughes et al. 2010). The same applies to corals. For instance, baselines for Caribbean reef benthic coverage were collected in the 1970s and quantified macroalgae to cover an average of 2% benthic space. In collections from 1996-2006, average macroalgal cover had risen to 40%, a 20-fold increase. Macroalgal cover in the Caribbean is now substantially higher than coral cover (Hughes 1994).

Between the coral attractor and the macroalgal attractor, the process of herbivory is a feedback that acts across the feedback threshold, reinforcing coral dominance and destabilising algal dominance (Fig. 0.1). As primary consumers, herbivores physically remove and control algae which can act to destabilise and control algal dominance (Hughes et al. 2007). The resilience of the algal attractor is weakened, i.e. the algal valley becomes shallower. Algae are therefore less competitive with increasing herbivory rates and herbivory can support coral dominance, i.e. the coral valley becomes deeper (Lirman 2001). However, like all feedbacks, the herbivory feedback that is effectively controlling algae can be weakened through a range of causes. Densities of herbivores could simply be too low (Cheal et al. 2010) and cannot keep up the grazing intensity necessary to effectively control algal populations (Williams et al. 2001). The herbivores are saturated with less algal mass than is available. Herbivores could also be present in sufficient densities but have a preferred food source that is alternative to the algal community composition that asserts its dominance at a given time (Ledlie et al. 2007). Similarly, many mature macroalgae become unpalatable as they grow (McClanahan et al. 2002) which can increase food handling time of herbivores (Vergés et al. 2011), causing herbivores to divert away to more palatable ones (Dell et al. 2016). Even in immature turf algal stages, algae are reported to retain sediment and thereby reduce herbivory (Bellwood and Fulton 2008; Goatley and Bellwood 2012; Tebbett et al. 2016). Additionally, when macroalgae form dense stands, herbivorous fishes have been observed to avoid

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macroalgal patches, potentially to circumvent predators that could be hiding in between the algae or to avoid excessive abrasion by the algal blades (Hoey and Bellwood 2011).

Studies show macroalgae efficiently outcompeting other benthic settlers (e.g. corals) by inhibition of their settlement (Diaz-Pulido et al. 2009), physical interference (Tanner 1995), chemical interference (Rasher and Hay 2010) or sediment retention (Birrell et al. 2005). In addition to reducing herbivory, reports of the common macroalgal genus *Sargassum* suggest the forming of dense stands as a mechanism to lessen physical stresses and to suppress microbes. The fitness of *Sargassum* recruits within dense stands was also significantly improved by depositing nutrients, propagules, and rhizomes into the sediment when mature algae decay (Dell et al. 2016). The same genus has also been shown to have attachment structures (holdfasts) extremely resistant to damage and physical disturbance such as grazing (Loffler and Hoey 2018; Loffler et al. 2018). *Sargassum* macroalgae have been observed to regrow readily from leftover holdfasts, shortening the time in which macroalgal feedbacks can be re-established (Ceccarelli et al. 2018).

Managing feedbacks on coral reefs of the Anthropocene

Comprehensive management approaches that build on our understanding of fundamental feedbacks in degraded coral reefs, can be used to trigger coral recovery (Hughes et al. 2010). Coral reefs already show high alterations in composition and there is a high probability that they will continue to do so as the Anthropocene accelerates (Graham et al. 2014). One likely future pathway of tropical reefs is a mosaic of habitat patches, where multiple patch reefs of different habitat types form an interconnected tropical seascape (Fulton et al. 2019). A mosaic habitat reefscape can consist of habitat patches such as corals, seagrass or macroalgae, that each can benefit different communities or life stages of individual species within those communities (e.g. fishes; Berkström et al. 2013; van Lier et al. 2018). Connectivity between the habitat patches is critical for functioning mosaic reefscales (Olds et al. 2018) carefully managed mosaic reefscales will demonstrate asymmetric patch sizes (Beger et al. 2010a). Yet, expanding patches of singular habitat type, such as uniform macroalgal communities (Fulton et al. 2019), can grow too large and undermine this connectivity. Self-reinforcing feedbacks can allow

uniform patches to efficiently expand when unchecked (Johns et al. 2018). In order to maximise the benefit of a mosaic reefscape, interventions are required that can manage undesirable patch expansion.

The expansion and succession of macroalgae could be halted when light availability is limited for extended time periods. This was shown for tropical macroalgae in a study at Kāneʻohe Bay, Hawaiʻi (Stimson and Conklin 2008). An unusually extended overcast period of 42 days caused significant die-offs in the algal community and assisted in the recovery of local corals. It is likely that this can be exploited. Macroalgae likely adapt to changing light regimes by diverting energy away from growth and achieving unpalatability towards maximising photosynthesis (Littler et al. 1988; Teichberg et al. 2013). Shading macroalgae could alter the re-allocation of nutrients within the algal tissue to favour herbivory. A study associated decreased grazing rates by herbivores on macroalgae with algal maturation and suggested the correlation between algal maturation and decreased palatability to herbivores as the mechanisms behind it (Duran et al. 2016). This could be traced back to nitrogen content in the algae as a driver of grazing rates. Studies associate lower carbon-to-nitrogen (C:N) -ratios in algae with higher palatability to herbivores (Vergés et al. 2011). For instance, two marine herbivorous gastropods have been reported to prefer diets with low C:N-ratios and increase growth rates on them (Barile et al. 2004; Van Alstyne et al. 2009). Similarly, seagrasses have been reported to show short-term reductions in N-content when grazed by fishes and urchins (Alcoverro and Mariani 2005; Vergés et al. 2008) and shifts from palatable algal communities to unpalatable ones seem to occur when herbivores are experimentally excluded (Thacker et al. 2001; Duran et al. 2016).

In summary, by utilising the interactions between shading and palatability, herbivores could be encouraged to graze areas where reefs have shifted to macroalgal dominance and control algal expansion. The key is that this interaction of processes has potential to both weaken algae-reinforcing feedbacks via shading and strengthen algae-destabilising feedbacks via herbivory (Fig. 0.2).

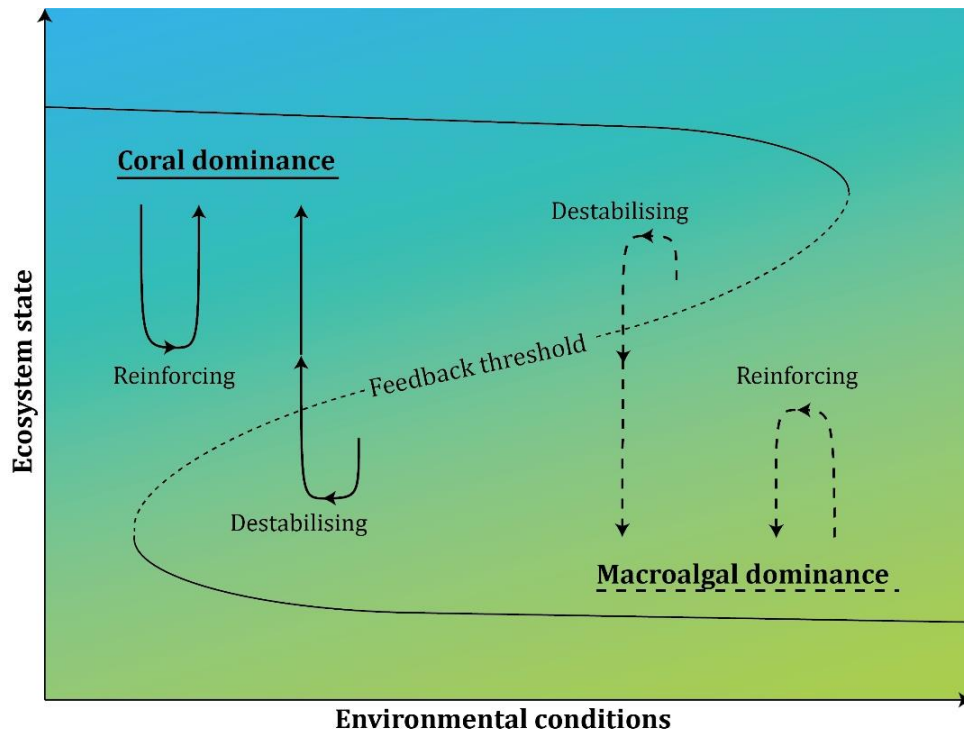


Figure 0.2 Alternative community states with respective feedbacks promoting coral (solid arrows) or macroalgal dominance (dashed arrows); destabilising feedbacks ‘pull’ the system over the feedback threshold into an alternative community state while reinforcing feedbacks strengthen one community state.

Sea urchins and herbivory

Herbivory has been repeatedly shown to be able to boost the feedback processes in the coral’s favour by reducing the competition pressure between corals and algae (Mumby et al. 2007) and even by clearing space that can allow corals to settle (Baird et al. 2003). Alongside fish herbivores, sea urchins have been reported as effective algal consumers on coral reefs (Odgen and Lobel 1978; McClanahan and Shafir 1990; Graham et al. 2017). Urchins have been suggested to be especially important for controlling algae in heavily fished areas (McClanahan 1992). Urchin abundance decreases have also been shown to be correlated with regional herbivorous fish increases (Carpenter 1988) highlighting their potential to substitute for depleted fish herbivore populations. In a system widely regarded as regime shifted to algal dominance, the recent urchin recovery in the Caribbean has been strongly correlated with macroalgal-cover recessions and coral recovery in both local and regional scales (Carpenter and Edmunds 2006; Myhre and Acevedo-Gutiérrez 2007). Similar to the importance to other reef organisms, structural complexity has been shown to increase urchin survival and therefore grazing effectiveness (Hereu et al.

2004) and to be essential to urchin retention in an area (Lee and Hessen 2006). Most studied urchins have been shown to be largely opportunistic grazers (Solandt and Campbell 2001), some even controlling physically and chemically defended macroalgae (Furman and Heck 2009) and turf algae (Carpenter 1988).

Most studies have explored urchin impacts in Caribbean or Kenyan coastlines (McClanahan 1992,1995; Carpenter and Edmunds 2006; Hughes et al. 2010), and few have attempted to actively utilise urchins in a focussed area. Whether urchins can be used to effectively control algal expansion or even clear algal patches and thereby aid coral recovery is yet to be determined. Maciá et al. (2007) conducted experiments transplanting urchins to high algal density areas to explore this ability. The urchins were recorded to graze the algae but vacated the area too quickly to show a controlling impact. According to the authors, there were no apparent signs of mortality or predation that led to the urchin loss. The potential of this approach to reveal the focussed impact of urchins on algae thus remains unexhausted and could be improved to determine urchins' potential as macroalgal controllers outside of the classically studied systems.

Seychelles as an ecological study site

My chosen study sites for ecological studies were located in the inner Seychelles (4°30'S, 55°30'E). I made this choice based on the rich data that is available for comparisons to historical baselines in juvenile coral densities and recent studies reporting extensive shifts to macroalgal dominance (e.g. Graham et al. 2015). My focus falls on the reefs surrounding the granitic islands of Mahé and Praslin (Fig. 0.3), which rise from the Seychelles Bank, an underwater plateau at average depths of 44 - 65 m. Extensive fringing reefs have developed their carbonate framework around the islands, and, at greater depths, the corals grow directly on the granitic substrate. In recent history, these reefs have been strongly affected by thermal anomalies that caused the 1998 coral bleaching event (~ 90 % loss; Goreau et al. 2000) and the 2016 coral bleaching event (~ 70 % loss; Wilson et al. 2019). Of the 21 reefs that I focus on in my thesis, 9 have undergone a benthic regime shift to macroalgal dominance after the 1998 bleaching event, the other 12 were recovering (Graham et al. 2015). My thesis will contribute to determining their recovery status following the 2016 bleaching event.

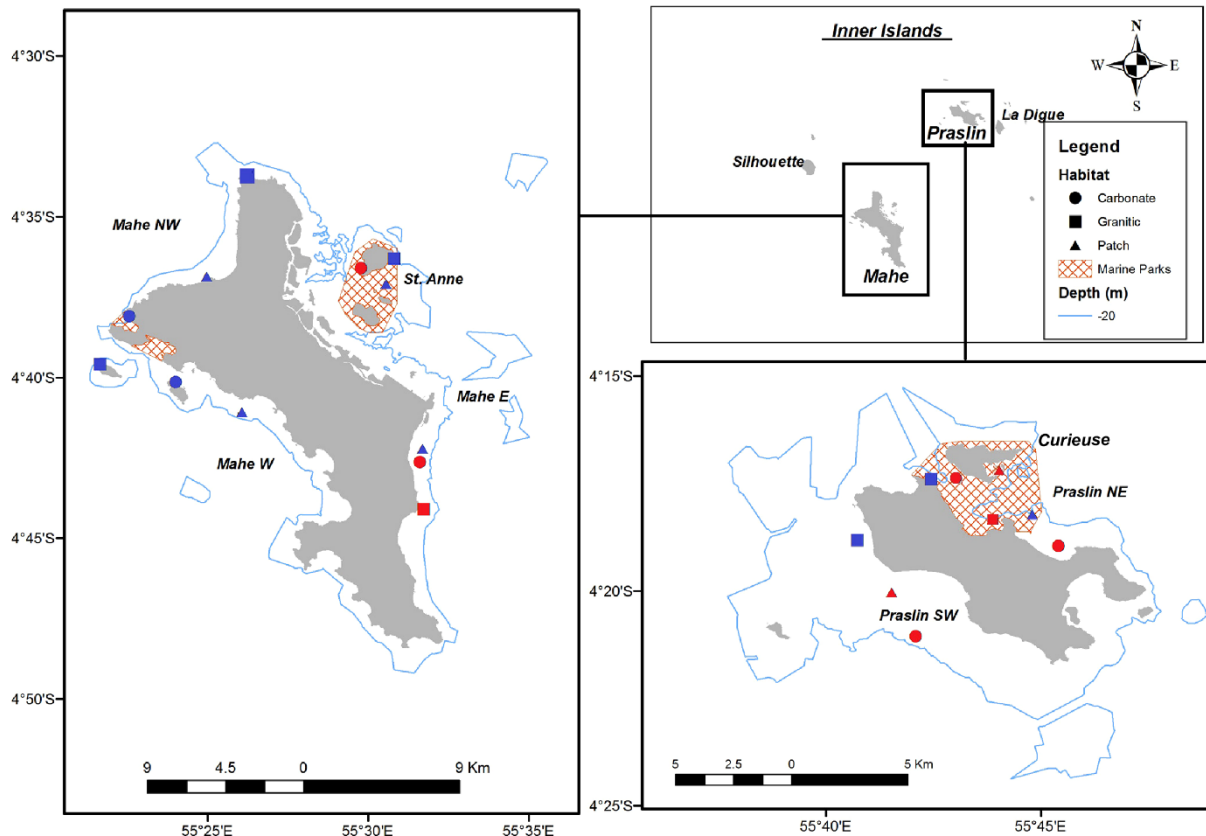


Figure 0.3 Map of Seychelles showing 21 study sites categorised into previous categorisations regime shifted to macroalgal dominance (red) and recovering (blue) from the 1998 bleaching event, adapted from Graham et al. (2015).

Coral reef social-ecological systems and associated feedbacks

While the described feedback processes above operate solely in the ecological component of degraded coral reefs, sustainable conservation management must consider connections between multiple ecosystems (Beger et al. 2010b) as well as connections between ecological and social components of a social-ecological system (SES) and can span across spatial and temporal scales (Cumming et al. 2014). Social-ecological feedbacks are indeed vital to the function and integrity of the SES because of their ability to feed the ecosystem state back to the human community (Fig. 0.4), for instance by indicating overharvesting of natural resources (Meyfroidt 2013). These feedback-driven cause-and-effect relationships allow human communities to capture, interpret, and respond to signals that indicate changes in ecosystems, a key factor for sustainable management in SES (Hoole and Berkes 2010; Hamann et al. 2015). If this signal-response chain is interrupted or re-routed onto external systems, the

break can allow ecological changes to occur and go unnoticed, increasing the potential for ecological collapse (Berkes 2007; Nyström et al. 2019). Therefore, knowing when and where these “missing feedbacks” occur, is of high priority for SES management (Barnett and Anderies 2014; Crona et al. 2016).

In coral reef SES, missing feedbacks have facilitated a range of social-ecological issues, such as poverty traps on Kenyan reef fisheries (Cinner 2011) or the iconic coral-to-algal regime shift on Jamaican coral reefs (Hardt 2009; Hughes et al. 2010), and will continue to do so until they are addressed. In order to address them, missing feedbacks must first be uncovered, but this is impeded by their absent nature. Social-ecological sustainability research has developed frameworks that can be used to uncover missing feedbacks that need to be applied to the diverse data types available for coral reef SES.

The red loop-green loop (RL-GL) concept first described by Cumming et al. (2014) can uncover missing feedbacks through the characterisation of SES dynamics along a spectrum of human resource dependence. Resource dependence on a national scale can follow two fundamentally different trajectories - one with weak local ecosystem ties and strong ties with distal systems (red loop), the other with strong local ecosystem ties and weak ties with distal systems (green loop). Both ends of the RL-GL spectrum also display a variant of unsustainable trajectories (red trap & green trap).

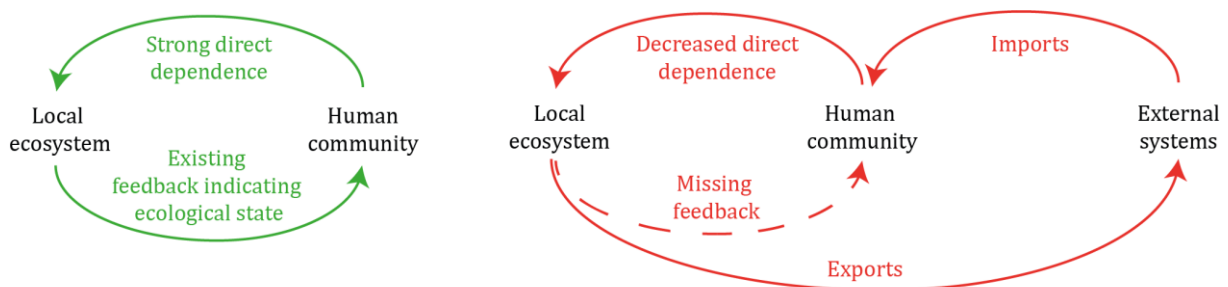


Figure 0.4 Schematic of existing and missing feedbacks in social-ecological systems.

Aims and thesis outline

My thesis aims to contribute to our knowledge of coral reef dynamics in the Anthropocene. I achieve this by using our current understanding of feedback processes on degraded coral reefs to conceptually and experimentally confront both ecological and social-ecological feedbacks that may have merit in triggering coral recovery. My thesis addresses the following overarching research questions:

1. Which habitat drivers best predict juvenile coral densities following bleaching?
2. Can macroalgae-reinforcing feedbacks be weakened through shading?
3. Can sea urchins effectively weaken macroalgal feedbacks given their current natural densities?
4. Can red and green loops uncover missing social-ecological feedbacks?

The overarching research questions are addressed in the following research chapters. **Chapter 1** gives predictions of coral recruitment density shortly following mass bleaching of corals in the inner Seychelles. **Chapter 2** assesses shading as a management tool in an experimental confrontation of macroalgal feedbacks to maximise the benefit of mosaic habitat reefs. **Chapter 3** uses survey and experimental methods to determine the potential role that sea urchins can play in reducing macroalgal cover with regards to current natural densities of urchins in Seychelles. **Chapter 1, 2, and 3** all tackle ecological coral reef recovery dynamics (Fig. 0.5). **Chapter 4** conceptually integrates two frameworks from social-ecological sustainability research to historical and current dynamics between human communities and coral reef ecosystems of Jamaica. All chapters are either published or submitted to international research journals and I indicate the status of each in each chapter's title page.

Thesis outline



Figure 0.5 Schematic of the individual rationales, research processes, and outcomes as well as the interplay of the four research chapters contained in this PhD-thesis.

1 UNCOVERING DRIVERS OF JUVENILE CORAL DENSITY FOLLOWING MASS BLEACHING

1.1 Abstract

Thermally induced mass coral bleaching is globally responsible for major losses of coral cover. Coral recovery from mass coral disturbances like the 2016 bleaching event hinges on successful recruitment of new coral colonies to the existing population. Juvenile corals as a life history stage represent survival and growth of new recruits. As such, habitat preferences of juvenile corals and how environmental parameters interact to drive coral recovery following a mass bleaching disturbance are important research areas. To expand our knowledge on this topic, we compared juvenile coral densities from before the 2016 bleaching event with those after the disturbance and identified abiotic and biotic characteristics of 21 reefs in the inner Seychelles that predict juvenile coral densities. Our results show that following the 2016 bleaching event, juvenile coral densities were significantly reduced by about 70 %, with a particularly large decline in juvenile *Acropora*. Macroalgae present a large obstacle to survival of juvenile corals in a post-bleaching setting, but their influence varies as a function of herbivore biomass, reef structure, and reef type. Higher biomass of herbivorous fish weakens the negative effect of macroalgae on juvenile corals and structural complexity on granitic reefs is a strong positive predictor of juvenile coral density. However, structural complexity on carbonate or patch reefs was negatively related to juvenile coral density, highlighting the importance of considering interactive terms in analyses. Our study emphasises the importance of habitat for juvenile coral abundance at both fine and seascape scales, adding to the literature on drivers of reef rebound potential following severe coral bleaching.

Published:

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1.2 Introduction

Mass coral bleaching events resulting from ocean warming have led to significant losses of coral cover across many of the world's reefs (Goreau et al. 2000; Hughes et al. 2017). Coral reefs have the ability to rebound from extensive coral bleaching, but it can take more than a decade for coral cover to reach pre-bleaching levels (Gilmour et al. 2013; Graham et al. 2015). Coral reef recovery depends on the reassembly of the habitat-forming hard coral (scleractinian) community (Connell et al. 1997), driven in part by coral recruitment – the replenishment of the local population by new individuals from within or outside an existing population (Hughes et al. 2010).

Successful coral recruitment is dependent on several important factors that can result in significant demographic bottlenecks. Firstly, recruitment depends on sufficient supply of coral larvae, requiring inputs of external larvae on well-connected reefs (Hughes and Tanner 2000; Elmhirst et al. 2009) or self-recruitment on geographically isolated reefs (Gilmour et al. 2013). Secondly, availability of suitable benthic space for coral settlement is important (Connell et al. 1997; Diaz-Pulido et al. 2009). Some benthic algae (e.g. turf algae or mature fleshy macroalgae) inhibit larval settlement of corals when the algal beds become too dense (Johns et al. 2018), whilst other surfaces, such as some crustose coralline algae (CCA), can be preferred settlement sites by coral larvae (Yadav et al. 2016). Thirdly, post-settlement mortality of juvenile corals (0.5 - 5 cm; Roth and Knowlton 2009) is high (Hughes et al. 2007). Two major drivers of early post-settlement mortality are competition with other benthic organisms, such as macroalgae (Rasher et al. 2011; Johns et al. 2018), and predation, for instance by corallivores and incidental predation by some herbivores (Cole et al. 2008; Doropoulos et al. 2012). Unstable substrates such as rubble have also been suggested to cause major coral recruit die-offs (Fox et al. 2003; Chong-Seng et al. 2014). Mortality rates gradually reduce with coral growth and most corals escape mortality once they have reached sizes above 5 cm (Doropoulos et al. 2015), allowing the corals to grow to reproductive sizes and contribute to the adult population (Hughes et al. 2010; Gilmour et al. 2013).

Coral reefs can recover from extensive coral mortality, provided key factors such as fishing, water quality, and anthropogenic climate change are kept within safe operating spaces (Norström et al. 2016).

However, the likelihood of experiencing mass coral bleaching events in the coming decades is increasing (Hughes et al. 2018). A long-term study by Graham et al. (2015) in the inner Seychelles determined the density of juvenile corals as one of five parameters that can positively predict the rebound potential of mass-bleaching disturbed coral reefs. Initial post-disturbance recovery rates are usually slow and global average increases in percent coral cover following mass bleaching are only 3 % (Graham et al. 2011). However, recovery rates can speed up exponentially once juvenile corals have grown into reproducing colonies (Gilmour et al. 2013) to create an efficient positive feedback that can result in rapid rates of coral cover expansion (Nyström et al. 2012).

Studies spanning multiple decades demonstrate that corals are affected by abiotic factors such as light, depth, and substratum orientation (Babcock and Mundy 1996; Roth and Knowlton 2009), seawater temperature (Edmunds 2004), or cryptic microhabitat orientation along a depth gradient (Edmunds et al. 2004) during early post settlement. Some biotic surfaces facilitate juvenile coral growth and survival, such as some CCA species (Arnold et al. 2010; Arnold et al. 2011; Yadav et al. 2016), calcareous polychaete worm tubes, biofilms (Arnold et al. 2010), and other coral skeletons (Norström et al. 2006). Conversely, other biotic factors inhibit coral recruitment, for instance macroalgae (Box and Mumby 2007; Arnold et al. 2010; Arnold and Steneck 2011), turf algae, and other invertebrates (Arnold et al. 2010; Arnold and Steneck 2011). More recently, interacting biotic processes have been identified, such as between herbivory of turf algae (Arnold et al. 2010) and how herbivore exploitation reduced algal consumption and ultimately affected juvenile coral densities (Steneck et al. 2018).

Despite the extensive body of research, most of our knowledge on the early life history of settled corals does not stem from recently disturbed reefs. With the likelihood of thermally driven coral bleaching events increasing across the tropics (Hughes et al. 2018), an improved understanding of the drivers of post-bleaching coral recruitment will help to identify which processes promote or inhibit coral recovery. A recent study on juvenile coral densities on the Great Barrier Reef following the 2016 bleaching event considered abiotic predictors (temperature, rugosity, location around island, depth) as well as one biotic predictor (coral taxon; Álvarez-Noriega et al. 2018), but post-bleaching influences of other environmental factors, such as herbivory, CCA or macroalgae, remain unclear. Thus, an important

research gap exists regarding post-bleaching habitat and biotic predictors of juvenile coral density. Insight into which cross-scale abiotic and biotic drivers predict juvenile coral densities and how they interact shortly after large-scale coral bleaching events will improve our understanding of how early coral reef recovery dynamics vary spatially following extensive bleaching. Our study addresses this gap by investigating reefs of the inner Seychelles one year after the 2016 bleaching event. We explore temporal patterns of juvenile coral densities before and after the 2016 bleaching event and investigate how key habitat characteristics interact to limit or facilitate juvenile coral density.

1.3 Methods

The inner Seychelles (4°30'S, 55°30'E) are mostly granitic islands with well-developed carbonate fringing reefs. In recent history, the inner Seychelles' coral reefs have been affected by two major bleaching events caused by thermal anomalies (in 1998: ~ 90 % loss; Goreau et al. 2000; and 2016: ~ 70 % loss; Wilson et al. In review). We surveyed 21 sites within the inner Seychelles in April 2017, 18 of which had been previously surveyed in 2008 and 2011. At each of the 21 sites, we recorded the abundances of diurnally active, non-cryptic, reef-associated fish species along with estimates of their individual total lengths at 8 replicate point counts (7 m radius) along the reef slope. We excluded any individual fish entering the cylindrical area once sampling had commenced from abundance estimates. To ensure accurate length estimates of fish, the surveying diver estimated the lengths of sized PVC pipes until accuracy was consistently within 4 % of actual lengths every day (Graham et al. 2007). After the survey, we converted estimated fish lengths from surveys into biomass using published length-weight relationships (Letourneur et al. 1998; Froese and Pauly 2018) and species assigned to feeding groups based on their diet and feeding behaviour (Wilson et al. 2008). Within the same point counts, we visually estimated structural complexity of the reef using a scale from 0 (no vertical reef) to 5 (exceptionally complex with numerous caves and overhangs) as per Polunin and Roberts (1993), which correlates strongly with a range of other methods for capturing the structural complexity of coral reefs (Wilson et al. 2007). We counted sea urchin abundance (Family: Diadematidae) within each point count area. Lastly, we randomly deployed a 50 x 50 cm quadrat repeatedly within each point-count and counted juvenile corals in it. The number of quadrat deployments in each point count area and associated juvenile

coral counts was limited to the maximum number that could be deployed within 8 min (3 - 13 quadrats per point count). Prior surveys of juvenile corals at these sites in 2008 and 2011 had used quadrat sizes of 33 x 33 cm for juvenile density (Chong-Seng et al. 2014; Harris et al. 2014), however we used larger 50 x 50 cm quadrats to obtain a better assessment of the habitat surfaces around juvenile corals. We searched each quadrat for juvenile corals with diameters up to 5 cm (Roth and Knowlton 2009), identified the corals to genus level, and measured their diameter to the nearest 0.1 cm. Colonies clearly resulting from shrinkage, fragmentation, or overgrowth of older colonies were not recorded (Hughes and Jackson 1985). We recorded the coral's attachment substrate and took a HD-photograph of each quadrat from above in a way that all borders of the quadrat were visible. We later analysed the photographs with Coral Point Count with extension for Excel (CPCe; Kohler and Gill 2006) to obtain percent cover values for the benthos categories: macroalgae, turf algae, CCA, sand, rubble, pavement (bare rock).

1.3.1 Statistical analysis

We analysed temporal variation in juvenile coral density between 2008 (Harris et al. 2014), 2011 (Chong-Seng et al. 2014), and 2017 at the 18 sites surveyed each year. To standardise varying sampling efforts, we averaged the juvenile coral abundances across quadrats, for each site of each year (18 sites of 3 years: $n = 54$), rounded to give an average coral abundance. Because different quadrat sizes were used throughout the years, we included the quadrat area as an offset variable, a pre-specified coefficient, in our models. To account for overdispersion of the response variable, we fitted generalised linear mixed models (GLMMs) from the 'lme4' package (Bates et al. 2015) in R (R-Core-Team 2018) for Poisson distributed errors. Our final models with 'site' as a random intercept term were selected based on Akaike information criterion (AIC; Zuur et al. 2009):

$$\text{Juvenile coral abundance}(All, Acropora, Favites, Porites) \sim \text{Year} + \text{offset}(\text{Area}) \\ + (1 | \text{Site})$$

We fitted GLMMs to total juvenile corals abundances, as well as to two common genera, *Acropora* and *Porites*. For a third genus, *Favites*, we fitted the same model structure but with Gaussian errors (linear

mixed model, LMM), using the ‘nlme’ package (Pinheiro et al. 2018). We conducted Tukey HSD post-hoc tests to identify significant year differences.

Using only the dataset for 2017, we analysed the data for 21 sites at the scale of the 7 m radius point counts to examine abiotic and biotic drivers of juvenile corals after 2016 bleaching. Because multiple quadrats were deployed within each point count, we averaged and rounded the resulting juvenile coral count across quadrats for each point count (n = 168). We expected juvenile coral density to be predicted by 7 biotic and abiotic variables measured at different scales (Table 1.1) and included ecologically sensible two-way interactions between variables.

Table 1.1: Biotic and abiotic variables considered in habitat predictor analysis to explain spatial variation in juvenile coral density.

Predictor	Rationale	Reference
Sand & rubble	Sand or sediment act as inhibitors to the settlement of coral larvae while unstable rubble can induce post-settlement mortality in corals.	(Fox et al. 2003; Birrell et al. 2005; Chong-Seng et al. 2014; Risk 2014; Cameron et al. 2016, Yadav et al. 2016)
Crustose coralline algae (CCA)	Coral larvae are able to settle and grow on certain CCA species. CCA can also act as a competitor for space with macroalgae as well as corals themselves.	(Harrington et al. 2004; Buenau et al. 2011; Vermeij et al. 2011; Yadav et al. 2016)
Macroalgae	Macroalgae are amongst the primary competitors for space with corals and can also induce post-settlement mortality to corals via physical and chemical pathways.	(McCook et al. 2001; Jompa and McCook 2003; Kuffner et al. 2006; Diaz-Pulido et al. 2009; Johns et al. 2018)
Herbivorous fish biomass	Feeding by herbivorous fish removes algae creating space for corals to settle and grow. The grazing impact scales with abundance and body size. Incidental predation by herbivorous fish on coral spat has also been reported.	(Bellwood et al. 2004; Lokrantz et al. 2008; Doropoulos et al. 2012; Mumby et al. 2013; Graham et al. 2015)
Sea urchin abundance	Similar to herbivorous fish, sea urchins can both facilitate and limit coral recruitment by (1) grazing algae that otherwise block potential coral settlement space and (2) incidental predation on coral spat.	(Glynn et al. 1979; Carpenter and Edmunds 2006; Furman and Heck 2009; Edgar et al. 2010; Hughes et al. 2010)
Structural complexity	Structurally complex reefs provide habitable space for a diverse range of organisms including fish or sea urchins and create niche space for coral settlement and survival.	(Vergés et al. 2011; Graham and Nash 2013; Rogers et al. 2014; Doropoulos et al. 2016)
Reef type	Three reef types surveyed: carbonate, patch and granite reefs; reef type can affect coral recruitment success.	(Jennings et al. 1995; Creed and Paula 2007; Graham et al. 2007; Burt et al. 2009; Wilson et al. 2012)

All variables were only weakly correlated and so the model was not biased by collinearity issues (Zuur et al. 2009). We scaled variables to a mean of 0 and standard deviation of 1, a recommended approach

for multi-model selection which allows for meaningful comparisons of effect sizes when variables are on different scales (e.g. benthic cover percent vs. structural complexity; Schielzeth 2010). ‘Reef type’ was originally a categorical variable with three reef types: carbonate, patch, and granite. After isolating the impact of each reef type on juvenile coral densities, granite stood out significantly from the other two reef types. To reduce the variables and interactions considered by our analysis to a number that can be sensibly interpreted with our given number of observations, we replaced ‘reef type’ as a categorical variable with a binary dummy variable that isolates the granite reef type and groups carbonate and patch reef types. To account for overdispersion and high frequencies of true zeros in the response variable (45.5 %), we fitted a zero-inflated negative binomial (ZINB) regression model via maximum likelihood estimation (Zuur et al. 2012). This is a two-part model that fits two distributions to the data – the first part fits a binomial distribution to the full dataset, treating the response variable as presence-absence data (zero component), while the second part fits a negative binomial distribution to all non-zero response data (i.e. where juvenile corals were present, count component). We initially fitted a zero-inflated mixed model (‘site’ as random factor) using the glmmTMB-package (Brooks et al. 2017) and one without a random effect using the ‘pscl’-package (Zeileis et al. 2008). Model selection based on AIC (Zuur et al. 2009) classed the model without random effect as better performing, indicating that autocorrelation does not bias our parameter estimates. One variable (‘sea urchins’) was excluded in backwards selection based on AIC, resulting in the final model:

$$\begin{aligned} \text{Juvenile coral density} &\sim \text{Sand \& rubble} + \text{CCA} + \text{Macroalgae} + \text{Herbivores} + \text{Complexity} \\ &+ \text{Reef type} + \text{Reef type} * \text{Complexity} + \text{Macroalgae} * \text{Complexity} \\ &+ \text{Macroalgae} * \text{Herbivores} \end{aligned}$$

The model validation of this final model did show a slight residual clustering in the model’s zero component which can be the case with zero-inflated models (Zuur et al. 2012). We visualized predicted relationships in ZINB models by predicting juvenile coral density across the observed range of each variable, holding all other variables to constant means of 0 (Schielzeth 2010). All statistical analyses were conducted in R (R Core Team 2018). We provide our R-scripts and model predictions at an open source repository (<https://github.com/JanDajka/SeyBabies-2016-bleaching>).

1.4 Results

1.4.1 Temporal patterns

Juvenile coral abundances in 2017 were less than half that of previous years (Fig. 1.1 A, GLMM, $z = -9.19$, $p < 0.001$). A post hoc test showed that 2017 abundances were significantly lower than those of 2008 (Tukey HSD, $Z-\Delta = 9.19$, $p < 0.001$) and 2011 ($Z-\Delta = 9.99$, $p < 0.001$) while 2008 and 2011 were not significantly different ($Z-\Delta = -0.912$, $p = 0.63$). This pattern was also the case for *Acropora* and *Porites* coral genera (Fig. 1.1 B, *Acropora* 2008-2017: $Z-\Delta = 3.82$, $p < 0.001$; *Acropora* 2011-2017: $Z-\Delta = 3.95$, $p < 0.001$; *Acropora* 2008-2011: $Z-\Delta = -0.31$, $p = 0.95$; *Porites* 2008-2017: $Z-\Delta = 4.82$, $p < 0.001$; *Porites* 2011-2017: $Z-\Delta = 4.48$, $p < 0.001$; *Porites* 2008-2011: $Z-\Delta = 0.53$, $p = 0.86$). Juvenile *Favites* abundances did not significantly differ between the years (*Favites* 2008-2017: $Z-\Delta = 2.29$, $p = 0.072$; *Favites* 2011-2017: $Z-\Delta = 2.4$, $p = 0.056$; *Favites* 2011-2008: $\Delta = -0.07$, $p = 0.997$).

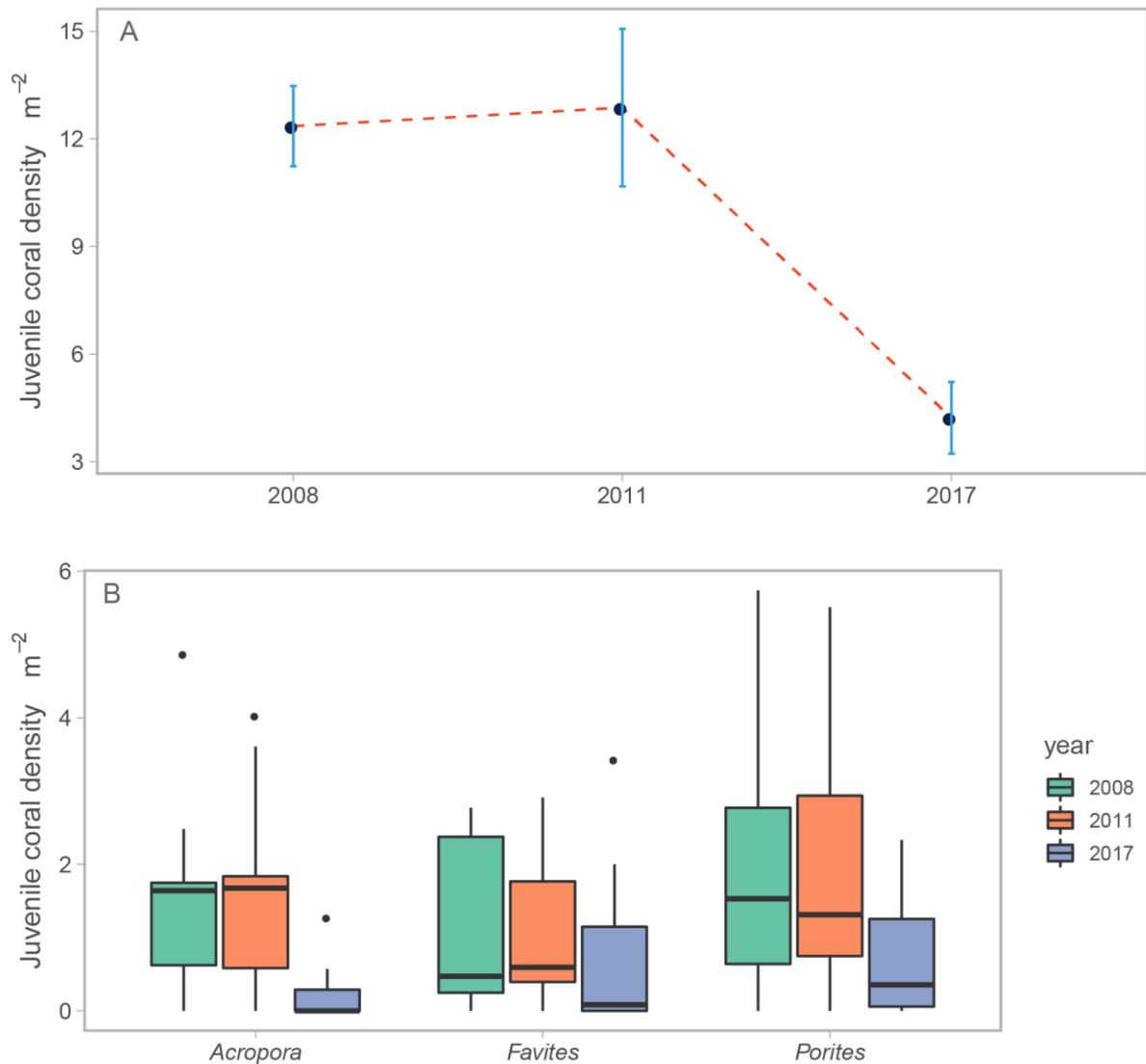


Figure 1.1 Average juvenile coral densities per square metre (\pm SE) of all sampled coral genera from 2008, 2011 and 2017, (A); average juvenile coral densities (\pm SE) of common coral genera *Acropora*, *Favites* and *Porites* from 2008, 2011 and 2017 (B).

1.4.2 Habitat predictors

Presence-absence data (zero model) indicated a negative effect of herbivores on juvenile corals (Fig. 1.2 A). Sand and rubble, granitic reef type, and macroalgae had very weak effects on juvenile coral densities, whilst CCA and complexity had positive effects. All interactions had a positive effect on coral densities. The interaction ‘macroalgae * herbivores’ highlight a positive indirect effect of herbivores on juvenile coral densities. The ‘macroalgae * complexity’ interaction showed how macroalgae slightly reduced the

positive effect that complexity alone had on juvenile coral densities while a granitic reef type increased the positive effect for complexity.

In the count component of the model, macroalgae, sand and rubble, and complexity had negative effects on juvenile coral densities (Fig 2 B). CCA and granitic reef type had very weak effects, while herbivores had a positive effect on juvenile coral densities. The ‘macroalgae * complexity’ interaction had a negative effect, the ‘granite * complexity’ interaction had a very weak effect, and the ‘macroalgae * herbivores’ interaction had a positive effect on juvenile coral densities.

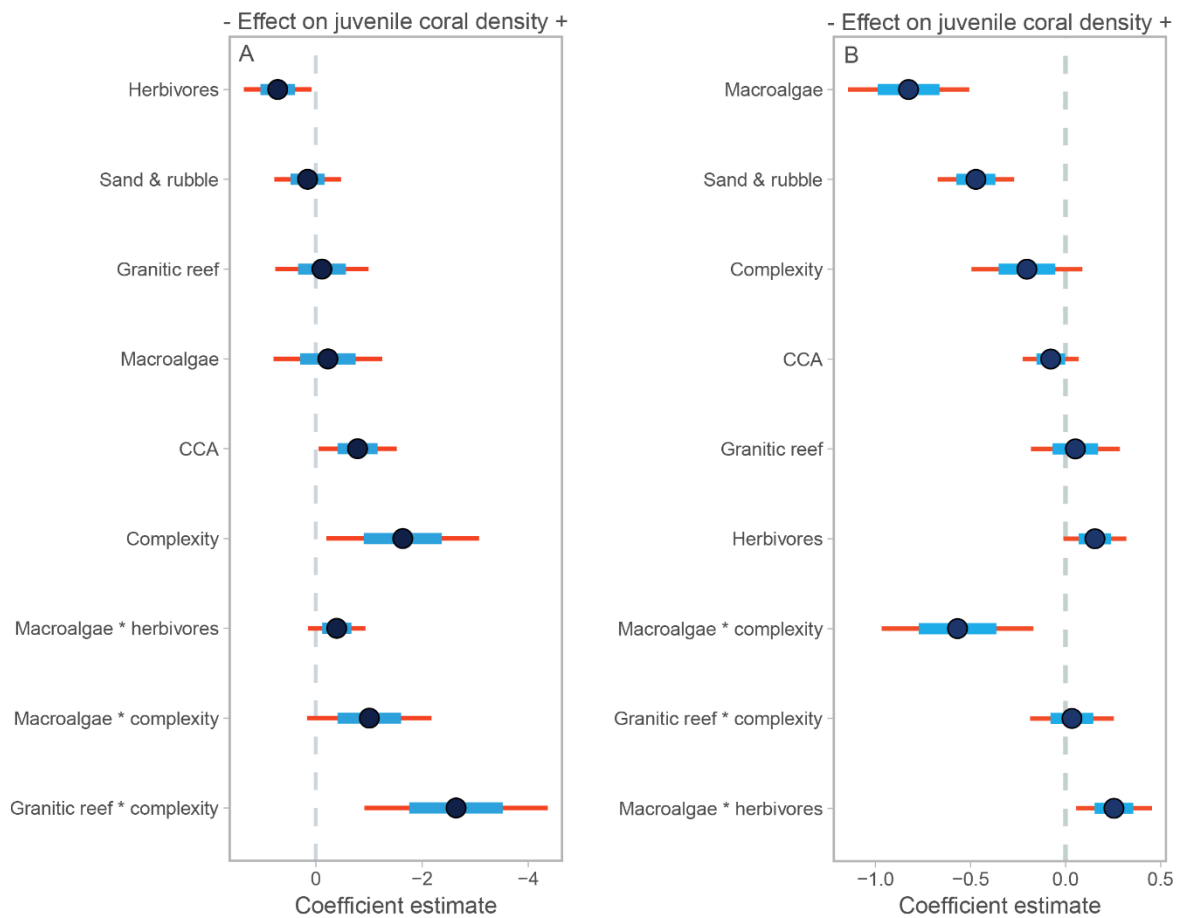


Figure 1.2 Effect size estimates of predictor coefficients in zero model with standard error (thick line) and 95% confidence intervals (thin line); zero-model component: positive coefficient estimates predict coral absences (0) and negative coefficient estimates predict coral presence (1), stronger negative values indicate stronger positive effect on juvenile coral density (A); count-model component: negative coefficient estimates predict lower juvenile coral density, positive coefficients predict higher density (B).

The zero-inflation model rarely predicted juvenile coral densities when cover of sand and rubble or macroalgae was greater than 50 %, however, when cover of these groups was low, predicted densities

reached of ~ 2.5 juvenile corals per m^2 (Fig. 1.3 A & B). In contrast, when CCA was absent, our model predicted ~ 1.5 juvenile corals per m^2 , and an expansion of up to 30 % CCA cover elevated that prediction above 2 juvenile corals (Fig. 1.3 C). The increasing standard error of additional CCA cover (30-60 %) resulting from few occurrences of high CCA cover values does not allow for further interpretation. The model predicted ~ 1.5 juvenile corals m^{-2} when herbivores were absent, and this number stayed relatively constant up to 250 $kg\ ha^{-1}$ herbivore biomass before falling to ~ 1 juvenile coral per m^2 at 900 $kg\ ha^{-1}$ herbivore biomass (Fig. 1.3 D). Further interpretation of this trend was not warranted due to large standard errors resulting from few occurrences of high herbivore biomass values.

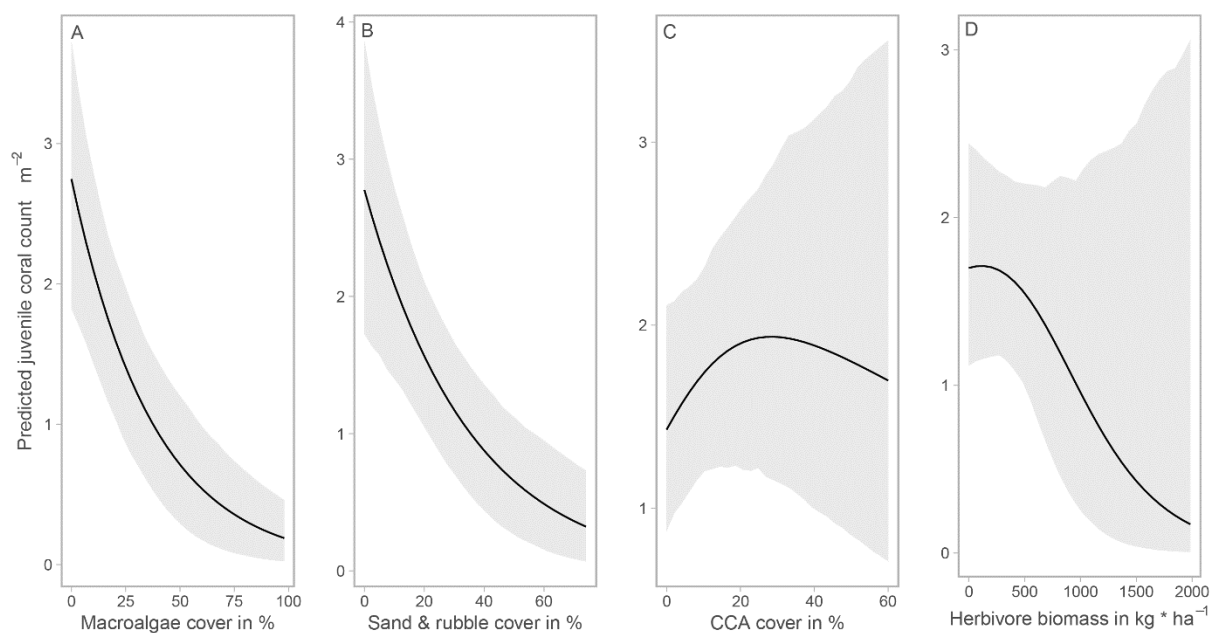


Figure 1.3 Model prediction trends of macroalgae (A), sand & rubble (B), CCA (C), and herbivores (D) for the count component of the zero-inflated negative binomial model, panels show the fitted effect (line) and 95 % confidence intervals (shaded bands) for each variable.

The ‘macroalgae * complexity’ interaction of our model predicted densities of ~ 1.2 juvenile corals m^{-2} on low (0-1 on the structural complexity scale) complexity reefs when macroalgal cover was above 50 %, but juveniles were rare on medium (1-3) or high (3-4) complexity reefs with macroalgal cover above 50 % (Fig. 1.4 A). When macroalgae cover was low (~ 10 %) however, high and medium complexity habitats supported juvenile coral densities ~ 5 juvenile corals m^{-2} while low complexity habitats only supported a maximum of ~ 2.5 juvenile corals m^{-2} . The prediction of high juvenile coral densities in the

high complexity habitat at 0 % macroalgae cover was also accompanied by a large standard error resulting from little occurrences of high complexity habitats without macroalgae in our data and was therefore not interpreted.

The ‘macroalgae * herbivore’ interaction led to highest densities reaching ~ 3.5 juvenile corals m^{-2} when both macroalgae cover (5 %) and herbivore fish biomass were low ($0-200 \text{ kg ha}^{-1}$; Fig. 1.4 B). At low herbivore biomass, increases in macroalgae cover to 50 % caused a reduction to ~ 0.5 juvenile corals m^{-2} . This reduction in juvenile corals occurred at 65 % macroalgae cover at medium ($200-400 \text{ kg ha}^{-1}$) herbivore biomass and to 85% macroalgae cover at high ($400-600 \text{ kg ha}^{-1}$) herbivore biomass. Yet, the maximum density of juvenile corals was also notably depressed as herbivore biomass increased. When herbivore biomass was low, the model predicted maximum densities of ~ 3.5 juvenile corals m^{-2} and ~ 3 juvenile corals m^{-2} at medium herbivore biomass. At high herbivore biomass, our model only predicted a maximum of ~ 2.3 juvenile corals m^{-2} .

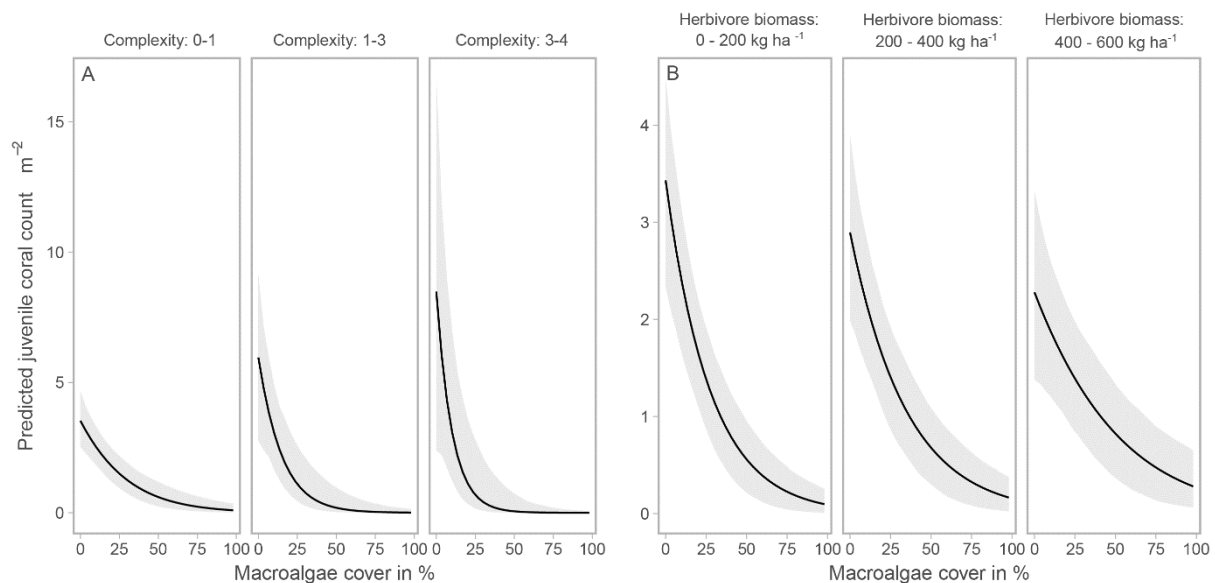


Figure 1.4 Model prediction trend for interactions macroalgae * structural complexity (A) and macroalgae * herbivore biomass (B) for the count component of the zero-inflated negative binomial model. Panels show the fitted effect (line) and 95 % confidence intervals (shaded bands) for each variable.

For the ‘reef type * complexity’ interaction, juvenile coral density decreased as complexity increased on carbonate and patch reefs (Fig. 1.5). For example, in granitic reefs, juvenile corals were absent at low complexity (0-1) but increased from ~ 0.5 to 2.2 juvenile corals m^{-2} at medium complexity (2-3). Both

the low complexity predictions on carbonate and patch reefs and the high complexity predictions on granitic reefs were accompanied by large prediction uncertainty and were therefore not interpreted.

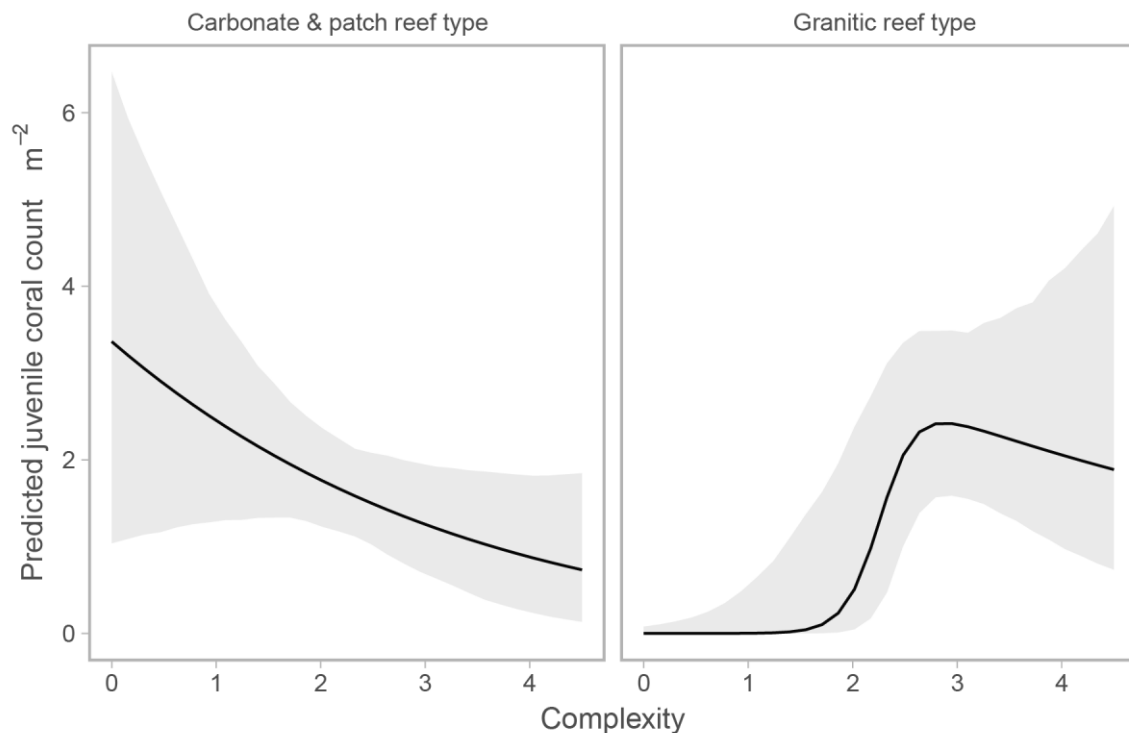


Figure 1.5 Model prediction trend for interaction reef type * structural complexity for the count component of the zero-inflated negative binomial model. Panels show the fitted effect (line) and 95 % confidence intervals (shaded bands).

1.5 Discussion

The densities of juvenile corals have been proposed as an important predictor of coral reef recovery from mass bleaching events (Hughes et al. 2010; Gilmour et al. 2013; Graham et al. 2015), yet predictors of juvenile corals themselves following large-scale bleaching are hitherto poorly explored. Following the 2016 bleaching event, we recorded a significant reduction of juvenile coral abundance in the inner Seychelles. High cover of macroalgae was associated with few juvenile corals shortly after a mass bleaching event, though interesting nuances were found in how their densities varied with interactions between macroalgal cover and other factors. Macroalgae appear to exploit structurally complex carbonate (limestone) reefs more efficiently and, as a result, may outcompete juvenile corals on these reefs; however, macroalgae cover on high complexity granitic reefs is generally low (Graham et al 2006). Increased biomass of herbivorous fish reduced the negative effect of macroalgae on juvenile

corals, though very high biomass of herbivores was associated with slightly lower density of juveniles when macroalgae was absent.

Our temporal findings depict the severity of the 2016 bleaching event to coral recruitment in the inner Seychelles via the loss of ~ 70 % juvenile coral abundance. This roughly matches the magnitude of adult coral cover loss for the same region (Wilson et al. In review). Loss in adult corals leads to lowered reproductive output and less larval supply (Hughes et al. 2000), which is problematic as the isolated coral communities of the inner Seychelles are likely reliant on self-recruitment (Graham et al. 2006). Before mass bleaching in 2016, the inner Seychelles' recovery from the 1998 bleaching event was slow for 7-10 years and then sped up exponentially at some sites (Graham et al. 2015), also typical for regions with coral recruitment from local sources (Gilmour et al. 2013). The 2016 bleaching event decimated juvenile *Acropora* corals. Fast-growing branching corals like *Acropora* tend to be among the most vulnerable to bleaching (Sheppard et al. 2002; Álvarez-Noriega et al. 2018) but can also drive the bulk of the coral reef's recovery (Emslie et al. 2008; Gilmour et al. 2013; Doropoulos et al. 2015). The low abundance of juvenile corals recorded post-bleaching, paired with their apparent inability to settle or survive on degraded sites (Chong-Seng et al. 2014) and reduced reproductive output of adults, suggests a significant delay of recovery in the inner Seychelles.

Our results indicate that macroalgal cover is a strong negative predictor of juvenile coral density. This supports the widely reported detrimental effect of macroalgae on coral recruitment (Diaz-Pulido et al. 2009; Rasher and Hay 2010; Johns et al. 2018; Steneck et al. 2018) in a post-bleaching setting and adds an interesting nuance with two interaction effects. Macroalgae inhibit settlement of coral larvae by blocking space (Diaz-Pulido et al. 2009; Johns et al. 2018) and increase the corals' post-settlement mortality by chemical and physical interference (Tanner 1995; Jompa and McCook 2003; Nugues et al. 2004; Rasher et al. 2011). It appears that increased structural complexity interacts with macroalgae to the detriment of juvenile corals. This might stem from an increased competitive pressure from macroalgae when coral larvae settle in more complex microhabitats or crevices (Doropoulos et al. 2016), as macroalgae that grow in complex structural elements avoid being grazed by herbivores (Bennett et al. 2010; Poray and Carpenter 2013). Because of the limited space in a crevice, corals experience more

contact with macroalgae (Rasher et al. 2011), exacerbating the effects of competition. This is underlined by more complex reefs supporting higher maxima of juvenile coral density when macroalgae cover is low or absent.

Higher biomass of herbivorous fish reduced the detrimental effect of macroalgae expansion on juvenile corals. In Seychelles, herbivorous fish biomass has increased following the 1998 bleaching event and is maintaining a productive inshore fishery (Robinson et al. 2018). Through their increased biomass, herbivorous fish graze more algal mass (Williams et al. 2001) which in turn opens settlement space for coral larvae (Doropoulos et al. 2013) and lessens the contact between corals and algae (Smith et al. 2006; Rasher et al. 2011). Herbivore biomass is a frequently highlighted parameter for coral reef recovery (Bellwood et al. 2004; Mumby et al. 2013) and was also one of the five positive predictors of coral recovery identified for Seychelles (Graham et al. 2015). Additionally, Steneck et al. (2018) found that herbivores reduced the negative effects of macroalgae and consequently had a beneficial effect on juvenile coral density in the Caribbean. In contrast, high herbivore biomass lowered the maximum density of juvenile corals in our study. This could be a result of incidental predation by herbivorous fish on coral spat (Doropoulos et al. 2012). Predation by herbivores, particularly scrapers, but also some grazers and detritivores, largely affects newly settled coral spat. These fish feed on a variety of reef substrates (e.g. turf algae, detritus), inadvertently removing coral recruits. This process largely affects corals within 3 months of settlement when they are still less than a centimetre in diameter, suggesting that predation by herbivorous fish is not visual and hence incidental (Doropoulos et al. 2016). This process might also relate to the macroalgae-complexity interaction, where maximum abundance of juvenile corals at 0 % macroalgae cover appeared depressed in high complexity habitats compared to medium and low complexity. High complexity habitats typically attract fish, such as corallivores or herbivores that seek shelter to ensure their own survival (Rogers et al. 2014). Feeding by these fishes can result in targeted or incidental predation on newly settled coral spat (Doropoulos et al. 2012), leading to depressed juvenile coral densities in highly complex reefs without macroalgae.

The presence of rubble and sand was also a strong negative predictor of juvenile coral density. It is well-reported that corals experience high post-settlement mortality on unconsolidated surfaces such as sand

due to its constant movement with wave energy and ability to smother or crush coral spat (Birrell et al. 2005; Risk 2014; Baldock et al. 2015). Periodic movement is also thought to prevent post-settlement survival of corals on unconsolidated rubble. The constant movement of rubble caused by waves results in newly settled corals being crushed (Fox et al. 2003; Yadav et al. 2016). Rubble was previously highlighted as a cause of serious demographic bottlenecks to corals in the inner Seychelles (Chong-Seng et al. 2014) and both patch and areas of carbonate reefs were often surrounded by sand and rubble (Pers. obs.).

Our data highlight the positive role of crustose coralline algae (CCA) on coral juvenile density. Some species of CCA have been reported to create suitable conditions for corals by acting as settlement cues to coral larvae (Ritson-Williams et al. 2010; Arnold and Steneck 2011; Yadav et al. 2016) or by suppressing macroalgal expansion (Belliveau and Paul 2002; Vermeij et al. 2011). Competition for space has also been reported between corals and CCA - as CCA covers more space, corals run the risk of being overgrown (Buenau et al. 2011). Our results show that CCA can be important for coral replenishment in post-bleaching scenarios.

An intriguing finding was the interaction between complexity and reef type. Paired with structural complexity, the granite reef type proved extremely beneficial to juvenile corals. We believe the benefit of granite in our study might be due to it being an unsuitable substrate for macroalgae rather than being a superior substrate for corals (Burt et al. 2009). Macroalgae attach to substrates via holdfasts which can penetrate the substrate up to 10 mm deep by exploiting the physical characteristics of mineral matrices. The density and matrices of granite and carbonate are very different (Morrison et al. 2009). It is likely that large fleshy macroalgae (e.g. *Sargassum*, *Turbinaria*) that commonly outcompete corals on carbonate reefs of the inner Seychelles cannot deeply penetrate the granitic mineral matrix (Milligan and DeWreede 2000), leading to an increased probability of algae dislodging as they grow (Thomsen 2004). Herbivorous fish could be assisting the coral's ability to more successfully exploit structural complexity on granitic reefs. Herbivore fish assemblages on granitic reefs in the inner Seychelles are more stable than those of carbonate and patch reef types (Graham et al. 2006). We found in our study

that the average herbivorous fish biomass was very similar for carbonate and patch reef types ($\sim 300 \text{ kg ha}^{-1}$), yet it was slightly elevated in the granite reef type ($\sim 400 \text{ kg ha}^{-1}$).

Our results have multiple implications for coral reef management. Our study reaffirms the negative effect macroalgae can have on coral recruitment and that reducing the competitive advantage of macroalgae is key to triggering a potential shift back to coral dominance on regime-shifted reefs via the support of positive or destabilising feedbacks (Nyström et al. 2012). Many coral reef systems appear currently locked in degraded states, for instance dominated by macroalgae. To break this locked state and push the system towards coral dominance, some negative feedback loops need to be interrupted and positive loops need to be engaged (Mumby and Steneck 2008). Herbivores can assist this feedback shift – our findings and recent findings from a large-scale study (Steneck et al. 2018) suggest that herbivores have a potential to weaken the effect of macroalgae on coral recruitment. High levels of herbivory also tend to push algal communities towards those dominated by calcareous forms (Littler and Littler 1984; Belliveau and Paul 2002), adding to habitats favouring coral reinforcing feedbacks, underlined by the positive effect of CCA detected in our study. A recent review by Ceccarelli et al. (2018) highlights the potential for physical removal of macroalgae to benefit coral, yet its effectiveness over large spatial and temporal scales will depend on whether the underlying drivers (e.g. eutrophication, overfishing of herbivores, ocean warming) that keep reefs locked in negative or reinforcing feedbacks favouring macroalgal dominance (Johns et al. 2018) are addressed (Norström et al. 2016). Our findings also highlight the importance of complex granite reefs for juvenile corals and that these habitats are potential coral refugia in Seychelles. Maintaining low levels of local stressors on complex granitic reefs may therefore be important for recovery.

Climate change and coral bleaching are reshaping coral reefs to a yet unknown extent. The 2016 bleaching event decimated the juvenile coral community of the inner Seychelles and concomitant obstacles such as macroalgal expansion have limited the ability for recovery on some reefs. As macroalgae interact with other reef characteristics such as structural complexity, herbivore biomass, and reef type, it becomes apparent that this obstacle has a very nuanced nature and addressing it will not be a straightforward process. If coral reef degradation progresses and the carbonate matrices break down,

sand and rubble patches will expand presenting another obstacle for coral recruitment. Should the more steadfast nature of granitic reefs prove a suitable refugia to future corals, a greater understanding of the mechanisms that underlie resilience on these reefs and their potential to re-seed nearby carbonate reefs is required.

Contribution of authors

JCD and NAJG conceived the ideas and designed the methodology; JCD, SKW, NAJG, KMCS, and AH contributed critically in acquisition of the data; JCD and JPWR analysed the data; JCD, NAJG and SKW interpreted the results. JCD wrote the first draft of the manuscript, and all authors contributed critically to drafts and gave final approval for publication.

2 WEAKENING MACROALGAL FEEDBACKS THROUGH SHADING ON DEGRADED CORAL REEFS

2.1 Abstract

Extensive and dense macroalgal fields can compromise the ecosystem function of habitat mosaics on reefs due to their limiting effect on patch connectivity. Macroalgae can maintain and increase their dominance with effective self-reinforcing feedback mechanisms. For instance, macroalgae can form dense beds, suppressing coral settlement and grazing by herbivores. This compromised ecosystem function can lead to major socio-economic and ecological changes. We shaded dense macroalgal beds with shade sails of two sizes and recorded changes to the underlying benthos and feeding rates of herbivorous fishes. The shade sails reduced the algae's ability to photosynthesise by 29 %. After six weeks, we recorded a 24 % macroalgae cover reduction under small sails and a 51 % reduction under large sails. Small shade sails reduced turf algal growth by 23 %, while large sails reduced growth by 82 %. Three months after removal of the shade sails, algal beds had almost completely regrown. During this regrowth period, herbivore bites taken from the experiment's substrates were recorded, with grazing impact reducing significantly with time. Our method is the first to achieve macroalgal reduction via the alteration of the light regime. While macroalgae regrew in this relatively short-term experiment, shading may be a viable reef management approach that aims to maximise habitat mosaics on coral reefs, particularly if used in combination with other intervention methods.

In review (04/04/2020):

Dajka, J.-C., Beasley, V., Gendron, G., Barlow, J. & Graham, N. A. J. Weakening macroalgal feedbacks through shading on degraded coral reefs. *Aquatic Conservation: Marine and Freshwater Ecosystems*

2.2 Introduction

Tropical coral reefs are changing globally, with corals reducing in cover and being replaced by other organisms such as algae (Hughes 1994; Cheal et al. 2010; Graham et al. 2015). Coral-algal regime shifts can substantially alter the ecological, social, and economic value of reefs (Moberg & Folke 1999; Hughes et al. 2010; Robinson et al. 2019), especially when systems become dominated by few weedy algal species of low complexity (Littler & Littler 1988; Hughes 1994; Mumby 2009). With an increasing frequency of disturbances threatening corals (Hughes et al. 2018), future predictions of coral-dominated systems, and the ecosystem services they support, are uncertain (Williams & Graham 2019; Woodhead et al. 2019). The changing compositions of reefs (Graham et al. 2014) may also give way to a mosaic of habitat patches, where multiple patch reef types form an interconnected tropical seascape (Nagelkerken et al. 2015; Harborne et al. 2016; Fulton et al. 2019). The mosaic can consist of habitat types such as corals, seagrass, and macroalgae, that each can benefit different communities or different life stages of individual species within those communities (e.g. fish; Berkström et al. 2013; van Lier et al. 2018). Connectivity between habitat types is critical for functioning reef mosaics (Olds et al. 2018). Substantial reductions in fish diversity can occur when the distance between coral and algal patches is greater than 500 m (van Lier et al. 2018) or 750 m when considering transient foragers (Berkström et al. 2013). Further, reef mosaic integrity and overall reef ecosystem function can decrease as individual, homogeneous habitats extend and increase the space between patch habitats (Olds et al. 2018). Therefore, patch connectivity should be considered in management in order to maximise the functioning of each patch (Fulton et al. 2019).

Conceptual models suggest that macroalgae can be very efficient at reinforcing dominance with feedback mechanisms (Mumby & Steneck 2008; Nyström et al. 2012; van de Leemput et al. 2016). Feedbacks are cause-effect loops where one aspect (A) affects another (B) which in turn feeds favouring conditions back to the original aspect (A). Observational and experimental studies have identified various macroalgal reinforcing feedbacks (Hoey & Bellwood 2011; Dell, Longo & Hay 2016; Johns et al. 2018; Loffler et al. 2018; Loffler & Hoey 2018). For example, once stands of the common tropical macroalgal genus *Sargassum* reach a certain density (A), they suppress grazing by fish herbivores (B),

and the reduction of feeding pressure then allows macroalgal fields to grow further (A; Hoey & Bellwood 2011). In addition, limited space in these fields prevents benthic settlement by other organisms such as corals (Dell, Longo & Hay 2016), and can lead to the development of microbe aggregations that cause diseases in remaining corals (Smith et al. 2006). The result can be an ever-expanding homogeneous field of weedy macroalgae (Mumby 2009) which can compromise reef mosaic connectivity (Berkström et al. 2013; van Lier et al. 2018).

In order to limit the extent of dense homogeneous macroalgal fields and maximise ecosystem function of mosaic-style habitats (Fulton et al. 2019), studies have investigated ways to reduce algal cover. Experiments that remove macroalgae manually, have had short lived success due to rapid regrowth likely from leftover algal attachment structures (holdfasts; Tanner 1995; McClanahan et al. 2001; Roff et al. 2015; Loffler et al. 2018; Loffler & Hoey 2018). In addition, turf algae can rapidly colonise open settlement space under favourable environmental conditions (e.g. sufficient nutrient and light levels; Littler & Littler 1992). Following an unusually long period of overcast weather (42 days) in Kāneʻohe Bay, Hawaii, a mass-macroalgal die-off occurred, likely caused by the lack of sufficient photosynthetically active radiation (PAR; Stimson & Conklin 2008). The macroalgae did not return for the 2 years of subsequent monitoring, suggesting that shading may be a feasible approach to weaken macroalgal feedbacks.

In this study we established an artificial shading experiment in a bay of Curieuse Island, Seychelles that was entirely dominated by dense macroalgal fields. The overarching objective was to create macroalgal free patches and attract herbivorous fish to these patches. We specifically asked 1) does a shading period of 42 days (6 weeks) result in a reduction of macroalgal cover?; and 2) do herbivorous fish graze more in patches of reduced macroalgal cover?

2.3 Methods

2.3.1 Study site and organisms

We conducted our study from January until June 2018 at Anse Papaie (4.28°S, 55.73°E), Curieuse Island, Seychelles. We chose the bay due to its continuous, thick macroalgal beds extending to relatively

deep water (6 m at high tide) and its status as a marine park to minimise boat traffic. The dominance by macroalgae likely developed following the 1998 bleaching event, that led to many Seychelles reefs shifting dominance from corals to macroalgae (Graham et al. 2015). Prevailing winds in the inner Seychelles come from the north-west between December and March and start turning into south-easterly winds in late March, staying this way until October, followed by intense rainfalls and winds through November and December (M Belmont and V Amelie, Seychelles Meteorological Services). With Anse Papaie on the eastern side of Curieuse, the bay remains relatively wind-sheltered from late January until mid-March. Macroalgae overstorey in the bay are primarily *Sargassum* spp. with some *Turbinaria* spp. present, while the understorey is primarily *Lobophora* spp. and *Dictyota* spp. *Sargassum* often display strong seasonality in growth patterns around the world. *Sargassum* seasonality in the inner Seychelles appears to be tied to the prevailing seasonal winds and currents (Bijoux 2013). *Sargassum* appear to senesce during the cloudy south-east wind period (from May to October) and regrow during the predominantly clear-sky north-west wind period (December to March). This led our choice of experimental timing (January to June), during which skies are predominantly clear and *Sargassum* are not subjected to senescence but instead are in a regrowth phase.

2.3.2 Experimental setup

We built submerged square-shaped shade sails (> 98 % UV-blockage certified according to Kookaburra Shade Sails, Sydney, Australia) of two sizes (4 m² & 9 m², five of each size) over continuous macroalgal fields. We mounted each shade sail on four threaded steel rods ($\phi = 22$ mm, length = 1.5 m), with the rods hammered 50 cm into the sediment to allow at least 1 m between the rod's end and the water's surface at low tide (to allow boat passage) and for the algae (~ 30 cm maximum height) not to touch the shade sails. We put the shade sail structures in place on 28/01/2018 and they remained fixed for 42 days until deconstruction on 11/03/2018 to prevent shifting winds from disrupting the experiment. We constructed control plots of solely steel rods (no shade sails) on the same reef. The total experimental setup included 16 plots (five 4 m² treatments, five 9 m² treatments, three 4 m² controls, three 9 m² controls) running in rows parallel to the shoreline, at a similar depth. Plots were separated to ensure there was no overlap in shade and control plots were 15 m from experimental plots. Altogether, the experiment covered roughly 450m².

As a summary, we present a list of materials used, the time and funds spent building the shading structures, and a picture of construction (Fig. 2.1):

- 64 threaded steel rods ($\phi = 22$ mm, length = 1.5 m), 4 per plot (5 GBP each, 320 GBP in total)
- 5 square Kookaburra shade sails 3 m * 3 m (50 GBP each, 250 GBP in total)
- 5 square Kookaburra shade sails 2 m * 2 m (39 GBP each, 195 GBP in total)

In our experiment, the structures were built by a team of 3 divers that measured the correct distance of individual rods to each other, hammered all rods into the sediment, and attached the shade sails in two days. The team was adhering to 8 working hours per day, 16 hours in total.

Individual shade sail above macroalgal field

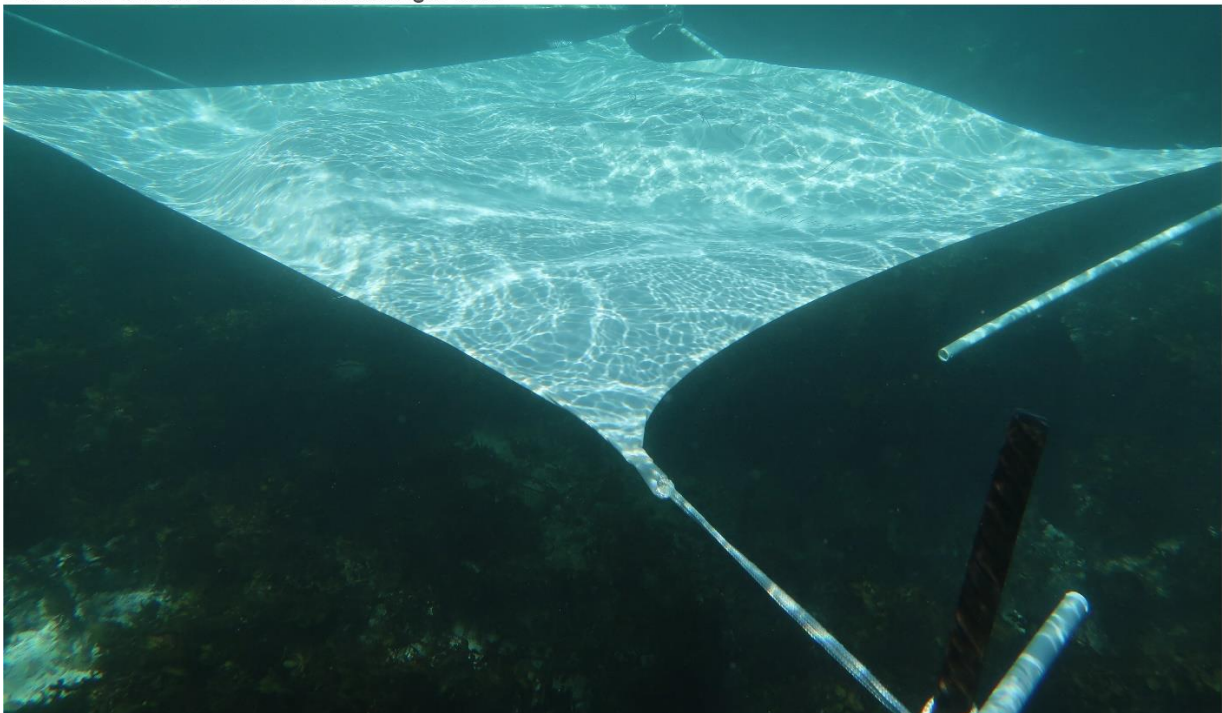


Figure 2.1 Shading structure (white bars seen in structural picture [top] are unessential to construction, they were used for camera attachment, which produced unreliable data and was therefore omitted from the paper)

2.3.3 Sampling and statistical analysis

All sampling was conducted using snorkel gear. We deployed HOBO pendant loggers to measure light intensity (in lux) underneath the sails (Fig. S2.1). We placed the loggers on PVC pipes (35 cm), keeping them above the macroalgal canopy and in the centre of each plot. Loggers were deployed in the first

week of shading from 11:00 to 16:00 h and took light intensity readings every 10 min. We repeated this method in control plots.

2.3.4 Macroalgal cover

We took planar view photographs of treatment and control plots immediately before installing and immediately after taking down the sails. We repeated the process monthly following sail removal, with the last picture taken on the 11/06/2018, 3 months following shading. These pictures were compared using “Coral Point Count with Excel extensions (CPCe)” (Kohler & Gill 2006) to obtain the change in percent macroalgal cover over time.

To statistically investigate the effects of sail size and time (fixed effects), we fitted generalised linear mixed models (GLMM) to macroalgae cover using the lme4-package in R (Bates et al. 2015). The model was fitted with ‘plot’ nested in ‘treatment’ as a random effect to address dependencies induced by repeated measures through time. To avoid having a percentage-based response variable, we used macroalgae cover as a binary response variable (1 = macroalgae, 0 = no macroalgae) with each randomly allocated point in our HD-photographs being one observation (n = 50 per photo, n = 4000 in total) and fitted it with a GLMM with a binomial distribution.

2.3.5 Settlement blocks: turf algal growth potential

To simulate benthic regrowth, we deployed one settlement block (10 x 10 cm, made from marine cement) in the centre of each treatment and control plot when the experiment started. The cement blocks remained under the sails for the entire time of active shading. We collected the blocks with the shade sail removal and analysed them for algae cover using photographs and CPCe (Kohler & Gill 2006). We fitted a GLMM with sail size and time as fixed effects and plot nested in treatment as a random effect. We did the same binary allocation as for macroalgal cover data (1 = turf algae, 0 = no turf algae) for the settlement blocks data (n = 30 per photo, n = 270 in total) and fitted a binomial GLMM to the data.

2.3.6 Photosynthetic efficiency

Every week during active shading and one additional week after, we collected three random basal blades from different plants of each plot from 09:00-10:00 am, at medium to high tide (~ 40 cm difference). We placed these blades in a black, optically opaque bag and, within a maximum of 30 min, took them

from the field site to a wet laboratory, where we kept the same light conditions for the duration of the experiment. We analysed each blade individually with a Junior pulse-amplitude modulation (PAM) chlorophyll fluorometer (Walz, Erlangen-Eltersdorf, Germany) using light curves that applied photo fluence rates of 120, 192, 273, 414, 574, 903, 1341, and 2010 $\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$ consecutively, with 1 min intervals in between. The interval time was sufficient to allow a return to a steady state following saturation pulses. We used the light curves to obtain the effective photochemical quantum yield ($Y(\text{II})_{\text{max}} = \Delta F / F_m'$) as a representative measurement of photosynthetic efficiency per plot per week. We fitted a linear mixed model (LMM) to photosynthetic efficiency data with sail size and time as fixed effects and plot as a random effect. The photosynthetic efficiency ($Y(\text{II})$) data met the assumptions of the LMM as an untransformed response variable with $Y(\text{II})$ recordings averaged for each plot ($n = 112$).

2.3.7 Herbivore feeding following experimental deconstruction

After removal of the shade sails, we monitored plots in March, April, and May 2018 with six digital video cameras (GoPro Hero 4). To quantify the herbivore feeding impact per m^2 on our experimental plots, we deployed the cameras at each plot for 4 hours between 10:00 and 14:00. We analysed a 1-hour film segment situated at least 30 min after deployment and at least 30 min before the end of the filming. We recorded each bite taken by an individual fish and recorded the species. We fitted an LMM to herbivore bite data with sail size and time as fixed effects and plot nested in treatment as a random effect. We \log_{10} -transformed the response variable of herbivore bites per m^2 with every fish being an individual observation ($n = 3859$).

Our models were not or only weakly biased by collinearity (Zuur, Ieno & Elphick 2010). The residual plots of all four models suggested good model fits. We conducted pair-wise comparison Tukey post-hoc test for the four models using the emmeans-package in R (Lenth et al. 2019). All analyses were conducted in R version 3.5.3 (R-Core-Team 2019). We provide our R-scripts and data at an open source repository (<https://github.com/JanDajka/SeyShading-2018>).

2.4 Results

2.4.1 Macroalgal cover

Macroalgal cover significantly declined from before shading (January) to after shading (March) on small plots of 4 m² (Fig. 2.2, 23.6 % reduction January vs. March shaded 4 m²: Tukey pair-wise comparison $z-\Delta_4 = 4.72$, $p = 0.003$) and large plots of 9 m² (51.2 % reduction January vs. March shaded 9 m²: $z-\Delta_9 = 10.25$ $p < 0.001$), while the controls showed non-significant increases in macroalgal cover (3.33 % increase January vs. March controls 4 m²: $z-\Delta_4 = -0.52$, $p = 1$; 2.67 % increase January vs. March controls 9 m²: $z-\Delta_9 = -0.41$, $p = 1$). Macroalgal cover returned following shade removal with significant differences still present after 2 months (12 % reduction January vs. May shaded 4 m²: $z-\Delta_4 = 4.24$, $p = 0.012$; 20.4 % reduction January vs. May shaded 9 m²: $z-\Delta_9 = 4.08$, $p = 0.02$). Three months after shade removal, both plot sizes had returned to similar macroalgal cover compared to before shading (1.2 % reduction January vs. June shaded 4 m²: $z-\Delta_4 = 0.24$, $p = 1$; 7.6 % reduction January vs. June shaded 9 m²: $z-\Delta_9 = 1.52$, $p = 0.99$). Controls showed little change throughout the experiment.

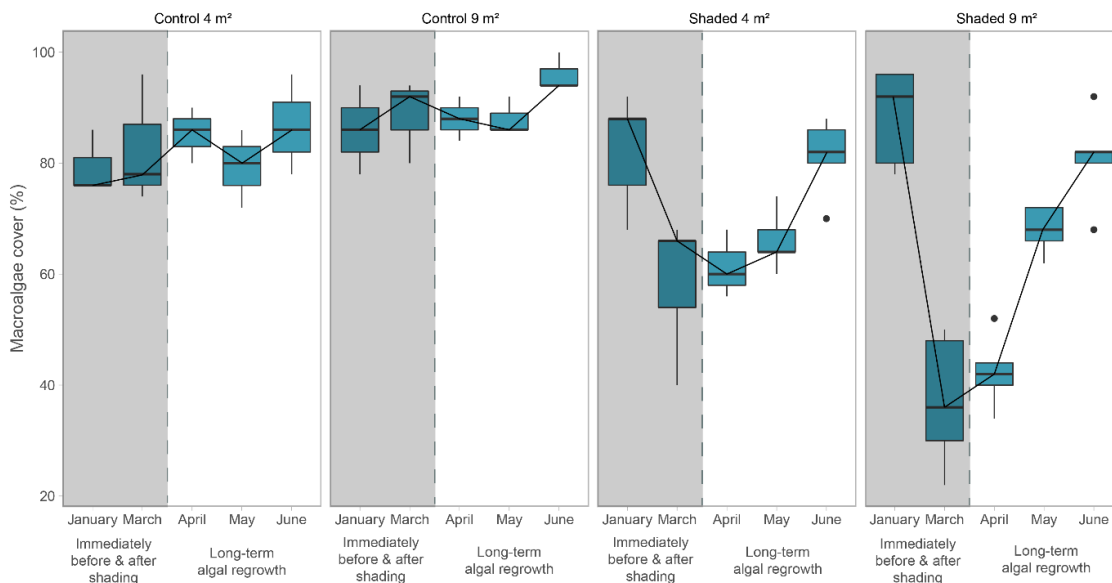


Figure 2.2 Macroalgal cover (in %) changes observed monthly in shaded plots and unshaded control plots of different sizes (4 m² & 9 m²) over the active shading period (grey area) and post-removal/algal regrowth period (white area); central line: mean, boxplot boundaries: interquartile range, outside dot: value is > 1.5 times and < 3 times the interquartile range beyond either end of the box, whiskers: \pm standard error.

2.4.2 Settlement blocks: turf algal growth potential

Turf algae covered most of the area on the previously clear settlement blocks in control plots (Fig. 2.3). In the small shade sail plots, turf algae covered on average 67.8 % (23.37 % reduction control vs. shaded 4 m² tiles: $z-\Delta_4 = 2.7$, $p = 0.02$), while in the larger shade plots turf only covered 8.89 % (81.9 % reduction control vs. shaded 9 m² tiles: $z-\Delta_9 = 7.1$, $p < 0.001$).

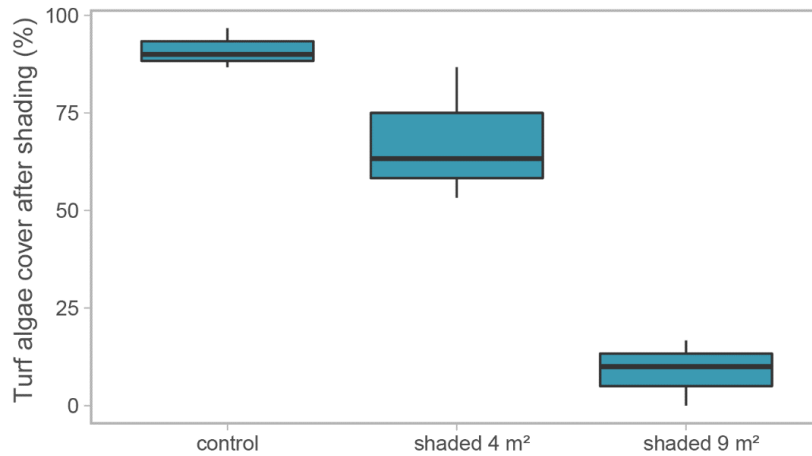


Figure 2.3 Turf algae cover (in %) observed on settlement blocks that were deployed in shaded plots of different sizes (4 m² & 9 m²) and unshaded control plots and collected following deconstruction of the experiment in March 2019; central line: mean, boxplot boundaries: interquartile range, whiskers: \pm standard error.

2.4.3 Photosynthetic efficiency

The photochemical quantum yield of photosystem II (Y(II)) of macroalgae in shaded conditions changed over the duration of the experiment, with noticeable decreases occurring in week 5 (Fig. 2.4). The diversion from baseline measurements taken before the experiment (week 1) were not significant throughout the experiment for shaded macroalgae in small plots (12 % reduction week 1 vs. week 5: $t-\Delta_4 = 2.6$, $p = 0.51$). For large plots on the other hand, the depression in photosynthetic efficiency for shaded macroalgae in week 5 was significant (29 % reduction week 1 vs. week 5: $t-\Delta_9 = 5.8$, $p < 0.001$) and remained significant until week 6, when we removed the shade sails (18 % reduction week 1 vs. week 6: $t-\Delta_9 = 0.1$, $p = 0.04$). Y(II) of macroalgae in control plots did not change significantly throughout the experiment.

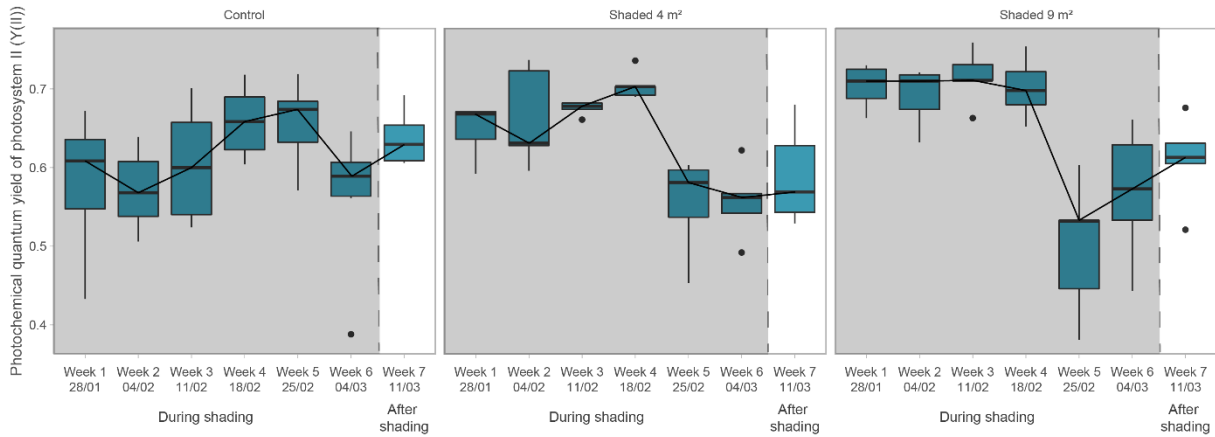


Figure 2.4 Photochemical quantum yield of photosystem II (Y(II)) of experimental *Sargassum* macroalgae throughout weeks of active shading (grey area) and one week after (white area) in shaded plots of different sizes (4 m² & 9 m²) and unshaded control plots; central line: mean, boxplot boundaries: interquartile range, outside dot: value is > 1.5 times and < 3 times the interquartile range beyond either end of the box, whiskers: ± standard error.

2.4.4 Herbivore feeding following shade sail removal

Regardless of plot size or herbivore functional group, bites taken from plots reduced with time following experiment deconstruction (Fig. 2.5). Herbivore feeding did not differ significantly between control plots and plots that were previously shaded for small (control vs. shaded 4 m²: $z\text{-}\Delta_4 = -1.415$, $p = 0.96$) or large plot sizes (control vs. shaded 9 m²: $z\text{-}\Delta_9 = -0.732$, $p = 0.99$).

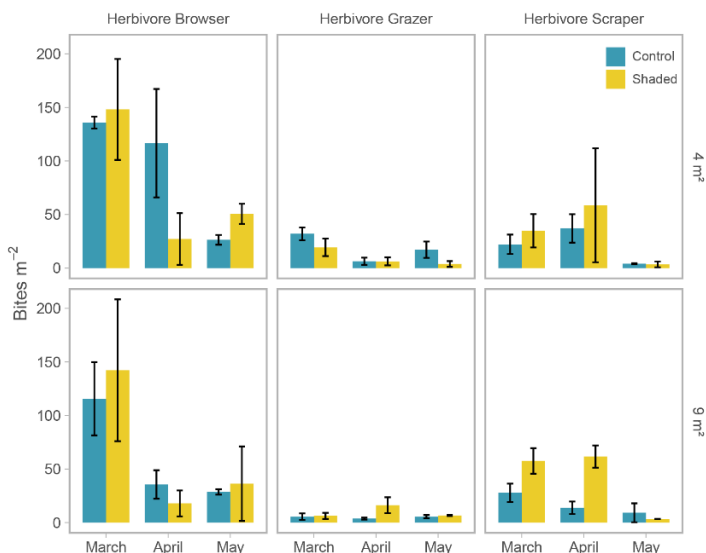


Figure 2.5 Bites per m² taken by three herbivore fish functional groups (browsers, grazers, scrapers) from shaded and control plots of different sizes (4 m² and 9 m²) in one-hour video samples; recordings were taken monthly following shade sail deconstruction, error bars: ± standard error.

However, there were significant differences between control and previously shaded plots in scraper feeding on large plots one month after shade-sail removal (control vs. shaded 9 m² for scrapers in April: $z-\Delta_9 = -4.78$, $p = 0.001$) which had subsided two months after removal (control vs. shaded 9 m² for scrapers in May: $z-\Delta_9 = -1.602$, $p = 0.99$).

2.5 Discussion

Our study demonstrates that using submerged shade sails, macroalgal reduction can be accomplished within 42 days or less, and that reduction scales with shade sail size. Shading also limits turf algal regrowth, potentially making space available to other benthic settlers. Once we removed the shade sails, we did not detect a significant increase in herbivore grazing in our experimental plots, which indicates that the macroalgae-reinforcing feedback was not sufficiently weakened. Our algal reduction method may be used in a reef management approach that pursues the maximisation of ecosystem services drawn from a habitat mosaic reefscape.

The prolonged shading likely hindered the algae's metabolic ability to a point where net-positive photosynthesis could not be sustained (Littler & Littler 1992; Shiu & Lee 2005; Teichberg, Fricke & Bischof 2013). Initially, *Sargassum* was able to acclimatise to the light regime changes and did not show a loss of photosynthetic efficiency for four weeks, although a darkening in blade colouration was visible from week 2 (pers. obs.). The initial acclimatisation to a darker light regime could be possible because the plant increases their light-harvesting pigment content to maximise photosynthesis when PAR is limiting (Littler, Littler & Lapointe 1988; Littler & Littler 1992; Abal et al. 1994; Lirman & Biber 2005). This photoadaptation in macroalgae is likely achieved by diverting energy away from growth and towards maximising photosynthesis, as reported for other tropical marine macroalgae (e.g. *Halimeda*; Littler, Littler & Lapointe 1988; Teichberg, Fricke & Bischof 2013). At week 5, the PAR that *Sargassum* plants were able to harvest in shaded conditions proved insufficient to sustain net-positive photosynthesis. It is possible that reactive metabolic by-products, such as oxygen radicals, caused oxidative damage to the plant photosystems (Shiu & Lee 2005). In addition, the constant variations in light-intensity reaching the algae induced by movement of the shade sails in wave action may have proven challenging to photoadaptation and the sustenance of net-positive photosynthesis (Taylor &

Long 2017). On the other hand, there is evidence suggesting that intermittent light regimes in seaweed canopies stimulate growth and often result in higher productivity within canopy environments (Bennett et al. 2015).

The decrease in photosynthetic efficiency likely resulted in the observed discolouration of the plants and eventually led to a disintegration of the algal thalli. This may have affected the palatability of the plants to herbivores. The palatability of macroalgae to herbivores seems to partly depend on the carbon-to-nitrogen ratio (C:N ratio) within the plant tissue (Vergés et al. 2011). Lower C:N ratios have been experimentally associated with increased herbivore palatability (Barile, Lapointe & Capo 2004; Van Alstyne, Pelletreau & Kirby 2009). Given that changing light-regimes affect plants' photosynthesis and therefore their ability to maintain a C:N ratio (Teichberg, Fricke & Bischof 2013), this ratio can be expected to have changed in our experiment. Unfortunately, we were unable to quantify palatability in our experiment due to the lack of necessary equipment on Curieuse (e.g. -80°C-freezer).

In addition to the decrease in photosynthetic efficiency, herbivorous fish, which are abundant in the area (Robinson et al. 2019), could have grazed on the experimental algae and thus contributed to the reduction in macroalgal cover observed. While we obtained grazing footage of herbivorous fish after the removal of the shade sails, we were unable to do so while the shade sails were in place. We could not set up a camera angle that could balance a view far above the macroalgal canopy (~ 30 cm maximum height) for us to see the substrate clear enough to identify the fish grazing and still be below the shade sail (~ 60 cm above the substrate at the lowest point). In order to obtain grazing footage while the shade sails were in place, we would have needed to build the shading structures higher above the substrate, which then would have reduced the shading efficiency and the ability for boats to pass overhead.

We did not weaken the macroalgae-reinforcing feedback sufficiently, as the experimental plots with reduced macroalgal cover after shading did not show significantly higher grazing rates by herbivorous fish compared to our controls. The macroalgae regrew to roughly pre-experimental cover levels within 3 months. After deconstruction on the 11th of March 2018, herbivorous fishes remained in the plot areas for the first post-experimental month and grazed more intensely on both the shaded and control plots in March. There are two plausible mechanisms for this. First, our experimental design may have lacked

statistical power to detect differences: grazing rates in post-shading plots were higher in March, but there was a high level of variability in these findings. This also has mechanistic support, for instance when scraping parrotfish seemed to preferentially target large shaded plots in the March surveys. Since scraping parrotfish target turf algae (Bellwood & Choat 1990; Streebman et al. 2002; Bonaldo, Hoey & Bellwood 2014; Clements et al. 2017) and our experiment cleared most macroalgae and exposed more open settlement space that turf algae could readily colonise, the scrapers might have preferred macroalgae-free feeding sites over those in between macroalgal stands, which they have been observed to avoid (Hoey & Bellwood 2011). A second but less likely explanation could be that herbivores may have become used to feeding around the structures, such that the intense grazing in March 2018 was a lag effect of the structural attraction, as reef fish have been demonstrated to be attracted by structures similar to ours (Kerry & Bellwood 2015).

Our observed regrowth rates of 3 months roughly match those of a previous study that also used percent cover as a metric - *Sargassum*: 2 months (McClanahan et al. 2001), *S. herporhizum*: < 1 month, *S. sinicola*: > 3 months (McCourt 1985). However, macroalgal biomass, and associated feedback mechanisms, may take longer to re-establish (Loffler & Hoey 2018). Our six-week shading method led to a significant reduction of macroalgal cover and we can suggest a combination of possible reduction mechanisms. An interesting question remains as to whether the algae regrew because of low herbivory, or the herbivores moved because the macroalgal feedbacks were not sufficiently weakened. Along our previous reasoning, we believe the latter. It could be that with the removal of the shade sails, the return to a normal light regime allowed the macroalgae to again reinforce their unpalatability to herbivores which then led to herbivore disengagement and regain of strength in the self-reinforcing feedback. There is also a notable difference in initial macroalgal cover between our two treatments and their associated controls (Fig. 2.2). This difference was induced by randomness and is not by design. It is further compounded by the low number of pens per treatment ($n = 5$) and per controls ($n = 3$). We believe that further replicates would have corrected this anomaly, but as mentioned before, our replicate numbers were based on logistical constraints. As a consequence, we refrained from cross-treatment comparisons of our macroalgal cover data and only compared each experimental week with the initial values of the same treatment or controls.

While other studies have reduced macroalgal cover by manual removal (McClanahan et al. 2001; Loffler et al. 2018; Loffler & Hoey 2018), our study is the first to do so via shading for a limited time frame. The time we were able to physically keep our shade sails in place was restricted by the increase in wave action. While our study confirmed that localised macroalgal reduction can be achieved within 42 days as indicated by an observational study (Stimson & Conklin 2008), we were unable to clear the plot of holdfasts. Given the resistant nature of the algae's holdfasts (Ceccarelli et al. 2018), we think that it would be interesting to see whether a longer shading time would result in a reduction of holdfasts, since most of the observed macroalgal regrowth following shade sail removal has likely come from leftover holdfasts (Loffler et al. 2018). Alternatively, since the shorter six-week time frame might be particularly interesting to management as the longer time frame might not be a realistic management tool (Ceccarelli et al. 2018), perhaps a combination with other intervention methods, e.g. shading areas manually cleared of holdfasts, could be of greater management use. We accurately measured the pre-shading density of holdfasts in situ but could only estimate the post-shading density from plot photos due to illness of the primary observer. Based on our photographs, we do believe holdfast densities decreased.

Although larger shade sails did result in a darker light regime which in turn resulted in more effective macroalgal removal, we want to note that shade sails even larger than 9 m² could present the problem of being too large. The 9 m² shade sails did present a slight loss in tension towards the end of our experiment. This could result in the centre of the shade sail dragging on the substrate and resulting in macroalgal reduction as result of abrasion rather than shading. While the loss in tension in our experiment was not as drastic that the sails experienced contact with the substrate or the algae, shade sails larger than 9 m² may well present this problem. Therefore, we advise future studies to be cautious of this issue and should it arise, opt for an approach that uses multiple 9 m² sails to cover a larger area rather than one larger sail.

We were unable to confirm that other benthic settlers (e.g. corals) can grow on the cleared settlement space because of the limited experimental period. Based on coral settlement studies that monitored coral settlement for 5 - 29 months (Babcock & Mundy 1996; Mangubhai, Harrison & Obura 2007; Yadav et al. 2016), we suggest that future studies find sites and/or shading structures that allow for a longer period

of uninterrupted shading to be able to observe a potential increase in coral recruits. We note that shading corals that have adapted to light regimes, for instance in depths of less than 3 m, might also entail negative effects on those corals (Rogers 1979). Shaded plots could instead provide settlement space for organisms that normally grow at greater depths or in turbid environments with comparable light regimes.

Our study tested a novel method of macroalgal reduction that could be used and further developed for localised intervention approaches that aim to manage productive reefs made up of a mosaic of interconnected habitat patches. We recognise the importance of natural macroalgal reefs (Fulton et al. 2019) and that macroalgae will increasingly be a part of ecological (Nagelkerken et al. 2015; Harborne et al. 2016) and socio-economic reef potential (Robinson et al. 2019). But since self-reinforcing feedbacks can lead macroalgae to dominate continuous stretches of reef and thereby expand beyond connectivity thresholds that are critical for a productive mosaic, reef management needs ways to address macroalgal expansion. While our method did not interrupt macroalgal-reinforcing feedbacks to the point where grazing rates by herbivorous fish significantly increase, it weakened them so that macroalgal cover could be significantly reduced. We present a method that reduced macroalgal cover by altering the light regime, that may be useful as part of a suite of intervention strategies, particularly to shade areas cleared of holdfasts, and perhaps aiding coral recruitment on newly provided settlement substrates.

Contribution of authors

JCD, NAJG, and JB conceived the ideas and designed the methodology; JCD, VB, and GG contributed critically in acquisition of the data; JCD analysed the data; JCD, NAJG, and JB interpreted the results. JCD wrote the first draft of the manuscript, and all authors contributed critically to drafts and gave final approval for publication.

3 INVESTIGATING SEA URCHIN DENSITIES CRITICAL TO MACROALGAL CONTROL ON DEGRADED CORAL REEFS

3.1 Abstract

Tropical sea urchins are often considered as macroalgal grazers with the ability to control macroalgal expansion on degraded coral reefs. However, this assumption relies heavily on geographically limited observations of select species, leading to the functional roles and main habitats of many tropical urchin species being poorly understood. We addressed these gaps for a common urchin species in the Seychelles, *Echinothrix calamaris*, in a two-part approach. Firstly, we surveyed urchin abundances on 21 reefs of the inner Seychelles and predicted their density using habitat predictors in a modelling approach. Patch-reef type best predicted increases in urchin abundances, while macroalgae best predicted decreases. Secondly, we experimentally investigated the macroalgae-urchin relationship by penning two urchin densities on macroalgal fields. Over six weeks, the highest density (4.44 urchins m⁻²) cleared 13 % of macroalgal cover. This moderate impact leads us to conclude that controlling macroalgal expansion is not likely to be one of the main functions of *E. calamaris* in the inner Seychelles given the current densities we found in our surveys (mean: 0.02 urchins m⁻², maximum: 0.16 urchins m⁻²). However, for other tropical urchin species, such as *Diadema antillarum*, controlling grazing on macroalgae was measured at high densities (~ 7.7 urchins m⁻²) and our results indicate that this could apply to *E. calamaris* as well. Patch reefs are where *E. calamaris* are most likely to control macroalgae on degraded coral reefs.

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3.2 Introduction

Tropical coral reefs are changing under recent anthropogenic pressures such as overfishing, near-shore pollution, and climate change (Norström *et al.* 2016). There are cases where overfished coral reefs do not recover from acute disturbances, such as thermally induced mass bleaching and undergo a regime shift to dominance of benthic states alternative to coral, such as macroalgal dominance (Done 1992; Mumby 2009; Graham *et al.* 2015). One of the key ecological controls of macroalgal expansion is herbivory (Bellwood *et al.* 2004; Hughes *et al.* 2007), and sea urchins are widely assumed to perform that function (Morrison 1988; McClanahan 1992; Solandt & Campbell 2001; Sumi & Scheibling 2005; Carpenter & Edmunds 2006; Stimson, Cunha & Philippoff 2007). However, that this macroalgae-controlling role can be assumed to extend universally to species across the globe, is unlikely.

Our knowledge about the role of sea urchins on degraded coral reefs is very limited in geographical extent (Caribbean: Carpenter 1988; Carpenter & Edmunds 2006; Kenya: McClanahan & Shafir 1990; Western Australia: Johansson, Bellwood & Depczynski 2010; Great Barrier Reef: Young & Bellwood 2011) and is based on very few species (McClanahan 1992; Young & Bellwood 2011). Especially prevalent is a single Caribbean species, *Diadema antillarum* (Maciá, Robinson & Nalevanko 2007; Hughes *et al.* 2010; Graham *et al.* 2013). This limitation to our knowledge of other urchin species also extends to the composition of their habitat (Benedetti-Cecchi & Cinelli 1995; Chiappone, Swanson & Miller 2002; Lee & Hessen 2006; Bodmer *et al.* 2015), and therefore where these other species are most likely to perform their respective functions, such as grazing. When long-spined sea urchins, *D. antillarum*, were reported to be the main controllers of macroalgal cover in the Caribbean, mean densities were reported at 7.7 urchins m⁻² (Hughes 1994). The urchins' macroalgae-controlling role was assumed to be critical on the overfished Caribbean reefs which were lacking the necessary biomass of herbivorous fishes. Afterwards, the urchins' macroalgae-controlling impact was virtually erased in a pivotal mass die-off from disease (Hughes *et al.* 2010). The more recent recovery of the Caribbean *D. antillarum* has been correlated with some returns in coral cover in the region (Carpenter & Edmunds 2006; Myhre & Acevedo-Gutiérrez 2007). In a large-scale model, some urchin species (*D. antillarum*, *Tripneustes ventricosus*, *Tripneustes esculentes* [Caribbean], *Echinometra mathaei* [Western Indian

Ocean]) have been suggested to be especially important for controlling algae in heavily fished areas (McClanahan 1992). While knowledge of the ecological dynamics associated with these urchin species is fairly extensive, the densities at which other urchin species in other geographic locations have notable macroalgae-controlling impact is poorly studied. The lack of understanding could prove detrimental to coral reef ecosystems if urchin populations are targeted for exploitation (Furesi *et al.* 2016; Parvez, Rahman & Yusoff 2016; Sato *et al.* 2017).

In addition, the macroalgae-controlling role of urchins could be used in a more targeted manner that is useful to coral reef management, yet few have attempted to actively utilise urchin grazing in a focussed area. Whether urchins can be used to effectively control algal expansion or even clear algal patches and thereby aid coral recovery is yet to be determined. Maciá *et al.* (2007) conducted experiments transplanting urchins to high algal density areas to explore this ability. The urchins were recorded to graze the algae but vacated the area too quickly to show a controlling impact. According to the authors, there were no apparent signs of mortality or predation that led to the urchin loss. The potential of this approach to reveal the focussed impact of urchins on algae thus remains unexhausted and could be improved to determine urchins' potential as macroalgal controllers outside of the classically studied systems.

We investigate the role of the short-spined urchin (*Echinothrix calamaris*) as potential macroalgal herbivores in the inner Seychelles. First, we conducted field surveys to observe urchin densities and benthic habitat use. With the resulting dataset, we modelled the habitat predictors of urchin abundance. Second, we experimentally relocated varying densities of *E. calamaris* into standardised pens located on dense, continuous fields of macroalgae to focus their grazing impact. Our study provides insights into the function of *E. calamaris* as a macroalgal controller that helps illuminate the ecological dynamics of degraded coral reefs.

3.3 Methods

3.3.1 Study organism and site

Our study species, the short-spined urchin (*Echinothrix calamaris*), is a common urchin species in the Western Indian Ocean and in our study area, the inner Seychelles (Kroh 2013). The inner Seychelles (4°30'S, 55°30'E) are largely granitic islands with well-developed carbonate fringing reefs that have been increasingly fragmented by large-scale disturbances in recent history. In particular, two major coral-bleaching events caused by thermal anomalies (in 1998: ~ 90 % coral loss; (Goreau *et al.* 2000); and 2016: ~ 70 % coral loss; (Wilson *et al.* 2019) have led to habitat fragmentation of coral reefs as well as to macroalgae-dominated habitat (average macroalgae cover of 42 %) on many reefs in the Seychelles (Graham *et al.* 2015). Prevailing winds in the inner Seychelles come from the north-west between December and March and start turning into south-easterly winds in late March, staying this way until October, followed by intense rainfall and wind through November and December (M Belmont and V Amelie, Seychelles Meteorological Services).

3.3.2 Benthic drivers of sea urchin abundance & statistical analysis

Surveys for the first part of our study were conducted in April 2017. We surveyed 21 sites of the inner Seychelles (Fig. S3.1) that were preselected by a range of long term studies starting in 1994 (Jennings, Grandcourt & Polunin 1995) and coarsely classified each site as one of three types; either continuous, well developed fringing reef with limestone framework (carbonate), continuous reef with granitic base (granite), or fragmented reef (patch). We conducted sampling during daytime hours from 9:00-16:00 in eight replicate areas (7 m radius) along the base of the reef slope of each site at the depth of 2-9 m depth covering up to 0.5 km of reef front and 2,500 m² of reef habitat. Individual replicates were at least 10 m apart, and within each replicate we visually estimated percent cover of macroalgae and corals. This visual estimation method strongly correlates with a range of other methods for capturing benthic cover and structural complexity of coral reefs (Wilson, Graham & Polunin 2007). We also visually estimated structural complexity of the reef using a scale from 0 (no vertical reef) to 5 (exceptionally complex with numerous caves and overhangs) as per Polunin and Roberts (1993). We counted *E. calamaris* within each replicate area. Lastly, within each 154 m² replicate (7 m radius), we recorded the abundances and

size (total length) of 134 diurnally active, non-cryptic, reef-associated fish species. The surveying diver calibrated size estimates of fish by estimating and confirming the lengths of pre-sized plastic pipes at the start of each sampling day until estimates were consistently within ~ 3 % of actual lengths to ensure accurate length estimates of fish (Graham *et al.* 2007). Large mobile fish in the cylinder were recorded first, followed by a systematic search for smaller site-attached fish. We converted estimated fish lengths from the resulting dataset into biomass using published length-weight relationships (Letourneur, Kulbicki & Labrosse 1998; Froese & Pauly 2011) and assigned recorded species to feeding groups based on their diet and feeding behaviour (Wilson *et al.* 2008).

We used the dataset resulting from the 21-reef site survey to analyse abiotic and biotic habitat predictors of sea urchin abundance at the scale of the radial replicates ($n = 168$). We expected urchin abundance to be predicted by 6 biotic and abiotic variables measured at the replicate scale and 1 measured at the site scale (Table 3.1). We also included one ecologically sensible two-way interaction between macroalgae and structural complexity which has yielded interesting results in previously published work resulting from the same surveys (Dajka *et al.* 2019). We recorded ‘reef type’ as a categorical variable with three reef types: carbonate, patch, and granite. After isolating the influence of each reef type on urchin abundance during data exploration, patch reefs stood out as most influential while carbonate and granite reefs showed comparable effects. Given our number of observations ($n = 168$), we replaced ‘reef type’ with a binary dummy variable that isolates the patch reef type and groups carbonate and granitic reef types to reduce our covariates to a number that can be sensibly interpreted. Our chosen variables did not present problematic variance inflation factors (Table 3.1), indicating that our model was not biased by collinearity issues (Zuur *et al.* 2009). We scaled variables to a mean of 0 and standard deviation of 1. This is a recommended approach for multi-model selection which allows for meaningful comparisons of effect sizes when variables are on different scales (e.g. structural complexity vs. reef type) (Schielzeth 2010). To account for overdispersion and high frequencies of true zeros in our response variable (45.8 %), we fitted a zero-inflated negative binomial (ZINB) regression; a two-part model that fits two distributions to the data (Zuur, Saveliev & Ieno 2012). The first part fits a binomial distribution to the full dataset, treating the response variable as presence-absence (i.e. 0 urchins or 1 urchin, zero component).

Table 3.1 Biotic and abiotic variables considered in habitat predictor analysis to explain spatial variation in sea urchin abundance, brackets include a variance inflation factor (VIF) that was determined during data exploration, the VIF is showing the degree of collinearity between our variables (values > 3 can start to show auto-correlation, Zuur, Ieno & Elphick 2010).

Predictor (VIF)	Rationale	Reference
Coral (1.6)	Sea urchins have been reported closely associating with live and dead coral, and also to graze on corals.	(Bak & van Eys 1975; Furman & Heck 2009; Johansson, Bellwood & Depczynski 2010; Young & Bellwood 2011)
Macroalgae (2.6)	Many sea urchin species throughout the world are considered macroalgal grazers.	(McClanahan 1999; Solandt & Campbell 2001; Sumi & Scheibling 2005; Carpenter & Edmunds 2006; Stimson, Cunha & Philippoff 2007; Johansson, Bellwood & Depczynski 2010)
Herbivorous fish biomass (1.2)	Sea urchins and fish herbivores have been considered as primary competitors.	(Carpenter 1988; McClanahan 1992)
Invertivorous fish biomass (1.2)	Invertivorous fish are considered primary predators of sea urchins	(McClanahan & Shafir 1990; McClanahan 1999; Hereu <i>et al.</i> 2004)
Structural complexity (1.5)	Structurally complex reefs provide habitable space for a diverse range of organisms including sea urchins or fish, and can increase urchin survival.	(Andrew & Underwood 1993; Benedetti-Cecchi & Cinelli 1995; Hereu <i>et al.</i> 2004; Lee & Hessen 2006; Bodmer 2019)
Patch reef type – site scale (1.5)	Three reef types surveyed: carbonate, patch and granite reefs; patch reef type is considered to be a facilitating habitat for sea urchins	(Jones & Andrew 1990; Andrew 1993; McClanahan 1999)

The second part fits a negative binomial distribution to all response data excluding true zeros (i.e. > 1 urchin, count component). We initially used a zero-inflated model with ‘site’ as a random factor using the glmmTMB-package (Brooks *et al.* 2017) and one without a random effect using the ‘pscl’-package (Zeileis, Kleiber & Jackman 2008). Model selection based on Akaike Information Criterion (AIC, Zuur *et al.* 2009) determined the latter model as better performing, suggesting that auto-correlation did not bias our parameter estimates. Backwards selection based on AIC (Table 3.2) excluded three variables (‘coral’, ‘herbivorous fish biomass’, ‘invertivorous fish biomass’) resulting in the final model:

$$\text{Sea urchin abundance} \sim \text{Macroalgae} + \text{Complexity} + \text{Patch reef type} + \text{Macroalgae} \\ * \text{Complexity}$$

Table 3.2 Model selection in backwards stepwise selection based on Akaike information criterion (AIC) and degrees of freedom (df).

Model	AIC	df	Excluded factors
Urchins ~ Macroalgae + Complexity + Coral + Patch reef + Herbivores + Invertivores + Macroalgae * complexity	667.92	19	None, global model
Urchins ~ Macroalgae + Complexity + Coral + Patch reef + Macroalgae * complexity	662.3	13	Herbivores Invertivores
Urchins ~ Macroalgae + Complexity + Patch reef + Macroalgae * complexity	661.1	11	Herbivores Invertivores Coral

During model validation, we found no alarming patterns in the model's residuals apart from the clustering in the model's zero component, which is expected with zero-inflated models (Zuur, Saveliev & Ieno 2012). To visualise the relationships between predicted urchin abundance across the observed range of each individual variable in our ZINB model, we held all other variables to constant means of 0 (Schielzeth 2010).

3.3.3 Experimental sea urchin penning & statistical analysis

The second part of our study was done from January to March 2018 on the degraded reefs of Anse Papaie (4.28°S, 55.73°E), Curieuse Island, one of the 21 sites surveyed in the first part of the study (Fig. S3.1). We chose the bay because it is a marine park, minimising disturbance to our experiment and because Anse Papaie is a degraded fringing coral reef, with high fragmentation and eroded structural complexity at 0.5 m to 7 m depths. The bay is almost universally covered by continuous macroalgal fields, with canopy and overstorey primarily made up of *Sargassum* spp. and some *Turbinaria* spp., while the understorey is primarily *Lobophora* spp. and *Dictyota* spp. *Sargassum* in particular often have strong seasonal patterns, mainly driven by temperature changes and nutrient limitation (McCourt 1984; Vuki & Price 1994; Hwang, Tsai & Lee 2004). *Sargassum* seasonality in the inner Seychelles appears to be tied to the prevailing seasonal winds and currents (Kalugina-Gutnik, Perestenko & Titlyanova 1992; Zvyagintsev & Ivin 1992; Bijoux 2013). *Sargassum* appear to senesce during the peak of the more cloudy season during the south-east winds (from May to October) and regrow (likely from leftover holdfasts) during the predominantly clear-sky season of north-west winds (December to March) (Bijoux 2013), leading to our choice of experimental timing (January to March).

In early January 2018, we built 13 individual experimental pens (2.25 m² area, each fenced with chicken wire and built with open top) on continuous macroalgal fields that grew on relatively flat surfaces to ensure the fences were flush with the sea floor. We stocked 5 pens with 10 *E. calamaris* (4.44 urchins m⁻²), 5 pens with 4 *E. calamaris* (1.78 urchins m⁻²), and 3 pens without urchins as controls. These stocking densities were the logistically highest attainable given the surrounding natural urchin abundances. The pens were dispersed randomly within the macroalgal field, although we kept a minimum distance of 1 m between each treatment pen and 5 m between control and treatment pens. On the 28th of January (week 1), we took HD-photographs of each pen from above. We repeated the process on the 18th of February (week 3) and the 11th of March (week 6). We compared the photographs using “Coral Point Count with Excel extensions (CPCe)” (Kohler & Gill 2006) to obtain a change in macroalgal cover over time.

To analyse the effects of ‘urchin stocking density’ and ‘time’ (fixed effects), we fitted generalised linear mixed models (GLMM) to our response variable ‘macroalgae cover’ using the lme4-package in R (Bates *et al.* 2015). The model was fitted with ‘plot’ as a random effect to address dependencies induced by repeated measures through time (Zuur, Ieno & Elphick 2010). To avoid having a percentage-based response variable, we used macroalgal cover as a binary response variable (1 = macroalgae, 0 = no macroalgae) with each randomly allocated point in our HD-photographs being one observation (n = 50 per photo, n = 1950 in total) and fitted it with a GLMM using a binomial distribution and the following formula:

$$\text{Macroalgae cover} \sim \text{Urchin stocking density} + \text{Time} + (1 | \text{Plot})$$

The plots of the GLMMs’ residuals did not show any alarming clustering or patterns and therefore suggest good model fits. Subsequently, we used a pair-wise comparison Tukey post-hoc test using the emmeans-package in R (Lenth *et al.* 2019).

All analyses were conducted in R version 3.5.3 (R-Core-Team 2019). We provide our R-scripts and dataset at an open source repository (<https://github.com/JanDajka/SeyUrchins-2018>).

3.4 Results

3.4.1 Benthic drivers of sea urchin abundance

Our model's zero component indicated a strong positive correlation of patch-reef type on sea urchin abundance, as well as weak positive correlation of the macroalgae-structural-complexity interaction and structural complexity (Fig. 3.1 A). Macroalgae displayed a strong negative correlation on urchin abundance in the zero component. The count component of our model showed a strong positive correlation for patch-reef type, and a weak positive correlation for macroalgae (Fig. 3.1 B), and a weak negative correlation of structural complexity on urchin abundance. The macroalgae-structural-complexity interaction displayed a strong negative correlation on urchin abundance in the count-component of our model. The sizes of the confidence intervals (thin lines) do not allow for a reliable interpretation of the weak correlation of the macroalgae-structural-complexity interaction and structural complexity in the zero component (Fig. 3.1 A) or macroalgae and structural complexity in the count component (Fig. 3.1 B).

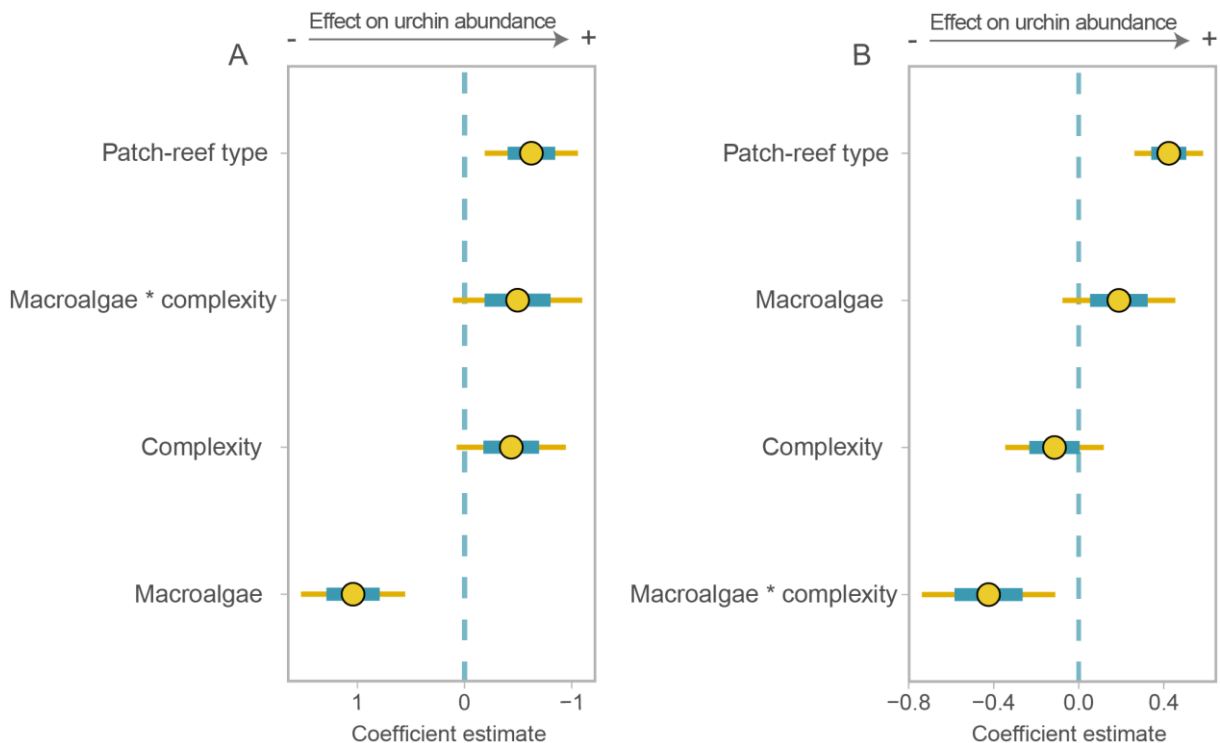


Figure 3.1 Effect size estimates of predictor coefficients in zero model with standard error (thick lines) and 95% confidence intervals (thin lines); zero-model component: positive coefficient estimates predict urchin absences (0) and negative coefficient estimates predict urchin presence (1), stronger negative values indicate stronger positive effect on urchin abundance (A); count-model component: negative coefficient estimates predict lower urchin abundance, positive coefficients predict higher abundance (B).

The predictor trends resulting from the count component of our model predict a steady decline in urchin abundance with increasing macroalgal cover (Fig. 3.2 A). Our model predicted ~ 3 urchins per replicate (0.019 urchins m²) per when macroalgae were absent, but ~ 2 urchins (0.013 urchins m²) when macroalgal cover extended to 5 % per replicate. Further interpretation of this trend was not warranted due to large standard errors resulting from few occurrences of macroalgal cover values above 5 %. Our model suggested that no urchins were found in replicates with > 90 % algal cover, while over 20 replicates were found where there were urchins present. The predictor trend of structural complexity predicts a slight increase of urchin abundances with increasing structural complexity (Fig. 3.2 B). In replicates with structural complexity of 2, the model trend predicted abundances of ~ 2.5 urchins (0.02 urchins m²) that increased to ~ 3 urchins (0.02 urchins m²) at a structural complexity of 4. The predictor trend at lower structural complexity is also uninterpretable due to the limited number of replicates with structural complexity below 2. Continuous reefs of granitic or carbonate base predicted abundances of ~ 1.5 urchins (0.01 urchins m²) while fragmented patch habitats predicted abundances of ~ 6.5 urchins (0.04 urchins m²) (Fig. 3.2 C). With increasing structural complexity, macroalgae correlated with a more severe decrease of urchin abundances (Fig. 3.2 D). As macroalgal cover increases from 0 % to 7.5 % per replicate, urchin abundances decrease with structural complexity as follows: predicted abundances decreased from ~ 3 urchins (0.02 urchins m²) to ~ 1 urchin (0.01 urchins m²) at structural complexity 0, from ~ 5 urchins (0.03 urchins m²) to ~ 1 (0.01 urchins m²) at structural complexity 2, and from ~ 7 (0.05 urchins m²) to ~ 0 urchins (0.002 urchins m²) at structural complexity 3.5.

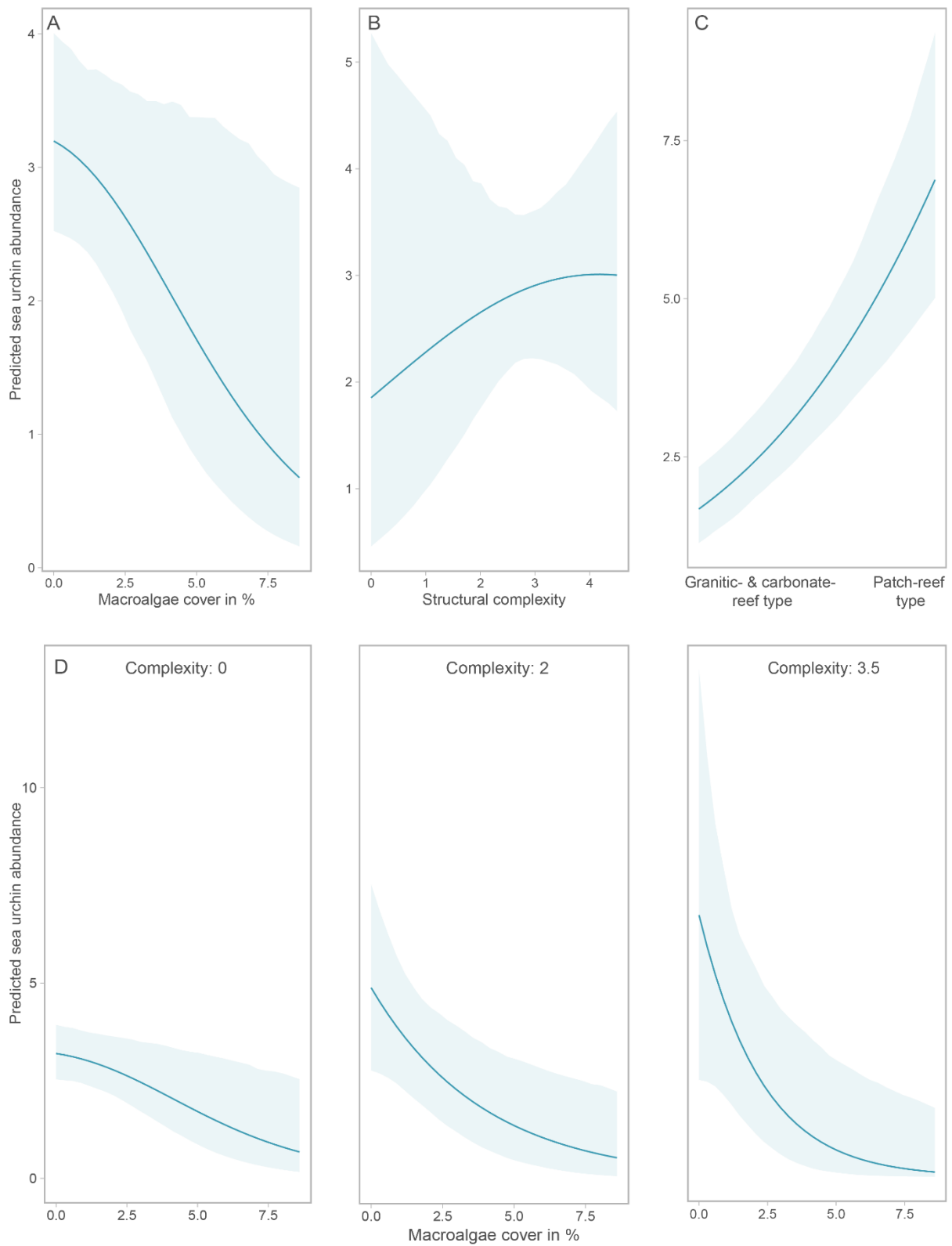


Figure 3.2 Model prediction trends of macroalgae (A), structural complexity (B), and patch-reef type (C), and for the interaction of macroalgae * structural complexity (D) for the count component of the zero-inflated negative binomial model, panels show the fitted effect (line) and 95 % confidence intervals (shaded bands) for each variable.

3.4.2 Experimental sea urchin penning

Macroalgal cover declined from the first week to the third week in pens stocked with 10 *E. calamaris* (Fig. 3.3, 13 % reduction: Tukey pair-wise comparison $z\text{-}\Delta_{10} = 3.074$, $p = 0.054$, Suppl. table 3.1). Pens stocked with 4 urchins as well as control pens displayed no notable differences in macroalgal cover over time (Fig. 3.3, Suppl. table 3.1).

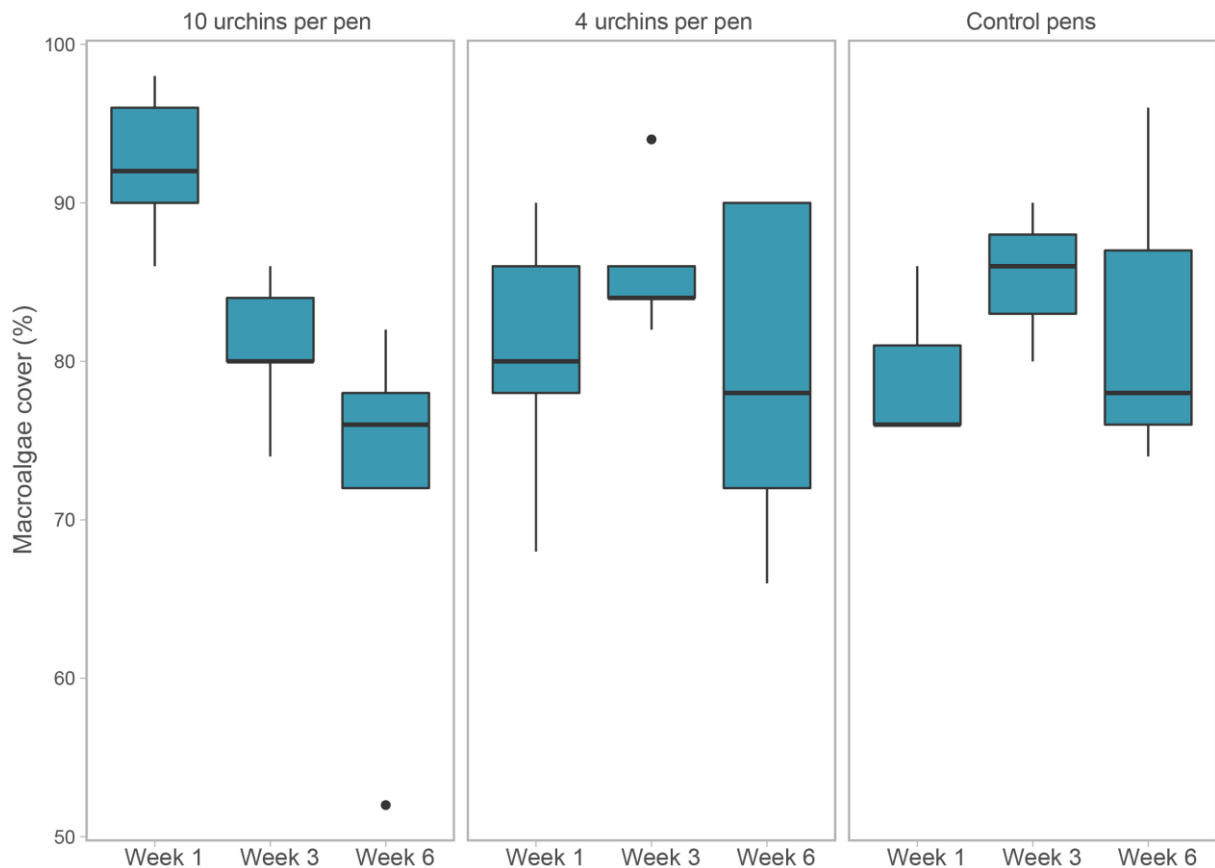


Figure 3.3 Macroalgal cover (in %) changes observed in three-week intervals inside the penned experimental plots for stocking densities of 10 & 4 *Echinothrix calamaris*, as well as controls; central line: mean, boxplot boundaries: interquartile range, outside dot: value is > 1.5 times and < 3 times the interquartile range beyond either end of the box, whiskers: \pm standard error.

3.5 Discussion

In our urchin penning experiment, short-spined urchins (*Echinothrix calamaris*) were able to achieve some macroalgal reduction within six weeks. While the experimental densities (4.44 urchins m^{-2}) required to achieve this reduction were far above mean and maximum densities we observed in surveys across the inner Seychelles (mean: 0.02 urchins m^{-2} , maximum: 0.16 urchins m^{-2}), there are studies that have recorded even higher densities of sea urchins in the Caribbean between 1970 and 1983 (mean: 7.7

urchins m^{-2} , maximum: > 20 urchins m^{-2}) before a die-off from disease (Hughes *et al.* 2010; Graham *et al.* 2013). Since this drastic mortality, Caribbean urchin densities have slightly risen again (mean 2000-2008: 0.3 urchins m^{-2}). The authors of another study that also relocated urchins (*Diadema antillarum*) from high density (1.40 ± 0.18 urchins m^{-2}), to low density (0.02 ± 0.01 urchins m^{-2}), non-fenced areas were able to achieve significant reductions in macroalgal cover by about 15 % before the urchins left the area (Maciá, Robinson & Nalevanko 2007). When we relocated similar densities of *E. calamaris* (1.78 urchins m^{-2}) into pens, we did not observe a significant reduction of macroalgal cover.

At lower densities, closer to those that we found naturally in the Seychelles, our model suggests that urchin abundance correlates positively with patch reefs and negatively with macroalgae. We also found a weak positive correlation of structural complexity on urchins in our model. Although, the negative correlation we found for macroalgae appeared to outweigh the positive correlation of structural complexity, leading to a more drastic reduction of urchin abundances on complex reefs as macroalgal cover expanded. The relationship between urchins and structural complexity in the wider literature is multi-faceted which might be why our results did not show clear patterns. Some studies report a positive relationship between urchins and structural complexity (Hereu *et al.* 2004; Lee 2006) while others, including a meta-analysis, report a negative relationship (Weil, Torres & Ashton 2005; Graham & Nash 2013). These discrepancies could stem from the varying behaviours, such as substrate-eroding and protection behaviours displayed by multiple urchin species. Some urchins, such as the substrate-boring urchin *E. mathaei*, tend to use crevices for protection (Khamala 1971; McClanahan & Kurtis 1991), while other species such as *D. antillarum* display gregarious behaviour in open areas (Levitan 1988; Graham & Nash 2013). We observed both hiding in crevices and gregarious behaviour in open areas with *E. calamaris* during our study (JCD, pers. obs.).

Increasing abundances of *E. calamaris* were more often found in areas with low macroalgal cover and more towards patch reef types. Perhaps the urchins graze down the macroalgae or they actively search open areas. Our combined experimental and observational evidence suggest the latter. In our penning experiment, only unnaturally high densities of urchins had an effect on algal densities (4.44 urchins m^{-2} vs 0.16 urchins m^{-2}) and locally common macroalgal genera like *Sargassum* were not overwhelmingly

grazed. As a whole, our findings align with the literature in that notable sea urchin grazing impacts on macroalgae appear to scale with local urchin densities (Carpenter & Edmunds 2006; Myhre & Acevedo-Gutiérrez 2007; Furman & Heck 2009; Hughes *et al.* 2010). The common urchin species in the Western Indian Ocean, *E. calamaris*, could have a macroalgal controlling effect like its Caribbean relative, but this is only likely if mean densities that we recently observed in the Seychelles were to exponentially rise (by 220 times).

The penning technique as we used it is unlikely to lend itself as an effective method for controlling macroalgal expansion on degraded coral reefs. This is mainly because of the large number of urchins that need to be transported into the pens in order to achieve macroalgal reduction. The technique may be enhanced by including structural elements into the pens, given the partly positive relationship between structural complexity and urchins in the literature (Hereu *et al.* 2004; Lee 2006). A longer penning time at higher stocking densities (minimum of 4.44 urchins m⁻²) could also prove effective in clearing the entire pen of macroalgae, seeing as macroalgal cover in pens stocked with 10 urchins declined continuously throughout our experiment.

It is also notable that the penning experiments of stocking densities with 4 urchins commenced with an average of ~ 81 % initial macroalgal cover while pens with 10 urchins commenced with ~ 92 % (Fig. 3). This difference was induced by a combination of the random placement of treatments and is compounded by the low number of pens per treatment (n = 5) and we believe that further replication would have rectified this irregularity but, in our case, we were logistically constraint to the numbers of replicates used. We therefore refrained from analysing our data across treatments and only compared each experimental week with the starting point of the same treatment.

Another note about our experiment is that macroalgal cover declined from week 3 to week 6 almost uniformly across all treatments as well as controls. We propose that the onset of south-easterly winds in March (see methods) towards the end of our experiment may have increased wave energy to the extent that similar amounts of macroalgae got removed by increased wind forces rather than by urchin feeding in week 6. This would explain why we see a similar reduction in macroalgal cover in the controls.

In addition, the macroalgal fields in our experiment were largely made up of *Sargassum*, an algal genus that *E. calamaris* may not have feeding preference for. Our HD-photographs allowed us to identify the macroalgae to genus level, which resulted in more than 90 % *Sargassum* cover in our experiment. However, since the photographs were taken from plantar view, this only represents the overstorey and we cannot make inferences about the understorey that might have been growing under the *Sargassum* canopy. *Lobophora* algae for instance can grow in the understorey of other algae (Roff *et al.* 2015) and if the *E. calamaris* did prefer these algae, we would not have picked up on it. Feeding preference towards certain algal genera and species has been reported for sea urchins (Solandt & Campbell 2001; Konar & Estes 2003; Stimson, Cunha & Philippoff 2007). Although, a notable non-selectivity has also been reported for the Caribbean urchin species, *D. antillarum*, grazing on several chemically and physically defended macroalgae (Solandt & Campbell 2001; Furman & Heck 2009) as well as turf algae (Carpenter 1985). In summary, we believe that *E. calamaris* might not have a feeding preference for *Sargassum*, but this does not exclude them preferring other macroalgae. This could be an explanation as to why *E. calamaris* show a different feeding behaviour to some other, better studied tropical urchins. Future feeding preference experiments for *E. calamaris* may illuminate whether *Sargassum* and other macroalgae are indeed not the urchins' preferred food sources.

In conclusion, the main function of *E. calamaris* in the Seychelles does not appear to be controlling macroalgal expansion given the natural densities we found in our study. It is likely that a drastic elevation of the species' density on degraded coral reefs could make the controlling effect on macroalgae measurable. Our model suggests that *E. calamaris* are most likely to congregate on patch reefs, especially if these patch reefs feature structurally complex elements and are low in macroalgal cover. This type of habitat is where their performed function would be most measurable and future studies should look to investigate these habitats to narrow down the function of *E. calamaris* in the Western Indian Ocean. Our study provides insights to the species' function as macroalgal controllers that add to our knowledge of degraded coral reef dynamics.

Contribution of authors

JCD and NAJG conceived the ideas and designed the methodology; JCD, VB, and GG contributed critically in acquisition of the data; JCD analysed the data; JCD and NAJG interpreted the results. JCD wrote the first draft of the manuscript, and all authors contributed critically to drafts and gave final approval for publication.

4 RED AND GREEN LOOPS HELP UNCOVER MISSING FEEDBACKS IN A CORAL REEF SOCIAL-ECOLOGICAL SYSTEM

4.1 Abstract

Social-ecological systems (SES) exhibit complex cause-and-effect relationships. Capturing, interpreting, and responding to signals that indicate changes in ecosystems is key for sustainable management in SES. Breaks in this signal-response chain, when feedbacks are missing, will allow change to continue until a point when abrupt ecological surprises may occur. In these situations, societies and local ecosystems can often become uncoupled. In this paper, we demonstrate how the red loop-green loop (RL-GL) concept can be used to uncover missing feedbacks and to better understand past social-ecological dynamics. Reinstating these feedbacks in order to recouple the SES may ultimately create more sustainable systems on local scales. The RL-GL concept can uncover missing feedbacks through the characterisation of SES dynamics along a spectrum of human resource dependence. Drawing on diverse qualitative and quantitative data sources, we classify SES dynamics throughout the history of Jamaican coral reefs along the RL-GL spectrum. We uncover missing feedbacks in red-loop and red-trap scenarios from around the year 600 until now. The Jamaican coral reef SES dynamics have moved between all four dynamic states described in the RL-GL concept: green loop, green trap, red loop, and red trap. We then propose mechanisms to guide the current unsustainable red traps back to more sustainable green loops, involving mechanisms of seafood trade and ecological monitoring. By gradually moving away from seafood exports, Jamaica may be able to return to green-loop dynamics between the local society and their locally sourced seafood. We discuss the potential benefits and drawbacks of this proposed intervention and give indications of why an export ban may insure against future missing feedbacks and could prolong the sustainability of the Jamaican coral reef ecosystem.

Our approach demonstrates how the RL-GL approach can uncover missing feedbacks in a coral reef SES, a way the concept has not been used before. We advocate for how the RL-GL concept in a feedback setting can be used to synthesise various types of data and to gain an understanding of past, present, and future sustainability that can be applied in diverse social-ecological settings.

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4.2 Introduction

Increased globalisation has been one of the underlying factors driving observed increases in human development (e.g. Human Development Index; Cumming & von Cramon-Taubadel 2018; United Nations Development Program 2018). However, the increased connectivity of economies, ecosystems, and human societies on a global level has been argued to be detrimental to the sustainability of local social-ecological systems (SES) when feedback relationships that indicate overharvesting of natural resources or environmental impacts are weakened or lost (Levin 1999; Berkes 2007; Nyström et al. 2019). This weakening – or decoupling – can emerge as the geographical distance between the location of consumption and production increases (Anderson 2010, Clapp 2014, Nyström et al. 2019). Overfishing of local fish stocks, for example, can be masked by importing fish caught elsewhere, leaving consumers relatively unaffected and unaware of ongoing changes in the ecosystem (Crona et al. 2016). For instance, the United Kingdom (UK) increased their imports of Atlantic cod from Iceland and the Faeroe Islands between the late 1980s and 1990s (Crona et al. 2016). Because cod was available in UK markets from multiple competing sources, the prices did not represent the decreasing cod stocks in local UK waters. This masked the mechanism for UK consumers to keep track of the increasing cod rarity and hence did not cause consumers to match their consumption patterns to the state of local ecosystem degradation. Such mechanisms are often referred to as “feedback mechanisms” because they have the potential to feed information about the state of a system back to society.

Capturing, interpreting, and responding to signals that indicate changes in ecosystems are key facets of sustainable management in SES. If feedbacks are ignored or masked (e.g. by trade), change is allowed to pass unnoticed until a point when an abrupt ecological surprise (i.e. regime shift) may occur. Once manifested, the new ecological state can be difficult, very costly, and potentially even impossible to reverse (Nyström et al. 2012). Pathways toward improved local sustainability have to feature managing feedbacks that underpin social-ecological trajectories.

Here, we demonstrate how the RL-GL concept highlights missing feedbacks and how it can be used to synthesise various types of data and to understand past, present, and future sustainability in diverse

social-ecological settings. Our study is the first that is integrating these two approaches to unpack social-ecological dynamics for improved sustainability of SES.

4.2.1 Reinstating missing feedbacks to recouple social-ecological systems

When feedbacks are masked, they are referred to as “missing feedbacks” (Barnett & Anderies 2014; Crona et al. 2016). In the context of social-ecological dynamics, this often means that the social system gets decoupled from the local ecosystem (Hoole & Berkes 2010), which opens unsustainable pathways that the SES may follow (Crona et al. 2016). To avoid this from happening it is critical to reinstate missing feedbacks and recouple the SES by “closing the loop” between humans and ecosystems (Patterson & Coelho 2008). A global example of this recoupling feedback approach is the current climate change discussion. Carbon taxes or carbon credits are meant to act as a “global” feedback to recouple anthropogenic changes to the atmospheric system back to society (Van der Ploeg 2014). Cod prices in the UK provide a local example; the missing feedbacks mentioned above could be reinstated by strengthening information flow from fishers to consumers or by directly increasing overfishing awareness in citizens and political actors through publicity (Crona et al. 2016). Another example of reinstating feedbacks comes from the Etosha National park in Namibia (Hoole & Berkes 2010). Decoupling was connected to the loss of Herero knowledge of the park, which led to failing wildlife conservation initiatives and exacerbated poverty levels in local Herero communities. Reinstating this missing feedback, through management collaboration between the park and Herero communities, as well as Herero inclusion in park management and as employees was used to re-instate feedbacks, ultimately improving the outcomes for the Herero and conservation management. Addressing missing feedbacks can have a transformational impact on the SES but it requires very detailed knowledge of the SES dynamics to uncover where feedbacks are missing (Patterson & Coelho 2008; Meyfroidt & Lambin 2009; Crona et al. 2016). Individual case studies are extremely variant in their display of feedback dynamics and detecting missing feedbacks will vary from case to case.

4.2.2 Using the ‘red loop-green loop’ model to identify missing feedbacks

We argue that a framing is required which assists with feedback classification and can identify missing feedback scenarios. The “red loop-green loop” (RL-GL) concept (Cumming et al. 2014) provides this framing for two differing forms of ecosystem dependence and sustainable resource use.

The RL-GL concept proposes that human resource dependence on a national scale tends to follow one of two fundamentally different trajectories that are reinforced by weak ties with local ecosystems and strong ties with distal systems (red loop), or strong ties with local ecosystems and weak ties with distal systems (green loop; Cumming & von Cramon-Taubadel 2018). In both red and green loop countries, the entire economy or certain economic sectors can evolve into trap situations that can severely threaten the long-term sustainability of the current trajectory (Cumming et al. 2014). Green traps can occur as the human population in a green-loop economy grows without adequate food production from the local ecosystem, leading to a spiral of increased overharvesting and environmental degradation (Steneck 2009). To avoid this green trap situation, societies can divert their dependence towards external ecosystem services, for instance by means of food import, which would lead towards red-loop dynamics. In a red-loop trajectory, the economy’s ecological impact reaches to distal ecosystems as well as the local system. For instance, reforestation in parts of Vietnam between 1987 to 2006 was achieved at the expense of forest displacement from other parts of the country as well as partly illegal imports from deforestation in neighbouring countries such as Cambodia and Laos (Meyfroidt & Lambin 2009). The example illustrates a red-trap situation where supply and consumption are maintained without recognition of the ecological degradation entails in other local ecosystems due to missing feedbacks.

In summary, as sectors in the economy relying on local ecosystems for resources approach a red trap and the economy as a whole increases its dependence on distal systems, the likelihood of missing feedbacks between the country’s society and local ecosystems increases. Therefore, societal and ecological dimensions of the SES run the risk of decoupling and a recoupling of the SES becomes more necessary for local system sustainability.

We argue that once the missing feedbacks have been identified, interventions to reinstate them could recouple local SES and move economic sectors out of red- or green-trap trajectories. Applying the RL-

GL concept to historical SES data can facilitate an understanding of how feedback dynamics have changed through time (Cumming et al. 2014; Hamann, Biggs & Reyers 2015) and what trajectory an economic sector is currently following (Cumming & von Cramon-Taubadel 2018). This can highlight points where the SES decoupled and thus identify opportunities to recouple the SES and avoid trap scenarios.

In this study, we apply the RL-GL framework to understand and classify the SES dynamics in the context of Jamaican coral reefs (Fig. 4.1), using mixed historical data dating back to roughly the year 600. With this historical understanding, we focus on uncovering missing feedbacks between the Jamaican people and their coral reef system. Lastly, we propose mechanisms that could move the current Jamaican coral reef SES out of recently assumed red-trap dynamics.

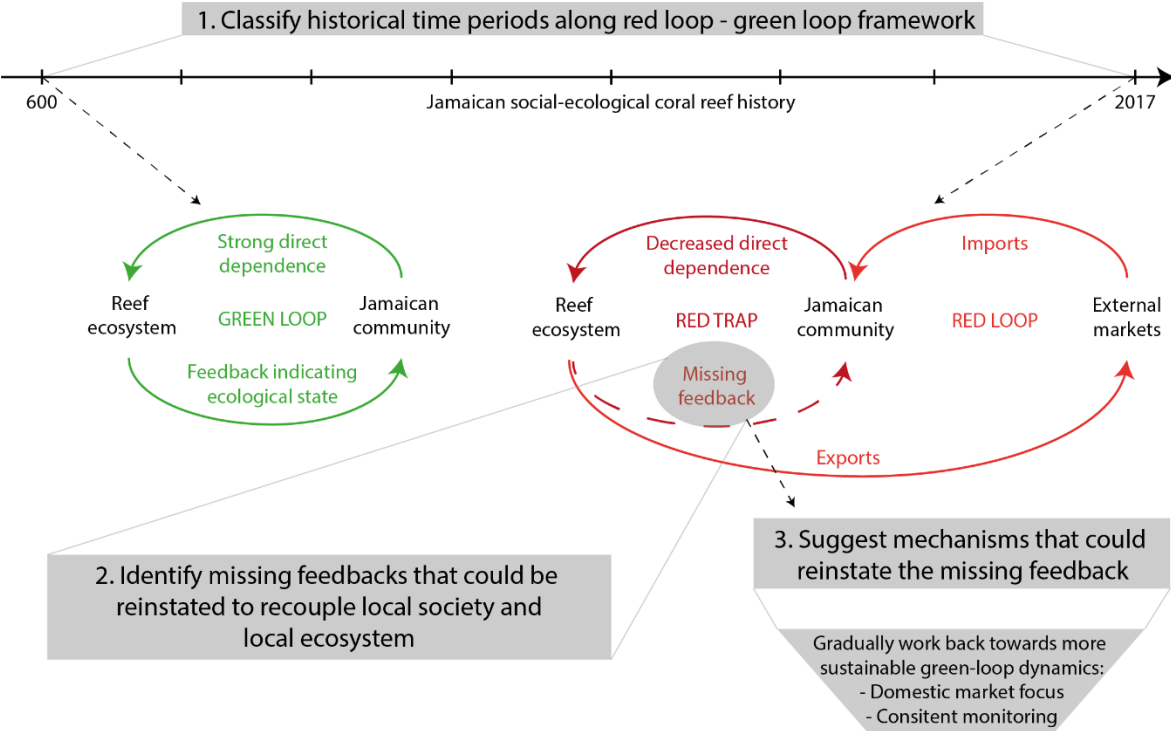


Figure 4.1 Summary schematic of our approach to 1) using red-loop green-loop classification of historical time periods to 2) uncovering missing feedbacks for which we suggest 3) mechanisms to reinstate the feedbacks and recouple the coral reef social-ecological system.

4.3 Jamaican coral reef SES dynamics through time

We identified and categorised social-ecological trajectories and feedbacks of Jamaican coral reefs across eight time periods (Table 4.1), from around 600 to the present. For the first six time periods (Ostionan, Meilican, Spanish occupation, British colonisation, Post-emancipation, and World Wars I & II), the available data are mostly qualitative. Hardt (2009) and Hicks et al. (2016) conclusively reconstructed the social-ecological dynamics for these time periods and we use them as our primary reference to infer about the nature (red or green loop) of those dynamics. Most quantitative data became available from 1950 and we use them to infer about social-ecological dynamics in the last two time periods (Post-war and Shifted reefs; Oswald 1963; Hughes 1994; Clayton 2001; Hardt 2009; Lingard et al. 2012; Hicks et al. 2016; FAOSTAT 2019).

Table 4.1: Historical data types and sources per time period of Jamaican history

Time period	Data type	References
Ostionan (600 - 900)	Qualitative:	(Hardt 2009; Hicks et al. 2016)
Meilican (900 - 1500)	Kitchen midden analyses	
Spanish occupation (1509 - 1655)	Qualitative:	(Beckwith 1929; Thompson 1945; Munro, Reeson & Gaut 1971; Hardt 2009; Hicks et al. 2016)
British colonisation (1656 - 1834)	Sailors' logbooks & historical	
Post-emancipation (1834 - 1900)	descriptions by naturalists,	
World Wars I & II (1901 - 1945)	historians & fisheries scientists	
Post-war (1946 - 1985)		(Oswald 1963; Hughes 1994; Clayton 2001; Hardt 2009; Lingard et al. 2012; Hicks et al.
Shifted reefs (1985 - 2017)	Quantitative: Fisheries, demographic, economic, and ecological data	2016; United Nations Development Program 2018; FAOSTAT 2019; World Bank 2019)

To illustrate social-ecological dynamics between the Jamaican society and their coral reefs over eight time periods, we used a mixed quantitative and qualitative approach. For each time period, we inferred Jamaican social-ecological dynamics from indicators of social change, changes in human population size, economic diversification, as well as ecological change (Fig. 4.2). We then focused on the social-ecological dynamics around local Jamaican coral reefs, viewed them as an individual economic sector, as well as through an RL-GL lens for each of the time periods and suggest mechanisms to approach green-loop dynamics in future scenarios (Fig. 4.3).

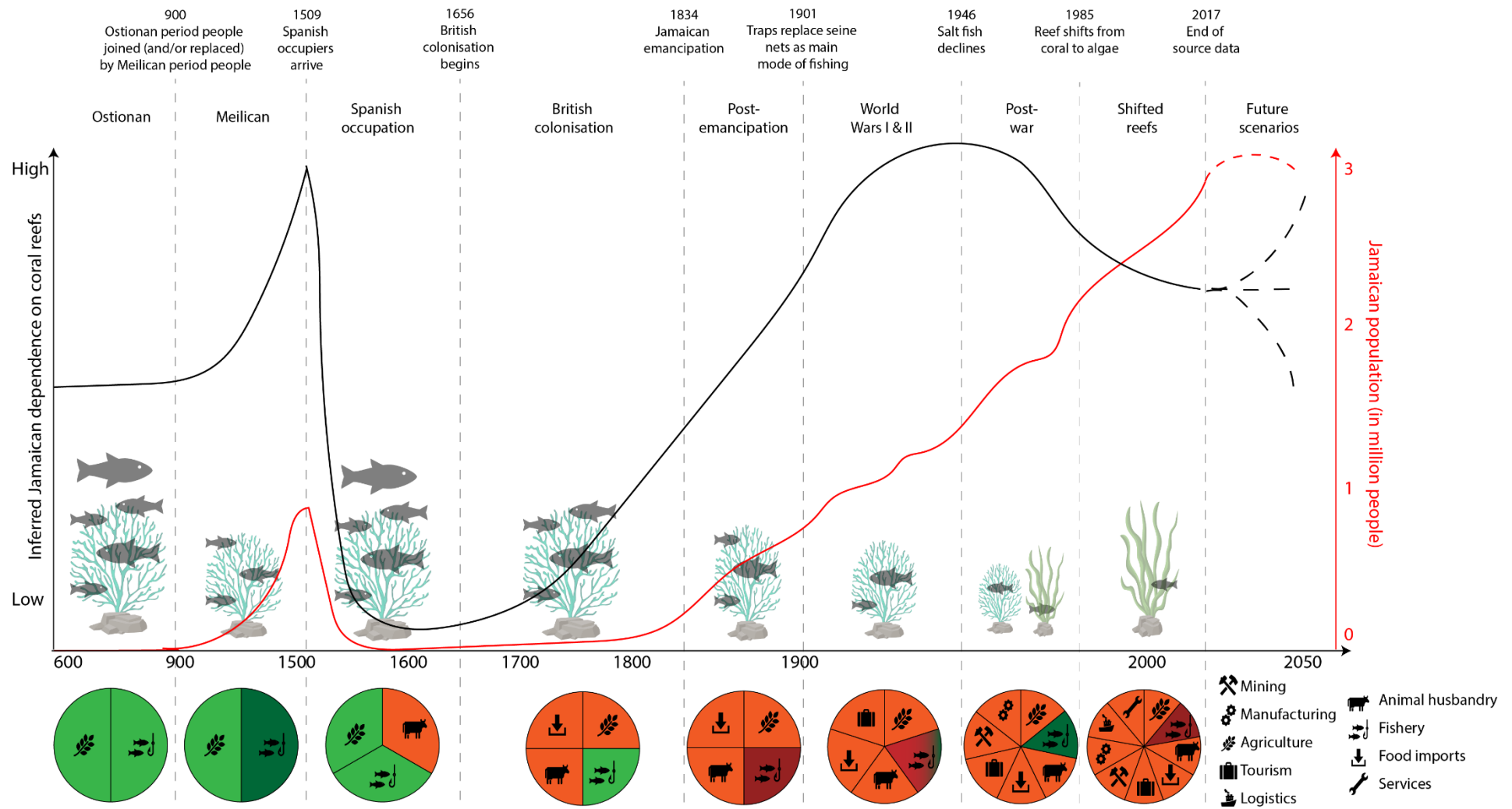


Figure 4.2 Jamaica's inferred dependence on coral reefs from low to high (black line) and human population (red line) through time. Time up to future scenarios is split into eight separate time periods and for each we determined ecological reef regime state of the reef (fish & coral/algae symbols) as well as major economic state of Jamaica (pie graphs). Colour of the pie graph segments indicates Jamaica's economic state along the RL-GL spectrum: green loop (light green), green trap (dark green), red loop (light red), red trap (dark red); population based on Hardt (2009; up to 1950) & United Nations, DESA, Population Division, World Population Prospects 2019, <http://population.un.org/wpp/> (from 1950).

4.3.1 Ostionan period (600s-900s): Green-loop dynamics

From roughly the 600s to 900s, Jamaica was inhabited by Ostionan period people and dependence on coral reefs was largely based on fishing (Fig. 4.2). This resource extraction increased with a growing human population with no indication of trade or other connections to other systems (Hardt 2009), as well as a relatively small population size, leading to the classification of this period as a green-loop state (Fig. 4.3).

4.3.2 Meilican period (900s-1500s): Green-trap dynamics

During the Meilican period, the human population on Jamaica grew rapidly and by 1500 had reached ~ 1 million people (Hardt 2009; Hicks et al. 2016; Fig. 4.2). Decreasing reef fish catch sizes indicate that the reef ecosystem was overexploited under the pressure of the growing human population and there is no evidence of trade prior to the first European contact that could have reduced pressure on the coral reef ecosystem (Hardt 2009). Based on gradually decreasing fish sizes in kitchen middens suggesting a “fishing down the food web” situation (Pauly & Palomares 2005), we concluded that the SES between the Jamaican people and the reef ecosystem during the Meilican period was characterised by green-trap dynamics (Fig. 4.3).

4.3.3 Spanish occupation period (1509-1655): Green-loop dynamics

With the Spanish occupation in 1509 the Jamaican population declined significantly due to the introduction of new diseases and harsh treatment of the local population (Hicks et al. 2016). By the mid-1510s, the population had been reduced by over 99 % from the Meilican period, to approximately 5,000 people, which lessened pressure on the reef ecosystem (Hardt 2009; Fig. 4.2). Pressure was further reduced via an alternate source of protein by the introduction of pigs and cattle from Spain (characteristic of a red-loop dynamic), resulting in a temporary recovery of reefs (Hardt 2009). Due to these two pressure reduction factors and minimal dependence on coral reef resources, the local SES returned to a green loop during Spanish occupation (Fig. 4.3).

4.3.4 British colonisation period (1656-1834): Green-loop dynamics

With the colonisation by the British in 1656, Jamaica was being developed into a hub for international trade. Sugar, coffee, and bananas were increasingly used as trade commodities for salt fish from the UK,

USA, and Canada (red-loop dynamic; Fig. 4.2). As a result of this resource diversification, reefs were further relieved from fishing pressure (Hardt 2009; Hicks et al. 2016). The human population of Jamaica started to grow rapidly with the increase in slavery (> 300,000 slaves by 1810) as the colonisers expanded their plantations (Hicks et al. 2016). Again, the reef system began to show signs of overexploitation around 1800 as reef fish were increasingly used as food for the plantation owners (Hardt 2009). During British colonisation, the Jamaican community gradually came to re-kindle their dependence on the reef system after barely depending on it during Spanish occupation. Although reef dependence was largely based on subsistence fishing, fishing regulations (e.g. minimum mesh size for fishing nets) put in place by the colonisers suggest that there was an awareness of changes occurring in the local SES and a feedback between society and the reef ecosystem existed (Hardt 2009). While the larger part of the Jamaican economy was involved in global trade and hence red-loop dynamics (Fig. 4.2), the coral reef SES dynamics remained localised and in a green loop (Fig. 4.3).

4.3.5 Post-emancipation period (1834-1900): Red-trap dynamics

With emancipation in 1834, Jamaica's human population surged towards Meilican levels (~ 1 million by 1900) and reef dependence shifted from feeding the local population to using reef fish as a trading commodity for salt fish (Fig. 4.2), which the Jamaican community had become used to during times of slavery (Hicks et al. 2016). The salt fish dependence was so strong that by the 1830s, local reef resources (including fish and coral) were traded to be able to import salt fish from the USA, Canada, and the UK (Hardt 2009). This indirect dependence on local reefs for trade masked the feedback within the SES and began to decouple the reef environment from the local society, likely for the first time in Jamaican history. The increased fishing of reef fish for trade with salt fish producing countries, shifted the coral reef SES dynamics from green loop to red trap (Fig. 4.3).

4.3.6 World Wars I & II period (1901-1945): From red- to green-trap dynamics

With the advent of tourism and urbanisation in the 1900s, red-trap dynamics were further reinforced (Beckwith 1929; Thompson 1945; Hicks et al. 2016; Fig. 4.2). Accelerated population growth in the early 1900s led Jamaicans to depend on reef resources for both subsistence and trade (Hardt 2009). Technological development of fishing gear, especially the adoption of wire mesh fish traps in the 1910s

(Munro, Reeson & Gaut 1971), caused a shift in dominant fishing mode from seine nets to traps (a technique with even heavier impact on purely reef dwelling fish) and spiralled further reef degradation (Hicks et al. 2016).

With the onset of World War II, trade suffered a dramatic decline and the Jamaican population had to increasingly rely on local reef fish for food instead of imported salt fish. Green-loop dynamics were forced to be resumed between Jamaican society and reef ecosystem and the SES began to recouple. In 1945, Jamaica's dependence on local fish stocks peaked (Hardt 2009) and overfishing of near-shore fish stocks was officially recognised for the first time by government fisheries scientist E. Thompson (1945). Due to a rapidly growing population (~1.3 million in 1945), limited economic diversification, and Jamaican reef dependence rising as a result, the human population quickly outgrew the provisioning capacities of the reef ecosystem (Hardt 2009). We argue that the SES could not sustain this quick fall-back on the reef ecosystem for resources during WWII and the resumed green-loop dynamics quickly manifested as green-trap dynamics (Fig. 4.3).

4.3.7 Post-war period (1946-1985): Green-trap dynamics

As Jamaica's dependence on local reefs for food peaked, the government established the Fisheries Division and developed an off-shore fishery (Oswald 1963) to be able to keep up with the increasing demand for seafood (Fig. 4.2). Thompson's suggestions to subsidise job transitions for fishers into other jobs were ignored, and the expansion of the reef fishery was instead heavily subsidised in the 1970s and 1980s (Hardt 2009), which reinforced the green-trap dynamics. In parallel, increasing urbanisation, tourism, and industrialisation (e.g. development of large-scale bauxite mining) were causing reef degradation through pollution of near-shore waters (Hardt 2009; Hicks et al. 2016). During the 1980s, Jamaica also reported the highest regional deforestation rates, leading to a substantial loss of mangroves (Agard et al. 2007). In 1983-84, reefs suffered surges of hurricane damage and a sea urchin disease, which in combination with overfishing led to an ecological regime shift where coral reefs became rapidly overgrown by algae (Hughes 1994). This regime shift and the noticeable catch reductions of reef-dwelling and reef-associated fish species due to overfishing (Suppl. panel 4.1) caused a further spatial expansion of Jamaica's fisheries so that the most productive fisheries were now in far off-shore

environments (Oswald 1963; Lingard et al. 2012). The combined effects of reduced catches from reef fisheries and resulting further fisheries off-shore expansion, as well as the coral reef regime shift, led Jamaican social-ecological reef dynamics to spiral into a green trap (Fig. 4.3). By the late 1980s, Jamaica's economy had diversified and moved into globally connected red-loop dynamics (e.g. revamping salt-fish trade), which in part compensated for the heavily degraded reef ecosystem (Fig. 4.2).

4.3.8 Shifted reefs period (1985-2017): Red-trap dynamics

Following the ecological regime shift, the reef system was severely degraded and the dependence of Jamaicans on the reefs was decreasing. The percentage of employed fishers in the rising Jamaican population declined (FAOSTAT 2019) and workers in non-ecosystem service sectors increased (Clayton 2001; Fig. 4.2). Jamaica's fisheries catches were largely made up of subsistence catches, but a part was, once again, used for exports (Suppl. panel 4.1; Lingard et al. 2012; FAOSTAT 2019). Resuming the resource extraction from the exhausted reef ecosystem for trade, again led to the missing feedback and repeated the decoupling of the SES we described for the post-emancipation period and dynamics of a red trap (Fig. 4.3).

4.3.9 Jamaica's recent red-loop economy supporting a red-trap coral reef SES

Although the Jamaican coral reef SES was kept in a red-trap situation between 1990 and 2017, the country increased its Human Development Index (HDI) from 0.638 to 0.732 (14.8% increase; United Nations Development Program 2018). Generally, red-loop and green-loop countries appear to separate along a gradient of the HDI, where HDI class 1 countries assume red loops and HDI class 4 countries assume green loops, while HDI class 2 and HDI class 3 countries are more difficult to classify and show characteristics of both loops (Cumming & von Cramon-Taubadel 2018). Economic diversification allowed Jamaica with its ~ 2.9 million population (Fig. 4.2), to be placed in an HDI class 1 in 2017 (United Nations Development Program 2018), at the median of red-loop countries (HDI of ~ 0.7; Cumming & von Cramon-Taubadel 2018). The economic stability gained from diversification has allowed some other nations to improve local ecosystem sustainability (Martens & Raza 2010; Hansen et al. 2018). A diversified economy is a relatively recent development for Jamaica that had not yet

developed when the local SES attempted to move away from red-trap dynamics (i.e. during the World Wars I & II period, Fig. 4.3). A diverse, largely red-loop economy that can lessen the requirements placed on the local coral reef SES could be of great assistance in intervening with current local reef SES red-trap dynamics, provided that the correct guidance is applied to proposed interventions. We propose a set of mechanisms for current Jamaican red-trap dynamics that are meant to reinstate a feedback between society and reef ecosystem to recouple both.

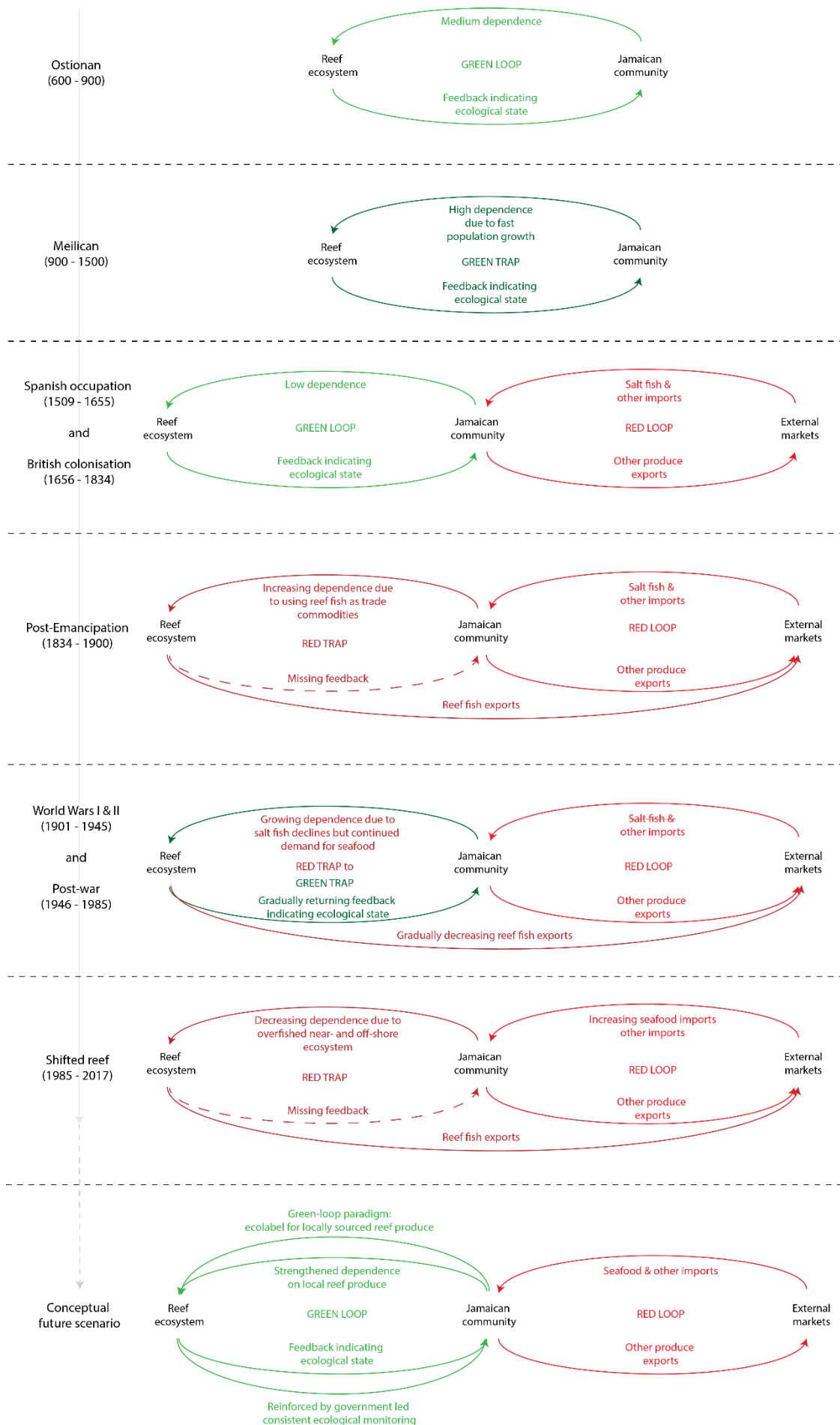


Figure 4.3 Schematic showing social-ecological dynamics focussed on the dependence of the Jamaican community on their coral reefs and categorisation of these dynamics along the spectrum of the RL-GL model leading to a concept of future dynamics where we suggest a conceptual system with mechanisms to reinstate the missing feedbacks and to recouple the social-ecological system.

4.4 Reinstating missing feedbacks in a local red-trap system

Based on the historical assessment of Jamaican SES dynamics, we discuss possible interventions that may lead to a recoupled Jamaican local reef SES. Highlighting missing feedbacks can help steer a system out of red-trap dynamics (Fig. 4.3). Importantly, we propose a set of mechanisms that are supposed to tackle the systemic design of the Jamaican coral reef SES rather than only few systemic parameters. This prioritisation of interventions is highlighted by the “Leverage Points” perspective (Meadows 1999; Abson et al. 2017; Fischer & Riechers 2019) and guided our proposed intervention. The leverage points perspective argues for prioritisation of interventions that have large transformational potential (deep leverage) over those that are usually used but have little to no impact (shallow leverage; Abson et al. 2017). These deep leverage points are difficult to implement because they often prioritise tackling system design and intent (deep leverage) over system parameters (shallow leverage), which is why they are under-used and under-researched (Fischer & Riechers 2019). Their transformational potential applies well to our case study and hence guides the interventions we are proposing to implement here.

4.4.1 Pursuing a green-loop coral reef social-ecological system design through seafood export bans

With an annual per capita fish consumption of 25.8 kg (2017), Jamaica ranks amongst the highest seafood consuming countries in the Americas. Yet, 79 % of Jamaica’s supply of all fishery products consumed domestically in 2017 stemmed from imports (FAOSTAT 2019). Our historical analysis of Jamaica shows that seafood exports were a main driver in decoupling the feedback within the coral reef SES, especially in the post emancipation period, World Wars I & II period, and the shifted reef period (Fig. 4.3).

We propose an intervention strategy following a deep leverage point in the system’s design (Abson et al. 2017). The local coral reef SES could be gradually designed towards green-loop dynamics in which

locally sourced reef produce are rerouted from exports to domestic markets. In envisaging the local reef SES, local seafood catches from the near-shore and off-shore environment would not serve as exports and only be used for domestic markets, including consumption (e.g. by locals) and sales (e.g. to tourists). A system averse to exports of locally sourced seafood would reinstate a direct feedback between the Jamaican society and the local reef ecosystem. However, for this reinstated feedback to be sustainable, and avoid a green trap scenario, careful monitoring and management of the resource will be necessary. This could lead to the desired recoupling of the Jamaican coral reef SES and enable movement towards locally connected green-loop dynamics within an otherwise globally connected red-loop system.

A coral reef SES in which seafood is locally sourced and used, would, according to RL-GL thinking, be more sustainable than the current red-trap situation (Cumming et al. 2014). For this reinstated feedback to have the desired effect, it is crucial that the information on the ecosystem's state that is fed back to the Jamaican society is reacted on appropriately. This means that the feedback is not ignored, as was the case in 1945 when the suggestions and warnings by fisheries scientist Thompson were ignored by the Jamaican government (Hardt 2009). Existing feedbacks that are ignored can also have destructive effects on the ecosystem (Degnbol & McCay 2007), although, our historical analysis of the Jamaica case indicates that missing feedbacks were more frequently occurring in the coral reef SES than ignored ones.

4.4.2 Strengthening green loops in other regions

Examples of mechanisms that can assist the transition from red-trap to green-loop dynamics exist in the literature. As in the cod example above, one mechanism to reinstate the missing feedbacks could be in strengthening information flow from fishers to consumers (Crona et al. 2016). Eco-labels could provide this transparency to consumers; specifically, labels with a "locally grown" claim have been suggested to be more highly valued by consumers in the United States (Loureiro & Hine 2002; Giovannucci, Barham & Pirog 2010; Onozaka & McFadden 2011). A "locally sourced" eco-label could lend itself to reinstate sustainable stewardship of local reef products. Besides such labelling schemes, education and public campaigns are central instruments for consumers to make informed decisions that can help reinstate feedbacks (Crona et al. 2016). Moreover, traceability is a key mechanism in this context to

ensure supply chains are devoid of unacceptable behaviour, ranging from illegal sourcing and forced labour to poor sanitation and mislabelling (Nyström et al. 2019).

Addressing unsustainable trajectories from deep within a SES is complex and sometimes difficult to monitor through time. For example, it has been suggested that many South-East Asian economies (van Mulekom et al. 2006) could alleviate malnutrition and poverty by redirecting the considerable resources gained through fishing away from exports and towards domestic use, particularly given the rich micronutrients yields in these catches (Hicks et al. 2019). For a region as large as South-East Asia, it is difficult to understand whether these suggestions have led to improvement, largely because the documentation is very inconsistent (Béné et al. 2016). However, shifts towards fishing for domestic markets have been noted in the province of Phang-nga, Thailand (Jones, Gray & Umponstira 2010) and the Philippines (Fabinyi 2016). Some South-East Asian countries might not be as economically well-placed to manifest a green-loop dynamic for their local reef ecosystems, since the marine seafood sector creates a large percentage of national revenue. For instance, Indonesia appears to favour an increase in marine seafood exports, believing that further development of marine resource exports (4.2 billion USD; FAOSTAT 2018) is vital for bringing Indonesia out of its recent economic crisis (Rizal et al. 2018).

A recent study from Seychelles demonstrated substantial catch declines in prized red snapper species, locally called “bourzwa” (Robinson et al. 2020), with exports leading to price increases to the point where the fish became unaffordable to locals. In attempts to protect livelihoods, lower the prices, and achieve recovery of the species’ stocks, export bans from 2020 have been proposed for bourzwa (Robinson & Graham 2020). Similar price dynamics might be driving the Jamaican affinity for imported fish consumption in our case study. Export bans could lead to price reduction in local reef fish, make it more affordable for locals, and hence increase their consumption. In the optimal case, this could gradually increase local seafood sustainability, as well as increase the perceived value of the local reef ecosystem and an increased sense of stewardship (Chapin et al. 2010) to gradually close the feedback loop.

The success of an export ban, however, depends on the availability of data to fully understand SES dynamics. In the Seychelles example, Robinson et al. (2020) use detailed fisheries data to show that

local markets were already buying four times as much bourzwa as is exported and elude to the limited likelihood that export bans may have on reducing bourzwa prices, and that other local fisheries management efforts will be key to sustainability (Robinson et al. 2020). Comparative data in Jamaica are very limited, with the most recent (2002) specific seafood export information noting lobster, conch, and “some fish” (FAOSTAT 2019). An export ban, if implemented, should be preceded and accompanied by detailed monitoring of fisheries data to uncover if similar dynamics to Seychelles could be at play in Jamaica. Similarly, an example from Palau, where the government banned 80 % of fishing from foreign vessels in their off-shore waters caused effort to transition to near-shore waters, increasing the pressure on reef fish species (Dacks et al. 2020).

The above examples demonstrate the possible effectiveness of an export ban for recoupling feedbacks within an SES. Yet, these case-studies also emphasise the importance of having detailed data to understand past, current and future SES dynamics. In the following section, we propose where further data could enhance the establishment of a green-loop coral reef SES.

4.4.3 Monitoring required for the green loop

Based on our historical analysis of SES dynamics, we argue that the diverse red-loop economy of Jamaica is at a point where the small export revenue derived from the local reef fishery (12.9 million USD) could be rerouted to domestic markets to increase local coral reef SES sustainability (FAOSTAT 2019). In our historical analysis, when Jamaica was forced to resume green-loop dynamics for the local reef SES during WWII, the economy had only five main sectors whereas today it has nine (World Bank 2019). Jamaica acts as a conceptual example in which we demonstrate how a diverse economy could help leverage a green-loop pathway for its local ecosystem dependence.

For a green loop through export bans to work, a thorough, species-specific comparison of seafood imports and exports needs to be established to be able to gauge the full benefit of an export ban (Robinson & Graham 2020). In addition, the local and international demand for species-specific seafood needs to be thoroughly understood so that the government can anticipate potential knock-on effects (Dacks et al. 2020).

Consistent ecological monitoring of the Jamaican reef system has usually been scarce, as we have seen through our historical analysis. The peak of ecological monitoring was likely during the benthic regime shift and even recently, consistent government-led ecological monitoring of the reefs has been spatially and temporally fragmented (Lapointe et al. 2011; Creary, Smith & Green 2012). Consistent monitoring should provide concurrent ecological awareness that would enable more reactive management to ecological change in the future.

The interventions we suggest above were formulated by searching for points in the system's design that we could leverage to prolong its sustainability. We decided to pursue the design of a green loop coral reef SES and we highlight the benefits and drawbacks for this pathway, but our suggestions are not exhaustive. For instance, within the leverage points framework, there are more pathways which could lead to different interventions (e.g. pursuing the alteration of the system's intent through alternative governance) which future studies could explore.

4.5 Conclusion

Within sustainability research there are different concepts to disentangle social-ecological dynamics. We demonstrate the value of examining complex dynamics through a conceptual lens by using Jamaica's complex coral reef SES dynamics as a case study. We identified a decoupling in the SES using the feedbacks concept - the feedbacks from coral reefs to Jamaican society had become masked. The resulting missing feedbacks were uncovered with the RL-GL concept. Throughout Jamaica's social-ecological history, the SES dynamics between people and the coral reef ecosystem have moved between all four dynamic states described in the RL-GL concept: green loop, green trap, red loop, and red trap.

Jamaica's society has experienced the effects of a degrading near-shore system in the past, at the very least in the form of changes in the types of seafood available for consumption. In its current form, the Jamaican economy has effectively diluted any severe repercussions through a rapidly diversifying economy. Historically, when rapidly growing human populations led to the near-shore system being heavily exploited, or when the dependence on other fisheries products were interrupted, Jamaica had relatively productive reef systems to fall back on. Whether this can be done again in the future will

depend on the intent of the SES and whether feedback mechanisms are in place to signal ecological condition.

We propose mechanisms that could guide transitions away from the red trap that the SES dynamics have currently settled on. We highlight examples of countries that have used a specific intervention in order to move from an unsustainable local red-trap situation to more sustainable green-loop dynamics. We suggest that a successful transition into green-loop dynamics will strongly depend on data availability and continued monitoring of the SES. Future studies should seek to draw on different and multi-disciplinary perspectives to explore this and other interventions and test their feasibility with empirical data.

We arrived at our conclusion through using a conceptual lens that highlights the feedbacks within RL-GL concept and applying it to Jamaica's rich social-ecological coral reef history to reveal potential future pathways. These pathways need to be carefully re-considered under the light of a range of proficiencies, including political, economic, and social expertise, before they can be successfully implemented. We want to highlight the practicality of how we applied the RL-GL concept to uncover missing feedbacks within complex social-ecological dynamics and encourage future studies to apply it to other systems to further advance sustainability research.

Contribution of authors

All authors conceived core ideas and contributed critically to the design of the study; JCD acquired and analysed the data; all authors interpreted the results. JCD wrote the first draft of the manuscript, and all authors contributed critically to subsequent drafts and gave final approval for publication.

GENERAL DISCUSSION

Coral reef recovery dynamics in the Anthropocene

My findings presented in this thesis add to two major realms of the understanding of dynamics on degraded coral reefs as the Anthropocene and associated reef stressors accelerate. Firstly, I provide new insights about feedback dynamics on degraded coral reef states, specifically about those related to the macroalgae-dominated state. Secondly, I open new avenues to coral reef management and future research to consider; more specifically, by providing tools to confront macroalgal feedbacks at local scales and to engage with missing social-ecological feedbacks at national scales. In addition, my models offer predictions about potential habitat types that could be vital to future coral reef recovery that should be of interest to management and research.

Feedback processes

The feedback research presented in my thesis can be coarsely divided into findings regarding existing ecological feedbacks and missing social-ecological feedbacks, all involving processes on degraded coral reef states that have shifted to macroalgal dominance.

Confronting existing feedbacks

Macroalgae-dominated reef states are well established within the general literature as a major obstacle to coral settlement (Birrell et al. 2005; Diaz-Pulido et al. 2009), likely due to efficient self-reinforcing feedbacks that quickly establish effective dominance of colonisable space (Roff et al. 2015; Dell et al. 2016; Johns et al. 2018). My results (**Chapter 1**) add to this understanding by highlighting macroalgae as one of the major obstacles to juvenile corals as well. By effectively creating two bottlenecks in the coral life-cycle (recruits and juveniles; Chong-Seng et al. 2014), macroalgae form a major hurdle to coral recovery. By increasingly limiting coral recruitment processes with self-reinforcing feedbacks, macroalgae prevent corals from re-establishing their own self-reinforcing feedbacks (van de Leemput et al. 2016) and allow efficient macroalgal expansion on shallow water reefs (McCook 1999; Hughes et al. 2007; Roff et al. 2015; Wilson et al. 2019). Strengthening macroalgal-reinforcing feedbacks thereby

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increase the resilience of the macroalgal state preventing reversal or reorganisation away from the macroalgal attractor (Fig. 5.1).

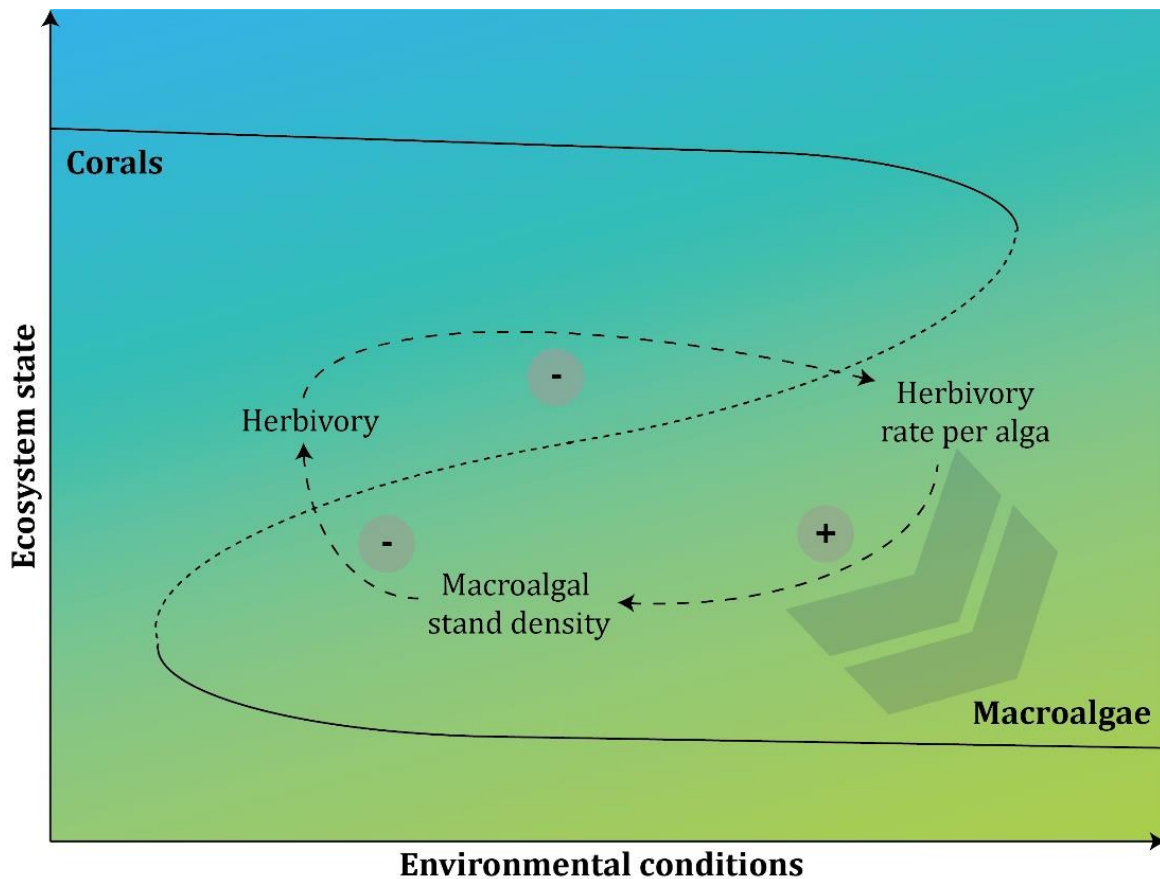


Figure 5.1 Illustration of strengthening macroalgae-reinforcing feedbacks increasing the resilience of the macroalgal state using the example of dense macroalgal stands deterring herbivorous fishes.

In **Chapter 2**, I show that the strength of these macroalgal-reinforcing feedbacks can be weakened on a local scale. My shading method confronts the following macroalgal-reinforcing feedback: expanding algal cover can lead to dense macroalgal fields, which may be avoided by herbivorous fishes, leading to a decreased herbivory rate per algae (Hoey and Bellwood 2011; van de Leemput et al. 2016; Fig. 5.1). I attempted to weaken this feedback via the use of shade sails that weaken the feedback in three ways (Fig. 5.2). In my experiment, the shade firstly reduced the photosynthetic efficiency of the algae, leading to a thinning of algal stands. Secondly, it is likely that the shading also affected algal palatability to herbivores, although I do not have evidence for this mechanism. Thirdly, the shade structures themselves attracted herbivorous fishes to the shaded algae. I interpret the reduction in macroalgal cover in shade

plots as an effective weakening of macroalgae-reinforcing feedbacks through the interaction of the above-mentioned mechanisms. The macroalgae-reinforcing feedback induced by dense macroalgal stands was effectively interrupted and macroalgal resilience was reduced in a small-scale experiment (Fig. 5.2). When shade sails were removed, the macroalgal feedbacks re-established over three months and the system clearly did not cross a threshold (Fig. 5.2, dotted line). I believe that, if the shading structures were in place for longer, a shift towards the coral attractor may have occurred. The results do provide evidence of effective reduction of macroalgal cover locally, which could be of use in combination with other interventions, such as manual holdfast removal and subsequent shading (Ceccarelli et al. 2018), and in managing productive habitat mosaic reefscape (van Lier et al. 2018; Fulton et al. 2019).

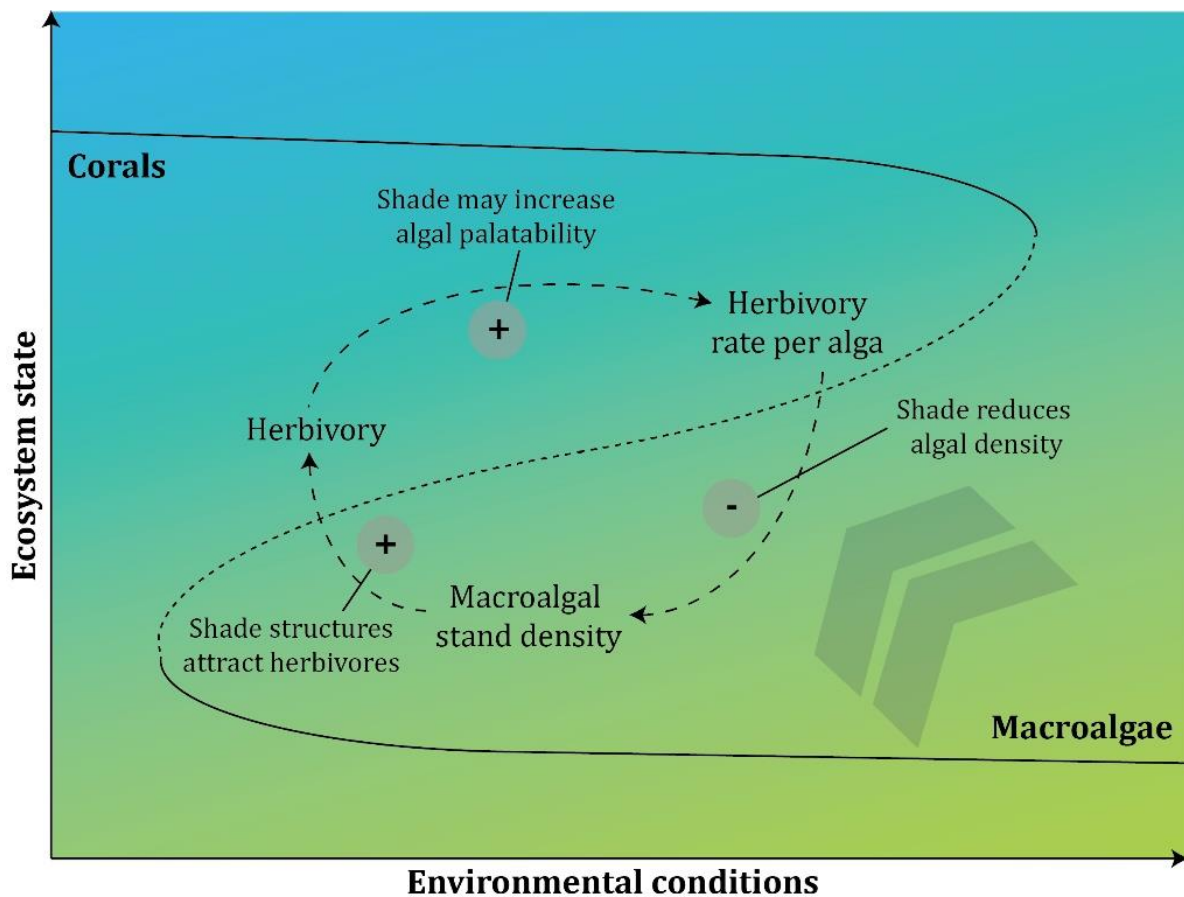


Figure 5.2. Illustration of weakening macroalgae-reinforcing feedback away from the macroalgal attractor based on the small-scale example of shading and herbivorous fish attraction.

Similar outcomes could be achieved by focussing herbivore grazing on small localised patches (Maciá et al. 2007; Bodmer 2019). I attempted this by penning sea urchins on macroalgal patches. This did not achieve a macroalgal reduction as effectively as the shading method. However, this could be due to the mechanisms behind sea urchin grazing. Urchins might be causing reduction amongst fleshy, tall macroalgal fields by structurally damaging the algal holdfasts (Tegner et al. 1995). Although, conclusive evidence is lacking, this damage to holdfasts could cause macroalgae to get detached with increased wave action (Lee 2006). In my experiment, urchins may have caused this structural damage to macroalgal holdfasts, but I did not observe much macroalgal detachment as a study site with least wave impact was chosen. I made this choice because both the shading and urchin penning experiments were running at the same time and in the same bay to be able to compare the macroalgal cover reduction achieved by both. To protect the shade sails from structural damage, I chose the least windy time at the study site. It would be interesting to see whether a similar urchin penning experiment conducted in a more wave-impacted site could achieve more reduction in macroalgal cover.

Confronting missing feedbacks

As much as existing ecological feedbacks can contribute to ecosystem degradation, so can interrupted feedbacks between human communities and the ecosystems on which they depend (Crona et al. 2016; Nyström et al. 2019). My results (**Chapter 4**) show how information of coral reef condition that is fed back to Jamaican society was interrupted repeatedly through time and how this has contributed to overall reef ecosystem degradation. While missing feedbacks are not often identified and considered in social-ecological systems in the literature, they appear to be an important feature that can hamper management of social-ecological systems, and seem especially prominent in food production systems such as fisheries (Levin 1999; Steneck 2009; Crona et al. 2016) and agricultural systems (Cumming et al. 2014; Nyström et al. 2019). My study is the first to explicitly highlight and confront them in a coral reef social-ecological system. The results highlight how the red-loop green-loop model can uncover these missing social-ecological feedbacks to highlight more sustainable future management pathways.

Management and research directions

Potential habitats of juvenile corals and sea urchins in the Anthropocene

My spatial modelling studies of juvenile corals (**Chapter 1**) and sea urchins (**Chapter 3**) present habitat predictors across 21 reefs in the inner Seychelles. The analyses for both juvenile corals and urchins were conducted on datasets of the same spatial scale (replicate point counts) and are hence comparable. The major comparable habitat predictors are macroalgae (percent cover), structural complexity (0-5 scale), and reef type (patch, carbonate, or granitic reef). Although I did include both juvenile corals as a potential predictor in the urchin models and vice versa, they never showed significantly correlated trends between each other.

While macroalgae negatively predicted both juvenile coral density and urchin abundance, structural complexity was a comparatively neutral predictor for urchins and more positive for juvenile corals. The uncertain relationship between urchins and structural complexity appears to match the unclear consensus of the literature. Some studies report negative relationships (Weil et al. 2005; Graham and Nash 2013) while others report positive relationships (Hereu et al. 2004; Lee 2006) between complexity and sea urchin densities. The trend between juvenile corals and structural complexity is also supported by the literature, with several studies reporting a positive relationship between complexity and juvenile corals (Vergés et al. 2011; Graham and Nash 2013; Rogers et al. 2014; Doropoulos et al. 2016), although I note that my findings include more detailed information through uncovering predictor interactions (see **Chapter 1**).

The interaction of complexity and the granitic reef type was the strongest positive predictor of juvenile coral density, while patch reef type was the strongest positive predictor for sea urchin density. Reef types might highlight potential refugia for future reef assemblages. Both trends are relatively unexplored in the wider literature. There are studies that hint at coral recruitment success being influenced by reef type (Jennings et al. 1995; Graham et al. 2007; Burt et al. 2009; Wilson et al. 2012) and studies that claim urchin abundance might be influenced by fragmented habitats, such as patch reefs (Jones and Andrew 1990; Andrew 1993; McClanahan 1999). Again, I note that my results found through predictor

interactions highlight that some more complex mechanisms (e.g. interaction reef type & macroalgae) might be at play.

In summary, my results suggest that juvenile corals could be expected to recover better on structurally complex, granitic reef habitats following future bleaching events, while sea urchins may perform their functional roles more on patch-reef habitats. Both trends should be considered for further research which could accentuate the importance of these habitats in the future and provide guidance for future coral reef management, for instance in updating zoning plans.

Combining shading and sea urchin penning to confront macroalgal feedbacks

Chapter 2 indicates that shading and herbivory by reef fishes may act together. However, the shading experiment did not encourage herbivorous fish grazing to persist following shade structure removal. The urchin penning method (**Chapter 3**) could maintain grazing focussed on the shaded area, especially following shade removal. Future studies could employ a combination of shading followed by urchin penning and investigate the potential for long-term regime reversals this combination might have on experimental patches of algal communities.

Both the shading (**Chapter 2**) and urchin penning method (**Chapter 3**) were conducted over a six-week time frame which allowed for a comparison of their respective effectiveness in macroalgal reduction. Urchin penning (highest stocking density of 4.44 urchins m⁻²) only achieved a reduction of 17 % macroalgal cover, while shading (largest shade sails of 9 m²) achieved a reduction of 82 %. In this regard, the effectiveness of penned urchin densities of 4.44 urchins m⁻² was closer to the effectiveness of small 4 m² shade sails. Both methods' effectiveness appears to scale with shade sail size or urchin stocking density, which could be valuable to future studies and management approaches.

Holdfast removal is essential to managing expanding macroalgal fields (Loffler et al. 2018). The two methods could be further combined with existing methods, such as manual holdfast removal (Ceccarelli et al. 2018). Manual holdfast removal could be followed by shading to keep algal regrowth at bay. Additionally, if future studies were to find that urchin penning is effective in areas with higher wave action (Tegner et al. 1995; Lee 2006), management could use urchin penning in areas with high wave action and a combination of shading and manual holdfast removal in areas with low wave action.

Flexibility with different method combinations could be especially beneficial for the maintenance of habitat mosaics of different sizes (Beger et al. 2010a) and functions (Fulton et al. 2019).

Confronting missing feedbacks for social-ecological system sustainability

I demonstrate how missing feedbacks can be uncovered using the red-loop green-loop framework from social-ecological sustainability research (**Chapter 4**). If developed further and applied to other SES, the concept presented could pave the way for practical applications, similarly to how the red-loop green-loop model has already been applied to empirical data such as the United Nations Human Development Index (HDI; Cumming and von Cramon-Taubadel 2018) and my approach demonstrated for coral reef SES could be similarly trailed by studies to empirically test my concept for coral reef SES.

Missing feedbacks within SES can damage ecosystems and uncovering them could ultimately lead to informed management plans that prolong ecosystem sustainability (Nyström et al. 2019). I apply the concept to rich data from Jamaican coral reef SES. Another next step could be to apply the concept to other SES with the aim to further test its conceptual utility. I used historical information to understand the social-ecological dynamics, highlighting that this approach is not limited to a certain source, range, or type of data. Jackson (2001) also used a variant of this mixed data approach and combined paleoecological, archaeological, historical, and ecological data to infer about historical overfishing of coastal ecosystems spanning from 125,000 years ago until the end of the 1900s. I apply the concept in a mixed-method approach to diverse data types ranging from qualitative historical to quantitative contemporary data.

In conclusion, the value of this thesis is both in adding to the knowledge pool of ecological and social-ecological dynamics on degraded coral reefs of the Anthropocene, as well as providing management tools to confront degraded state dynamics.

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APPENDIX A: SUPPLEMENTARY MATERIAL

Supplementary table 1.1: Tukey HSD results for significant differences between individual years

Tukey multiple comparisons of means, 95% family-wise confidence level				
Comparison	Estimate	Standard error	Z-ratio	p-value
2008-2011 all corals	-00918527	01007356	-0912	06328
2008-2017 all corals*	14078811	01531937	919	<0001
2011-2017 all corals*	14997339	01501209	999	<0001
2008-2011 <i>Acropora</i>	-00805806	02640742	-0305	095
2008-2017 <i>Acropora</i> *	28013390	07331233	3821	00004
2011-2017 <i>Acropora</i> *	28819196	07295555	395	00002
2008-2011 <i>Favites</i>	-00231273	03301440	-007	09973
2008-2017 <i>Favites</i>	07546504	03301440	2286	00719
2011-2017 <i>Favites</i>	07777778	03236202	2403	00559
2008-2011 <i>Porites</i>	01135194	02156242	0526	08584
2008-2017 <i>Porites</i> *	16897016	03502626	4824	<0001
2011-2017 <i>Porites</i> *	15761822	03518651	4480	<0001

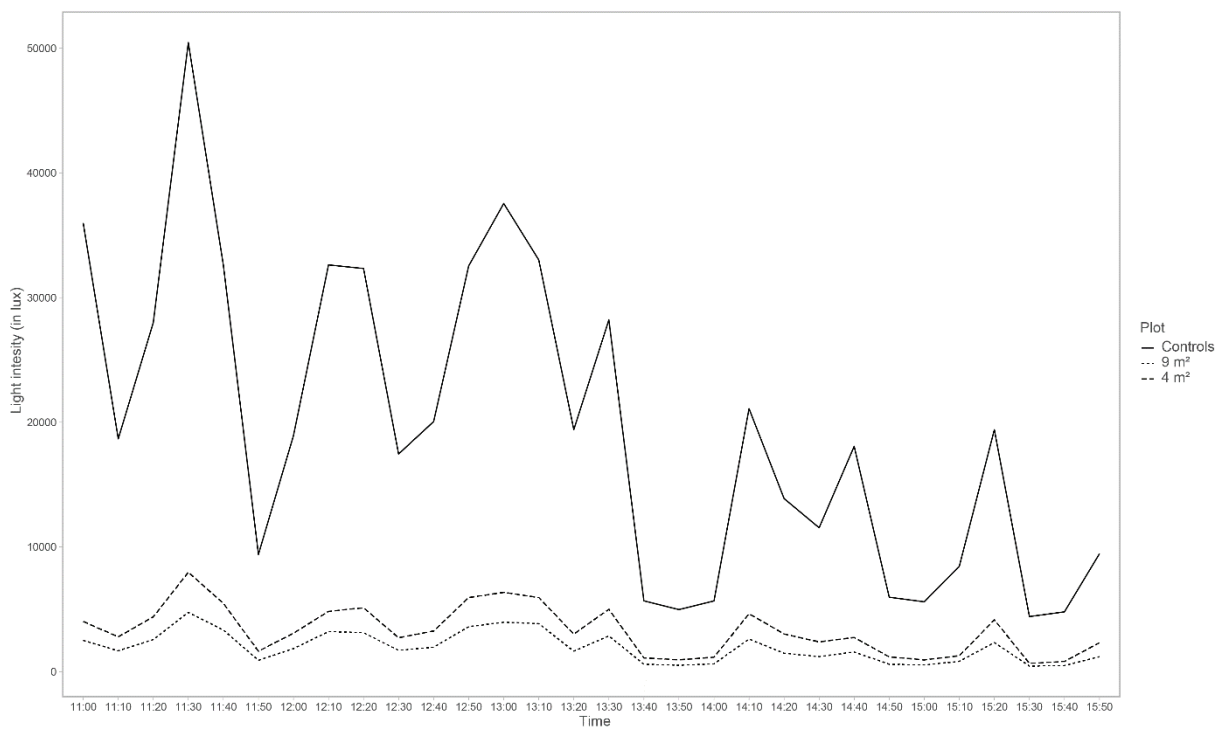


Figure S2.1 HOBO pendant logger readings of light intensity (in lux) below the small and large shade sails as well as control plots during first week of shading from 11:00-16:00 h

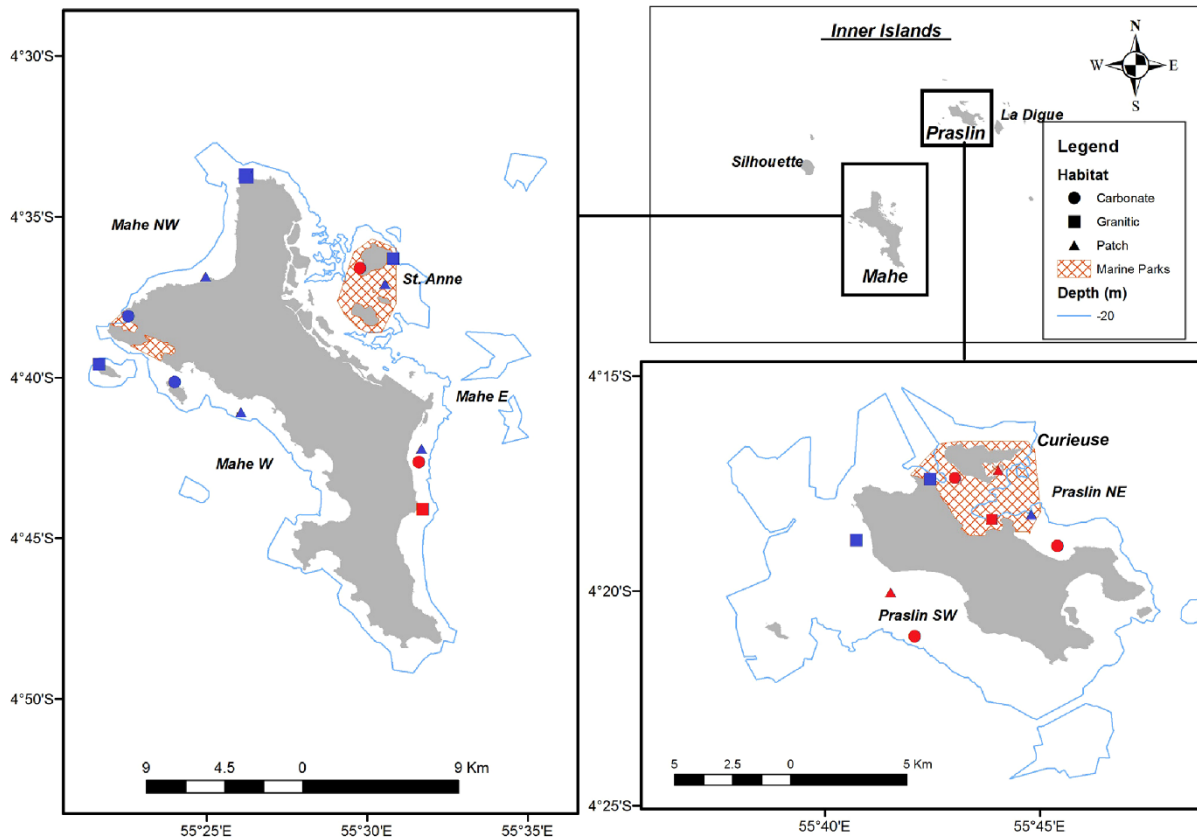


Figure S3.1 Map of Seychelles showing 21 study sites categorised into previous categorisations regime shifted to macroalgal dominance (red) and recovering (blue) from the 1998 bleaching event, adapted from Graham et al. (2015).

Supplementary table 3.1: Tukey HSD results for significant differences between individual experiment weeks and urchin stocking densities

Tukey multiple comparisons of means, 95% family-wise confidence level				
Comparison	Estimate	Standard error	Z-ratio	p-value
10 urchins week 1 - 10 urchins week 3	10812	0352	3074	00543
10 urchins week 1 - 10 urchins week 6	14802	0345	4293	00006
4 urchins week 1 - 4 urchins week 3	-04028	0315	-1277	09382
4 urchins week 1 - 4 urchins week 6	01710	0299	0572	09997
Control week 1 - control week 3	-04223	0402	-1050	09808
Control week 1 - control week 6	-02414	0395	-0611	09996

Supplementary panel 4.1 Jamaica's reef fisheries state and the demand for available seafood

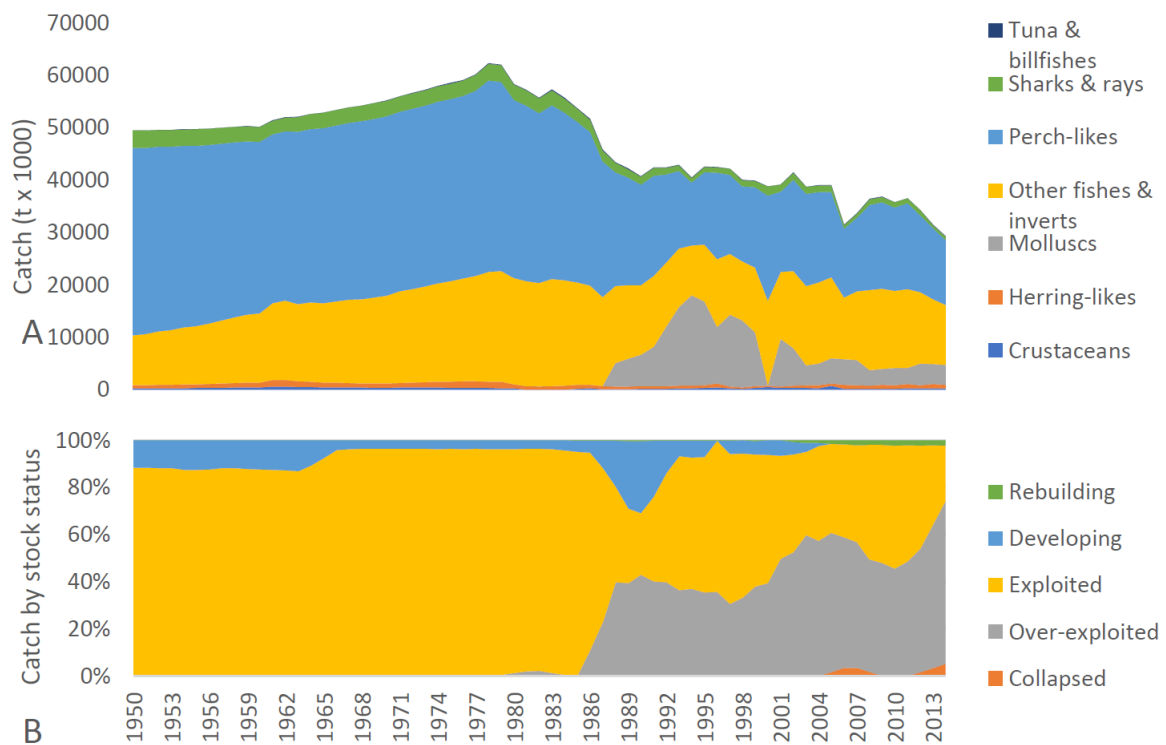


Figure S1. Jamaican catches of commercial fishing groups (A) Percentage of Jamaica's catches from stocks divided by stock status (B) from 1950-2014, reconstructed for www.seaaroundus.org by Lingard et al. (2012).

Jamaica's fisheries are heavily dependent on reef catches (i.e. sharks & rays, perch-likes, molluscs, Fig. S1 A; Lingard et al. 2012). Historically, the fishery can be divided into two periods, before and after the mid-1980s (Fig. S1 B) – a split aligning with the benthic regime shift from coral to algae that Jamaican reefs experienced at the same time (Hughes 1994).

Intense overfishing leading up to the regime shift caused overexploited fishing stocks to change from < 1 % in 1985 to 40 % in 1988. This figure has since risen to 69 % in 2014 (Fig. S1 B).

With Jamaica's own catches declining (Fig. S1 A & B), imports had to be elevated (Fig. S2) to sustain the growing daily seafood consumption from 31.2 g (1990) to 37.3 g (2010; <https://www.globaldietarydatabase.org/our-data/data-visualizations/dietary-data-country>).

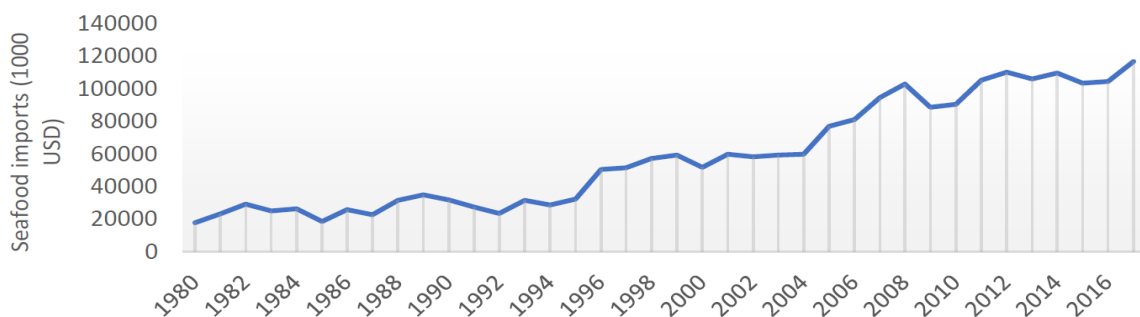


Figure S2. Jamaican imports of seafood products from 1980-2017 (FAOSTAT 2019).

APPENDIX B: PUBLICATIONS ARISING FROM THESIS

Dajka, J.-C., Wilson, S. K., Robinson, J. P. W., Chong-Seng, K. M., Harris, A. & Graham, N. A. J. (2019) Uncovering drivers of juvenile coral density following mass bleaching. *Coral Reefs* 38:637–649, <https://doi.org/10.1007/s00338-019-01785-w>

Dajka, J.-C., Woodhead, A. J., Riechers, M., Graham, N. A. J., Norström, A. V., Nyström, M. (2020) Red and green loops help uncover missing feedbacks in a coral reef social-ecological system, *People and Nature*, <https://doi.org/10.1002/pan3.10092>



Uncovering drivers of juvenile coral density following mass bleaching

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Abstract Thermally induced mass coral bleaching is globally responsible for major losses of coral cover. Coral recovery from mass coral disturbances like the 2016 bleaching event hinges on successful recruitment of new coral colonies to the existing population. Juvenile corals as a life history stage represent survival and growth of new recruits. As such, habitat preferences of juvenile corals and how environmental parameters interact to drive coral recovery following a mass bleaching disturbance are important research areas. To expand our knowledge on this topic, we compared juvenile coral densities from before the 2016 bleaching event with those after the disturbance and identified abiotic and biotic characteristics of 21 reefs in the inner Seychelles that predict juvenile coral densities. Our results show that following the 2016 bleaching event, juvenile coral densities were significantly reduced by about

70%, with a particularly large decline in juvenile *Acropora*. Macroalgae present a large obstacle to survival of juvenile corals in a post-bleaching setting, but their influence varies as a function of herbivore biomass, reef structure, and reef type. Higher biomass of herbivorous fish weakens the negative effect of macroalgae on juvenile corals, and structural complexity on granitic reefs is a strong positive predictor of juvenile coral density. However, structural complexity on carbonate or patch reefs was negatively related to juvenile coral density, highlighting the importance of considering interactive terms in analyses. Our study emphasises the importance of habitat for juvenile coral abundance at both fine and seascape scales, adding to the literature on drivers of reef rebound potential following severe coral bleaching.

Keywords Coral reef recovery · Recruitment · Coral bleaching · Coral reef ecology · Macroalgae · Seychelles

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Introduction

Mass coral bleaching events resulting from ocean warming have led to significant losses of coral cover across many of the world's reefs (Goreau et al. 2000; Hughes et al. 2017). Coral reefs have the ability to rebound from extensive coral bleaching, but it can take more than a decade for coral cover to reach pre-bleaching levels (Gilmour et al. 2013; Graham et al. 2015). Coral reef recovery depends on the reassembly of the habitat-forming hard coral (scleractinian) community (Connell et al. 1997), driven in part by coral recruitment—the replenishment of the local population by new individuals from within or outside an existing population (Hughes et al. 2010).

Successful coral recruitment is dependent on several important factors that can result in significant demographic bottlenecks. Firstly, recruitment depends on sufficient supply of coral larvae, requiring inputs of external larvae on well-connected reefs (Hughes and Tanner 2000; Elmhirst et al. 2009) or self-recruitment on geographically isolated reefs (Gilmour et al. 2013). Secondly, availability of suitable benthic space for coral settlement is important (Connell et al. 1997; Diaz-Pulido et al. 2010). Some benthic algae (e.g. turf algae or mature fleshy macroalgae) inhibit larval settlement of corals when the algal beds become too dense (Johns et al. 2018), while other surfaces, such as some crustose coralline algae (CCA), can be preferred settlement sites by coral larvae (Yadav et al. 2016). Thirdly, post-settlement mortality of juvenile corals (0.5–5 cm; Roth and Knowlton 2009) is high (Hughes et al. 2007). Two major drivers of early post-settlement mortality are competition with other benthic organisms, such as macroalgae (Rasher et al. 2011; Johns et al. 2018), and predation, for instance by corallivores and incidental predation by some herbivores (Cole et al. 2008; Doropoulos et al. 2012). Unstable substrates such as rubble have also been suggested to cause major coral recruit die-offs (Fox et al. 2003; Chong-Seng et al. 2014). Mortality rates gradually reduce with coral growth, and most corals escape mortality once they have reached sizes above 5 cm (Doropoulos et al. 2015), allowing the corals to grow to reproductive sizes and contribute to the adult population (Hughes et al. 2010; Gilmour et al. 2013).

Coral reefs can recover from extensive coral mortality, provided key factors such as fishing, water quality, and anthropogenic climate change are kept within safe operating spaces (Norström et al. 2016). However, the likelihood of experiencing mass coral bleaching events in the coming decades is increasing (Hughes et al. 2018). A long-term study by Graham et al. (2015) in the inner Seychelles determined the density of juvenile corals as one of the five parameters that can positively predict the rebound potential of mass bleaching-disturbed coral reefs. Initial post-disturbance recovery rates are usually slow, and global average increases in per cent coral cover following mass bleaching are only 3% (Graham et al. 2011). However, recovery rates can speed up exponentially once juvenile corals have grown into reproducing colonies (Gilmour et al. 2013) to create an efficient positive feedback loop that can result in rapid rates of coral cover expansion (Nyström et al. 2012).

Studies spanning multiple decades demonstrate that corals are affected by abiotic factors such as light, depth, and substratum orientation (Babcock and Mundy 1996; Roth and Knowlton 2009), seawater temperature (Edmunds 2004), or cryptic microhabitat orientation along a depth gradient (Edmunds et al. 2004) during early post-

settlement. Some biotic surfaces facilitate juvenile coral growth and survival, such as some CCA species (Arnold et al. 2010; Arnold and Steneck 2011); Yadav et al. 2016), calcareous polychaete worm tubes, biofilms (Arnold et al. 2010), and other coral skeletons (Norström et al. 2006). Conversely, other biotic factors inhibit coral recruitment, for instance macroalgae (Box and Mumby 2007; Arnold et al. 2010; Arnold and Steneck 2011), turf algae, and other invertebrates (Arnold et al. 2010; Arnold and Steneck 2011). More recently, interacting biotic processes have been identified, such as between herbivory of turf algae (Arnold et al. 2010) and how herbivore exploitation reduced algal consumption and ultimately affected juvenile coral densities (Steneck et al. 2018).

Despite the extensive body of research, most of our knowledge on the early life history of settled corals does not stem from recently disturbed reefs. With the likelihood of thermally driven coral bleaching events increasing across the tropics (Hughes et al. 2018), an improved understanding of the drivers of post-bleaching coral recruitment will help to identify which processes promote or inhibit coral recovery. A recent study on juvenile coral densities on the Great Barrier Reef following the 2016 bleaching event considered abiotic predictors (temperature, rugosity, location around island, depth) as well as one biotic predictor (coral taxon; Álvarez-Noriega et al. 2018), but post-bleaching influences of other environmental factors, such as herbivory, CCA, or macroalgae, remain unclear. Thus, an important research gap exists regarding post-bleaching habitat and biotic predictors of juvenile coral density. Insight into which cross-scale abiotic and biotic drivers predict juvenile coral densities and how they interact shortly after large-scale coral bleaching events will improve our understanding of how early coral reef recovery dynamics vary spatially following extensive bleaching. Our study addresses this gap by investigating reefs of the inner Seychelles one year after the 2016 bleaching event. We explore temporal patterns of juvenile coral densities before and after the 2016 bleaching event and investigate how key habitat characteristics interact to limit or facilitate juvenile coral density.

Methods

The inner Seychelles (4°30'S, 55°30'E) are mostly granitic islands with well-developed carbonate fringing reefs. In recent history, the inner Seychelles' coral reefs have been affected by two major bleaching events caused by thermal anomalies (in 1998: ~ 90% loss, Goreau et al. 2000; and in 2016: ~ 70% loss, Wilson et al., in review). We surveyed 21 sites within the inner Seychelles in April 2017, 18 of which had been previously surveyed in 2008 and 2011.

At each of the 21 sites, we recorded the abundances of diurnally active, non-cryptic, reef-associated fish species along with estimates of their individual total lengths at 8 replicate point counts (7 m radius) along the reef slope. We excluded any individual fish entering the cylindrical area once sampling had commenced from abundance estimates. To ensure accurate length estimates of fish, the surveying diver estimated the lengths of sized PVC pipes until accuracy was consistently within 4% of actual lengths every day (Graham et al. 2007). After the survey, we converted estimated fish lengths from surveys into biomass using published length–weight relationships (Letourneur et al. 1998; Froese and Pauly 2018) and species assigned to feeding groups based on their diet and feeding behaviour (Wilson et al. 2008). Within the same point counts, we visually estimated the structural complexity of the reef using a scale from 0 (no vertical reef) to 5 (exceptionally complex with numerous caves and overhangs) as per Polunin and Roberts (1993), which correlates strongly with a range of other methods for capturing the structural complexity of coral reefs (Wilson et al. 2007). We counted sea urchin abundance (family: Diadematidae) within each point count area. Lastly, we randomly deployed a 50 × 50 cm quadrat repeatedly within each point count and counted juvenile corals in it. The number of quadrat deployments in each point count area and associated juvenile coral counts was limited to the maximum number that could be deployed within 8 min (3–13 quadrats per point count). Prior surveys of juvenile corals at these sites in 2008 and 2011 had used quadrat sizes of 33 × 33 cm for juvenile density (Chong-Seng et al. 2014; Harris et al. 2014); however, we used larger 50 × 50 cm quadrats to obtain a better assessment of the habitat surfaces around juvenile corals. We searched each quadrat for juvenile corals with diameters up to 5 cm (Roth and Knowlton 2009), identified the corals to genus level, and measured their diameter to the nearest 0.1 cm. Colonies clearly resulting from shrinkage, fragmentation, or overgrowth of older colonies were not recorded (Hughes and Jackson 1985). We recorded the coral's attachment substrate and took a HD photograph of each quadrat from above in a way that all borders of the quadrat were visible. We later analysed the photographs with Coral Point Count with extension for Excel (CPCe; Kohler and Gill 2006) to obtain percent cover values for the benthos categories: macroalgae, turf algae, CCA, sand, rubble, and pavement (bare rock).

Statistical analysis

We analysed temporal variation in juvenile coral density between 2008 (Harris et al. 2014), 2011 (Chong-Seng et al. 2014), and 2017 at the 18 sites surveyed each year. To

standardise varying sampling efforts, we averaged the juvenile coral abundances across quadrats, for each site of each year (18 sites of 3 yr: $n = 54$), rounded to give an average coral abundance. Because different quadrat sizes were used throughout the years, we included the quadrat area as an offset variable, a pre-specified coefficient, in our models. To account for overdispersion of the response variable, we fitted generalised linear mixed models (GLMMs) from the 'lme4' package (Bates et al. 2015) in R (R-Core-Team 2018) for Poisson-distributed errors. Our final models with 'site' as a random intercept term were selected based on Akaike information criterion (AIC; Zuur et al. 2009):

$$\text{Juvenile coral abundance (All, Acropora, Favites, Porites)} \\ \sim \text{year} + \text{offset (area)} + (1|\text{site})$$

We fitted GLMMs to total juvenile corals abundances, as well as to two common genera, *Acropora* and *Porites*. For a third genus, *Favites*, we fitted the same model structure but with Gaussian errors (linear mixed model, LMM), using the 'nlme' package (Pinheiro et al. 2018). We conducted Tukey HSD post hoc tests to identify significant year differences.

Using only the dataset for 2017, we analysed the data for 21 sites at the scale of the 7-m-radius point counts to examine abiotic and biotic drivers of juvenile corals after 2016 bleaching. Because multiple quadrats were deployed within each point count, we averaged and rounded the resulting juvenile coral count across quadrats for each point count ($n = 168$). We expected juvenile coral density to be predicted by 7 biotic and abiotic variables measured at different scales (Table 1) and included ecologically sensible two-way interactions between variables. All variables were only weakly correlated, and so the model was not biased by collinearity issues (Zuur et al. 2009). We scaled variables to a mean of 0 and standard deviation of 1, a recommended approach for multi-model selection which allows for meaningful comparisons of effect sizes when variables are on different scales (e.g. benthic cover in percent vs. structural complexity; Schielzeth 2010). 'Reef type' was originally a categorical variable with three reef types: carbonate, patch, and granite. After isolating the impact of each reef type on juvenile coral densities, granite stood out significantly from the other two reef types. To reduce the variables and interactions considered by our analysis to a number that can be sensibly interpreted with our given number of observations, we replaced 'reef type' as a categorical variable with a binary dummy variable that isolates the granite reef type and groups carbonate and patch reef types. To account for overdispersion and high frequencies of true zeros in the response variable (45.5%), we fitted a zero-inflated negative binomial (ZINB)

Table 1 Biotic and abiotic variables considered in habitat predictor analysis to explain spatial variation in juvenile coral density

Predictor	Rationale	References
Sand and rubble	Sand or sediment acts as inhibitors to the settlement of coral larvae, while unstable rubble can induce post-settlement mortality in corals	Fox et al. (2003), Birrell et al. (2005), Chong-Seng et al. (2014), Risk (2014), Cameron et al. (2016), Yadav et al. (2016)
Crustose coralline algae (CCA)	Coral larvae are able to settle and grow on certain CCA species. CCA can also act as a competitor for space with macroalgae as well as corals themselves	Buenau et al. (2011), Vermeij et al. (2011), Yadav et al. (2016)
Macroalgae	Macroalgae are among the primary competitors for space with corals and can also induce post-settlement mortality to corals via physical and chemical pathways	McCook et al. (2001), Jompa and McCook (2003), Diaz-Pulido et al. (2010), Johns et al. (2018)
Herbivorous fish biomass	Feeding by herbivorous fish removes algae creating space for corals to settle and grow. The grazing impact scales with abundance and body size. Incidental predation by herbivorous fish on coral spat has also been reported	Bellwood et al. (2004), Lokrantz et al. (2008), Doropoulos et al. (2012), Mumby et al. (2013), Graham et al. (2015)
Sea urchin abundance	Similar to herbivorous fish, sea urchins can both facilitate and limit coral recruitment by (1) grazing algae that otherwise block potential coral settlement space and (2) incidental predation on coral spat	Glynn et al. (1979), Carpenter and Edmunds (2006), Furman and Heck (2009), Edgar et al. (2010), Hughes et al. (2010)
Structural complexity	Structurally complex reefs provide habitable space for a diverse range of organisms including fish or sea urchins and create niche space for coral settlement and survival	Vergés et al. (2011), Graham and Nash (2013), Rogers et al. (2014), Doropoulos et al. (2016)
Reef type	Three reef types were surveyed: carbonate, patch, and granite reefs; reef type can affect coral recruitment success	Jennings et al. (1995), Graham et al. (2007), Burt et al. (2009), Wilson et al. (2012)

regression model via maximum likelihood estimation (Zuur et al. 2012). This is a two-part model that fits two distributions to the data—the first part fits a binomial distribution to the full dataset, treating the response variable as presence–absence data (zero component), while the second part fits a negative binomial distribution to all non-zero response data (i.e. where juvenile corals were present, count component). We initially fitted a zero-inflated mixed model (‘site’ as random factor) using the *glmmTMB* package (Brooks et al. 2017) and one without a random effect using the ‘*pscl*’ package (Zeileis et al. 2008). Model selection based on AIC (Zuur et al. 2009) classed the model without random effect as better performing, indicating that auto-correlation does not bias our parameter estimates. One variable (‘sea urchins’) was excluded in backward selection based on AIC, resulting in the final model:

Juvenile coral density \sim Sand and rubble + CCA
 + macroalgae + herbivores + complexity
 + reef type + reef type * complexity
 + macroalgae * complexity + macroalgae * herbivores

The model validation of this final model did show a slight residual clustering in the model’s zero component which can be the case with zero-inflated models (Zuur et al. 2012). We visualised predicted relationships in ZINB models by predicting juvenile coral density across the

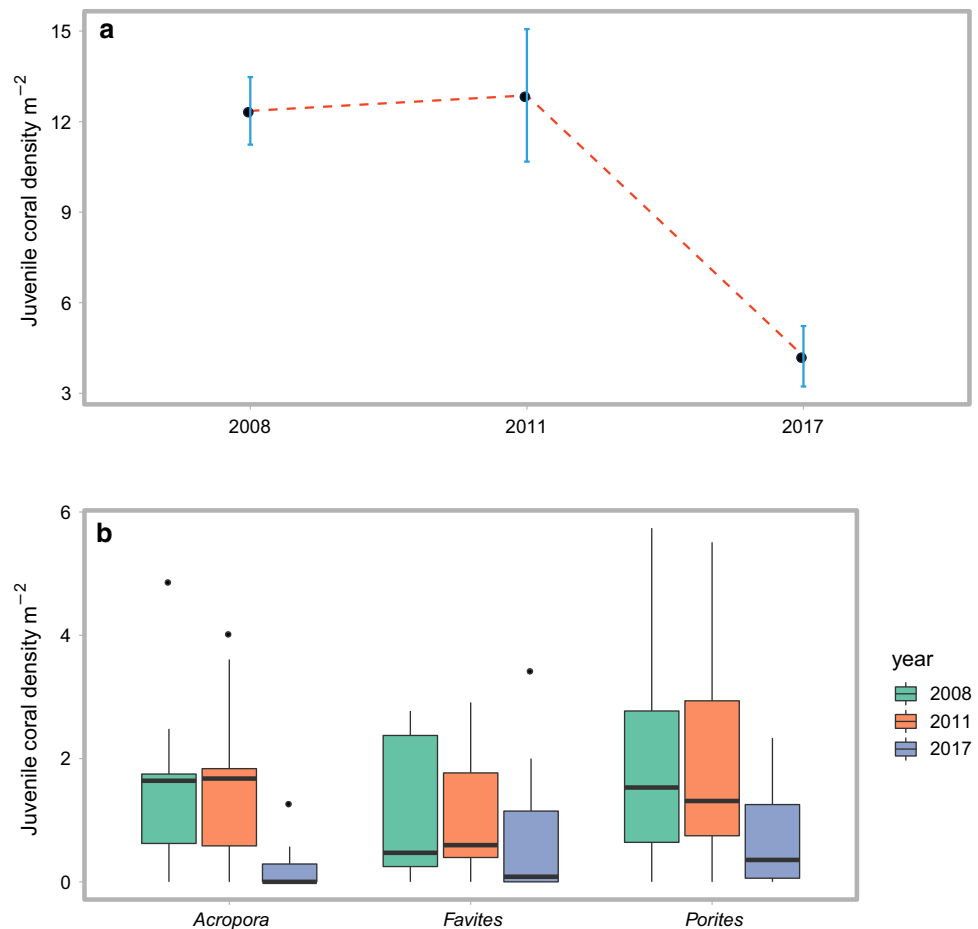
observed range of each variable, holding all other variables to constant means of 0 (Schielzeth 2010). All statistical analyses were conducted in R (R Core Team 2018). We provide our R-scripts and model predictions at an open-source repository (<https://github.com/JanDajka/SeyBabies-2016-bleaching>).

Results

Temporal patterns

Juvenile coral abundances in 2017 were less than half that of previous years (Fig. 1a, GLMM, $z = -9.19$, $p < 0.001$). A post hoc test (Table S1) showed that 2017 abundances were significantly lower than those of 2008 (Tukey HSD, $Z-\Delta = 9.19$, $p < 0.001$) and 2011 ($Z-\Delta = 9.99$, $p < 0.001$), while 2008 and 2011 were not significantly different ($Z-\Delta = -0.912$, $p = 0.63$). This pattern was also the case for *Acropora* and *Porites* coral genera (Fig. 1b, *Acropora* 2008–2017: $Z-\Delta = 3.82$, $p < 0.001$; *Acropora* 2011–2017: $Z-\Delta = 3.95$, $p < 0.001$; *Acropora* 2008–2011: $Z-\Delta = -0.31$, $p = 0.95$; *Porites* 2008–2017: $Z-\Delta = 4.82$, $p < 0.001$; *Porites* 2011–2017: $Z-\Delta = 4.48$, $p < 0.001$; *Porites* 2008–2011: $Z-\Delta = 0.53$, $p = 0.86$). Juvenile *Favites* abundances did not significantly differ between the years (*Favites* 2008–2017: $Z-\Delta = 2.29$,

Fig. 1 Average juvenile coral densities per square metre (\pm SE) of all sampled coral genera from 2008, 2011, and 2017 (a); average juvenile coral densities (\pm SE) of common coral genera *Acropora*, *Favites*, and *Porites* from 2008, 2011, and 2017 (b)



$p = 0.072$; *Favites* 2011–2017: $Z\text{-}\Delta = 2.4$, $p = 0.056$; *Favites* 2011–2008: $\Delta = -0.07$, $p = 0.997$).

Habitat predictors

Presence–absence data (zero model) indicated a negative effect of herbivores on juvenile corals (Fig. 2a). Sand and rubble, granitic reef type, and macroalgae had very weak effects on juvenile coral densities, while CCA and complexity had positive effects. All interactions had a positive effect on coral densities. The interaction ‘macroalgae * herbivores’ highlighted a positive indirect effect of herbivores on juvenile coral densities. The ‘macroalgae * complexity’ interaction showed how macroalgae slightly reduced the positive effect that complexity alone had on juvenile coral densities while a granitic reef type increased the positive effect for complexity.

In the count component of the model, macroalgae, sand and rubble, and complexity had negative effects on juvenile coral densities (Fig. 2b). CCA and granitic reef type had very weak effects, while herbivores had a positive effect on juvenile coral densities. The ‘macroalgae * complexity’ interaction had a negative effect, the ‘granite *

complexity’ interaction had a very weak effect, and the ‘macroalgae * herbivores’ interaction had a positive effect on juvenile coral densities.

The zero-inflation model rarely predicted juvenile coral densities when cover of sand and rubble or macroalgae was greater than 50%; however, when cover of these groups was low, predicted densities reached ~ 2.5 juvenile corals m^{-2} (Fig. 3a, b). In contrast, when CCA was absent, our model predicted ~ 1.5 juvenile corals m^{-2} and an expansion of up to 30% CCA cover elevated that prediction above 2 juvenile corals (Fig. 3c). The increasing standard error of additional CCA cover (30–60%) resulting from few occurrences of high CCA cover values does not allow for further interpretation. The model predicted ~ 1.5 juvenile corals m^{-2} when herbivores were absent, and this number stayed relatively constant up to 250 kg ha^{-1} herbivore biomass before falling to ~ 1 juvenile coral m^{-2} at 900 kg ha^{-1} herbivore biomass (Fig. 3d). Further interpretation of this trend was not warranted due to large standard errors resulting from few occurrences of high herbivore biomass values.

The ‘macroalgae * complexity’ interaction of our model predicted densities of ~ 1.2 juvenile corals m^{-2} on low

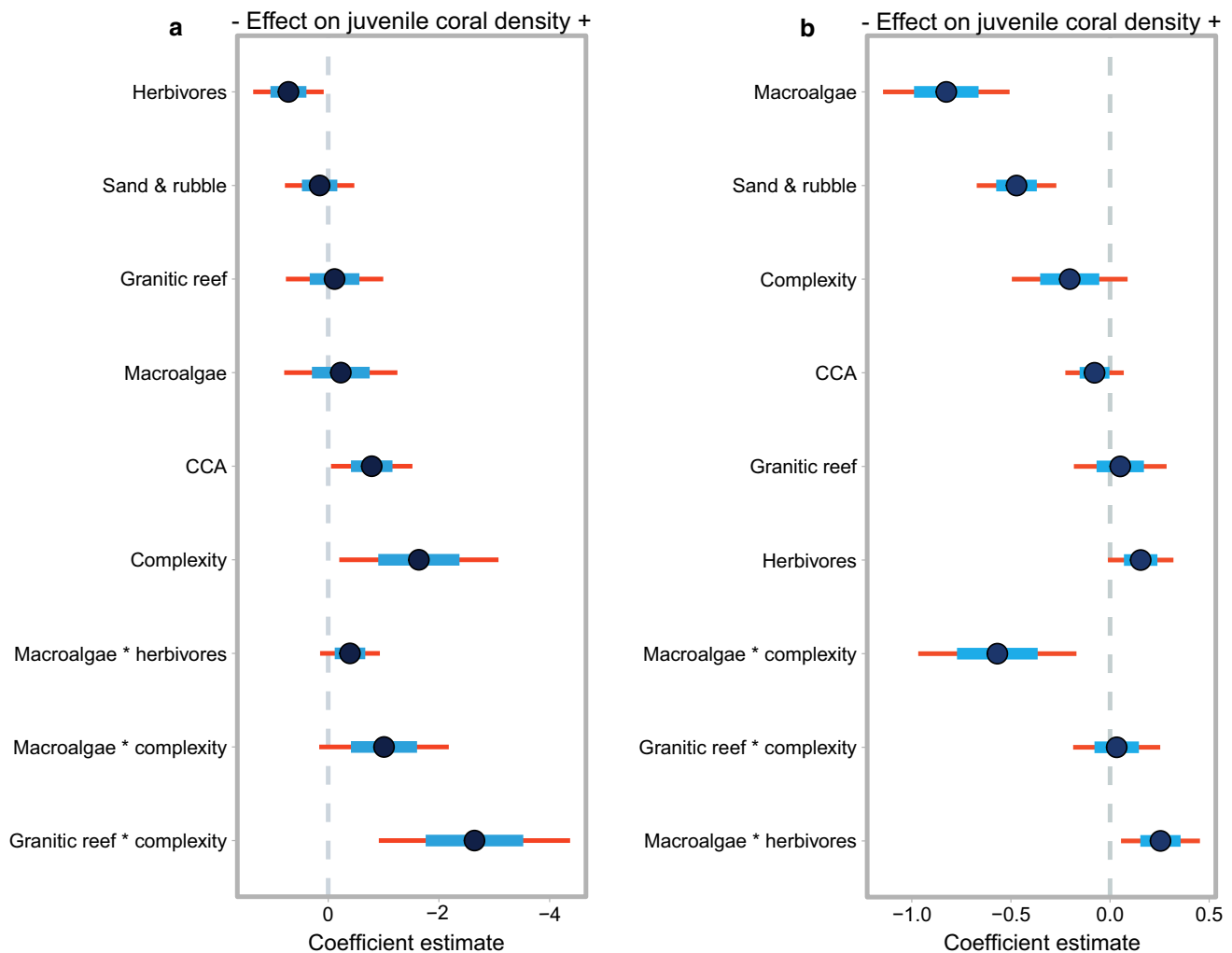


Fig. 2 Effect size estimates of predictor coefficients in zero model with standard error (thick line) and 95% confidence intervals (thin line); zero model component: positive coefficient estimates predict coral absences (0) and negative coefficient estimates predict coral

presence (1), stronger negative values indicate stronger positive effect on juvenile coral density (a); count model component: negative coefficient estimates predict lower juvenile coral density and positive coefficients predict higher density (b)

(0–1 on the structural complexity scale)-complexity reefs when macroalgal cover was above 50%, but juveniles were rare on medium (1–3)- or high (3–4)-complexity reefs with macroalgal cover above 50% (Fig. 4a). When macroalgae cover was low ($\sim 10\%$), however, high- and medium-complexity habitats supported juvenile coral densities ~ 5 juvenile corals m^{-2} , while low-complexity habitats only supported a maximum of ~ 2.5 juvenile corals m^{-2} . The prediction of high juvenile coral densities in the high-complexity habitat at 0% macroalgae cover was also accompanied by a large standard error resulting from little occurrences of high-complexity habitats without macroalgae in our data and was therefore not interpreted.

The ‘macroalgae * herbivore’ interaction led to highest densities reaching ~ 3.5 juvenile corals m^{-2} when both macroalgae cover (5%) and herbivore fish biomass were low (0–200 $kg\ ha^{-1}$; Fig. 4b). At low herbivore biomass,

increases in macroalgae cover to 50% caused a reduction to ~ 0.5 juvenile corals m^{-2} . This reduction in juvenile corals occurred at 65% macroalgae cover at medium (200–400 $kg\ ha^{-1}$) herbivore biomass and to 85% macroalgae cover at high (400–600 $kg\ ha^{-1}$) herbivore biomass. Yet, the maximum density of juvenile corals was also notably depressed as herbivore biomass increased. When herbivore biomass was low, the model predicted maximum densities of ~ 3.5 juvenile corals m^{-2} and ~ 3 juvenile corals m^{-2} at medium herbivore biomass. At high herbivore biomass, our model only predicted a maximum of ~ 2.3 juvenile corals m^{-2} .

For the ‘reef type * complexity’ interaction, juvenile coral density decreased as complexity increased on carbonate and patch reefs (Fig. 5). For example, in granitic reefs, juvenile corals were absent at low complexity (0–1) but increased from ~ 0.5 to 2.2 juvenile corals m^{-2} at

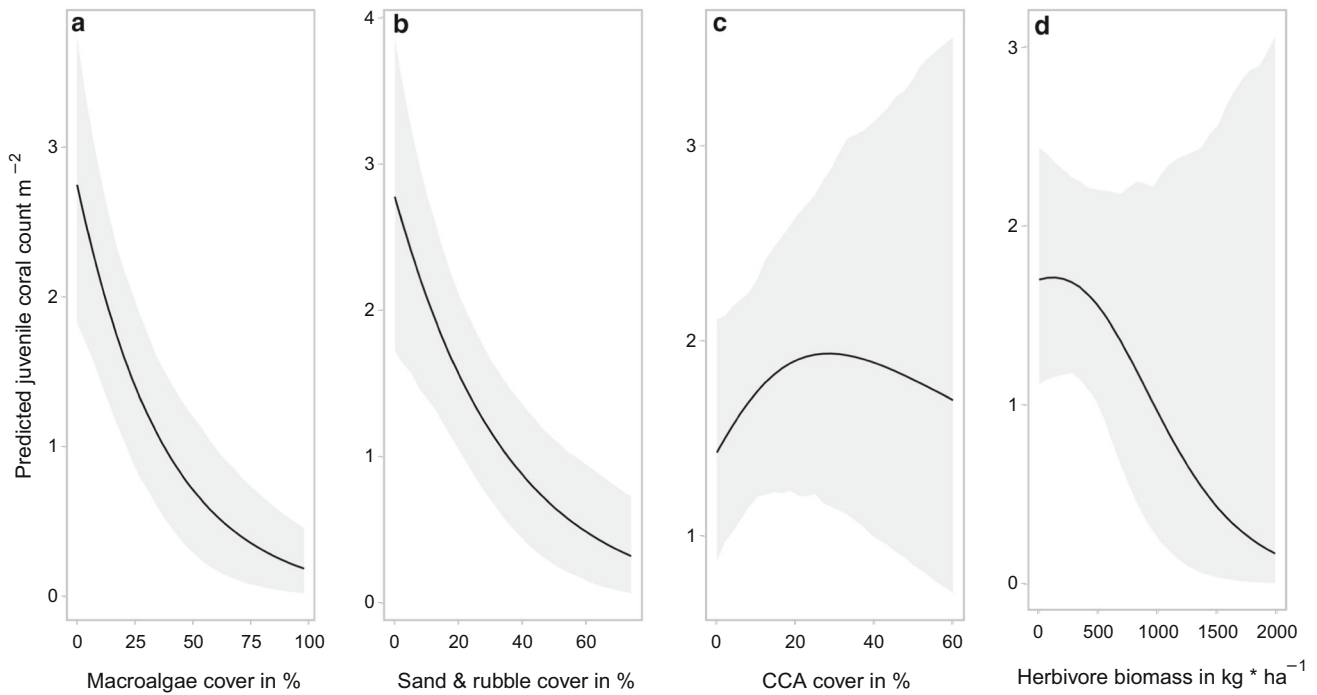


Fig. 3 Model prediction trends of macroalgae (a), sand and rubble (b), CCA (c), and herbivores (d) for the count component of the zero-inflated negative binomial model; panels show the fitted effect (line) and 95% confidence intervals (shaded bands) for each variable

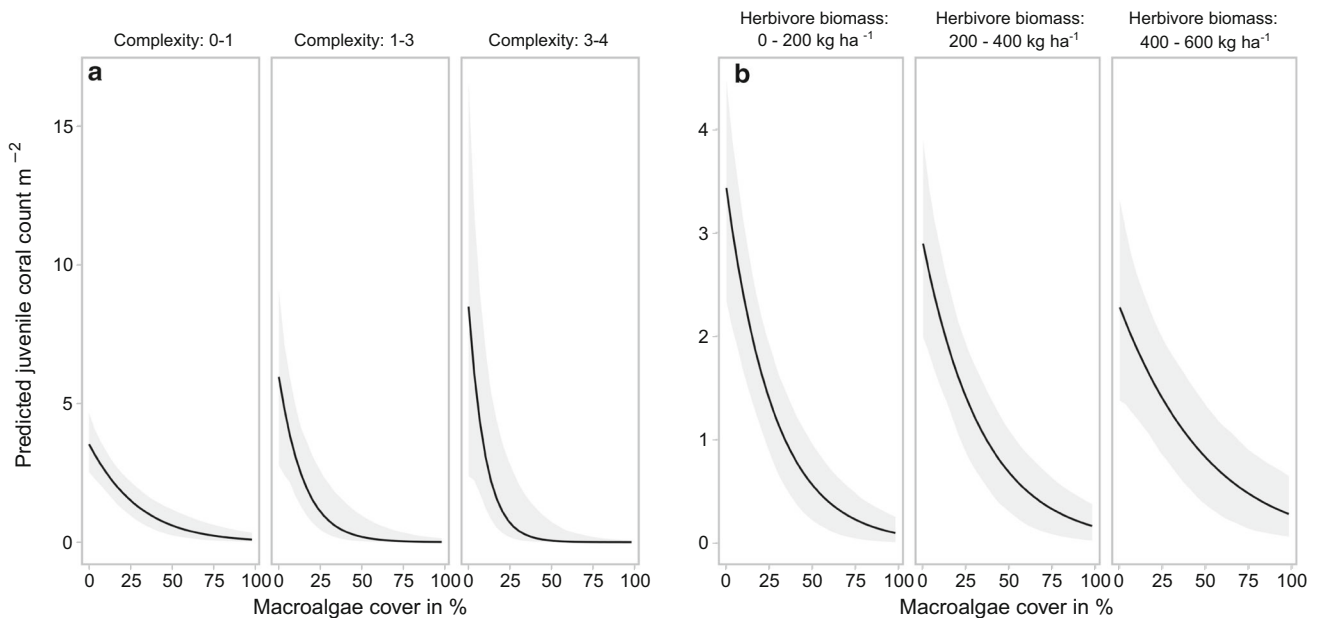


Fig. 4 Model prediction trend for interactions macroalgae * structural complexity (a) and macroalgae * herbivore biomass (b) for the count component of the zero-inflated negative binomial model. Panels

show the fitted effect (line) and 95% confidence intervals (shaded bands) for each variable

medium complexity (2–3). Both the low-complexity predictions on carbonate and patch reefs and the high-complexity predictions on granitic reefs were accompanied by large prediction uncertainty and were therefore not interpreted.

Discussion

The densities of juvenile corals have been proposed as an important predictor of coral reef recovery from mass bleaching events (Hughes et al. 2010; Gilmour et al. 2013;

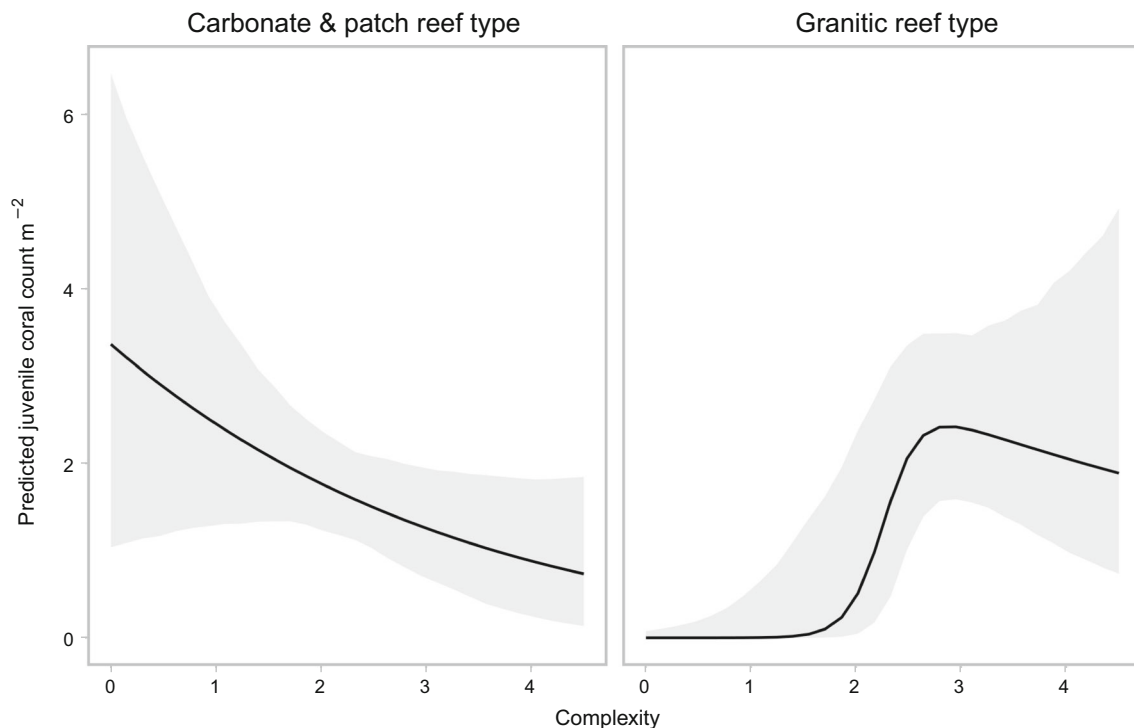


Fig. 5 Model prediction trend for interaction reef type * structural complexity for the count component of the zero-inflated negative binomial model. Panels show the fitted effect (line) and 95% confidence intervals (shaded bands)

Graham et al. 2015), yet predictors of juvenile corals themselves following large-scale bleaching are hitherto poorly explored. Following the 2016 bleaching event, we recorded a significant reduction in juvenile coral abundance in the inner Seychelles. High cover of macroalgae was associated with few juvenile corals shortly after a mass bleaching event, though interesting nuances were found in how their densities varied with interactions between macroalgal cover and other factors. Macroalgae appear to exploit structurally complex carbonate (limestone) reefs more efficiently and, as a result, may outcompete juvenile corals on these reefs; however, macroalgae cover on high-complexity granitic reefs is generally low (Graham et al. 2006). Increased biomass of herbivorous fish reduced the negative effect of macroalgae on juvenile corals, though very high biomass of herbivores was associated with slightly lower density of juveniles when macroalgae were absent.

Our temporal findings depict the severity of the 2016 bleaching event to coral recruitment in the inner Seychelles via the loss of ~ 70% juvenile coral abundance. This roughly matches the magnitude of adult coral cover loss for the same region (Wilson et al., in review). Loss in adult corals leads to lowered reproductive output and less larval supply (Hughes et al. 2000), which is problematic as the isolated coral communities of the inner Seychelles are likely reliant on self-recruitment (Graham et al. 2006).

Before mass bleaching in 2016, the inner Seychelles' recovery from the 1998 bleaching event was slow for 7–10 years and then sped up exponentially at some sites (Graham et al. 2015), also typical for regions with coral recruitment from local sources (Gilmour et al. 2013). The 2016 bleaching event decimated juvenile *Acropora* corals. Fast-growing branching corals like *Acropora* tend to be among the most vulnerable to bleaching (Sheppard et al. 2002; Álvarez-Noriega et al. 2018) but can also drive the bulk of the coral reef's recovery (Emslie et al. 2008; Gilmour et al. 2013; Doropoulos et al. 2015). The low abundance of juvenile corals recorded post-bleaching, paired with their apparent inability to settle or survive on degraded sites (Chong-Seng et al. 2014) and reduced reproductive output of adults, suggests a significant delay of recovery in the inner Seychelles.

Our results indicate that macroalgal cover is a strong negative predictor of juvenile coral density. This supports the widely reported detrimental effect of macroalgae on coral recruitment (Diaz-Pulido et al. 2010; Rasher and Hay 2010; Johns et al. 2018; Steneck et al. 2018) in a post-bleaching setting and adds an interesting nuance with two interaction effects. Macroalgae inhibit settlement of coral larvae by blocking space (Diaz-Pulido et al. 2010; Johns et al. 2018) and increase the corals' post-settlement mortality by chemical and physical interference (Tanner 1995; Jompa and McCook 2003; Nugues et al. 2004; Rasher et al.

2011). It appears that increased structural complexity interacts with macroalgae to the detriment of juvenile corals. This might stem from an increased competitive pressure from macroalgae when coral larvae settle in more complex microhabitats or crevices (Doropoulos et al. 2016), as macroalgae that grow in complex structural elements avoid being grazed by herbivores (Bennett et al. 2010; Poray and Carpenter 2013). Because of the limited space in a crevice, corals experience more contact with macroalgae (Rasher et al. 2011), exacerbating the effects of competition. This is underlined by more complex reefs supporting higher maxima of juvenile coral density when macroalgae cover is low or absent.

Higher biomass of herbivorous fish reduced the detrimental effect of macroalgae expansion on juvenile corals. In Seychelles, herbivorous fish biomass has increased following the 1998 bleaching event and is maintaining a productive inshore fishery (Robinson et al. 2018). Through their increased biomass, herbivorous fish graze more algal mass (Williams et al. 2001) which in turn opens settlement space for coral larvae (Doropoulos et al. 2013) and lessens the contact between corals and algae (Smith et al. 2006; Rasher et al. 2011). Herbivore biomass is a frequently highlighted parameter for coral reef recovery (Bellwood et al. 2004; Mumby et al. 2013) and was also one of the five positive predictors of coral recovery identified for Seychelles (Graham et al. 2015). Additionally, Steneck et al. (2018) found that herbivores reduced the negative effects of macroalgae and consequently had a beneficial effect on juvenile coral density in the Caribbean. In contrast, high herbivore biomass lowered the maximum density of juvenile corals in our study. This could be a result of incidental predation by herbivorous fish on coral spat (Doropoulos et al. 2012). Predation by herbivores, particularly scrapers, but also some grazers and detritivores, largely affects newly settled coral spat. These fish feed on a variety of reef substrates (e.g. turf algae, detritus), inadvertently removing coral recruits. This process largely affects corals within 3 months of settlement when they are still less than a centimetre in diameter, suggesting that predation by herbivorous fish is not visual and hence incidental (Doropoulos et al. 2016). This process might also relate to the macroalgae–complexity interaction, where maximum abundance of juvenile corals at 0% macroalgae cover appeared depressed in high-complexity habitats compared to medium- and low-complexity habitats. High-complexity habitats typically attract fish, such as corallivores or herbivores, that seek shelter to ensure their own survival (Rogers et al. 2014). Feeding by these fishes can result in targeted or incidental predation on newly settled coral spat (Doropoulos et al. 2012), leading to depressed juvenile coral densities in highly complex reefs without macroalgae.

The presence of rubble and sand was also a strong negative predictor of juvenile coral density. It is well reported that corals experience high post-settlement mortality on unconsolidated surfaces such as sand due to its constant movement with wave energy and ability to smother or crush coral spat (Birrell et al. 2005; Risk 2014; Baldock et al. 2015). Periodic movement is also thought to prevent post-settlement survival of corals on unconsolidated rubble. The constant movement of rubble caused by waves results in newly settled corals being crushed (Fox et al. 2003; Yadav et al. 2016). Rubble was previously highlighted as a cause of serious demographic bottlenecks to corals in the inner Seychelles (Chong-Seng et al. 2014), and both patch and areas of carbonate reefs were often surrounded by sand and rubble (Pers. obs.).

Our data highlight the positive role of crustose coralline algae (CCA) on coral juvenile density. Some species of CCA have been reported to create suitable conditions for corals by acting as settlement cues to coral larvae (Ritson-Williams et al. 2010; Arnold and Steneck 2011; Yadav et al. 2016) or by suppressing macroalgal expansion (Belliveau and Paul 2002; Vermeij et al. 2011). Competition for space has also been reported between corals and CCA—as CCA covers more space, corals run the risk of being overgrown (Buenau et al. 2011). Our results show that CCA can be important for coral replenishment in post-bleaching scenarios.

An intriguing finding was the interaction between complexity and reef type. Paired with structural complexity, the granite reef type proved extremely beneficial to juvenile corals. We believe the benefit of granite in our study might be due to it being an unsuitable substrate for macroalgae rather than being a superior substrate for corals (Burt et al. 2009). Macroalgae attach to substrates via holdfasts which can penetrate the substrate up to 10 mm deep by exploiting the physical characteristics of mineral matrices. The density and matrices of granite and carbonate are very different (Morrison et al. 2009). It is likely that large fleshy macroalgae (e.g. *Sargassum*, *Turbinaria*) that commonly outcompete corals on carbonate reefs of the inner Seychelles cannot deeply penetrate the granitic mineral matrix (Milligan and DeWreede 2000), leading to an increased probability of algae dislodging as they grow (Thomsen 2004). Herbivorous fish could be assisting the coral's ability to more successfully exploit structural complexity on granitic reefs. Herbivore fish assemblages on granitic reefs in the inner Seychelles are more stable than those of carbonate and patch reef types (Graham et al. 2006). We found in our study that the average herbivorous fish biomass was very similar for carbonate and patch reef types ($\sim 300 \text{ kg ha}^{-1}$), yet it was slightly elevated in the granite reef type ($\sim 400 \text{ kg ha}^{-1}$).

Our results have multiple implications for coral reef management. Our study reaffirms the negative effect macroalgae can have on coral recruitment and that reducing the competitive advantage of macroalgae is key to triggering a potential shift back to coral dominance on regime-shifted reefs via the support of positive or destabilising feedback loops (Nyström et al. 2012). Many coral reef systems appear currently locked in degraded states, for instance dominated by macroalgae. To break this locked state and push the system towards coral dominance, some negative feedback loops need to be interrupted and positive loops need to be engaged (Mumby and Steneck 2008). Herbivores can assist this feedback shift—our findings and recent findings from a large-scale study (Steneck et al. 2018) suggest that herbivores have a potential to weaken the effect of macroalgae on coral recruitment. High levels of herbivory also tend to push algal communities towards those dominated by calcareous forms (Littler and Littler 1984; Belliveau and Paul 2002), adding to habitats favouring coral reinforcing feedbacks, underlined by the positive effect of CCA detected in our study. A recent review by Ceccarelli et al. (2018) highlights the potential for physical removal of macroalgae to benefit coral, yet its effectiveness over large spatial and temporal scales will depend on whether the underlying drivers (e.g. eutrophication, overfishing of herbivores, ocean warming) that keep reefs locked in negative or reinforcing feedback loops favouring macroalgal dominance (Johns et al. 2018) are addressed (Norström et al. 2016). Our findings also highlight the importance of complex granitic reefs for juvenile corals and that these habitats are potential coral refugia in Seychelles. Maintaining low levels of local stressors on complex granitic reefs may therefore be important for recovery.

Climate change and coral bleaching are reshaping coral reefs to a yet unknown extent. The 2016 bleaching event decimated the juvenile coral community of the inner Seychelles, and concomitant obstacles such as macroalgal expansion have limited the ability for recovery on some reefs. As macroalgae interact with other reef characteristics such as structural complexity, herbivore biomass, and reef type, it becomes apparent that this obstacle has a very nuanced nature and addressing it will not be a straightforward process. If coral reef degradation progresses and the carbonate matrices break down, sand and rubble patches will expand, presenting another obstacle for coral recruitment. Should the more steadfast nature of granitic reefs prove suitable refugia to future corals, a greater understanding of the mechanisms that underlie resilience on these reefs and their potential to re-seed nearby carbonate reefs is required.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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Red and green loops help uncover missing feedbacks in a coral reef social–ecological system

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Abstract

1. Social–ecological systems (SES) exhibit complex cause-and-effect relationships. Capturing, interpreting, and responding to signals that indicate changes in eco-systems is key for sustainable management in SES. Breaks in this signal–response chain, when feedbacks are missing, will allow change to continue until a point when abrupt ecological surprises may occur.
2. In these situations, societies and local ecosystems can often become uncoupled. In this paper, we demonstrate how the red loop–green loop (RL–GL) concept can be used to uncover missing feedbacks and to better understand past social–ecological dynamics. Reinstating these feedbacks in order to recouple the SES may ultimately create more sustainable systems on local scales.
3. The RL–GL concept can uncover missing feedbacks through the characterization of SES dynamics along a spectrum of human resource dependence. Drawing on diverse qualitative and quantitative data sources, we classify SES dynamics throughout the history of Jamaican coral reefs along the RL–GL spectrum. We uncover missing feedbacks in red-loop and red-trap scenarios from around the year 600 until now. The Jamaican coral reef SES dynamics have moved between all four dynamic states described in the RL–GL concept: green loop, green trap, red loop and red trap.
4. We then propose mechanisms to guide the current unsustainable red traps back to more sustainable green loops, involving mechanisms of seafood trade and ecological monitoring. By gradually moving away from seafood exports, Jamaica may be able to return to green-loop dynamics between the local society and their locally sourced seafood. We discuss the potential benefits and drawbacks of this proposed intervention and give indications of why an export ban may insure against future missing feedbacks and could prolong the sustainability of the Jamaican coral reef ecosystem.
5. Our approach demonstrates how the RL–GL approach can uncover missing feedbacks in a coral reef SES, a way the concept has not been used before.

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We advocate for how the RL–GL concept in a feedback setting can be used to synthesize various types of data and to gain an understanding of past, present and future sustainability that can be applied in diverse social–ecological settings.

KEYWORDS

coral reef management, historical, interventions, Jamaica, leverage points, mixed methods, regime shift, sustainability

1 | INTRODUCTION

Increased globalization has been one of the underlying factors driving observed increases in human development (e.g. Human Development Index; Cumming & von Cramon-Taubadel, 2018; United Nations Development Program, 2018). However, the increased connectivity of economies, ecosystems and human societies on a global level has been argued to be detrimental to the sustainability of local social–ecological systems (SES) when feedback relationships that indicate overharvesting of natural resources or environmental impacts are weakened or lost (Berkes, 2007; Levin, 1999; Nyström et al., 2019). This weakening—or decoupling—can emerge as the geographical distance between the location of consumption and production increases (Anderson, 2010; Clapp, 2014; Nyström et al., 2019). Overfishing of local fish stocks, for example, can be masked by importing fish caught elsewhere, leaving consumers relatively unaffected and unaware of ongoing changes in the ecosystem (Crona et al., 2016). For instance, the United Kingdom (UK) increased their imports of Atlantic cod from Iceland and the Faeroe Islands between the late 1980s and 1990s (Crona et al., 2016). Because cod was available in UK markets from multiple competing sources, the prices did not represent the decreasing cod stocks in local UK waters. This masked the mechanism for UK consumers to keep track of the increasing cod rarity and hence did not cause consumers to match their consumption patterns to the state of local ecosystem degradation. Such mechanisms are often referred to as ‘feedback mechanisms’ because they have the potential to feed information about the state of a system back to society.

Capturing, interpreting and responding to signals that indicate changes in ecosystems are key facets of sustainable management in SES. If feedbacks are ignored or masked (e.g. by trade), change is allowed to pass unnoticed until a point when an abrupt ecological surprise (i.e. regime shift) may occur. Once manifested, the new ecological state can be difficult, very costly and potentially even impossible to reverse (Nyström et al., 2012). Pathways toward improved local sustainability have to feature managing feedbacks that underpin social–ecological trajectories.

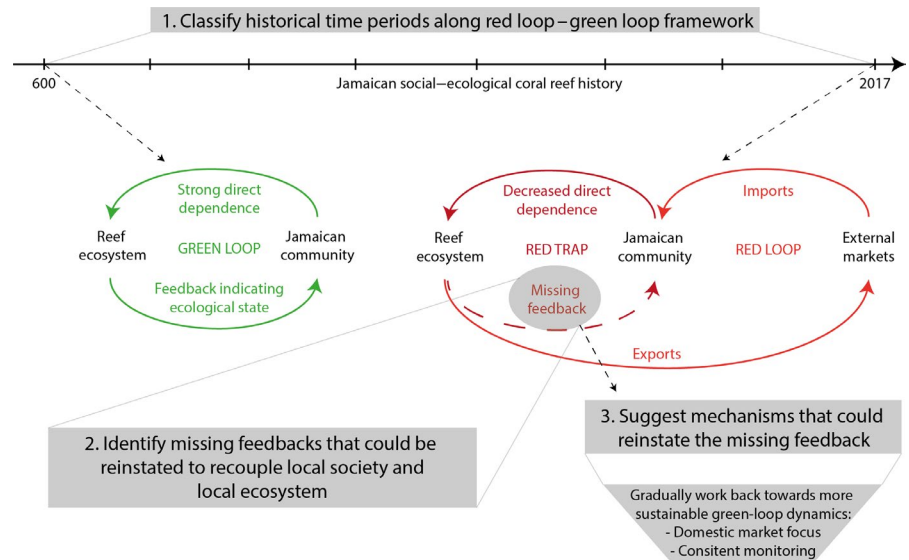
Here, we demonstrate how the RL–GL concept highlights missing feedbacks and how it can be used to synthesize various types of data and to understand past, present and future sustainability in diverse

social–ecological settings. Our study is the first that is integrating these two approaches to unpack social–ecological dynamics for improved sustainability of SES.

1.1 | Reinstating missing feedbacks to recouple social–ecological systems

When feedbacks are masked, they are referred to as ‘missing feedbacks’ (Barnett & Anderies, 2014; Crona et al., 2016). In the context of social–ecological dynamics, this often means that the social system gets decoupled from the local ecosystem (Hoole & Berkes, 2010), which opens unsustainable pathways that the SES may follow (Crona et al., 2016). To avoid this from happening it is critical to reinstate missing feedbacks and recouple the SES by ‘closing the loop’ between humans and ecosystems (Patterson & Coelho, 2008). A global example of this recoupling feedback approach is the current climate change discussion. Carbon taxes or carbon credits are meant to act as a ‘global’ feedback to recouple anthropogenic changes to the atmospheric system back to society (Van der Ploeg, 2014). Cod prices in the UK provide a local example; the missing feedbacks mentioned above could be reinstated by strengthening information flow from fishers to consumers or by directly increasing overfishing awareness in citizens and political actors through publicity (Crona et al., 2016). Another example of reinstating feedbacks comes from the Etosha National park in Namibia (Hoole & Berkes, 2010). Decoupling was connected to the loss of Herero knowledge of the park, which led to failing wildlife conservation initiatives and exacerbated poverty levels in local Herero communities. Reinstating this missing feedback, through management collaboration between the park and Herero communities, as well as Herero inclusion in park management and as employees was used to reinstate feedbacks, ultimately improving the outcomes for the Herero and conservation management. Addressing missing feedbacks can have a transformational impact on the SES but it requires very detailed knowledge of the SES dynamics to uncover where feedbacks are missing (Crona et al., 2016; Meyfroidt & Lambin, 2009; Patterson & Coelho, 2008). Individual case studies are extremely variant in their display of feedback dynamics and detecting missing feedbacks will vary from case to case.

FIGURE 1 Summary schematic of our approach to (1) using red-loop green-loop classification of historical time periods to (2) uncovering missing feedbacks for which we suggest (3) mechanisms to reinstate the feedbacks and recouple the coral reef social–ecological system



1.2 | Using the ‘red loop–green loop’ model to identify missing feedbacks

We argue that a framing is required which assists with feedback classification and can identify missing feedback scenarios. The ‘red loop–green loop’ (RL–GL) concept (Cumming et al., 2014) provides this framing for two differing forms of ecosystem dependence and sustainable resource use.

The RL–GL concept proposes that human resource dependence on a national scale tends to follow one of two fundamentally different trajectories that are reinforced by weak ties with local ecosystems and strong ties with distal systems (red loop), or strong ties with local ecosystems and weak ties with distal systems (green loop; Cumming & von Cramon-Taubadel, 2018). In both red- and green-loop countries, the entire economy or certain economic sectors can evolve into trap situations that can severely threaten the long-term sustainability of the current trajectory (Cumming et al., 2014). Green traps can occur as the human population in a green-loop economy grows without adequate food production from the local ecosystem, leading to a spiral of increased overharvesting and environmental degradation (Steneck, 2009). To avoid this green-trap situation, societies can divert their dependence towards external ecosystem services, for instance by means of food import, which would lead towards red-loop dynamics. In a red-loop trajectory, the economy’s ecological impact reaches to distal ecosystems as well as the local system. For instance, reforestation in parts of Vietnam between 1987 and 2006 was achieved at the expense of forest displacement from other parts of the country as well as partly illegal imports from deforestation in neighbouring countries such as Cambodia and Laos (Meyfroidt & Lambin, 2009). The example illustrates a red-trap situation where supply and consumption are maintained without recognition of the ecological degradation entails in other local ecosystems due to missing feedbacks.

In summary, as sectors in the economy relying on local ecosystems for resources approach a red trap and the economy as a whole increases its dependence on distal systems, the likelihood of missing

feedbacks between the country’s society and local ecosystems increases. Therefore, societal and ecological dimensions of the SES run the risk of decoupling and a recoupling of the SES becomes more necessary for local system sustainability.

We argue that once the missing feedbacks have been identified, interventions to reinstate them could recouple local SES and move economic sectors out of red- or green-trap trajectories. Applying the RL–GL concept to historical SES data can facilitate an understanding of how feedback dynamics have changed through time (Cumming et al., 2014; Hamann, Biggs, & Reyers, 2015) and what trajectory an economic sector is currently following (Cumming & von Cramon-Taubadel, 2018). This can highlight points where the SES decoupled and thus identify opportunities to recouple the SES and avoid trap scenarios.

In this study, we apply the RL–GL framework to understand and classify the SES dynamics in the context of Jamaican coral reefs (Figure 1), using mixed historical data dating back to roughly the year 600. With this historical understanding, we focus on uncovering missing feedbacks between the Jamaican people and their coral reef system. Lastly, we propose mechanisms that could move the current Jamaican coral reef SES out of recently assumed red-trap dynamics.

2 | JAMAICAN CORAL REEF SES DYNAMICS THROUGH TIME

We identified and categorized social–ecological trajectories and feedbacks of Jamaican coral reefs across eight time periods (Table 1), from around 600 to the present. For the first six time periods (Ostionan, Meilican, Spanish occupation, British colonization, Post-emancipation and World Wars I & II), the available data are mostly qualitative. Hardt (2009) and Hicks, Crowder, Graham, Kittinger, and Cornu (2016) conclusively reconstructed the social–ecological dynamics for these time periods and we use them as our primary reference to infer about the nature (red or green loop) of those dynamics.

Time period	Data type	References
Ostionan (600–900) Meilican (900–1500)	Qualitative: Kitchen midden analyses	Hardt (2009) and Hicks et al. (2016)
Spanish occupation (1509–1655) British colonization (1656–1834) Post-emancipation (1834–1900) World Wars I & II (1901–1945)	Qualitative: Sailors' logbooks & historical descriptions by naturalists, historians & fisheries scientists	Beckwith (1929), Hardt (2009), Hicks et al. (2016), Munro et al. (1971) and Thompson (1945)
Post-war (1946–1985) Shifted reefs (1985–2017)	Quantitative: Fisheries, demographic, economic and ecological data	Clayton (2001), FAOSTAT (2019), Hardt (2009), Hicks et al. (2016), Hughes (1994), Lingard et al. (2012), Oswald (1963), United Nations Development Program (2018) and World Bank (2019)

TABLE 1 Historical data types and sources per time period of Jamaican history

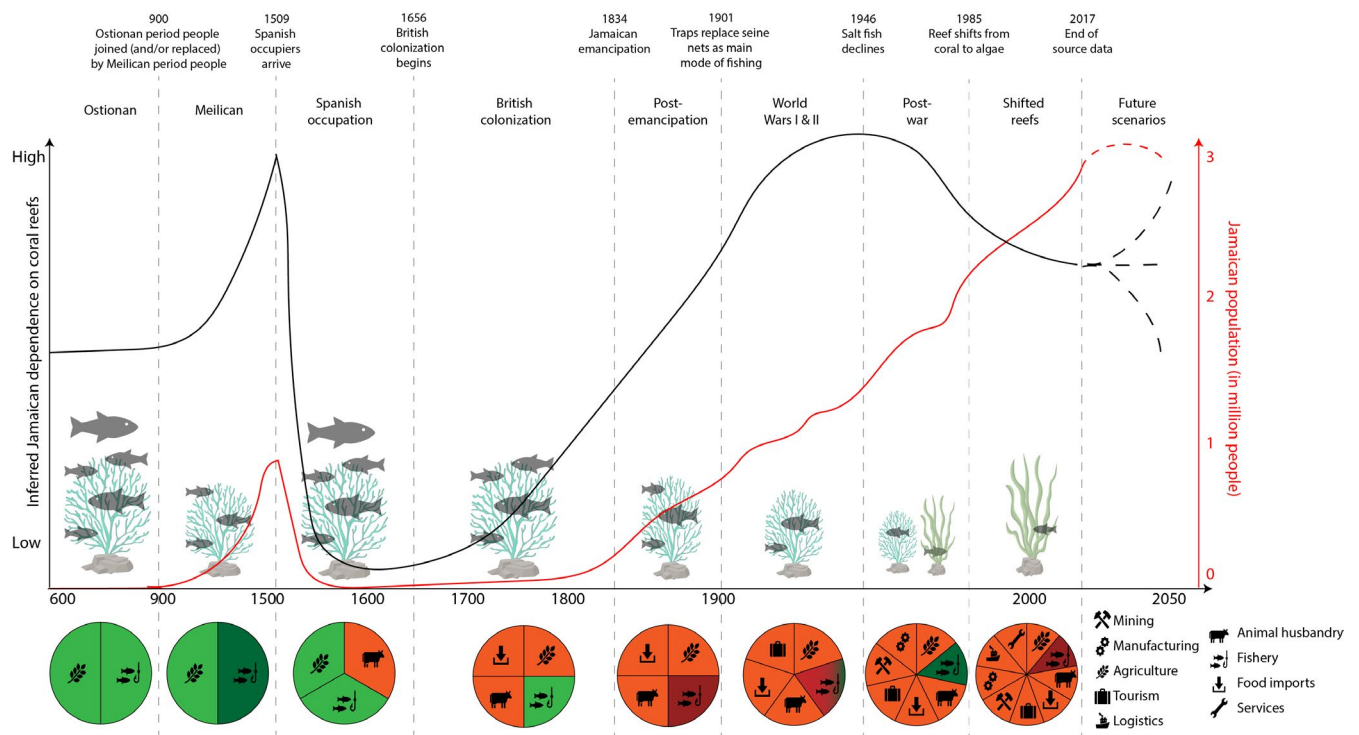


FIGURE 2 Jamaica's inferred dependence on coral reefs from low to high (black line) and human population (red line) through time. Time up to future scenarios is split into eight separate time periods and for each we determined ecological reef regime state of the reef (fish & coral/algae symbols) as well as major economic state of Jamaica (pie graphs). Colour of the pie graph segments indicates Jamaica's economic state along the RL–GL spectrum: green loop (light green), green trap (dark green), red loop (light red), red trap (dark red); population based on Hardt (2009; up to 1950) & United Nations, DESA, Population Division, World Population Prospects 2019, <http://population.un.org/wpp/> (from 1950)

Most quantitative data became available from 1950 and we use them to infer about social–ecological dynamics in the last two time periods (Post-war and Shifted reefs; Clayton, 2001; FAOSTAT, 2019; Hardt, 2009; Hicks et al., 2016; Hughes, 1994; Lingard et al., 2012; Oswald, 1963).

To illustrate social–ecological dynamics between the Jamaican society and their coral reefs over eight time periods, we used a mixed quantitative and qualitative approach. For each time period, we inferred Jamaican social–ecological dynamics from indicators of social change, changes in human population size, economic

diversification, as well as ecological change (Figure 2). We then focused on the social–ecological dynamics around local Jamaican coral reefs, viewed them as an individual economic sector, as well as through an RL–GL lens for each of the time periods and suggest mechanisms to approach green-loop dynamics in future scenarios (Figure 3).

2.1 | Ostionan period (600s–900s): Green-loop dynamics

From roughly the 600s–900s, Jamaica was inhabited by Ostionan period people and dependence on coral reefs was largely based on fishing (Figure 2). This resource extraction increased with a growing



FIGURE 3 Schematic showing social–ecological dynamics focussed on the dependence of the Jamaican community on their coral reefs and categorization of these dynamics along the spectrum of the RL–GL model leading to a concept of future dynamics where we suggest a conceptual system with mechanisms to reinstate the missing feedbacks and to recouple the social–ecological system

human population with no indication of trade or other connections to other systems (Hardt, 2009), as well as a relatively small population size, leading to the classification of this period as a green-loop state (Figure 3).

2.2 | Meilican period (900s–1500s): Green-trap dynamics

During the Meilican period, the human population on Jamaica grew rapidly and by 1500 had reached ~1 million people (Hardt, 2009; Hicks et al., 2016; Figure 2). Decreasing reef fish catch sizes indicate that the reef ecosystem was overexploited under the pressure of the growing human population and there is no evidence of trade prior to the first European contact that could have reduced pressure on the coral reef ecosystem (Hardt, 2009). Based on gradually decreasing fish sizes in kitchen middens suggesting a ‘fishing down the food web’ situation (Pauly & Palomares, 2005), we concluded that the SES between the Jamaican people and the reef ecosystem during the Meilican period was characterized by green-trap dynamics (Figure 3).

2.3 | Spanish occupation period (1509–1655): Green-loop dynamics

With the Spanish occupation in 1509 the Jamaican population declined significantly due to the introduction of new diseases and harsh treatment of the local population (Hicks et al., 2016). By the mid-1510s, the population had been reduced by over 99% from the Meilican period, to approximately 5,000 people, which lessened pressure on the reef ecosystem (Hardt, 2009; Figure 2). Pressure was further reduced via an alternate source of protein by the introduction of pigs and cattle from Spain (characteristic of a red-loop dynamic), resulting in a temporary recovery of reefs (Hardt, 2009). Due to these two pressure reduction factors and minimal dependence on coral reef resources, the local SES returned to a green loop during Spanish occupation (Figure 3).

2.4 | British colonization period (1656–1834): Green-loop dynamics

With the colonization by the British in 1656, Jamaica was being developed into a hub for international trade. Sugar, coffee and bananas were increasingly used as trade commodities for salt fish from the UK, USA and Canada (red-loop dynamic; Figure 2). As a result of this resource diversification, reefs were further relieved from fishing pressure (Hardt, 2009; Hicks et al., 2016). The human population of Jamaica started to grow rapidly with the increase in slavery (>300,000 slaves by 1810) as the colonizers expanded their plantations (Hicks et al., 2016). Again, the reef system began to show signs of overexploitation around 1800 as reef fish were increasingly used as food for the plantation owners (Hardt, 2009). During British colonization, the Jamaican community gradually came to re-ignite their

dependence on the reef system after barely depending on it during Spanish occupation. Although reef dependence was largely based on subsistence fishing, fishing regulations (e.g. minimum mesh size for fishing nets) put in place by the colonizers suggest that there was an awareness of changes occurring in the local SES and a feedback between society and the reef ecosystem existed (Hardt, 2009). While the larger part of the Jamaican economy was involved in global trade and hence red-loop dynamics (Figure 2), the coral reef SES dynamics remained localized and in a green loop (Figure 3).

2.5 | Post-emancipation period (1834–1900): Red-trap dynamics

With emancipation in 1834, Jamaica's human population surged towards Meilican levels (~1 million by 1900) and reef dependence shifted from feeding the local population to using reef fish as a trading commodity for salt fish (Figure 2), which the Jamaican community had become used to during times of slavery (Hicks et al., 2016). The salt fish dependence was so strong that by the 1830s, local reef resources (including fish and coral) were traded to be able to import salt fish from the USA, Canada and the UK (Hardt, 2009). This indirect dependence on local reefs for trade masked the feedback within the SES and began to decouple the reef environment from the local society, likely for the first time in Jamaican history. The increased fishing of reef fish for trade with salt fish producing countries, shifted the coral reef SES dynamics from green loop to red trap (Figure 3).

2.6 | World Wars I & II period (1901–1945): From red- to green-trap dynamics

With the advent of tourism and urbanization in the 1900s, red-trap dynamics were further reinforced (Beckwith, 1929; Hicks et al., 2016; Thompson, 1945; Figure 2). Accelerated population growth in the early 1900s led Jamaicans to depend on reef resources for both subsistence and trade (Hardt, 2009). Technological development of fishing gear, especially the adoption of wire mesh fish traps in the 1910s (Munro, Reeson, & Gaut, 1971), caused a shift in dominant fishing mode from seine nets to traps (a technique with even heavier impact on purely reef-dwelling fish) and spiralled further reef degradation (Hicks et al., 2016).

With the onset of World War II, trade suffered a dramatic decline and the Jamaican population had to increasingly rely on local reef fish for food instead of imported salt fish. Green-loop dynamics were forced to be resumed between Jamaican society and reef ecosystem and the SES began to recouple. In 1945, Jamaica's dependence on local fish stocks peaked (Hardt, 2009) and overfishing of near-shore fish stocks was officially recognized for the first time by government fisheries scientist E. Thompson (1945). Due to a rapidly growing population (~1.3 million in 1945), limited economic diversification and Jamaican reef dependence rising as a result, the human

population quickly outgrew the provisioning capacities of the reef ecosystem (Hardt, 2009). We argue that the SES could not sustain this quick fall-back on the reef ecosystem for resources during WWII and the resumed green-loop dynamics quickly manifested as green-trap dynamics (Figure 3).

2.7 | Post-war period (1946–1985): Green-trap dynamics

As Jamaica's dependence on local reefs for food peaked, the government established the Fisheries Division and developed an off-shore fishery (Oswald, 1963) to be able to keep up with the increasing demand for seafood (Figure 2). Thompson's suggestions to subsidize job transitions for fishers into other jobs were ignored, and the expansion of the reef fishery was instead heavily subsidized in the 1970s and 1980s (Hardt, 2009), which reinforced the green-trap dynamics. In parallel, increasing urbanization, tourism and industrialization (e.g. development of large-scale bauxite mining) were causing reef degradation through pollution of near-shore waters (Hardt, 2009; Hicks et al., 2016). During the 1980s, Jamaica also reported the highest regional deforestation rates, leading to a substantial loss of mangroves (Agard et al., 2007). In 1983–1984, reefs suffered surges of hurricane damage and a sea urchin disease, which in combination with overfishing led to an ecological regime shift where coral reefs became rapidly overgrown by algae (Hughes, 1994). This regime shift and the noticeable catch reductions of reef-dwelling and reef-associated fish species due to overfishing (Figure S1) caused a further spatial expansion of Jamaica's fisheries so that the most productive fisheries were now in far off-shore environments (Lingard et al., 2012; Oswald, 1963). The combined effects of reduced catches from reef fisheries and resulting further fisheries off-shore expansion, as well as the coral reef regime shift, led Jamaican social–ecological reef dynamics to spiral into a green trap (Figure 3). By the late 1980s, Jamaica's economy had diversified and moved into globally connected red-loop dynamics (e.g. revamping salt fish trade), which in part compensated for the heavily degraded reef ecosystem (Figure 2).

2.8 | Shifted reefs period (1985–2017): Red-trap dynamics

Following the ecological regime shift, the reef system was severely degraded and the dependence of Jamaicans on the reefs was decreasing. The percentage of employed fishers in the rising Jamaican population declined (FAOSTAT, 2019) and workers in non-ecosystem service sectors increased (Clayton, 2001; Figure 2). Jamaica's fisheries catches were largely made up of subsistence catches, but a part was, once again, used for exports (Figure S1; FAOSTAT, 2019; Lingard et al., 2012). Resuming the resource extraction from the exhausted reef ecosystem for trade, again led to the missing feedback and repeated the decoupling of

the SES we described for the post-emancipation period and dynamics of a red trap (Figure 3).

2.9 | Jamaica's recent red-loop economy supporting a red-trap coral reef SES

Although the Jamaican coral reef SES was kept in a red-trap situation between 1990 and 2017, the country increased its Human Development Index (HDI) from 0.638 to 0.732 (14.8% increase; United Nations Development Program, 2018). Generally, red-loop and green-loop countries appear to separate along a gradient of the HDI, where HDI class 1 countries assume red loops and HDI class 4 countries assume green loops, while HDI class 2 and HDI class 3 countries are more difficult to classify and show characteristics of both loops (Cumming & von Cramon-Taubadel, 2018). Economic diversification allowed Jamaica with its ~2.9 million population (Figure 2), to be placed in a HDI class 1 in 2017 (United Nations Development Program, 2018), at the median of red-loop countries (HDI of ~0.7; Cumming & von Cramon-Taubadel, 2018). The economic stability gained from diversification has allowed some other nations to improve local ecosystem sustainability (Hansen et al., 2018; Martens & Raza, 2010). A diversified economy is a relatively recent development for Jamaica that had not yet developed when the local SES attempted to move away from red-trap dynamics (i.e. during the World Wars I & II period, Figure 3). A diverse, largely red-loop economy that can lessen the requirements placed on the local coral reef SES could be of great assistance in intervening with current local reef SES red-trap dynamics, provided that the correct guidance is applied to proposed interventions. We propose a set of mechanisms for current Jamaican red-trap dynamics that are meant to reinstate a feedback between society and reef ecosystem to recouple both.

3 | REINSTATING MISSING FEEDBACKS IN A LOCAL RED-TRAP SYSTEM

Based on the historical assessment of Jamaican SES dynamics, we discuss possible interventions that may lead to a recoupled Jamaican local reef SES. Highlighting missing feedbacks can help steer a system out of red-trap dynamics (Figure 3). Importantly, we propose a set of mechanisms that are supposed to tackle the systemic design of the Jamaican coral reef SES rather than only few systemic parameters. This prioritization of interventions is highlighted by the 'Leverage Points' perspective (Abson et al., 2017; Fischer & Riechers, 2019; Meadows, 1999) and guided our proposed intervention. The leverage points perspective argues for prioritization of interventions that have large transformational potential (deep leverage) over those that are usually used but have little to no impact (shallow leverage; Abson et al., 2017). These deep leverage points are difficult to implement because they often prioritize tackling system design and intent (deep leverage)

over system parameters (shallow leverage), which is why they are under-used and under-researched (Fischer & Riechers, 2019). Their transformational potential applies well to our case study and hence guides the interventions we are proposing to implement here.

3.1 | Pursuing a green-loop coral reef social-ecological system design through seafood export bans

With an annual per capita fish consumption of 25.8 kg (2017), Jamaica ranks amongst the highest seafood consuming countries in the Americas. Yet, 79% of Jamaica's supply of all fishery products consumed domestically in 2017 stemmed from imports (FAOSTAT, 2019). Our historical analysis of Jamaica shows that seafood exports were a main driver in decoupling the feedback within the coral reef SES, especially in the post-emancipation period, World Wars I & II period and the shifted reef period (Figure 3).

We propose an intervention strategy following a deep leverage point in the system's design (Abson et al., 2017). The local coral reef SES could be gradually designed towards green-loop dynamics in which locally sourced reef produce are rerouted from exports to domestic markets. In envisaging the local reef SES, local seafood catches from the near-shore and off-shore environment would not serve as exports and only be used for domestic markets, including consumption (e.g. by locals) and sales (e.g. to tourists). A system averse to exports of locally sourced seafood would reinstate a direct feedback between the Jamaican society and the local reef ecosystem. However, for this reinstated feedback to be sustainable, and avoid a green-trap scenario, careful monitoring and management of the resource will be necessary. This could lead to the desired recoupling of the Jamaican coral reef SES and enable movement towards locally connected green-loop dynamics within an otherwise globally connected red-loop system.

A coral reef SES in which seafood is locally sourced and used, would, according to RL-GL thinking, be more sustainable than the current red-trap situation (Cumming et al., 2014). For this reinstated feedback to have the desired effect, it is crucial that the information on the ecosystem's state that is fed back to the Jamaican society is reacted on appropriately. This means that the feedback is not ignored, as was the case in 1945 when the suggestions and warnings by fisheries scientist Thompson were ignored by the Jamaican government (Hardt, 2009). Existing feedbacks that are ignored can also have destructive effects on the ecosystem (Degnbol & McCay, 2007), although, our historical analysis of the Jamaica case indicates that missing feedbacks were more frequently occurring in the coral reef SES than ignored ones.

3.2 | Strengthening green loops in other regions

Examples of mechanisms that can assist the transition from red-trap to green-loop dynamics exist in the literature. As in the cod example

above, one mechanism to reinstate the missing feedbacks could be in strengthening information flow from fishers to consumers (Crona et al., 2016). Eco-labels could provide this transparency to consumers; specifically, labels with a 'locally grown' claim have been suggested to be more highly valued by consumers in the United States (Giovannucci, Barham, & Pirog, 2010; Loureiro & Hine, 2002; Onozaka & McFadden, 2011). A 'locally sourced' eco-label could lend itself to reinstate sustainable stewardship of local reef produce. Besides such labelling schemes, education and public campaigns are central instruments for consumers to make informed decisions that can help reinstate feedbacks (Crona et al., 2016). Moreover, traceability is a key mechanism in this context to ensure supply chains are devoid of unacceptable behaviour, ranging from illegal sourcing and forced labour to poor sanitation and mislabelling (Nyström et al., 2019).

Addressing unsustainable trajectories from deep within a SES is complex and sometimes difficult to monitor through time. For example, it has been suggested that many South-East Asian economies (van Mulekom et al., 2006) could alleviate malnutrition and poverty by redirecting the considerable resources gained through fishing away from exports and towards domestic use, particularly given the rich micronutrient yields in these catches (Hicks et al., 2019). For a region as large as South-East Asia, it is difficult to understand whether these suggestions have led to improvement, largely because the documentation is very inconsistent (Béné et al., 2016). However, shifts towards fishing for domestic markets have been noted in the province of Phang-nga, Thailand (Jones, Gray, & Umponstira, 2010) and the Philippines (Fabinyi, 2016). Some South-East Asian countries might not be as economically well-placed to manifest a green-loop dynamic for their local reef ecosystems, since the marine seafood sector creates a large percentage of national revenue. For instance, Indonesia appears to favour an increase in marine seafood exports, believing that further development of marine resource exports (4.2 billion USD; FAOSTAT, 2018) is vital for bringing Indonesia out of its recent economic crisis (Rizal, Herawati, Zidni, Apriliani, & Ismail, 2018).

A recent study from Seychelles demonstrated substantial catch declines in prized red snapper species, locally called 'bourzwa' (Robinson et al., 2020), with exports leading to price increases to the point where the fish became unaffordable to locals. In attempts to protect livelihoods, lower the prices and achieve recovery of the species' stocks, export bans from 2020 have been proposed for bourzwa (Robinson & Graham, 2020). Similar price dynamics might be driving the Jamaican affinity for imported fish consumption in our case study. Export bans could lead to price reduction in local reef fish, make it more affordable for locals and hence increase their consumption. In the optimal case, this could gradually increase local seafood sustainability, as well as increase the perceived value of the local reef ecosystem and an increased sense of stewardship (Chapin et al., 2010) to gradually close the feedback loop.

The success of an export ban, however, depends on the availability of data to fully understand SES dynamics. In the Seychelles example, Robinson et al. (2020) use detailed fisheries data to show that local markets were already buying four times as much bourzwa as is exported and elude to the limited likelihood that export bans may

have on reducing bourzwa prices, and that other local fisheries management efforts will be key to sustainability (Robinson et al., 2020). Comparative data in Jamaica are very limited, with the most recent (2002) specific seafood export information noting lobster, conch and 'some fish' (FAOSTAT, 2019). An export ban, if implemented, should be preceded and accompanied by detailed monitoring of fisheries data to uncover if similar dynamics to Seychelles could be at play in Jamaica. Similarly, an example from Palau, where the government banned 80% of fishing from foreign vessels in their off-shore waters caused effort to transition to near-shore waters, increasing the pressure on reef fish species (Dacks, Lewis, James, Marino, & Oleson, 2020).

The above examples demonstrate the possible effectiveness of an export ban for recoupling feedbacks within an SES. Yet, these case studies also emphasize the importance of having detailed data to understand past, current and future SES dynamics. In the following section, we propose where further data could enhance the establishment of a green-loop coral reef SES.

3.3 | Monitoring required for the green loop

Based on our historical analysis of SES dynamics, we argue that the diverse red-loop economy of Jamaica is at a point where the small export revenue derived from the local reef fishery (12.9 million USD) could be rerouted to domestic markets to increase local coral reef SES sustainability (FAOSTAT, 2019). In our historical analysis, when Jamaica was forced to resume green-loop dynamics for the local reef SES during WWII, the economy had only five main sectors whereas today it has nine (World Bank, 2019). Jamaica acts as a conceptual example in which we demonstrate how a diverse economy could help leverage a green-loop pathway for its local ecosystem dependence.

For a green loop through export bans to work, a thorough, species-specific comparison of seafood imports and exports needs to be established to be able to gauge the full benefit of an export ban (Robinson & Graham, 2020). In addition, the local and international demand for species-specific seafood needs to be thoroughly understood so that the government can anticipate potential knock-on effects (Dacks et al., 2020).

Consistent ecological monitoring of the Jamaican reef system has usually been scarce, as we have seen through our historical analysis. The peak of ecological monitoring was likely during the benthic regime shift and even recently, consistent government-led ecological monitoring of the reefs has been spatially and temporally fragmented (Creary, Smith, & Green, 2012; Lapointe, Thacker, Hanson, & Getten, 2011). Consistent monitoring should provide concurrent ecological awareness that would enable more reactive management to ecological change in the future.

The interventions we suggest above were formulated by searching for points in the system's design that we could leverage to prolong its sustainability. We decided to pursue the design of a green loop coral reef SES and we highlight the benefits and drawbacks for this pathway, but our suggestions are not exhaustive. For instance, within the leverage points framework, there are more pathways

which could lead to different interventions (e.g. pursuing the alteration of the system's intent through alternative governance) which future studies could explore.

4 | CONCLUSION

Within sustainability research there are different concepts to disentangle social-ecological dynamics. We demonstrate the value of examining complex dynamics through a conceptual lens by using Jamaica's complex coral reef SES dynamics as a case study. We identified a decoupling in the SES using the feedbacks concept—the feedbacks from coral reefs to Jamaican society had become masked. The resulting missing feedbacks were uncovered with the RL-GL concept. Throughout Jamaica's social-ecological history, the SES dynamics between people and the coral reef ecosystem have moved between all four dynamic states described in the RL-GL concept: green loop, green trap, red loop and red trap.

Jamaica's society has experienced the effects of a degrading near-shore system in the past, at the very least in the form of changes in the types of seafood available for consumption. In its current form, the Jamaican economy has effectively diluted any severe repercussions through a rapidly diversifying economy. Historically, when rapidly growing human populations led to the near-shore system being heavily exploited, or when the dependence on other fisheries products were interrupted, Jamaica had relatively productive reef systems to fall back on. Whether this can be done again in the future will depend on the intent of the SES and whether feedback mechanisms are in place to signal ecological condition.

We propose mechanisms that could guide transitions away from the red trap that the SES dynamics have currently settled on. We highlight examples of countries that have used a specific intervention in order to move from an unsustainable local red-trap situation to more sustainable green-loop dynamics. We suggest that a successful transition into green-loop dynamics will strongly depend on data availability and continued monitoring of the SES. Future studies should seek to draw on different and multi-disciplinary perspectives to explore this and other interventions and test their feasibility with empirical data.

We arrived at our conclusion through using a conceptual lens that highlights the feedbacks within RL-GL concept and applying it to Jamaica's rich social-ecological coral reef history to reveal potential future pathways. These pathways need to be carefully re-considered under the light of a range of proficiencies, including political, economic and social expertise, before they can be successfully implemented. We want to highlight the practicality of how we applied the RL-GL concept to uncover missing feedbacks within complex social-ecological dynamics and encourage future studies to apply it to other systems to further advance sustainability research.

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CONFLICT OF INTERESTS

On behalf of all authors, the corresponding author states that there is no conflict of interest.

AUTHORS' CONTRIBUTIONS

All authors conceived core ideas and contributed critically to the design of the study; J.-C.D. acquired and analysed the data; all authors interpreted the results. J.-C.D. wrote the first draft of the manuscript, and all authors contributed critically to subsequent drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data used in this paper have already been published or archived elsewhere (see Table 1).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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