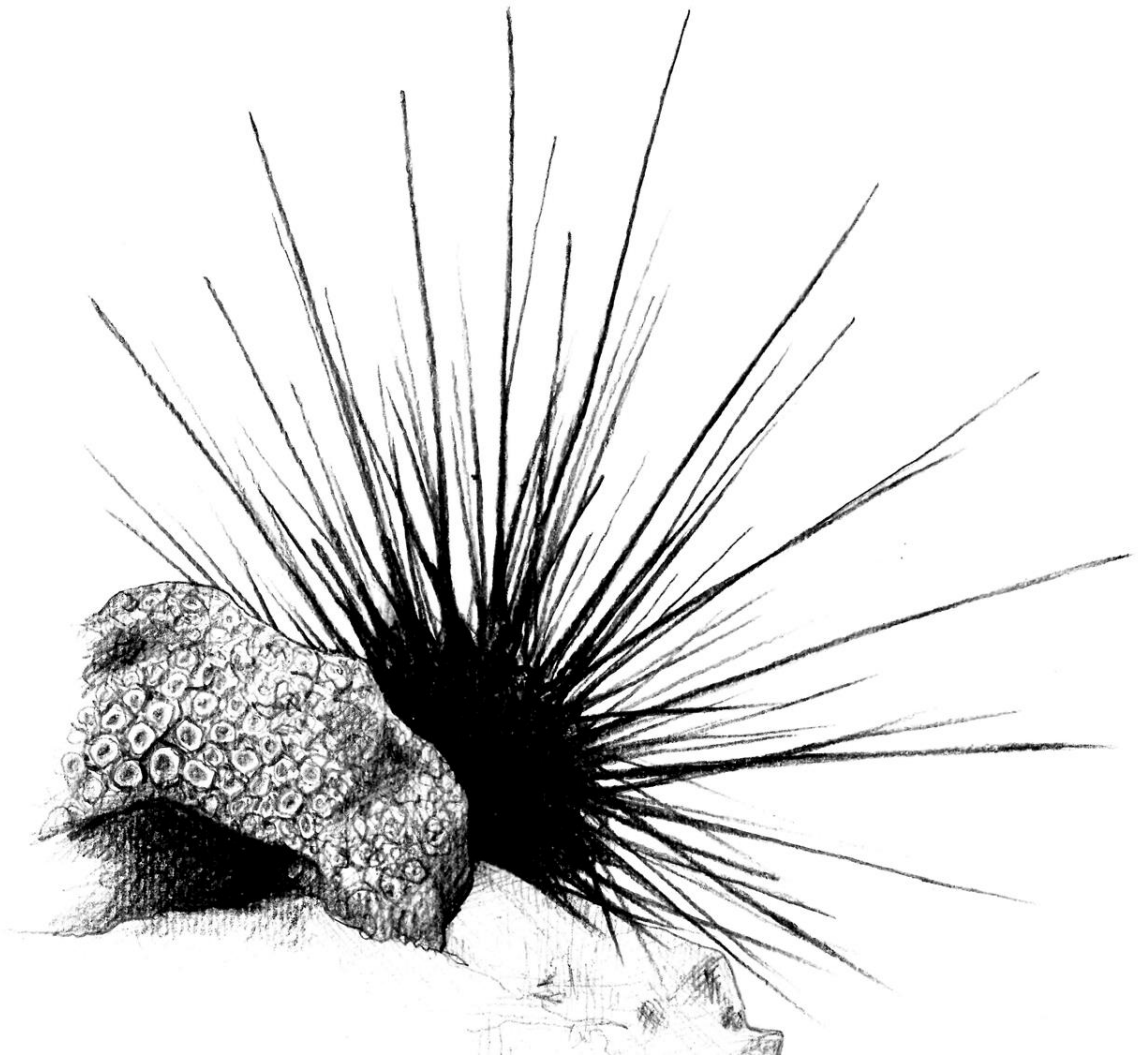


**Restoration of the long-spined sea
urchin, *Diadema antillarum*, to
Caribbean coral reefs**



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Thesis abstract

Coral reefs are among the most valuable and threatened ecosystems on Earth. Lower species diversity, and subsequently reduced resilience, make Caribbean reefs especially vulnerable to anthropogenic stressors. Overfishing and disease have reduced Caribbean herbivore abundances and their associated compensatory dynamics, leading to a 53% decrease in scleractinian coral cover since the 1970s. The long-spined sea urchin, *Diadema antillarum*, is an important Caribbean herbivore, and its functional extinction in the early 1980s, coupled with a subsequent lack of recovery, makes its restoration a conservation priority. A combination of *in situ* ecological surveys and environmental manipulations are coupled with *ex situ* experimental studies to aid *D. antillarum* restoration efforts. The thesis begins by assessing the relative impacts of fish and urchin grazing on the structure and diversity of reef communities and concludes that, whilst reestablishment of *D. antillarum* ecosystem functions may not represent a long-term conservation solution, it will provide short-term resilience benefits. A lab-based investigation then indicates that *D. antillarum* will be, at least partially, resistant to predicted future sea surface temperature increases, and observed negative fitness consequences may be mitigated by artificial structures; population restoration is therefore worthwhile in the context of climate change. Exploration of an isolated population boom then identifies a dearth of predation refugia, created by region-wide reef flattening, as the major barrier to recovery, and deployment of experimental artificial reefs demonstrates that augmentation of reef complexity is a viable strategy for increasing population size and reversing phase shifts. Restoration of *D. antillarum* will undoubtedly contribute to long-term ecosystem persistence, and insights contained within this thesis may help facilitate the difficult transition of Caribbean coral reefs to their future stable state.

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1 Chapter One – Introduction

1.1 The value of coral reefs

Coral reefs are ecologically and socio-economically important ecosystems that cover approximately 0.1% of the Earth's surface (Kohn 2002). Our understanding of coral reef biodiversity is limited, but it is estimated that they are home to over two million species (Knowlton et al. 2010). The multitude of organismal interactions that result from this biodiversity provides ecosystem services that up to 500 million people across the world are reliant upon; either directly for food provision, or indirectly for tourism and coastal protection (Wilkinson 2008). Scleractinian (hard) corals are the architects of coral reef ecosystems because they lay down calcium carbonate skeletons and create a structured environment that provides living space and promotes biodiversity (Heck and Wetstone 1977; Lee 2006; Alvarez-Filip et al. 2009). Up to 32% of all coral species are threatened with extinction, which makes them one of the most vulnerable groups of organisms in the world (Foden et al. 2013), yet just 5.2% of the ranges of threatened coral taxa lie within the boundaries of marine protected areas (Jenkins and Van Houtan 2016). In 2007, it was estimated that if the current extent of exploitation were to continue unabated until 2050, there would be 196,041 km² less coral reef than is needed to meet future food demands (Newton et al. 2007); the negative impacts of this deficit are likely to be most keenly felt in some of the world's poorest areas (Mora and Sale 2011).

Regular methodological advancements have made obtaining a holistic estimate of the total economic value of the world's coral reefs difficult. In 1997, the value of coral reefs was estimated as US\$8,384 ha⁻¹ yr⁻¹ (Costanza et al. 1997), but an updated analysis that accounts for storm and erosion protection services, as well as income generated from recreation, has seen this estimate increase 44-fold to US\$352,249 ha⁻¹ yr⁻¹ (Costanza et al. 2014). Whilst gaining an accurate global valuation can be

problematic, there are a plethora of studies that provide useful insights on a local-scale, e.g. estimates of the total economic value of coral reefs around Bermuda range from US\$488 million to US\$1.1 billion; 56% of this revenue is generated by tourism, 37% by coastal protection services, and just 0.7% from fishing activities (Sarkis et al. 2013). The significant coral loss caused by anthropogenic stress in the Caribbean over the last four decades has therefore had far-reaching socio-economic consequences and makes this region an urgent conservation priority (Jackson et al. 2014).

1.2 Ecosystem resilience

This thesis concerns the restoration of the long-spined sea urchin, *Diadema antillarum*, an ecologically, and therefore economically, important coral reef herbivore in the Caribbean. Disease-driven loss of *D. antillarum* ecosystem functions in the early 1980s demarcates the start of a period of ongoing major decline in Caribbean coral reef health, and reestablishment of this key echinoid may help slow, or even stop, this process of deterioration. Before presenting an in-depth species profile, including discussion of fundamental biology and ecology, ecosystem functions, current population status, and previous restoration attempts, it is necessary to provide an overview of the concept of ecosystem resilience and stability; an essential theory that must be considered by any conservation manager attempting to preserve biodiversity, ecosystem function and economic value.

Ecosystem resilience is normally defined as the ability of an ecosystem to resist and/or recover from large-scale disturbance events (Holling 1973; Sasaki et al. 2015). Resilience is conferred by species richness because it promotes functional redundancy and response diversity; this is known as the ‘insurance hypothesis’ (McCann 2000). Biodiverse ecosystems have high levels of functional redundancy because they

contain many species belonging to the same functional group, meaning that, in the event of species extirpation they are able to compensate for one another (Peterson et al. 1998; Elmqvist et al. 2003; Folke et al. 2004; Mumby et al. 2006; Roff and Mumby 2012; Loreau and Mazancourt 2013; Micheli et al. 2014). Response diversity is closely linked to functional redundancy and encompasses the variety of responses that different species within a functional group have to a common disturbance event; where response diversity is high, ecosystem functions are more likely to be maintained (Elmqvist et al. 2003).

As well as providing insurance against large-scale future climatic events, diversity is also important for promoting stability of ecosystem function. The diversity-stability hypothesis indicates that function is maintained because of the existence of a network of complex organismal interactions (McCann 2000), meaning that the loss of a single species can have a ripple effect throughout the entire ecosystem; the close correlation between diversity and primary productivity is often used to exemplify this idea (e.g. Tilman et al. 1997). The importance of diversity for maintaining stability has been questioned (May 1973), as strong interspecies interactions are destabilising and may leave ecosystems vulnerable to catastrophic collapse. However, it has been noted that the majority of species interact only weakly, therefore, in most ecosystems diversity is likely to have a stabilising effect (McCann 2006). As we progress through the Anthropocene, it is possible that biodiversity losses will increase the strength of organismal interactions and disrupt ecosystem function (McCann and Hastings 1997).

Whilst diversity is important, it is not the only thing that must be considered when trying to preserve resilience at the ecosystem level. Luck et al. (2003) highlight the need to think about the identity and characteristics of populations living within the

target ecosystem. In the context of a large-scale disturbance event, they emphasise the importance of; (1) Large population sizes to increase the probability of species survival and persistence, (2) High population richness within the landscape to maximise rates of recolonisation and recovery, (3) A geographically wide population distribution to minimise the probability of simultaneous extirpation of a species across the entire landscape, and, (4) High genetic diversity to facilitate recovery.

Oliver et al. (2015) also provide a more nuanced discussion of the mechanisms that confer resilience to an ecosystem and emphasise the need to think of them operating at three different spatial scales. (1) At the species level, resilience is dependent upon; (i) Response diversity, (ii) Population growth rate, (iii) Levels of adaptive phenotypic plasticity, (iv) Genetic diversity, and (v) The extent of Allee effects. (2) At the community level, resilience is determined by; (i) The correlation between response and effect traits, i.e. the extent to which an individual's response to disturbance impacts their ecosystem functions, (ii) The degree of functional redundancy, and (iii) The structure of the interaction network, e.g. in ecosystems with highly specialised interactions even slight disturbances can lead to trophic cascades and ecosystem collapse. (3) At the landscape level, resilience is reliant on; (i) Habitat/spatial heterogeneity, (ii) Metapopulation dynamics, (iii) Size of the landscape, and (iv) The potential for the landscape to exist in an alternative stable state.

Many ecosystems are able to exist in multiple ecologically stable states, e.g. coral reefs can be dominated by scleractinian corals or macroalgae, and sub-Saharan forests can also exist as grasslands; from an anthropogenic perspective, these states will provide different ecosystem services therefore one maybe more desirable than the other (Elmqvist et al. 2003). When resilience is eroded by multiple large-scale

disturbance events (Ghedini et al. 2015; Sasaki et al. 2015), phase shifts can occur as ecosystems move from one basin of attraction to another (Scheffer et al. 2001); stable states with wider basins of attraction are able to cope with more regular disturbances without experiencing noticeable changes to ecosystem function (Elmqvist et al. 2003). Whilst phase shifts can happen over long periods of time (Hughes et al. 2013), they usually occur suddenly after multiple perturbations have reduced the width of the basin of attraction to such an extent that a specific ecological threshold/tipping point has been surpassed (Scheffer et al. 2001).

Here it is necessary to make a distinction between phase shifts and alternative stable states (Petraitis and Dudgeon 2004). A phase shift is a unidirectional change in the dominant state of an ecosystem that occurs when prevailing environmental conditions are altered beyond a tipping point (Norstrom et al. 2009), whereas an alternative stable state is just one iteration of many potential community structures that can exist simultaneously within a given set of environmental parameters (Beisner et al. 2003). It is nigh-on impossible to forcibly change an ecosystem from one alternative stable state to another because both are able to persist under the same environmental regime (Petraitis and Dudgeon 2004). Phase shifts, on the other hand, are reversible because there is a tipping point that exists between the two different dominant states; this tipping point is determined by the threshold values of various biotic and abiotic factors (Hughes et al. 2010), and may not necessarily be the same in both the forward and backward directions (hysteresis; Scheffer et al. 2001; Bellwood et al. 2006; Beisner et al. 2011).

Disturbances can be classified as pulse-type or press-type. Pulse-type disturbances are one-off (acute) events that can take ecosystems back a successional stage, but, unless they occur regularly, are unlikely to stimulate a phase shift by

themselves, e.g. coral bleaching (Anthony et al. 2015). Press-type disturbances are chronic and operate to reduce resilience over time, which eventually leads to phase shifts by increasing species sensitivities to pulse-type events, reducing recovery rates and altering community-level interactions, e.g. rising sea surface temperatures. Historically, ecosystems have been resilient to natural disturbances because they tend to be pulse-type, but human activity has seen many previously acute threats become chronic and the increase in press-type disturbances over recent decades has stimulated phase shift in myriad ecosystems (Elmqvist et al. 2003).

Compensatory dynamics can provide resilience by absorbing disturbance events so that there is no net change to overall ecosystem function (Gonzalez and Loreau 2009). In all biomes, disturbance events lead to expansion of weedy species and in resilient ecosystems, this is usually accompanied by an increase in herbivore population size that keeps these newly dominant taxa in check (Ghedini et al. 2015). Typically, the size of the compensatory effect and the disturbance event are closely correlated, e.g. disturbance events cause expansion of turf algae in kelp forests, which releases grazers from intraspecific competition that then keep the algae at low levels; larger disturbances stimulate more turf algal growth and greater increases in grazer population size (Ghedini et al. 2015).

Coral reefs are space limited environments, which creates intense interspecific competition between benthic organisms; especially between slow growing scleractinian corals and fast growing macroalgae (McCook et al. 2001). On healthy reef systems, usually identified by their high coverage of scleractinian coral, macroalgal overgrowth is prevented, and hence scleractinian coral domination is maintained, because the water is oligotrophic (Hallock and Schlager 1986; McClanahan et al. 2002; Szmant 2002; Fabricius 2005) and there is an abundance of

vertebrate and invertebrate herbivores (Mumby et al. 2006; Lee 2006; Hughes et al. 2007; Roff and Mumby 2012). Regular press- and pulse-type stressors erode the resilience of coral reef ecosystems and operate to increase the likelihood of macroalgal phase shift, whereby the system moves from a scleractinian-coral-dominated to macroalgae-dominated state (Norstrom et al. 2009). Most fast growing macroalgae have simple 2D growth structures meaning that, when they dominate, the availability of living space, and thus biodiversity and resilience, are reduced (Done 1992). For this reason, the percentage cover of scleractinian coral is normally used as a proxy of reef health (e.g. Kramer 2003).

Fortunately, there is evidence to suggest that that macroalgal dominance is likely to constitute a phase shift and not an alternative stable state (Dudgeon et al. 2010). This finding provides hope to coral reef conservationists aiming to restore ecosystem function and resilience, and numerous experimental manipulations have demonstrated that augmentation of herbivore populations may help to alter environmental parameters and facilitate phase shift reversal (e.g. Hughes et al. 2007; Idjadi et al. 2010; Bonaldo and Bellwood 2011; Ghedini et al. 2015).

1.3 The current state and future of Caribbean coral reefs

Caribbean coral reef ecosystems are significantly less resilient than other global hotspots (Mumby et al. 2007; Hughes et al. 2010; Nystrom and Folke 2001), largely because the relatively low species diversity of the region means there is a lack of functional redundancy (Roff and Mumby 2012); compared to the Indo-Pacific, the Caribbean has just 28% and 14% of the diversity of fishes and corals respectively (Bellwood et al. 2004).

Over the last three decades, a perfect storm of threats has converged in the Caribbean and drastically altered coral reefs throughout the region. The most recent regional assessment estimates that hard coral cover decreased from 34.8% in 1970 to just 16.3% in 2012, and these decreases were accompanied by large increases in macroalgae from a mean value of 7% in 1984 to 23.6% in 1998 from which point they have remained relatively stable (Jackson et al. 2014). Occurrence of an epidemic of white-band disease in the early 1980s, coupled with loss of herbivory through disease and overharvesting, stimulated processes of reef flattening, which have created low complexity reef systems that cannot support high levels of biodiversity (Lee 2006; Alvarez-Filip et al. 2009; Jackson et al. 2014).

Given the large number of threats currently occurring on the world's coral reefs, it is unlikely that they will persist in their current state for much longer (Green et al. 2008; Côté and Darling 2010; Darling et al. 2012). Many reefs in the Caribbean have already undergone major transitions with regard to the dominant corals they support, as an increasing frequency and severity of disturbance events is causing stress-sensitive corals to be replaced by their stress-tolerant counterparts (Côté and Darling 2010). In particular, corals of the genera *Montastrea* and *Orbicella* are being replaced by *Porites*, *Agaricia* and *Undaria* (Aronson et al. 2004; Green et al. 2008; Côté and Darling 2010; Yakob and Mumby 2011; Darling et al. 2012; Garcia-Hernandez et al. 2017). Poritids and agaricids have opportunistic life-histories that enable them to colonise in otherwise unfavourable environmental conditions (Darling et al. 2012). Agaricids are especially competitive on degraded reefs because they can reproduce parthenogenetically, meaning that, unlike their competitors, they do not become mate-limited (Darling et al. 2012).

Changes in community composition are creating new frameworks within which conservation managers must operate if they are to have any success in securing the future of the world's coral reefs (Oliver et al. 2015). Caribbean reefs dominated by stress-tolerant corals are much more resistant to bleaching and disease (Côté and Darling 2010; Yakob and Mumby 2011), therefore conservation initiatives aimed at preserving community compositions may actually do more harm than good; a proposition which is supported by the observation that the severity of bleaching events is often highest within marine protected areas (Côté and Darling 2010). These new *Agaricia/Undaria* and *Porites* dominated reefs may not be 'ideal' as they support a slightly lower biodiversity than a healthy *Montastrea/Orbicella* reef (Alvarez-Filip 2009; Côté and Darling 2010). However, the likelihood that *Montastrea/Orbicella* reefs will persist into the next century is rapidly diminishing, and most researchers would agree that a slightly sub-optimal reef is better than no reef at all.

When making decisions, Caribbean coral reef conservationists must account for how the structure of reef communities is likely to shift under current and future environmental conditions so that they are better equipped to assist them with the potentially difficult transition to their new stress-tolerant state (Oliver et al. 2015). *D. antillarum* is an obvious conservation target from this perspective as replacement of lost herbivory will provide a compensatory effect that will remove macroalgae, encourage coral recruitment and confer ecosystem resilience against future pulse- and press-type disturbances (Hoegh-Guldberg et al. 2007; Hoegh-Guldberg and Bruno 2010; Anthony et al. 2015; Ghedini et al. 2015).

1.4 Species profile: *Diadema antillarum*

1.4.1 Taxonomy

There are eight species within the genus *Diadema*, which has the widest biogeographical range of any echinoid taxon. The clearest morphological marker of the genus is their distinctive long-spines (Muthiga and McClanahan 2013) but it is difficult to identify individuals to species level on the basis of gross morphology. *Diadema* spp. are, therefore, normally distinguished from one another by their unique biogeographical distributions, e.g. identification of *D. antillarum* in the Caribbean is easy because it is the only *Diadema* species found in the tropical Western-Atlantic (Muthiga and McClanahan 2013). *D. antillarum* was first described by Philippi in 1845, and its species name is derived from the fact that it was first found in the Dutch Antilles (Rodriguez et al. 2013); it is known by the common name of the long-spined sea urchin (Kroh 2014).

1.4.2 *D. antillarum* distribution

D. antillarum are found throughout the Caribbean Sea from the Florida Keys to the coast of Brazil (Lessios et al. 2001). Their depth range extends from just under the surface to roughly 70 m (Muthiga and McClanahan 2013). There is a negative correlation between depth and *D. antillarum* density (Morrison 1988; Cho and Woodley 2000; Moses and Bonem 2001; Debrot and Nagelkerken 2006; Petit 2009; Martin-Blanco et al. 2010; Williams et al. 2010), meaning that their ecological influence is greatest in the shallows (Morrison 1988).

D. antillarum has a home-range of approximately 4m² (Petit 2009), and, once settled, they remain faithful to their home crevice. Difficulties associated with tagging urchins mean that we know relatively little about their movements, however, on a local

scale there are numerous factors that affect distribution. There is a clear relationship between *D. antillarum* population density and habitat structure (e.g. Dumas et al. 2007; Bodmer et al. 2015; Alvarado et al. 2016; Rogers and Lorenzen 2016; Chapter 5), as more complex environments provide living space and predation refugia. Predation cues are another major determiner of echinoid population distribution because of impacts on aggregative behaviour, e.g. in *Lytechinus variegata* the presence of predator stimuli causes dispersal (Snyder and Snyder 1970; Vadas and Elner 2003).

Hydrodynamic forces have a large effect on echinoids, and the *Diadema* body plan makes them especially vulnerable to wave and tide action (Siddon and Witman 2003; Tuya et al. 2006; Petit 2009; Rodriguez et al. 2014). *D. antillarum* abundances therefore tend to be greatest at depths of 3-6 m, where it is shallow enough that there is ample food but deep enough that the risk of dislodgement is minimised. *D. antillarum* distribution is also influenced by competitive interactions with aggressive damselfish that exclude echinoids from their territories (Sammarco and Williams 1982).

1.4.3 Morphology

D. antillarum is a regular echinoid with a slightly dorso-ventrally compressed circular test that can reach up to 10 cm in diameter (Ogden and Carpenter 1987). Regular echinoids have three distinct classes of appendages that adorn their tests; spines, tube feet and pedicellariae. Tubercles, structures that exist at the interface between the test and the spines, are present on both the interambulacral and ambulacral zones (Fig. 1.1).

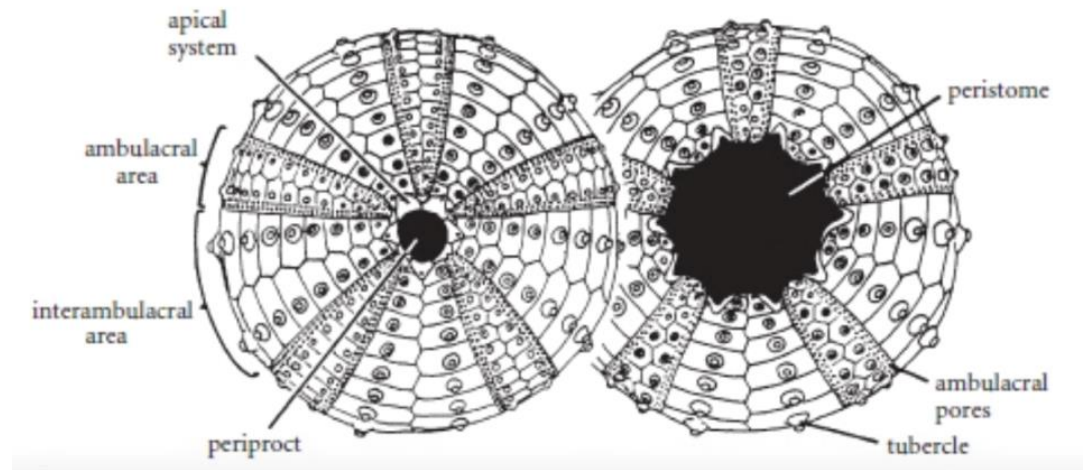


Figure 1.1. Basic anatomy of the exterior skeletal morphology of a regular echinoid.

Diagram has been included to highlight the location of the ambulacral and interambulacral areas (Benton and Harper 2013).

The larger defensive spines are found in the interambulacral zone, whereas smaller, secondary spines, primarily used for locomotion, are found in the ambulacral zone. The barbs of *D. antillarum* spines point towards the distal tip of the appendage (Randall et al. 1964), and the restricted-pivot mechanism that joins them to the test reduces spine mobility but increases strength to maximise their utility against predation (Fig. 1.2; Smith 1980).

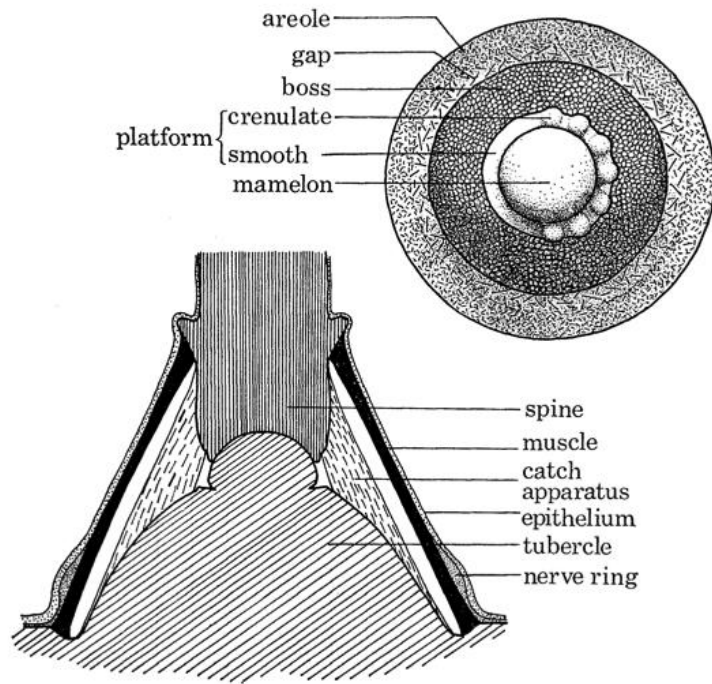


Figure 1.2. Basic structure of a spine and how it connects to the test via the tubercle. The shape of the base of the spine exactly matches the shape of the mamelon at the top of the tubercle. Muscle fibres known as the “catch apparatus” connect the spine to the mamelon where there is another set of muscle fibres that attach the spine to the test itself. An epithelial layer that contains photosensitive melanin and a mild toxin surrounds the whole structure (Smith 1980).

The peristome is formed as a result of the convergence of the ambulacral and interambulacral plates, which, as they curve upwards and inwards, create an internal structure known as the perignathic girdle. The girdle provides the large surface area required for the attachment of the muscles associated with the Aristotle’s Lantern (Duncan 1885). In *D. antillarum*, the Aristotle’s Lantern is made up of five pairs of buccal plates that each form a tooth, and there are up to 60 different types of muscle that surround the structure and anchor it to the perignathic girdle (Duncan 1885). The large muscle mass in the peristome makes *D. antillarum* a prolific macroalgal grazer (Randall et al. 1964).

1.4.4 *Light sensitivity*

Urchins have no differentiated light detecting receptors, but *D. antillarum* will respond to changes in the light environment. They have concentrations of melanin-containing melanophores around their tube feet and at the ambulacral margins (Millott and Yoshida 1959; Ullrich-Luter et al. 2013). Melanin gives *D. antillarum* its black colour and provides it with the ability to react to changes in light intensity (Millott 1954; Raible et al. 2006) as light stimuli cause expansion of the melanophores, which induces a nervous signal and invokes a behavioural response. The light detection system is diffuse and covers the entirety of the individual (Millott and Yoshida 1959). *D. antillarum* is most active at night (Tuya et al. 2004), and is therefore vulnerable to attack from visual predators during the day (Lamb et al. 2007); it is likely that this diffuse light detecting system evolved as an innate mechanism to survive during the least active part of their diurnal cycle (Raible et al. 2006).

Experimental manipulations demonstrate that urchins only respond to changes in light intensity if they occur over the surface of the test. The spines have no photodetecting capabilities and denuded urchins will continue to respond to changes in the light environment (Millott and Yoshida 1959). *D. antillarum* responds to light stimuli in one of two ways: (1) If the stimulus is directional then the whole organism will move either towards or away from the stimulus, (2) If the stimulus is non-directional then the response is limited to isolated organs, such as the spines (Millott and Yoshida 1960a; Millott 1976). Shadows will often be caused by predators and therefore they evoke an excitatory response in the spines, which decreases the efficacy of predatory attack (Raible et al. 2006). Conversely, increased light intensity has an inhibitory response that suppresses spine movement; when the threat of predation has

been removed, reduction of spine movement allows energy to be conserved (Millott and Yoshida 1960b; Millott 1976).

1.4.5 Feeding

D. antillarum is a generalist herbivore that feeds on multiple algal species (Ogden and Lobel 1978). This lack of discrimination means that they remove huge volumes of macroalgae from Caribbean reefs, which in turn facilitates scleractinian coral domination. Based on their chemotactic responses, *D. antillarum* has the following feeding preference hierarchy; *Lobophora* spp. > *Halimeda* spp. > *Dictyota* spp. > *Sargassum* spp. > *Galaxaura* spp. Despite *Galaxaura* spp. being the least preferred algal genus, it is the most beneficial to *D. antillarum* in terms of weight gain (Shunula and Ndibalema 1986; Rodriguez-Barreras et al. 2015b), presumably because of its high calcium carbonate concentration. These results imply that calcified algal species are important for *D. antillarum* but they are grazed less regularly as they do not release chemical attractants as readily as non-calcified species (Soldant and Campbell 2001), and they are more difficult to digest (Hay 1984).

D. antillarum is cellulase deficient (Lawrence et al. 2013) which makes mature macroalgae, with tough cell walls, unpalatable (Ogden and Lobel 1978; Soldant and Campbell 2001). They also have notably high alginase activity, which breaks down alginate, the main polysaccharide found in brown algae. This high concentration of alginase makes *D. antillarum* a keystone of contemporary Caribbean reefs (Lawrence et al. 2013), because brown macroalgae are one of the key drivers of current macroalgal phase shifts.

While *D. antillarum* is primarily herbivorous, its indiscriminate grazing of the benthos can lead to inadvertent corallivory (Ogden and Carpenter 1987; Edmunds and

Carpenter 2001). Recent isotope analysis has also revealed that they regularly assimilate carbon and nitrogen from non-algal sources, and their average trophic level ranges between 2.35 and 3.24. This indicates that *D. antillarum* is actually omnivorous; an assertion supported by the finding that up to 33% of the gut contents of *D. africanum* in the eastern Atlantic is comprised of invertebrates (Rodríguez-Barreras et al. 2015b).

1.4.6 Reproduction and recruitment

D. antillarum is a dioecious, external fertiliser that spawns asynchronously (Levitan 1988). This evolutionary quirk was thought to have evolved because for the majority of their evolutionary history *D. antillarum* were present at very high abundances and asynchronous spawning reduced reproductive competition whilst also ensuring fertilisation success (Levitan 1988). However, this widely held view is called into question by a number of paleontological studies which find that *D. antillarum* actually persisted at very low densities for the majority of its evolutionary history, and population booms only occurred because overfishing in the 20th century reduced competition and predation (Hay 1981; Cramer et al. 2016; Cramer et al. 2017). Regardless, the major driver of *D. antillarum* fertilisation success is adult population density (Levitan 1991). These findings are congruent with experiments conducted on the heterospecific echinoid, *Strongylocentrotus droebachiensis*, where 60-95% of fertilisations occurred within 20 cm of the spawning site, and beyond 2 m from the spawning site fertilisation success was reduced to zero (Pennington 1985).

Unlike fertilisation success, *D. antillarum* recruitment is density-independent and levels are similar in high and low-density adult populations (Tuya et al. 2006; Miller et al. 2009; Levitan et al. 2014). *D. antillarum* recruitment is affected by

numerous factors including accidental grazing or attack of settlers by aggressive heterospecific echinoid species such as *Echinometra lucunter* (Hunt and Scheibling 1997; Lacey et al. 2013). Recruitment is therefore more successful in structurally complex environments that provide predation refugia (Andrew 1993; Hunt and Scheibling 1997; Hereu et al. 2005; Clemente et al. 2007).

1.5 *Diadema antillarum* die-off: causes, consequences and recovery

1.5.1 *Mass mortality (1983-84)*

D. antillarum ecological dynamics were drastically altered in the early 1980s when an unknown water-borne pathogen spread throughout the entire Caribbean and reduced populations by 95-100% (Bak et al. 1984; Hughes et al. 1985; Liddell and Ohlhorst 1986; Lessios 1988; Levitan 1988; Carpenter 1990; Lessios 2005; Betchel et al. 2006). The disease was first detected in Panama in 1983 where densities decreased from 14,000 ha⁻¹ in January to just 0.5 ha⁻¹ in May (Lessios et al. 1984a). The disease reached all areas of the tropical Western-Atlantic, including Bermuda, by January 1984 (Lessios et al. 1984b). The pathogen is generally thought to have spread on prevailing Caribbean currents, however, this hypothesis can only explain patterns of infection for the Gulf of Mexico and Bermuda, but not for the rest of the Caribbean; it is proposed that the disease is more likely to have spread through ship ballast water (Phinney et al. 2001).

On average it took one to four weeks for infected individuals to die (Lessios et al. 1984a). The first symptom of the disease was an accumulation of sediment on the spines followed by spine detachment and loss of pigmentation. As the infection progressed it caused the tube feet to become flaccid and no longer fully retractable meaning that infected individuals could not anchor to the substrate. The disease also

triggered behavioural changes that caused individuals to abandon their cryptic habit leading to dramatically increased predation rates (Lessios 1984a; Hughes et al. 1985).

Three lines of evidence support the assertion that mass-mortality was caused by disease and not another causative agent. Firstly, pollutants have been ruled out as a possible cause because *D. antillarum* was the only affected species, and it is unlikely that a pollutant's potency would be maintained for such a prolonged period over the 3.5 million km² area of the tropical Western-Atlantic (Lessios et al. 1984a). Pollutant-induced mortality is also usually accompanied by a high abundance of gram-positive rod bacteria and *Escherichia coli* in the bacteriofauna of infected individuals; gut bacterial content of pre- and post-mortality *D. antillarum* populations was similar (Bauer and Agerter 1987). Secondly, anomalous fluctuations in sea surface temperature (SST) that occurred in the early 1980s cannot account for the mass-mortality because they were not as widespread as the die-off. Thirdly, there is a precedent for species-specific pathogen-caused echinoid mass-mortality having occurred in *S. droebachiensis* (Scheibling and Hamm 1991). *S. droebachiensis* populations off the coast of Nova Scotia, Canada, have classic boom-bust ecological dynamics and suffer regular mass-mortalities (Scheibling 1984), but between October and December 1982, disease reduced populations by an unprecedented 70% (Scheibling 1984).

Most of the literature refers to the causative agent of the mass-mortality as 'an unknown waterborne pathogen'. Bauer and Agerter (1987) identified *Clostridium perfringens* in the bacteriofauna of *D. antillarum*. *C. perfringens* is a swarming, spore forming, non-motile and anaerobic bacterial species, and is therefore a good candidate for disease-causation. When incubated with *D. antillarum*, the bacterium always

caused death within six days. However, it has not been verified as the cause of the mass-mortality.

1.5.2 Ecosystem functions and impacts of mass-mortality

At high densities, *D. antillarum* will consume the entire daily growth of macroalgae (Carpenter 1984; Petit 2009). There is therefore a very strong negative correlation between *D. antillarum* population size and percentage cover of macroalgae, as well as a closely linked positive relationship with scleractinian coral cover (Wanders 1977; Bak et al. 1984; Liddell and Ohlhorst 1986; Hughes et al. 1987; Ogden and Carpenter 1987; Carpenter 1988; Lessios 1988; Levitan 1988; Carpenter 1990; Haley and Solandt 2001; Solandt and Campbell 2001; Chiappone et al. 2002; Miller et al. 2003; Tuya et al. 2004; Carpenter 2005; Lessios 2005; Mumby et al. 2006; Macia et al. 2007; Chiappone et al. 2008; Roff and Mumby 2012; Chiappone et al. 2013). Improvements in metrics of coral reef health are also associated with either natural, or artificial enhancement of *D. antillarum* population densities (Cho and Woodley 2000; Edmunds and Carpenter 2001; Nedimyer and Moe 2003; Carpenter and Edmunds 2006; Myhre and Acevedo-Gutierrez 2007; Leber et al. 2008; Bruno et al. 2009; Idjadi et al. 2010; Martin-Blanco et al. 2010). The loss of *D. antillarum* ecological function therefore led to Caribbean-wide macroalgae increases of up to 50% (Carpenter et al. 2008), and is undoubtedly a major contributing factor to the 80% coral loss observed in the Caribbean from 1970-2000 (Gardner et al. 2003).

In St Croix (US Virgin Islands), loss of urchin ecosystem functions decreased macroalgae primary productivity by up to 37%, despite a 50% increase in algal biomass (Carpenter 1988); reefs with reduced energy availability support lower biodiversity, and therefore resilience. There are two hypotheses that may explain the

reduction in primary productivity associated with *D. antillarum* mass-mortality; (1) The canopy effect created by large macroalgae stands creates shade that decreases the efficacy of photosynthesis on the reef. (2) The calorific content of *D. antillarum* faecal pellets is up to ten times greater than any other reef organism, and the mass-mortality reduced this fertilisation effect (Lewis 1967; Hawkins and Lewis 1982).

Relative to areas devoid of *D. antillarum*, rates of juvenile coral recruitment have been found to be up to 11 times greater in ‘urchin zones’ (Edmunds and Carpenter 2001). These findings agree with numerous others which find a positive correlation between *D. antillarum* population size and juvenile coral recruit abundance (Sammarco and Williams 1982; Nedimyer and Moe 2003; Carpenter and Edmunds 2006; MacIntyre et al. 2008; Furman and Heck 2009; Idajadi et al. 2010). Since the mass-mortality event, *Dictyota* macroalgae have proliferated to reach coverages >50% in some parts of the Caribbean (Kuffner et al. 2006). *Dictyota* spp. not only compete with juvenile corals for space, but produce toxic compounds that prevent juvenile coral recruitment, and even induce mortality (Kuffner et al. 2006).

Whilst *D. antillarum* grazing activity is well-known for influencing the ecological dynamics of Caribbean coral reefs, it also affects the abiotic environment. At high densities, *D. antillarum* can remove up to 2.7 kg m⁻² year⁻¹ of calcium carbonate from the reef (Bak et al. 1984). Whilst high echinoid densities cause reef flattening (Carreiro-Silva and McClanahan 2001; Brown-Saracino et al. 2006; Bronstein and Loya 2014), intermediate densities are beneficial because their localised removal of CaCO₃ creates habitat complexity (Lee 2006), which promotes coral recruitment, biodiversity and ecosystem function (Heck and Wetstone 1977; Aronson and Precht 1995; Graham and Nash 2013). Prior to mass-mortality, *D. antillarum* was responsible for 80-90% of all bioerosion on Caribbean coral reefs (Perry et al. 2014).

Today, population densities are so low that the bioerosion provided by *D. antillarum* is negligible (Perry et al. 2014), and loss of this key ecosystem function is a driver of ubiquitous ‘reef flattening’ in the region (Gardner et al. 2003; Alvarez-Filip et al. 2009).

An often-overlooked ecosystem function of *D. antillarum* is the role that the spine canopy plays in the protection of fish fry and small invertebrates. At high population densities, aggregations of *D. antillarum* can provide protection to a wealth of small reef-dwelling organisms and promote their survival, many of which have their own ecosystem functions necessary for the maintenance of a healthy coral reef (Randall et al. 1964).

Experimental manipulations in the late 1980s indicate that population densities as high as 6-8 individuals m^{-2} are needed for ecosystem functions to be active (Ogden and Carpenter 1987), but more recent findings suggest that this is an overestimate and that *D. antillarum* may start to have beneficial impacts on reef systems at densities as low as 0.6-1.0 individuals m^{-2} (Miller et al. 2006; Mumby et al. 2006; Myhre and Acevedo-Gutierrez 2007).

1.5.3 Recovery and current population status

Discovery Bay, Jamaica, is one of the few localities where both pre and post-mortality data are available. After initially poor recovery, encouraging natural increases in *D. antillarum* populations have been observed. Pre-mortality densities around Discovery Bay ranged from 8.1 m^{-2} (Haley and Solandt 2001) to 14 m^{-2} (Liddell and Ohlhorst 1986). However, mass-mortality reduced populations to nearly 0 m^{-2} (Betchel et al. 2006). After the die-off, Betchel et al. (2006) documented a 15-year period of population stasis where densities remained just above 0 m^{-2} until 1999.

Moses and Bonem (2001) report slightly more encouraging figures but still found that, 15 years after the disease, populations had recovered to just 5-10% of their pre-mortality densities. In 1998-99, *D. antillarum* populations suddenly increased up to a density of 0.16 m⁻² (Moses and Bonem 2001), but, despite this ‘recovery’, *D. antillarum* population densities remain one to two orders of magnitude lower than their pre-mortality densities (Mumby et al. 2006).

A series of papers periodically released by Lessios have documented the lack of recovery of *D. antillarum* off the coast of Panama. Maximum pre-mortality densities recorded in Panama were as high as 70 m⁻², with an average density of 3.5 m⁻² (Robertson 1991). Disease reduced populations to just 0.0001 m⁻², and by February 1984, they had increased to 0.004 m⁻² but there was little more recovery beyond this initial augmentation (Lessios et al. 1984a). In 1988, surveys of 17 sites along the San Blas islands off the coast of Panama found no urchins (Lessios 1988), and, when the sites were revisited eight years later, populations had recovered to just 3.5% of their pre-mortality densities (Lessios 1995); even after two decades, population densities were just 6.5% of what they had been prior to 1983 (Lessios 2005). This lack of recovery has been blamed on the geographical position of Panama as it is located upstream of potential larval sources (Lessios 2016).

Unlike Discovery Bay and Panama, the Florida Keys were struck by a second mass-mortality event in 1991 (Chiappone et al. 2008). The Florida Keys had naturally lower pre-mortality *D. antillarum* densities than other Caribbean reef systems because of high storm frequency and a lack of upstream larval supply (Chiappone et al. 2008; Miller et al. 2009). Between the two mass mortalities, populations experienced significant recovery and reached densities of up to 0.58 m⁻². However, the second

mortality event reduced populations to just 0.01 m⁻² and the subsequent recovery has been notably less successful than the first (Chiappone et al. 2008).

The initial recovery was fast because overfishing in the Florida Keys removed the threat of predation (Chiappone et al. 2013). It is likely that the second mortality event was localised to the Florida Keys because, by 1991, *D. antillarum* recovery throughout the rest of the Caribbean was limited, therefore only Floridian reefs had high enough *D. antillarum* densities to facilitate disease spread (Chiappone et al. 2013). In 2002, just 16 individuals were found across 80 surveys conducted along a 200 km stretch of Floridian coastline (Chiappone et al. 2002). By 2007, recovery appeared to be underway, although densities remained low (0.27 m⁻²) (Chiappone et al. 2008), but there is some evidence of populations remaining stable at ca. 0.5 m⁻² from 2000 to 2009 (Pomory et al. 2014).

Many studies examining the extent of *D. antillarum* population recovery have found no evidence of significant density increases. Populations in the following locations have all failed to recover; US Virgin Islands (Carpenter 1988; Levitan 1988b; Miller et al. 2003), Dominica (Steiner and Williams 2006), Curacao (Debrot and Nagelkerken 2006; Vermeij et al. 2010), Barbados (Hunte and Younglao 1988), Costa Rica (Alvarado et al. 2004; Myhre and Acevedo-Gutierrez 2007; Cortes et al. 2010), Mexico (Lacey et al. 2013), Puerto Rico (Weil et al. 2005; Williams and Garcia-Sais 2010; Williams et al. 2010; Ruiz-Ramos et al. 2011; Williams et al. 2011; Rodriguez-Barreras 2014), and Venezuela (Noriega et al. 2006).

1.6 Threats to coral reefs

Loss of *D. antillarum* ecosystem functions is one of several major environmental pressures facing contemporary Caribbean coral reefs. Initially, *D. antillarum* population collapse was a pulse-type stressor, but the lack of significant recovery over the last three decades has converted it to press-type stressor (Anthony et al. 2015). Restoring *D. antillarum* grazing functions will reintroduce a compensatory dynamic to Caribbean coral reefs and enhance ecosystem resilience in response to a plethora of global and local threats (Ghedini et al. 2015).

1.6.1 Global threats

Global threats are a direct result of anthropogenic fossil fuel combustion and associated greenhouse gas release. The combined effects of ocean warming and acidification have caused ocean carbonate budgets to plummet (Perry et al. 2014). Today, only 26% of coral reefs are actively accreting, while 21% have negative carbonate budgets, and the remaining 53% are ‘budget neutral’ (Perry et al. 2012). When coupled with high UV irradiance, rising SST causes oxidative stress within the photosynthetic pathways of symbiotic zooxanthellae (Roth 2014), and they are therefore expelled from their coral host (Brown 1997); a phenomenon known as coral bleaching. Most scleractinian corals on shallow reef systems gain ca. 80% of their energy requirements from the photosynthetic products provided by their symbionts (Gorbunov et al. 2001), therefore if coral bleaching persists for long periods, mortality will occur.

The first global mass-bleaching event to have occurred for >3000 years occurred in 1998. On some reefs SSTs increased by >4°C for prolonged periods (Aronson et al. 2002), which led to 90% coral mortality on the Great Barrier Reef

(Hoegh-Guldberg 1999), and 100% coral mortality in some lagoons of the Belizean barrier reef (Aronson et al. 2002). This loss of live coral cover led to extensive phase shifts as dead coral skeletons were colonised by macroalgal recruits (Alvarez-Filip et al. 2009). If healthy *D. antillarum* populations had existed in the Caribbean, it is possible that their compensatory dynamics would have reduced the extent of macroalgal overgrowth and subsequent biodiversity and resilience loss (Ghedini et al. 2015).

Early data pertaining to the 2016 mass-bleaching of the Great Barrier Reef reveals that the incidence of bleaching was up to 4-times higher than in 1998 or 2002 (Hughes et al. 2017), and taxonomic differences in species' abilities to resist bleaching are likely to lead to dramatic shifts in coral community compositions (Côté and Darling 2010; Hughes et al. 2017). Most climate change researchers agree that mass-bleaching events will increase in frequency (IPCC 1996; Sheppard 2003; Baker et al. 2008; Hughes et al. 2018) and may become biennial events by 2050 (Donner et al. 2005).

Ocean acidification has been identified as one of the nine planetary processes which, if boundaries are transgressed, will have large ecological and humanitarian impacts. Recent estimations indicate that we are dangerously close to the tipping point in several (Rockstrom et al. 2009; Steffen et al. 2015), but that the ocean acidification boundary of $\geq 80\%$ pre-industrial aragonite levels has not yet been breached (Steffen et al. 2015). Ocean acidification has three major negative impacts. Firstly, increased hydrogen ion concentrations lower pH, which interferes with organismal calcification pathways. Secondly, increased incidence of the 'carbonate ion to bicarbonate ion' reaction decreases aragonite availability and impairs skeletal growth (Fabry et al. 2008). Thirdly, dissolution of CO_2 leads to hypercapnia and reduction of oxygen

availability for respiration (Hoffman and Todgham 2010). Each species has its own evolutionary idiosyncrasies and adaptive quirks, which makes it impossible to make generalisations about the impacts of ocean acidification, however, it is clear that organisms from across a wide range of taxa will be affected (Hoffman and Todgham 2010).

1.6.2 Local threats: The Caribbean

Local threats are pulse and press-type stressors that operate to reduce resilience and ecosystem function at a specific location. It has been postulated that most coral loss in the Caribbean is attributable to localised environmental stress (Gardner et al. 2003), which is good news for conservation managers because isolated local threats are easier to combat than broad global stressors.

Perhaps the most notorious threat facing the Caribbean is the invasion of the non-native lionfish (*Pterois volitans/miles*) from the Indo-Pacific. Their indiscriminate diet, high fecundity, large-scale dispersal and hardy larval stage (Morris et al. 2009), means they have become established on reefs throughout the Caribbean since their accidental introduction in 1984. Lionfish reduce juvenile fish recruitment by up to 79% in the tropical Western-Atlantic (Albins and Hixon 2008), which reduces herbivorous fish populations and stimulates macroalgae phase shifts (Lesser and Slattery 2011). In areas with large human populations, culling-focused management programmes have reduced invasive lionfish densities and partially mitigated the negative consequences of their introduction (Côté et al. 2014); although deep mesophotic reefs may offer populations refuge from this management approach (Andradi-Brown et al. 2017ab). There is also some evidence showing that populations

are now naturally decreasing because of interspecific competition and predation by native fish species (Benkwitt et al. 2017).

Overfishing is a global phenomenon affecting reefs on a local scale (Jackson et al. 2001). Overfishing reduces resilience and contributes to macroalgal phase shifts through numerous mechanisms. Firstly, removal of piscivores causes trophic cascades; damselfish have been released from predation pressures and, because of their farming behaviours, macroalgae cover has increased (Cramer et al. 2017). Secondly, removal of filter feeders, such as bivalves, causes eutrophication that not only stimulates macroalgae growth, but can lead to eutrophication, which creates hypoxic environments (Jackson et al. 2001). Overfishing has also increased incidence of density-dependent disease epidemics in lower trophic levels because associated increased population densities create the ideal conditions for pathogen spread (Hochachka and Dhondt 2000; Lafferty 2004).

The most severe local threat to Caribbean reef systems is the loss of herbivory associated with overharvesting and/or disease (Pandolfi et al. 2003). Coral reefs have been overfished for thousands of years (Jackson et al. 2001), and steady declines in the abundance and biomass of key fish grazers from the Scaridae and Acanthuridae families are, at least partially, responsible for dramatic decreases in scleractinian coral cover (Williams and Polunin 2001; Williams et al. 2001; Mumby et al. 2006); when herbivorous fish are removed from a reef, macroalgae cover can increase from 4% to 53% (Hughes et al. 2007). Legislation to protect herbivorous fish populations, largely through the establishment of marine protected areas (MPAs; Gill et al. 2017), should be enforced alongside *D. antillarum* conservation efforts to maximise compensatory dynamics and resilience of Caribbean coral reefs.

1.7 *D. antillarum* restoration initiatives

Conservation managers are attempting to safeguard coral reefs under highly unpredictable circumstances, but there is agreement that efforts to protect herbivore populations in the Caribbean will help to increase resilience over the next century and provide these valuable ecosystems with a fighting chance of survival (Hoegh-Guldberg et al. 2007; Hoegh-Guldberg and Bruno 2010; Perry et al. 2014; Ghedini et al. 2015; Cramer et al. 2017). Clear associations between their population size and commonly accepted metrics of reef health, make *D. antillarum* an obvious conservation target (Precht and Precht 2015), and many conservationists have attempted to augment populations with varying degrees of success. Several studies call into question the validity of *D. antillarum* restoration. While it is beyond doubt that *D. antillarum* play a key role in the prevention of phase shifts, it is less clear whether or not augmentation of their populations will facilitate their reversal; simply removing the factor that initially stimulated phase shifts may not be sufficient to undo its effects (Petraitis and Dudgeon 2004; Bellwood et al. 2006; Côté and Darling 2010; Hoey and Bellwood 2011).

However, restoration studies on the Florida Keys found that *D. antillarum* population enhancement increased juvenile coral recruit abundance (Nedimyer and Moe 2003; Rodriguez-Barreras et al. 2015a); a finding which is echoed by the results of Macia et al.'s (2007) Jamaican study. Transplanted urchins also had a high survival rate and were even resilient to two major storms that occurred during the study period. These studies not only show that reintroduction of *D. antillarum* can be beneficial to Caribbean reefs, but also that artificial populations are robust to both low and high level disturbances.

Miller et al. (2006) attempted to restock populations to mean densities of 4 m^{-2} but populations repeatedly ‘relaxed’ to 1 m^{-2} ; high mortality was attributed to predation on reintroduced juveniles due to a lack of 3D structure. This highlights that reintroduction can be successful, but the factor(s) preventing recovery must first be removed. Nedimyer and Moe (2003) also found that reintroduced populations relax to a density of 1 m^{-2} , but their interpretation of these results was more positive; conservationists should only augment to a density of 1 m^{-2} as this density is sufficient to replace lost *D. antillarum* ecosystem functions (Nedimyer and Moe 2003).

The most successful *D. antillarum* restoration programme to date has been led by Stacey Williams in Puerto Rico. She uses settlement plates to capture *D. antillarum* larvae and rear them in the lab until they are large enough to defend themselves against reef predators. Mortality of settlers is high (up to 80%), but recruits, defined as juveniles that have developed beyond their larval stage, exhibit a high level of survivorship. Williams (2016) reports huge decreases in macroalgae within just one week of reintroduction of lab-reared urchins. Survival rates were highest for individuals reintroduced as part of a large aggregation, therefore Williams advocates simultaneous release of up to 100 individuals (Williams 2016). These results are preliminary, but promising, and provide hope that *D. antillarum* restoration is an achievable conservation aim. However, a separate reintroduction study found that population increases do not persist in the long-term (beyond 3-4 months) and population mortality can be as high as 94.8% (Leber et al. 2008); low rates of survivorship can probably be attributed to low habitat complexity and juvenile predation (Miller et al. 2006; Leber et al. 2008).

1.8 Study sites and the Mesoamerican Barrier Reef System (MBRS)

This thesis aims to advance understanding of *D. antillarum* restoration on the Mesoamerican Barrier Reef System (MBRS). The MBRS is the second largest barrier reef in the world; extending over 1000 km from the Yucatan Peninsula in Mexico to the Bay Islands of Honduras (Almada-Villela et al. 2002). The Declaration of Tulum was signed in 1997 by the presidents of Mexico, Belize, Guatemala and Honduras (Kramer and Kramer 2000), and 100 marine protected areas covering an area of 45,000 km² were established, however, most of these are considered ‘paper parks’, lacking proper enforcement (Almada-Villela et al. 2002).

Study sites for this thesis are located in Honduras, at the very southern extent of the MBRS (Fig. 1.3). Roatan and Utila are the two major constituents of the Bay Islands located approximately 40-60 km north of mainland Honduras; both are tourist hotspots which is placing their reefs under considerable stress. The reefs of the Bay Islands are the most species rich within the MBRS but, they also have the highest incidence of coral disease, with an average of 4.4% of all corals showing signs of infection (Almada-Villela et al. 2002). Banco Capiro is a reef system located about 8 km offshore from the mainland in Tela Bay on the northern coast of Honduras, roughly 60 km away from the Bay Islands.

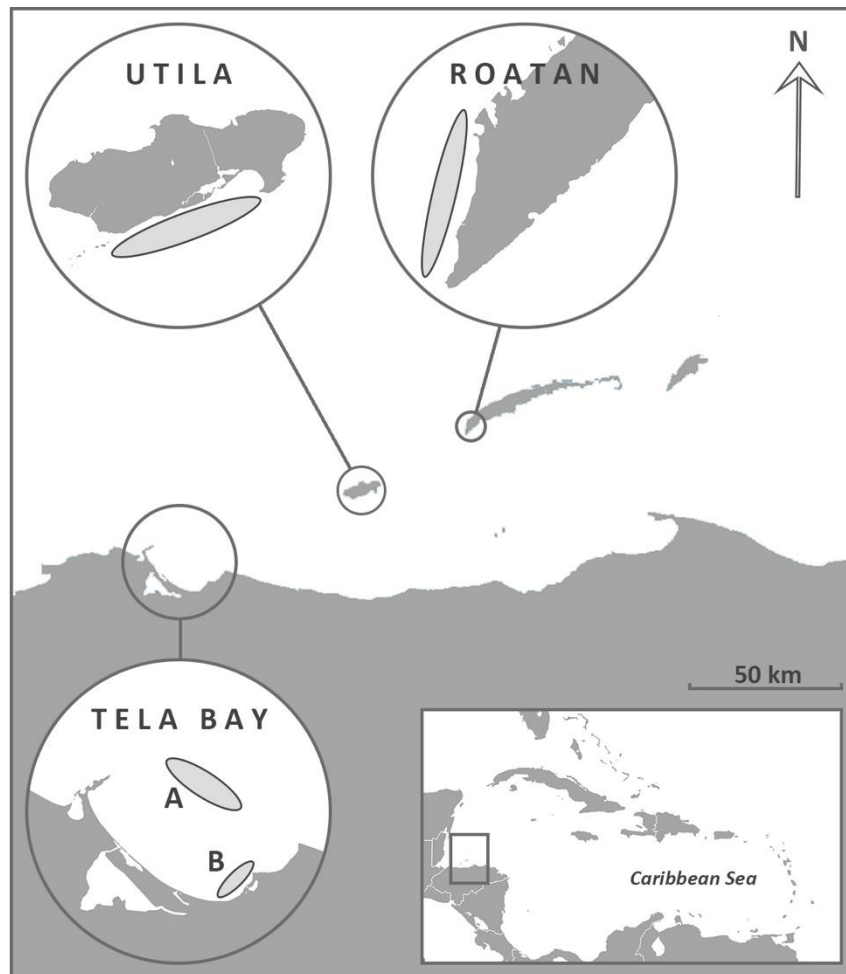


Figure 1.3. Map showing location of Honduras within the Caribbean, and location of study sites within Honduras. Grey ovals represent areas over which data were collected. Grey oval labelled 'A' = Banco Capiro; grey oval labelled 'B' = La Ensenada.

The population of Honduras doubled every 25 years throughout the 20th century and reached approximately 6.25 million by the year 2000 (Harborne et al. 2001); the current population estimate is over 9 million (Worldometers 2018). Honduran reefs are therefore threatened by increased anthropogenic disturbances (Heyman and Kjerfve 2001). There have been some attempts to protect Honduran reefs; the Acuerdo Dos places restrictions on coastal development around Roatan, but fines for non-compliance are so low that they are often cheaper than the permits (Forest 1998).

The reefs of Central America have been largely neglected by researchers despite the fact that they account for approximately 3.7% of the world's coral reefs. Honduran reef systems are particularly understudied because of Honduras' history of political unrest (Alvarado et al. 2013). At the point of publication, Alvarado et al. (2013) found only 13 peer-reviewed papers about echinoderms in Guatemala, El Salvador, Nicaragua and Honduras collectively. The paucity of data from the reefs of Honduras, coupled with the high threat level it is experiencing because of human population expansion, makes this area a research priority.

1.9 Aims and objectives

The overarching aim of this thesis is to better understand the ecology and functional role of *D. antillarum* in order to assess the potential for restoring its populations in the Caribbean. It initially focuses on the potential effects of *D. antillarum* restoration on benthic community composition and diversity relative to other conservation strategies aimed at augmenting herbivorous fish populations. It continues by presenting the first thermal tolerance work ever conducted on *D. antillarum*, and a discussion of the likely effects that rising SST will have on their future survivorship. The thesis then attempts to identify the major ecological barriers responsible for continued suppression of populations >30 years after the mass-mortality event. Finally, the results of the above studies are combined with a more in-depth exploration of the role of structural complexity in *Diadema* survival. Results are used to underpin the deployment of a series of experimental artificial reefs on a degraded reef system, and the efficacy of this as an approach to *D. antillarum* population restoration is assessed. Ultimately, it is hoped that this series of ecological assessments, behavioural studies and natural experiments will provide key

information currently missing from the literature that will help decision makers to maximise their limited conservation resources.

1.9.1 Aim one – assessing the impact of dominant grazer identity on the structure and diversity of Caribbean benthic communities

Banco Capiro is an urchin-grazed reef with *D. antillarum* population densities far in excess of those required for their ecosystem functions to be active, but with herbivorous fish biomass well below the equivalent threshold. Roatan is a fish-grazed reef, with a high herbivorous fish biomass but very low urchin population size, and Utila is an under-grazed reef where both *D. antillarum* abundance and herbivorous fish biomass are significantly lower than their ecologically relevant thresholds. Before attempting species restoration, it is important to consider the potential effects that population augmentation may have on the target ecosystem, therefore the first aim is to critically evaluate the impact that *D. antillarum* grazing has on community composition and diversity of a Caribbean coral reef relative to fish herbivory. This aim is addressed using the following objectives:

1. To assess how grazer identity impacts current metrics of coral reef health by looking at relationships between *D. antillarum* abundance and herbivorous fish biomass, and percent cover of scleractinian coral and macroalgae.
2. To assess how grazer identity impacts the diversity of four major taxonomic groups on a Caribbean coral reef; mature scleractinian coral, juvenile scleractinian coral, macroalgae, and macroinvertebrates.
3. To discuss the merits of using percent cover of scleractinian coral as a measure of ecosystem health relative to diversity metrics, and the impact that this will

have on attempts to restore *D. antillarum* populations in the context of future climatic changes.

1.9.2 Aim two – testing *D. antillarum* resilience to rising sea surface temperatures (SST) to assess their likelihood of survival in a warming world

There is an extensive literature pertaining to the likely effects of rising SST on coral physiology and future survivorship, but there is a paucity of studies looking at how key non-coral organisms will be affected by these same climatic changes. Before limited conservation resources are invested in *D. antillarum* population restoration, it is necessary to ask how future-proof they are; if it transpires that ocean warming is likely to have a large detrimental effect on *D. antillarum* fitness, management resources may be more effective if allocated to other initiatives. Reef flattening has left *D. antillarum* vulnerable to predation and they are therefore increasingly reliant on their innate predator avoidance behaviours (PAB), defined as the number of long-defensive spines that move in response to a shadow/predatory stimulus. The second aim is therefore to assess how the near- (by 2039) and long-term (by 2100) temperature increases predicted by the Intergovernmental Panel on Climate Change (IPCC) may affect future survivorship of *D. antillarum*, and to discuss the implications of these findings for population restoration efforts in a warming world. The following objectives are encompassed by this aim:

1. To use lab-based trials to assess differences of innate *D. antillarum* predator avoidance behaviours (PAB) between three different climate change scenarios;

- (i) Current SST (CSST) = 29.7°C, (ii) Medium severity scenario = CSST + 1.4°C, (iii) Worst-case scenario = CSST +3.1°C.
2. To assess how life-history stage (i.e. adult or juvenile) attenuates observed responses.
 3. To assess how adult phenotype (i.e. black-spined or white-spined) affects observed responses.
 4. To incorporate a site comparison of Utila and Banco Capiro, to see how differences in the level of habitat structure at the individual's site of origin may alter relationships between *D. antillarum* PAB and SST. Results of this objective enable assessment of the role that habitat structure has to play in protecting *D. antillarum* populations in the future.

1.9.3 Aim three – exploring ecological barriers to D. antillarum population recovery

With scleractinian coral cover of just 12%, and *D. antillarum* population densities <0.01 m⁻² (Bodmer et al. 2015; Chapter 5), Utila is representative of a ‘typical’ Caribbean coral reef ecosystem. Banco Capiro, on the other hand, boasts a mean scleractinian coral cover of 62%, and *D. antillarum* population densities >2 m⁻² (Bodmer et al. 2015; Chapter 5), and is therefore an ‘atypical’ reef system that may be the healthiest found in the Caribbean today. The third aim of this thesis is to compare these two highly contrasting reefs systems and identify the ecological variable(s) that may account for the three order of magnitude difference in *D. antillarum* population size. This aim is achieved using the following objectives:

1. To use replicate surveys to quantify differences in the levels of numerous ecological variables of interest that have been hypothesised to prevent *D. antillarum* population recovery. Abundances of the following are assessed; (i) Scleractinian hard coral cover, (ii) Macroalgae cover, (iii) Heterospecific competitor abundance, (iv) Interspecific fish competitor abundance, (v) *D. antillarum* fish predator abundance, (vi) Habitat Assessment Scores (HAS; Gratwicke and Speight 2005) used to estimate reef complexity.
2. To use correlative analyses to assess the impact of each variable of interest on *D. antillarum* population size.
3. To look for key differences in the above relationships between Utila and Banco Capiro, thus enabling identification of a variable that can account for the large discrepancy in *D. antillarum* population size.

1.9.4 Aim four – assessing the ecological importance of habitat structure for D. antillarum and evaluating the use of artificial reefs as a population restoration strategy

Results from the studies used to address aims 1-3 indicate the following; (1) *D. antillarum* population restoration will help secure the future of Caribbean coral reefs, (2) *D. antillarum* are likely to be somewhat resilient to imminent increases in SST, and individuals from more structured reefs may be afforded a degree of protection against any negative consequences associated with climate change, (3) Populations are failing to recover from mass-mortality because associated processes of reef flattening have created a dearth of refugia and left individuals vulnerable to predation. These findings reveal that support of *D. antillarum* populations through the deployment of artificial reefs may be an appropriate management strategy. The fourth

and final aim of this thesis is to couple findings from novel 3D models used to elucidate *in-situ* *D. antillarum* habitat preferences, with *ex-situ* lab-based climate change trials to assess whether provision of artificial structure is a viable conservation strategy for population restoration. The chapter concludes by evaluating the impact that deployment of 30 experimental artificial reefs had on *D. antillarum* population size, and associated metrics of reef health, on a degraded Caribbean reef system between 2015 and 2017. The objectives were as follows:

1. To use new and highly accurate 3D modelling technologies to demonstrate that *D. antillarum* preferentially select areas of high habitat complexity.
2. To build on the behavioural studies used to address aim two, and experimentally investigate the hypothesis that habitat structure has an important role to play in mitigating the negative fitness effect of rising SST. Together, objectives 1 and 2 provide two further lines of evidence in support of the use of artificial reef structures as a mechanism for promoting *D. antillarum* population restoration.
3. To use a combination of macroinvertebrate population assessments and photo quadrats to evaluate changes in *D. antillarum* population status and associated metrics of ecosystem health after deployment of 30 experimental artificial reefs on a degraded Caribbean reef system over three successive field seasons from 2015 to 2017.

2 Chapter Two – The impact of dominant grazer identity on the diversity of Caribbean coral reef benthic and macroinvertebrate communities: a natural experiment

2.1 Thesis logic: part one

D. antillarum is widely accepted as an important Caribbean coral reef herbivore, and its restoration is therefore a priority for the region. However, the relative merits of urchin conservation initiatives versus those aimed at protecting herbivorous fish populations are debated. In a world of limited time, manpower, and financial resource, it is essential that managers are provided with adequate information to make the decisions that will most benefit coral reefs in the region. The first step in a thesis aiming to identify a viable method to stimulate *D. antillarum* recovery, is therefore to assess the likely impacts that this initiative will have on the diversity and community composition of target reefs in relation to other proposed strategies. Data presented in Chapter 2, show how various metrics of reef health differ between urchin-grazed and fish-grazed reefs, and therefore enable assessment of the potential utility of *D. antillarum* restoration.

2.2 Chapter summary

Long-term trends in the decline of Caribbean coral reef health have been precipitated by the loss of herbivory associated with overfishing and disease. Historically, the long-spined sea urchin, *Diadema antillarum*, and herbivorous fish belonging to the Acanthuridae and Scaridae families, have been the dominant reef grazers, and their restoration is therefore a conservation priority for the region. The relative importance of urchins and fish is debated, but studies suggest that biomass thresholds of $\sim 80 \text{ g m}^{-2}$ and $\sim 18 \text{ g m}^{-2}$, respectively, must be exceeded for ecosystem functions to occur. Here, a natural gradient of herbivore biomass and dominant grazer across three reef systems in Honduras is used to assess the differential impacts of fish versus urchin grazing on the structure and diversity of Caribbean benthic communities; Banco Capiro is classified as an urchin-grazed reef, Roatan is a fish-grazed reef, and Utila is an under-grazed reef. Urchin grazing is shown to maintain abundant coral communities ($67.98 \pm 11.76 \%$ cover) of fast-growing taxa, which provide complex structure and thus promote macroinvertebrate diversity. It is predicted that anthropogenic disturbances throughout the Caribbean will create a stable state dominated by fast-growing coral taxa, and this change in community composition may be facilitated by *D. antillarum* grazing behaviours. However, coral diversity is lower on urchin-grazed than fish-grazed reefs, and therefore resilience may be reduced. Restoration of *D. antillarum* populations in the short-term may facilitate macroalgal phase shift reversal but reductions in diversity may leave reefs vulnerable to collapse. *D. antillarum* restoration efforts should be coupled with longer-term management strategies aimed at increasing fish herbivore biomass to maximise coral cover and diversity of the macroinvertebrate community whilst also boosting long-term ecosystem resilience.

2.3 Introduction

Cost-benefit analysis of ecosystem restoration efforts has revealed that, in comparison to nine other major biomes, coral reefs require the greatest resource input for the smallest gains (de Groot et al. 2012). On coral reefs therefore, prevention is far better than a cure: conservationists should be focussed on slowing, and ultimately stopping, declines in reef health, rather than hoping to rebuild them from the bottom-up. Globally, loss of herbivores, through a combination of disease and overfishing is a major contributor to scleractinian coral loss (Jackson et al. 2001), but because of a comparative lack of functional redundancy (Nystrom and Folke 2001; Mumby et al. 2007; Hughes et al. 2010), the effects are most keenly felt in the Caribbean (Pandolfi et al. 2003). The result is a phase shift towards dominance by macroalgae at the expense of coral cover (Kramer 2003; Norstrom et al. 2009). The link between diversity and ecosystem persistence is an important consideration for managers aiming to conserve coral reefs, and highlights the need for interventions to be designed in line with the precautionary principle to protect as much diversity as possible (Lauck et al. 1998; Bellwood et al. 2004; Mumby et al. 2006).

Species belonging to the parrotfish (Scaridae) and surgeonfish (Acanthuridae) families are the dominant fish herbivores on Caribbean reefs (Lewis 1986; Williams et al. 2001), and numerous studies have found clear negative relationships between herbivorous fish biomass and macroalgae abundance (e.g. Mumby et al. 2007; Edwards et al. 2014); according to assessments made by Williams and Polunin (2001), the healthiest reefs in the Caribbean should have a combined Scaridae and Acanthuridae biomass of $\sim 18 \text{ g m}^{-2}$. Historical overfishing has impacted the Caribbean for 1000s of years (Jackson et al. 2001), and herbivorous fish exclusion experiments demonstrating macroalgal increases from 4% to 53% (Hughes et al. 2007) indicate

that the steady decline of Scaridae and Acanthuridae is one of the likely drivers of Caribbean-wide macroalgal phase shifts. *D. antillarum* is the other dominant macroalgal grazer in the Caribbean (Carpenter and Edmunds 2006; Macia et al. 2007; Lessios 2016), and population densities exceeding one individual m⁻² are required for them to have an ecosystem-level impact (Mumby et al. 2006).

While many researchers agree that healthy populations of herbivorous fish and *D. antillarum* are both required to maintain Caribbean coral dominance (e.g. Williams et al. 2001; Williams and Polunin 2001; Mumby et al. 2006; Roff and Mumby 2012; Williams et al. 2017), there is significant debate surrounding the relative contribution of feeding behaviours in each of these taxonomic groups to overall grazing intensity, and their role in structuring the benthic community. Several studies find no relationship between *D. antillarum* abundance and macroalgae cover (Lacey et al. 2013; Cramer et al. 2016, 2017), others state that urchin grazing is only important on heavily overfished reefs (Bruno et al. 2009), and Morrison (1988) indicates that the impact of *D. antillarum* is restricted to the shallows.

A recent analysis of the fossil record also suggests that *D. antillarum* has in fact been rare over the last 3000 years (Cramer et al. 2016). The study proposes that, throughout this time period, scleractinian coral cover has been largely determined by parrotfish abundance, and that there is no evidence of a causal relationship with *D. antillarum* population density (Greenstein 1989; Cramer et al. 2016). These findings support the assertion that the historical importance of *D. antillarum* has been overstated, because populations immediately prior to the mass-mortality were artificially inflated as an indirect consequence of overfishing of their predators (Bruno et al. 2009). However, conclusions drawn from these studies must be treated with caution as echinoids are often underrepresented in the fossil record due to the fragility

of the tests and spines (Greenstein 1989; Donovan 2005). One must also consider that overfishing is not a recent phenomenon (Jackson 2001), so the importance of *D. antillarum* ecosystem functions in recent centuries and decades is a primary concern, regardless of their significance in past millennia.

Many studies contradict these conclusions and suggest that *D. antillarum* is more important than herbivorous fish. Robertson (1991) found that after the mass-mortality Acanthuridae abundance increased by 160-250% but, despite this, macroalgae continued to proliferate to the detriment of scleractinian coral. Enhanced acanthurid numbers may have failed to control the macroalgal overgrowth because the grazing behaviours of herbivorous fish are only effective when macroalgae abundances are relatively low (Hoey and Bellwood 2011). If these assertions are correct, then as macroalgal abundance continues to rise, herbivorous fish may become increasingly ineffective at maintaining Caribbean coral reef health. Most studies attempt to estimate the relative impacts that fish and urchins have on benthic composition, but Carpenter (1988) identified differences in macroalgae physiology driven by dissimilarities in the structure of the grazing community. He concluded that urchin-grazed reefs have a higher rate of primary productivity than fish-grazed reefs, and are therefore able to support a higher level of total biodiversity.

Disagreements over the relative importance of urchin-grazing and fish-grazing create difficulties in identifying the most appropriate conservation management strategies. Most studies evaluating the impact of grazing use the relative percentage covers of scleractinian coral and macroalgae as their metric of ecosystem health (Gardner et al. 2003; Kramer 2003), and very few, if any, assess the effect that grazer identity has on the *diversity* of the benthic community. If the precautionary principle is invoked, conservationists should be primarily concerned with protecting

biodiversity and function to confer ecosystem resilience (Mumby et al. 2007; Hughes et al. 2010) rather than simply promoting increased coral cover. Prioritising abundance over diversity may ultimately miss fundamental changes in the functioning of coral reefs.

Limited resources force managers to make value judgements to prioritise conservation targets and strategies, meaning it is vital for proxies to accurately reflect the ecological dynamics of target systems so that informed decisions can be made. Many researchers advocate a single-species approach to Caribbean reef conservation and suggest that efforts should be focussed on *D. antillarum* population restoration (Nedimyer and Moe 2003; Macia et al. 2007; Precht and Precht 2015). If successful, it will almost certainly increase scleractinian coral cover throughout the region, but the biodiversity impacts of this strategy, relative to alternative conservation initiatives focussed on protection of herbivorous fish, have not yet been assessed.

Previous studies have shown that *D. antillarum* abundances $>1 \text{ m}^{-2}$ (Mumby et al. 2006), and herbivorous fish biomasses $>18 \text{ g m}^{-2}$ (Williams et al. 2001) are required for their ecosystem functions to be active. Here, these thresholds are used to identify a natural gradient of herbivore abundance and biomass that exists across three geographically related but ecologically dissimilar reef systems along the northern coast of Honduras; Banco Capiro (Tela Bay), Utila and Roatan. This natural gradient is used to assess the relative impacts of fish and urchin grazing on the structure and diversity of Caribbean benthic communities. The impact that grazer identity has on Caribbean coral reefs is then elucidated by:

1. Establishing the nature and extent of grazing in the three reef systems.
2. Assessing differences in relative percentage covers of scleractinian coral and macroalgae, and the abundance of juvenile coral recruits in relation to grazing type.
3. Assessing differences in the diversity and community composition of the major components of the benthic community, including mature scleractinian corals, juvenile scleractinian corals, macroalgae and macroinvertebrates.

2.4 Methods

2.4.1 Site description

Data were collected in June-August 2016 on three reef systems on the northern coast of Honduras (Fig. 1.3). According to currently accepted metrics, with average scleractinian coral and macroalgae covers of 62% and 7% respectively (Bodmer et al. 2015; Chapter 5), Banco Capiro is one of the healthiest reefs in the Caribbean, but it has been heavily exploited by artisanal fishers for many decades. In 2017, Tela Bay, encompassing Banco Capiro, was granted status as a marine protected area (MPA) by the Honduran government but so far little has been done to enforce new regulations. This contrasts starkly with the grassroots establishment of the Roatan Marine Park (RMP) in 1989, which has proved relatively successful at protecting the reefs of the island. Protection afforded by the RMP has aided the maintenance of a mean scleractinian coral cover of ~30%, but a high mean macroalgae cover of up to 33% (HRI 2012). Despite efforts from local conservation organisations, the reefs around the south shore of Utila remain unprotected and, with mean scleractinian coral and macroalgal covers of 12% and 41% respectively (Bodmer et al. 2015; Chapter 5), it can be considered more representative of the wider Caribbean.

All surveys were conducted using SCUBA. Twenty replicate 2 x 30m belt transects were completed on each reef system at a consistent depth of 10 m. Between five and 10 study sites were selected on each reef system (Table 2.1) to encompass a suitable geographical range to provide accurate representations of the reef systems as a whole. Between two and seven surveys were completed at each study site, and pseudoreplication was avoided by following a different compass heading for each replicate. *D. antillarum* abundance, herbivorous fish biomass, juvenile coral recruit abundance, macroinvertebrate abundance, and relative percentage cover of the benthos were all quantified on every survey. All replicates across the study sites were pooled so that the total replicate number for each reef system (Banco Capiro, Utila and Roatan) was twenty.

2.4.2 Assessing benthic community composition and diversity

Line-point intercept transects were used to calculate benthic cover. The 30 m transect tape was filmed by holding a GoPro Hero 4 (1080 HD, 60 frames per sec) video camera approximately 15-30cm above the seafloor, and the benthic component lying under the tape at every 25 cm interval was recorded to species level. One hundred and twenty data points were generated for each transect and these were converted to an estimate of the relative percent cover of the following groups; scleractinian coral, fleshy macroalgae, turf algae, sponge, octocoral, other sessile benthic invertebrates (e.g. zoanthids), and non-biotic features (i.e. sand, rock, rubble and dead coral). The 120 data points were also tallied by species so that diversity indices and matrices could be calculated.

Table 2.1. GPS coordinates of the mooring buoys from which transects were conducted and number of replicate transects for each surveyed study site in the Honduran reef systems of Banco Capiro, Utila and Roatan.

Banco Capiro		
Site	GPS	n
Aldrid's	N 15.86496 W 87.49841	7
Butterfingers	N 15.86351 W 87.49525	5
Canyon	N 15.86414 W 87.50662	2
Kisci's Garden	N 15.86550 W 87.50017	3
Mushroom Mountain	N 15.86497 W 87.49730	3
Utila		
Site	GPS	n
Black Coral Wall	N 16.08305 W 86.91699	3
Coral View	N 16.08823 W 86.91094	2
Lighthouse	N 16.08498 W 86.90032	3
Little Bight	N 16.07926 W 86.92942	4
Stingray Point	N 16.06890 W 86.95477	4
Sturch Bank	N 16.08960 W 86.90350	4
Roatan		
Site	GPS	n
Bikini Bottom	N 16.29783 W 86.60091	2
Black Rock	N 16.25131 W 85.57065	2
Blue Channel	N 16.29951 W 86.60091	2
Divemaster's Choice	N 16.18828 W 86.35507	2
El Aquario	N 16.30246 W 86.59821	2
Moonlight	N 16.30546 W 86.59741	2
The Bight	N 16.29783 W 86.60052	2
Turtle Crossing 1	N 16.29351 W 86.60373	2
Turtle Crossing 2	N 16.29280 W 86.60259	2
Turtle Crossing 3	N 16.29216 W 86.60363	2

2.4.3 Quantifying grazing and juvenile coral recruit and macroinvertebrate abundances

Stereo-video technology allows dual-footage of transects to be collected from a precision-manufactured housing that, once calibrated, facilitates accurate fish length measurements and more accurate sample area control. Stereo-video surveys (SVS) were used in conjunction with EventMeasure software v3.51 (SeaGIS, Melbourne,

Australia) to quantify Scaridae and Acanthuridae biomass. Over the study period, two SVS systems were deployed; one using Cannon HFS21 cameras and the other using GoPro Hero 3 Silver editions. Each SVS transect was 30 m long, and the parameters of the EventMeasure software were set so that fish were only measured when within 2.5 m either side of, and 5 m above, the camera system; for further details of the SVS protocol see Watson et al. (2010), and Andradi-Brown et al. (2016). The mass of individual fish was estimated by combining length measurements provided by EventMeasure with known conversion constants extracted from Fishbase, using the formula $W = aL^b$ (W = weight, L = length, and a and b = species specific conversion constants). Individual masses from all Acanthuridae and Scaridae encountered on the transect were combined and then converted to a biomass estimate of ‘herbivorous fish biomass g m^{-2} ’.

D. antillarum abundance was assessed using 30 x 2m belt transects. The urchin surveyor would swim 1m either side of the transect tape recording the number of individuals encountered within the 60 m^2 survey area, and these values were transformed to *D. antillarum* individuals m^{-2} . On Banco Capiro and Utila, a subsample of individuals was removed from the reef ($n = 100$ from each reef system), using techniques outlined in Bodmer et al. (2017; Chapter 3), and their mass was recorded to the nearest 0.1 g. *D. antillarum* biomass per m^2 was calculated by multiplying the population density estimates by the mean mass of individuals from the reef system. Logistical and time constraints mean that these data were unavailable from Roatan but *D. antillarum* mass does not vary hugely by geographical region, therefore the mean values from Banco Capiro and Utila were used to estimate these metrics.

Along each transect, the number of juvenile coral recruits (defined as any scleractinian coral colony measuring <4 cm in their longest dimension as per Edmunds and Carpenter (2001)) was also counted as well as macroinvertebrates, both on a per m² basis. All individuals were identified to the highest possible taxonomic resolution.

2.4.4 Statistical methods

Kruskall-Wallis and Conover-Iman post-hoc tests including the Bonferroni correction were conducted to assess how each ecological variable differed by reef system. A series of Generalised Linear Models (GLMs) were then used to assess how percentage cover of scleractinian coral, fleshy macroalgae and turf algae relate to *D. antillarum* biomass, herbivorous fish biomass and site. Benthic cover values were converted to proportions and GLMs with quasi-binomial error terms were run to account for overdispersion in the data. The relationship between the abundance of juvenile coral recruits and herbivores was tested using a GLM assuming a Poisson distribution. In all cases, model selection was performed using hypothesis testing, and analyses were carried out in R v. 3.3.1 (R Core Team 2016) and RStudio v0.99.903 (RStudio Team 2015).

The species richness of mature and juvenile scleractinian corals, fleshy macroalgae, and macroinvertebrates was quantified and Simpson's Diversity Indices (SI) were calculated for each of these taxonomic groups. SI was calculated for each taxonomic group on each transect using the following formula: $1 - \sum \frac{N(N-1)}{\sum n(n-1)}$, where N = total number of individuals found, and n = total number of individuals of each species. Differences in diversity between sites were tested in PRIMER 7 (Clarke and Gorley 2015) using ANOSIM, and visual represented using non-metric multidimensional scaling (nMDS). Prior to construction of the dissimilarity matrices,

data were square-root transformed to reduce the impact of dominant species. Similarity percentage (SIMPER) analysis identified the factors associated with diversity disparities, whilst RELATE and BEST analyses were employed to investigate whether observed differences between site could be attributed to variation in *D. antillarum* abundance and/or herbivorous fish biomass.

2.5 Results

2.5.1 Benthic composition

Both metrics of coral health differed significantly amongst all three reef systems; hard coral cover (Fig. 2.1c) was two- and three-fold higher on Banco Capiro (67.98 ± 2.63 %; mean \pm 1SE) than Roatan (33.43 ± 1.57 %) and Utila (22.23 ± 1.66 %) respectively ($H_2 = 44.53$, $p < 0.001$). This corresponded to similar differences in the abundance of juvenile coral recruits ($H_2 = 40.91$, $p = 1.31 \times 10^{-9}$); Banco Capiro had 3.02 ± 0.30 individuals m^{-2} , Roatan had 1.69 ± 0.10 individuals m^{-2} , and Utila had just 0.76 ± 0.06 individuals m^{-2} (Fig. 2.1b). Given these findings, differences in the abundance of fleshy macroalgae (e.g. *Dictyota* spp.) match expectations, with coverage on Banco Capiro (12.85 ± 1.58 %) being ca. 50% lower than on Roatan (25.58 ± 1.48 %), which in turn, was ca. 20% lower than on Utila (32.62 ± 2.07 %) (Fig. 2.1e). Whilst the percentage cover of turf algae on Banco Capiro (4.83 ± 0.57 %) remained lower than on either of the other sites, it did not differ significantly from that found on Utila (5.96 ± 0.78 %). However, despite Roatan being the intermediary for all other benthic components, turf algae cover (12.48 ± 1.39 %) was up to three times higher ($H_2 = 22.54$, $p < 0.001$) (Fig. 2.1f).

2.5.2 Grazing levels in relation to benthic composition

The mean mass of adult *D. antillarum* from this study was 83.53 ± 4.27 g. When combined with the findings of Mumby et al. (2006), this implies that a mean *D. antillarum* biomass of 83.53 ± 4.27 g m⁻² is required for their ecosystem functions to be activated. Herbivorous fish biomass of 18 g m⁻² is required for fish grazing to impact benthic communities in the Caribbean (Williams et al. 2001), therefore these threshold values can be used to assign reefs to one of four grazing categories; fully-grazed, urchin-grazed, fish-grazed and under-grazed.

On Banco Capiro, the mean abundance of *D. antillarum* was 1.32 ± 0.08 individuals m⁻², and the average mass of an individual was 84.10 ± 3.36 g, meaning that the average urchin biomass was 111.01 ± 1.28 g m⁻². With a mean value of 1.28 ± 0.52 g m⁻², herbivorous fish biomass on Banco Capiro was two orders of magnitude lower than the urchin biomass, and only ca. 7% of the required grazing threshold. Banco Capiro can therefore be classified as an urchin-grazed reef.

Conversely, Roatan can be designated as a fish-grazed reef. Herbivorous fish biomass exceeded the ecological relevance threshold at 28.37 ± 13.16 g m⁻². However, with *D. antillarum* densities of only 0.07 ± 0.02 m⁻², urchin biomass on Roatan (5.85 ± 0.43 g m⁻²) is 14-times lower than the threshold requirement for urchin-grazing.

On Utila, *D. antillarum* had an average mass of 82.95 ± 5.17 g and mean population density of 0.004 ± 0.002 m⁻², which equates to a biomass of just 0.33 ± 0.05 g m⁻². When coupled with herbivorous fish biomass of just 6.11 ± 1.79 g m⁻², Utila can be classified as an under-grazed reef. Significant differences in herbivorous fish ($H_2 = 24.82$, $p < 0.001$), and *D. antillarum* ($H_2 = 45.23$, $p < 0.001$) biomasses were identified between all sites (Fig. 2.1a; Fig. 2.1b).

When the effects of *D. antillarum* abundance, herbivorous fish biomass and site were tested against each component of benthic composition, no interactions were significant, and they were dropped from the models. *D. antillarum* population size had a positive relationship with hard coral cover ($F_1 = 5.00, p = 0.03$) and abundance of juvenile coral recruits ($F_1 = 5.87, p = 0.02$), and a negative relationship with fleshy macroalgae cover ($F_1 = 13.48, p < 0.001$). There was no relationship between *D. antillarum* density and cover of turf algae ($F_1 = 1.59, p = 0.21$) (Fig. 2.2).

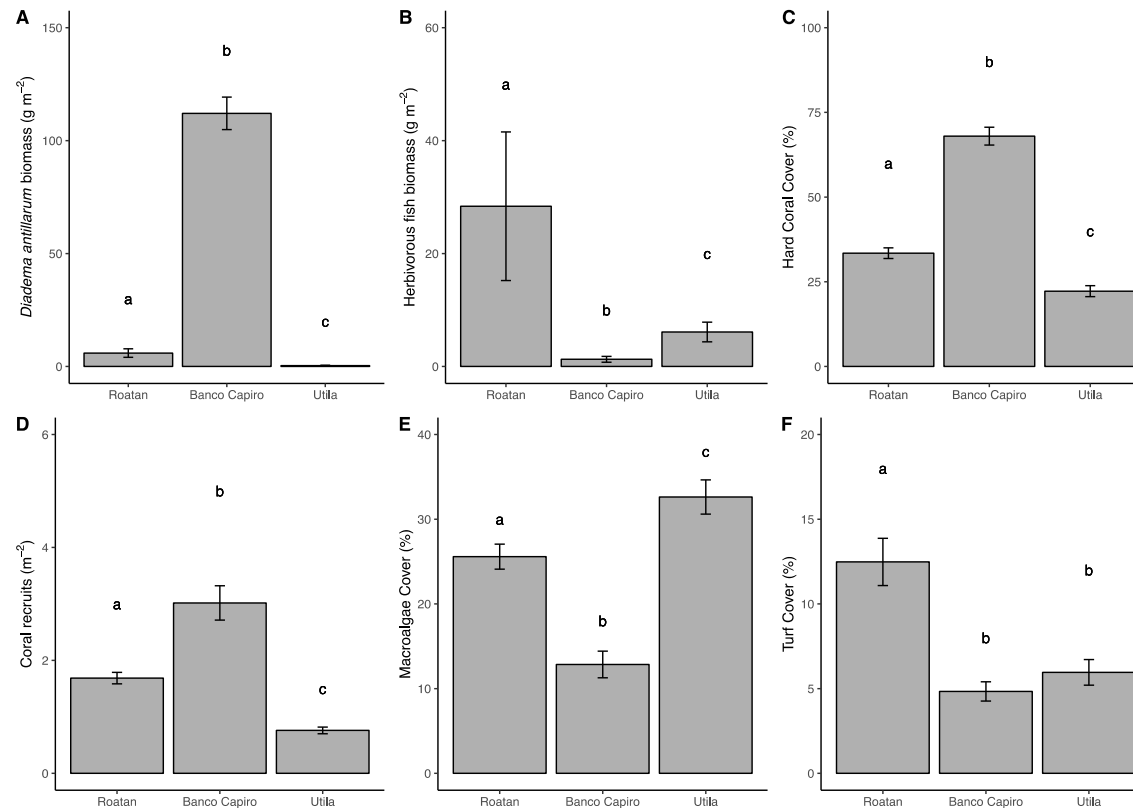


Figure 2.1. Differences in the relative abundances of different ecological variables of interest between a fish-grazed reef (Roatan), an urchin-grazed reef (Banco Capiro), and an under-grazed reef (Utila). Moving clockwise from the top left, variation in the following is shown; 2.2a. *D. antillarum* abundance, 2.2b. Herbivorous fish biomass, 2.2c. Scleractinian coral cover, 2.2d. Abundance of juvenile coral recruits, 2.2e. Fleshy macroalgae cover, and, 2.2f. Turf algae cover. Bars and error lines represent mean \pm 1SE, and post-hoc letter assignments show where differences lie.

There was no relationship between herbivorous fish biomass and hard coral cover ($F_1 = 1.07, p = 0.30$), abundance of juvenile coral recruits ($F_1 = 1.12, p = 0.29$), or fleshy macroalgae cover ($F_1 = 0.01, p = 0.92$), but there was a significant negative relationship between herbivorous fish biomass and turf algae cover ($F_1 = 6.82, p = 0.01$) (Fig. 2.2).

2.5.3 Coral species diversity

The diversity of mature coral colonies differed significantly between all study sites ($R = 0.78; p = 0.001$) (Fig. 2.3). Species richness on Banco Capiro (7.15 \pm 0.60 species per transect) was ca. 40% lower than on Roatan (12.20 \pm 0.47 species per transect) and Utila (11.90 \pm 0.67 species per transect) ($F = 15.77; p < 0.001$), and this difference was reflected in the Simpson's Diversity Index (SI) ($F = 114.10; p < 0.001$; Banco Capiro = 0.44 \pm 0.04; Utila = 0.88 \pm 0.01; Roatan = 0.85 \pm 0.01) (Fig. 2.4). With an average dissimilarity of 77.41%, SIMPER analysis revealed that the greatest disparity in diversity of mature coral colonies existed between Banco Capiro and Utila. Relative abundances of *Undaria tenuifolia*, *Porites asteroides*, *U. agracites* and *Orbicella annularis* accounted for >50% of this observed difference, and variation in the distribution of these same four species also largely accounted for the 73.14% dissimilarity observed between Banco Capiro and Roatan. Although the diversity of mature coral colonies differed significantly between Roatan and Utila, the average dissimilarity value of 54.03% means that these two reef systems were more similar to each other than either was to Banco Capiro.

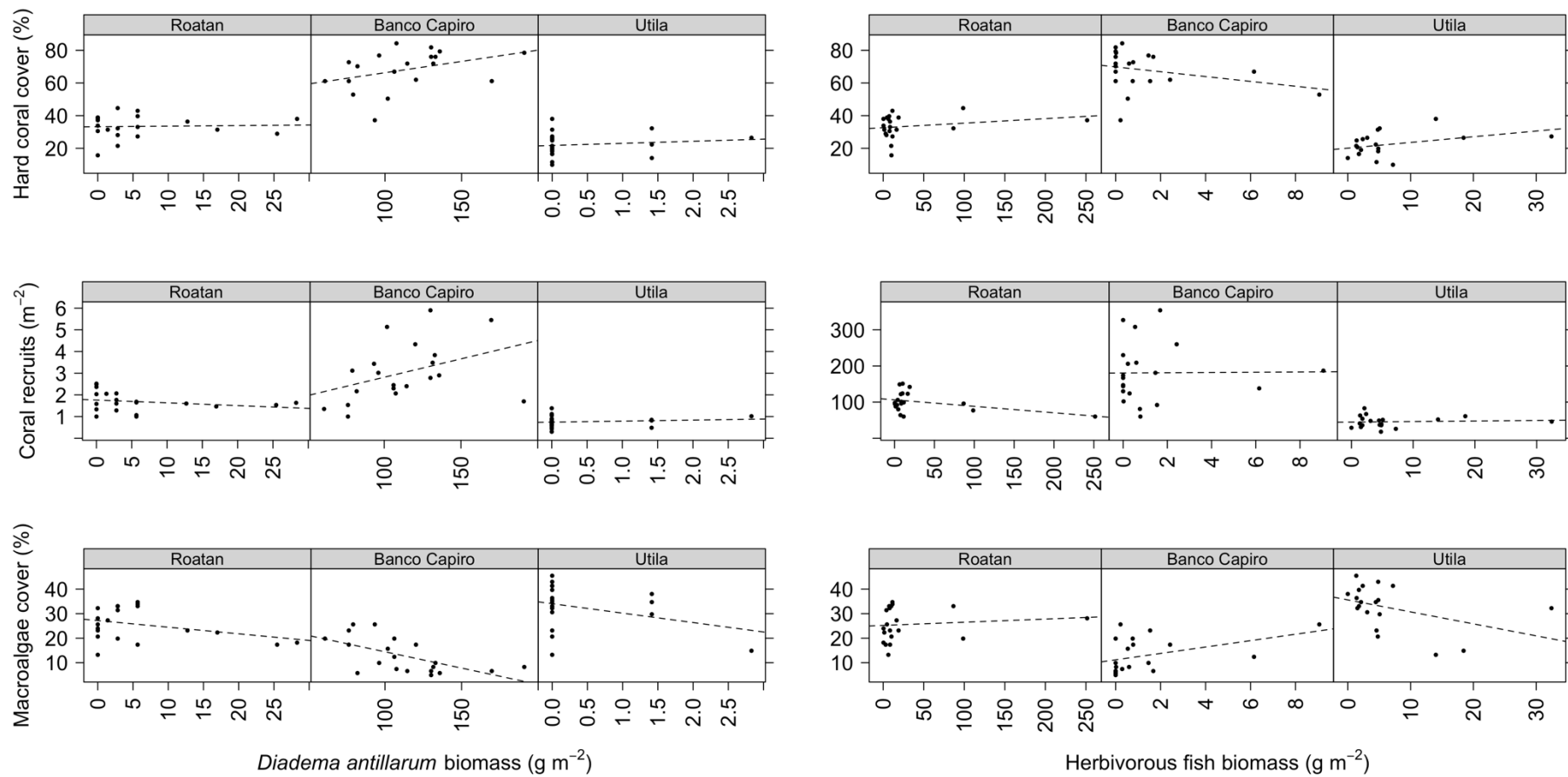


Figure 2.2. Relationships between *D. antillarum* abundance and herbivorous fish biomass and different metrics of coral reef health including; percent cover of scleractinian coral, fleshy macroalgae and turf algae, and abundance of juvenile coral recruits.

Whilst the difference in diversity between reef systems was lower than for their adult counterparts (Figs. 2.4 and 2.5), the same patterns of variation were observed in the juvenile coral recruits ($R = 0.72$; $p = 0.001$) (Fig. 2.3). On Utila (0.87 ± 0.01) and Roatan (0.85 ± 0.01), the SI values for juvenile coral diversity were similar, but diversity on Banco Capiro (0.71 ± 0.02) was 18% and 16% lower, respectively ($F = 32.45$; $p < 0.001$) (Fig. 2.4). Again, this finding is supported when species richness is used as the diversity metric ($F = 25.13$; $p < 0.001$); Banco Capiro (8.75 ± 0.61 species 60m^{-2}) has the lowest coral recruit diversity, and Utila (11.90 ± 0.67 species 60m^{-2}) is less diverse than Roatan (14.85 ± 0.54 species 60m^{-2}) (Fig. 2.5).

Again, >50% of the 66.72% dissimilarity between Utila and Banco Capiro was explained by differences in *U. tenuifolia*, *P. asteroides*, *U. agracites* and *O. annularis*, and these four species explain ca. 40% of the 59.84% dissimilarity between Roatan and Banco Capiro. When Utila and Roatan were compared, the average dissimilarity value was 49.55%, meaning that the composition of the juvenile coral community was more similar than that of the mature corals.

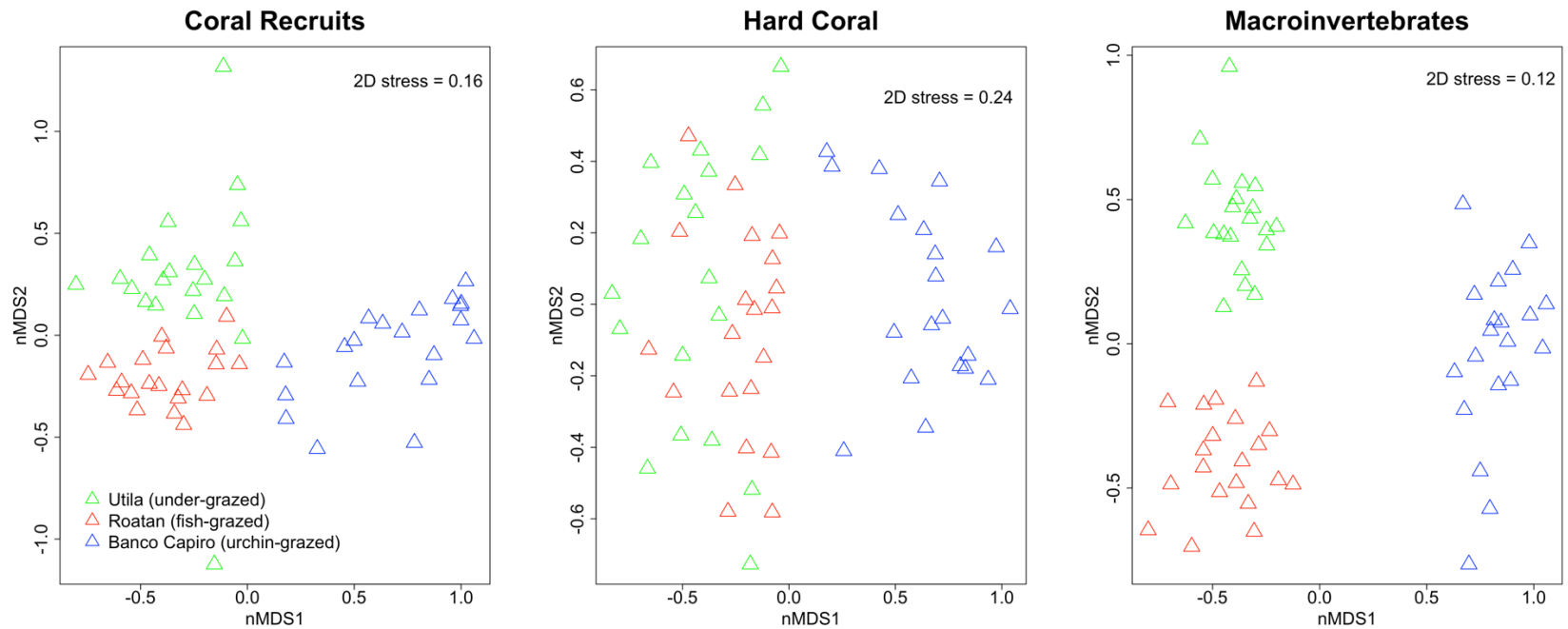


Figure 2.3. Non-metric multidimensional scaling (nMDS) plot showing dissimilarity in the diversity of juvenile scleractinian corals, hard coral, and macroinvertebrates between a fish-grazed reef (Roatan), an urchin-grazed reef (Banco Capiro), and an under-grazed reef (Utila). For the coral recruit community SIMPER average dissimilarity values; Roatan : Banco Capiro = 60%, Roatan : Utila = 50%, Banco Capiro : Utila = 67%. For mature hard coral SIMPER average dissimilarity values; Roatan : Banco Capiro = 73%, Roatan : Utila = 54%, Banco Capiro : Utila = 77%. Macroinvertebrate community SIMPER average dissimilarity; Roatan : Banco Capiro = 62%, Roatan : Utila = 81%, Banco Capiro : Utila = 78%.

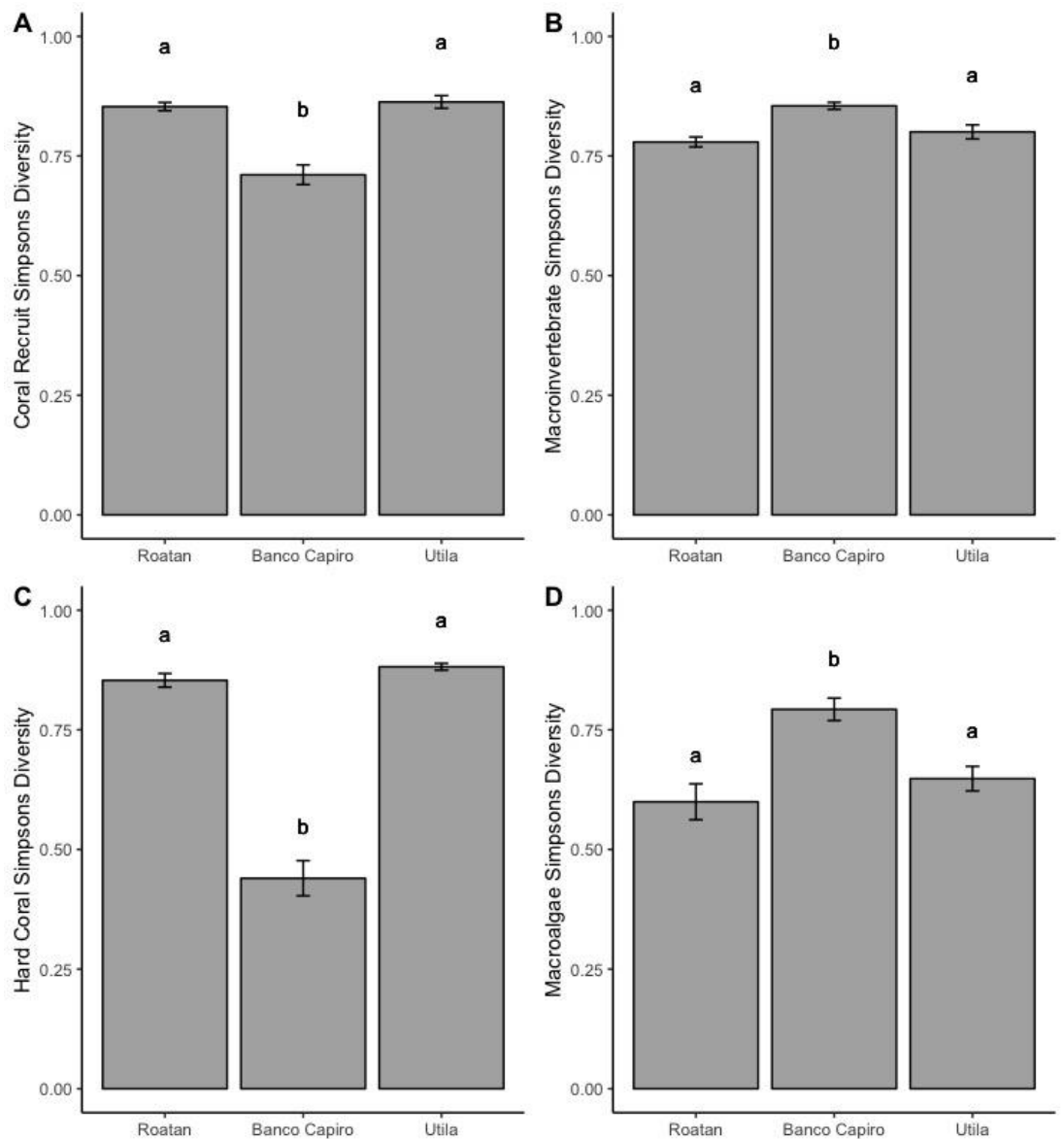


Figure 2.4. Comparison of means (SE) of Simpson's Diversity Indices for (A) juvenile coral recruits, (B) mature hard coral, (C) macroinvertebrates and (D) macroalgae between Roatan (a fish-grazed reef), Banco Capiro (an urchin-grazed reef), and Utila (an under-grazed reef). Bars and error lines represent mean \pm 1SE, and post-hoc letter assignments show where differences lie.

When SI was used as the diversity metric, macroinvertebrate diversity was significantly higher on Banco Capiro (0.85 ± 0.01) than on Roatan (0.78 ± 0.01) and Utila (0.80 ± 0.01) ($F = 105.2$; $p < 0.001$) (Fig. 2.4). Species richness between Banco

Capiro and Roatan differed by <1 species 60m^{-2} ($F = 1.51$; $p = 0.71$), but the average dissimilarity between the two sites was 61.66%. 50% of this dissimilarity could be assigned to differences in the relative abundances of *Siphonodictyon coralliphagum* (a yellow encrusting sponge) and sea pens (both of which were entirely absent from Banco Capiro), *Diadema antillarum*, sea rods (octocorals) and *Rhaphidophylus venosus* (an orange encrusting sponge). Macroinvertebrate diversity on Utila had an intermediate SI value of 0.80 ± 0.01 , but a significantly lower species richness than either of the other study sites (Utila = 10.10 ± 0.39 species 60m^{-2} ; Banco Capiro = 21.50 ± 0.54 species 60m^{-2} ; Roatan = 22.25 ± 0.94 species 60m^{-2}) ($F = 105.20$; $p < 0.001$) (Fig. 2.5), and SIMPER analysis revealed that it was slightly more similar to Banco Capiro (average dissimilarity = 77.95%) than Roatan (average dissimilarity = 80.81%).

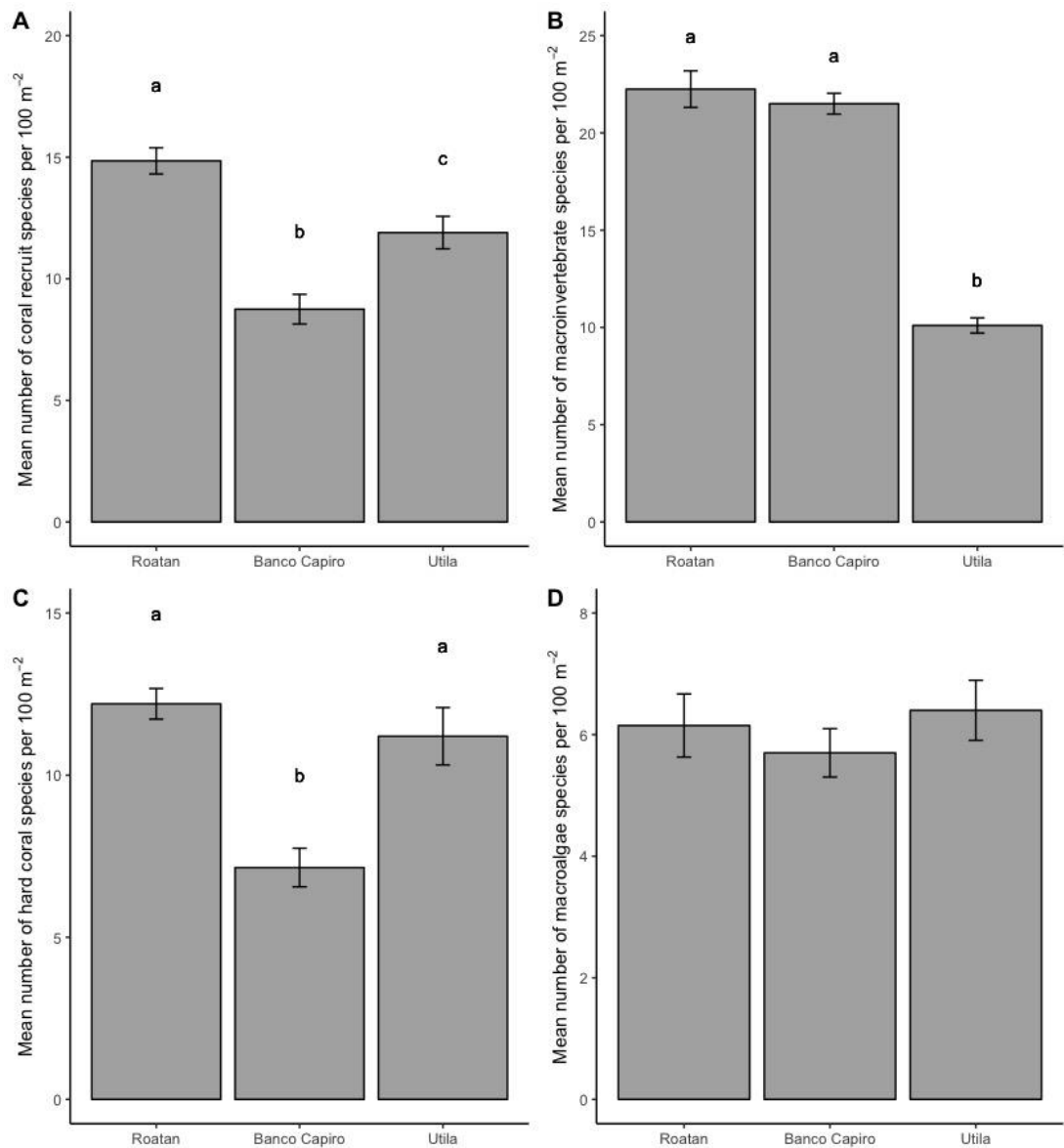


Figure 2.5. Comparison of means (SE) of species richness for (A) juvenile coral recruits, (B) mature hard coral, (C) macroinvertebrates and (D) macroalgae between Roatan (a fish-grazed reef), Banco Capiro (an urchin-grazed reef), and Utila (an under-grazed reef). Bars and error lines represent mean \pm 1SE, and post-hoc letter assignments show where differences lie; if absent there are no statistically significant differences between sites.

2.6 Discussion

Percentage cover of hard coral is the widely accepted metric used to assess coral reef ecosystem health. However, advancements in ecological theory have shown that the level of diversity within different functional groups is the major indicator of long-term ecosystem persistence (Elmqvist et al. 2003; Folke et al. 2004). Diversity begets functional redundancy, which buffers ecosystems against the catastrophic loss of any single species (Rosenfeld 2002); in a biodiverse habitat with a high degree of functional overlap, loss of ecosystem functions associated with a species extirpation is compensated for by expansion of populations belonging to functionally related groups. In low-biodiversity habitats, the probability of this compensation is highly reduced.

Stark differences in benthic composition between Banco Capiro, Roatan and Utila suggest that grazer identity may have a marked impact on the structure of Caribbean coral reef benthic communities. It is not surprising to find that under-grazed reefs have significantly lower scleractinian coral, and higher fleshy macroalgae, cover than those where at least one component of the herbivore community is present at ecologically relevant levels. These results concur with the extensive literature on the importance of *D. antillarum* ecosystem functions (e.g. Lee 2006; Chiappone et al. 2013), and indicate that urchin-grazed reefs have a higher scleractinian coral cover than fish-grazed reefs, and *D. antillarum* abundance is a better predictor of benthic coverage than herbivorous fish biomass. Using percentage cover of scleractinian coral and fleshy macroalgae as a measure of reef health might therefore lead managers to conclude that a single species approach to Caribbean reef conservation through the restoration of *D. antillarum* (Precht and Precht 2015) should be prioritised over protection of herbivorous fish populations.

However, this conclusion may be altered by considering the effect that grazer identity has on the *diversity* of different components of Caribbean reef benthic communities. Analyses clearly show disparity in the diversity of mature and juvenile scleractinian corals, macroalgae and macroinvertebrates between Banco Capiro, Roatan and Utila.

Here two metrics of diversity are used because they both provide valuable insights into the impacts of grazer identity on the benthic community. Species richness is an intuitive measure that provides information about the number of different taxonomic groups found within an ecosystem, but it does not account for the relative abundances of these species. The Simpson's Diversity Index (SI) emphasises the importance of evenness and incorporates measures of species richness with their relative abundance. At the most basic level this study questions how urchin and fish herbivory affect species survivorship on Caribbean coral reefs, therefore richness is the more appropriate diversity metric. However, when addressing questions related to ecosystem resilience, species richness alone is not an adequate measure of diversity, as a species' ecosystem function is related to its abundance.

Urchin-grazed reefs may support a lower Simpson's diversity and species richness of both mature and juvenile scleractinian corals because *D. antillarum* is an inadvertent corallivore (Ogden and Carpenter 1987). On Banco Capiro, both diversity metrics decrease between the two scleractinian life-history stages, and this may be because juvenile coral recruits are more vulnerable to predation than mature coral colonies. Therefore, whilst urchin-grazing creates settlement substrates by reducing macroalgae, it also serves to remove juvenile coral recruits before they reach maturity (Edmunds and Carpenter 2001). Urchin-grazing must therefore favour dominance of corals of fast-growing ruderal species, such as *Undaria* spp. and *Agaricia* spp. (Côté

and Darling 2010; Darling et al. 2012), that quickly escape their vulnerable juvenile stages. This hypothesis is supported by the observation that the dissimilarities in coral diversity between Banco Capiro and Utila/Roatan are driven by differences in the relative abundances of *Undaria tenuifolia*, *Undaria agracites*, and *Undaria humilis*, which were much more abundant on the urchin-grazed reef than the fish- and under-grazed reefs.

Domination of Banco Capiro by *D. antillarum* may also reduce coral diversity because, as a single species, its grazing has a uniform effect on the system, which favours dominance of particular aspects of the benthic community over others e.g. fast-growing agaricids. The functional group termed here as “herbivorous fish”, is comprised of up to 11 different species from across the Acanthuridae and Scaridae. Each species will interact with, and shape, the benthic community in a unique fashion, thus preventing the dominance of a single coral species or group of species. The volume of macroalgae removed by herbivorous fish is less than that removed by *D. antillarum* (Carpenter 1988), and therefore total scleractinian coral cover is lower on fish-grazed than urchin-grazed reefs, but herbivorous fish have a greater variety of grazing interactions with the benthic community than their urchin counterparts, meaning that coral diversity is ultimately higher. Species richness and Simpson’s diversity of scleractinian hard coral is similar on Roatan and Utila, likely because of the deficit of urchin herbivory.

Whilst non-scleractinian-coral macroinvertebrate species richness is similar on fish- and urchin-grazed reefs, the diversity is 61.66% dissimilar with respect to the identities of the species that form the community. The macroinvertebrate community on the fish-grazed reefs of Roatan is sponge dominated, whereas echinoderms and

crustaceans dominate on the urchin-grazed reefs of Banco Capiro. The under-grazed reefs of Utila have >50% fewer species than either of the grazed reefs.

These differences in macroinvertebrate species richness and community composition are likely driven by the close relationship between diversity and complexity of underlying reef architecture (Alvarez-Filip et al. 2009). Urchin-grazed reefs support greater cover of scleractinian coral whose calcium carbonate skeletons create a structured environment (Lee 2006) that is exploited by mobile macroinvertebrates requiring environmental protection from predation (Done 1992). In comparison, fish-grazed reefs have lower scleractinian coral cover and architectural complexity, which provides fewer survival benefits to echinoderms and crustaceans. However, whilst fish-grazing may not support high abundance and diversity of mobile macroinvertebrates, it does remove macroalgae and reduce space competition for benthic non-scleractinian-coral macroinvertebrates (McCook et al. 2001), which may account for the high sponge species richness. Grazer-identity appears not impact macroinvertebrate species *richness*, but it may influence species *composition* at a community level; this assertion is supported by patterns of difference in the macroinvertebrate SI values. On the under-grazed reefs of Utila, low scleractinian coral cover is coupled with high macroalgae cover, therefore neither mobile nor benthic non-scleractinian-coral macroinvertebrates are supported.

Interestingly, while macroinvertebrate abundance and species richness is higher on Roatan than Utila, Simpson's diversity is lower on fish-grazed than under-grazed reefs. This phenomenon can probably be attributed to differences in fish invertivore biomass. Relative to Banco Capiro, the low scleractinian coral cover on Roatan and Utila leaves macroinvertebrates vulnerable to predation (Lee 2006). However, fish populations on Roatan are larger than on Utila so the frequency of

predation of vulnerable macroinvertebrates may be higher, and the evenness of the community may be reduced.

It must be noted that, apart from the macroinvertebrate community, diversity on Roatan and Utila is always more similar than either site is to Banco Capiro (Fig. 2.3). *D. antillarum* abundance on Utila is three orders of magnitude lower than the necessary threshold for urchin-grazing and, although the herbivorous fish biomass is approximately three times under the threshold value for fish-grazing, it is still of the same order of magnitude. This indicates that, while the reefs of Utila are most certainly under-grazed, the grazing that does occur is carried out by herbivorous fish; it is therefore unsurprising that Utilan reef communities are more similar to the fish-grazed reefs of Roatan than the urchin-grazed reefs of Banco Capiro.

Respectively, urchin and fish grazing are driving the development of high-abundance-low-diversity and low-abundance-high-diversity coral communities. These results suggest that restoration of *D. antillarum* ecosystem functions may create habitats dominated by corals of the genera *Agaricia* and *Undaria*, and the 3D structure provided by this coral framework will promote diversity of the macroinvertebrate community. For Caribbean conservationists aiming to improve reef health, targeted single-species restoration of *D. antillarum* seems like an appealing approach. However, associated reductions in coral diversity may reduce long-term ecosystem resilience and ultimately leave reefs vulnerable to collapse as a result of disease and large-scale stochastic weather events (Bellwood 2004; Roff and Mumby 2012). If lack of resilience in the coral community leads to ecosystem collapse, habitat structure promoting high macroinvertebrate richness and evenness will disappear and negate any benefits associated with urchin-grazing.

However, an increasing body of evidence is emerging to suggest that, under future climatic and environmental conditions, coral diversity on Caribbean reefs will decrease and become dominated by previously rare opportunistic coral species, from genera such as *Agaricia* and *Undaria* (Côté and Darling 2010; Darling et al. 2012). If the diversity of the Caribbean coral community is going to be reduced by wide-scale threats largely beyond the control of conservationists (Côté and Darling 2010), perhaps perspective must shift to work within the constraints of this new reality (Oliver et al. 2015). Agaricids are complex corals able to support a high level of associated biodiversity and it is evident that restoration of *D. antillarum* may serve to promote their growth.

In an ideal world, coral reefs should have high coral cover, diversity and resilience (Fig. 2.6). These data suggest that, to achieve this aim, conservationists should be striving towards conservation approaches that protect both *D. antillarum* and herbivorous fish populations; protection of urchin-grazing will maximise scleractinian coral cover and macroinvertebrate species richness and community evenness, while maintenance of fish-grazing will promote diversity in the coral community and confer resilience to the system.

While focusing on *D. antillarum* restoration may not be a long-term solution to Caribbean coral reef conservation, limited resources, and increasing imminent threat levels throughout the region, mean that it may be the best and fastest solution currently available to increase ecosystem health in the short-term. Immediate improvements will buy time for the design of longer term, and more sustainable, conservation initiatives focussed on augmentation of herbivorous fish populations. Adoption of this dual approach to Caribbean herbivore population enhancement may

enable conservationists to achieve their ultimate aim of increasing coral reef diversity and resilience before these systems become too degraded to be recovered.

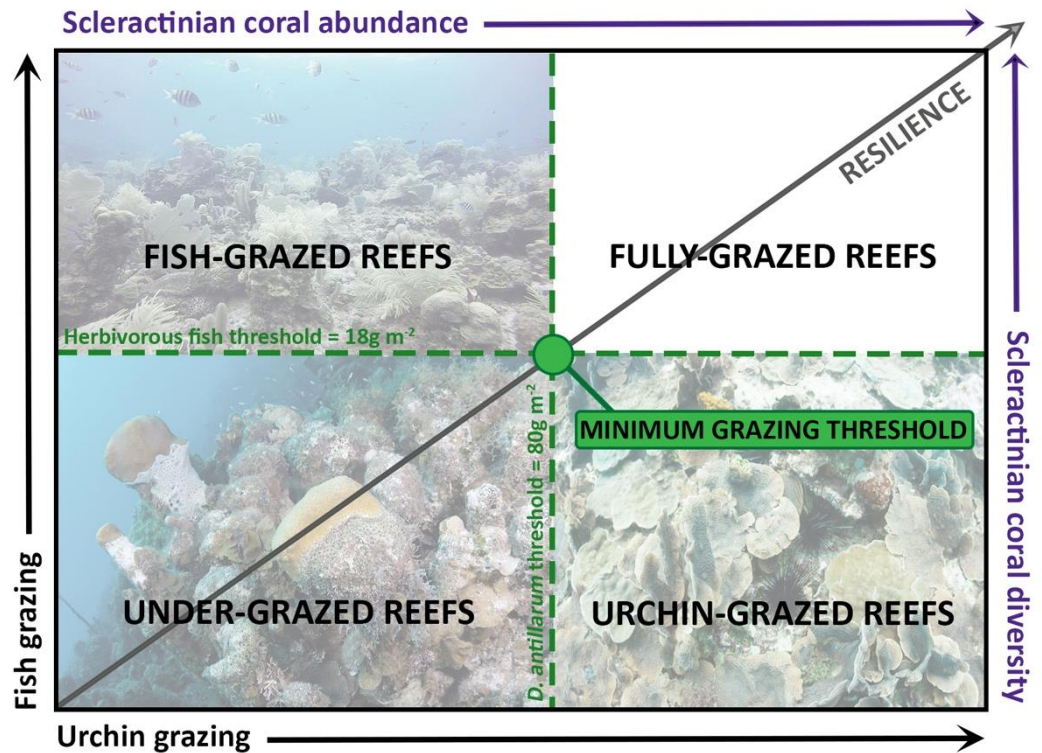


Figure 2.6. Schematic showing the theorised relationship between grazing level, hard coral abundance, hard coral diversity, and ecosystem resilience. Reefs surpassing the 18 g m^{-2} biomass threshold for fish-grazing are expected to have low coral abundance, but high coral diversity and intermediate resilience. Reefs over the 80 g m^{-2} urchin biomass threshold are likely to have high coral abundance but low coral diversity, and therefore also have an intermediate level of resilience. Under-grazed reefs that lie below both herbivore biomass thresholds will have low hard coral abundance and diversity and poor resilience. Fully-grazed reefs that exceed both the herbivorous fish and *D. antillarum* biomass thresholds are rare, but are predicted to have high coral abundance and diversity and therefore the greatest long-term ecosystem resilience. Photo credits: Adam Laverty, Matt Bassett, and Dan Exton.

3 Chapter Three – Interacting effects of temperature, habitat and phenotype on predator avoidance behaviour in *Diadema antillarum*: implications for restorative conservation

3.1 Thesis logic: part two

Having established that *D. antillarum* restoration is likely to confer ecosystem resilience, at least in the short-term, it was necessary to evaluate their possible responses to imminent and future predicted climatic changes. Conservationists must make decisions within the context of global warming and, despite the potential benefits, if long-term *D. antillarum* survival is threatened by rising SST, investment in their conservation may ultimately prove futile. Data presented in Chapter 3 enable managers to assess the ‘future-proofness’ of *D. antillarum*, and to assess whether restoration efforts are worthwhile in a warming world.

3.2 Chapter summary

Efforts to restore *D. antillarum* populations may be hampered by the currently unknown effects of short and long-term elevated SST. This chapter investigates how a key behavioural trait, predator avoidance behaviour (PAB), was affected by elevated SST in 180 individuals from two contrasting Honduran reef systems; Utila (flattened reef structure, dearth of predation refugia), and Banco Capiro (complex reef structure, abundant refugia). PAB was defined as the percentage of long defensive spines that moved in response to a shadow stimulus. Initiation of PAB is chemically mediated by melanin, which breaks down at elevated water temperatures, meaning that, as SST rises, *D. antillarum* may become increasingly vulnerable to predation. Local current SST (CSST; 29.7°C) was compared with two IPCC predicted long-term climate change scenarios under laboratory conditions. PAB decreased by 13.98-15.37% at CSST +1.4°C and 31.67-42.44% at CSST +3.1°C. Trial temperatures were similar to maxima recorded in the Caribbean during the 2016 El Niño, therefore results also represent likely responses to worst-case short-term acute temperature anomalies. Juveniles maintained higher PAB than adults, indicating increased reliance on anti-predation behaviours. White phenotypes from Utila's flattened reef maintained higher PAB than black counterparts, likely due to increased conspicuousness to visual predators. Habitat complexity may mitigate temperature-driven losses in natural behavioural defence mechanisms. *D. antillarum* is likely to be resilient to near-term (<2039) SST increases and periodic temperature stresses but may struggle in the long-term under worst-case scenario conditions.

3.3 Introduction

As architects of tropical reef ecosystems (Aronson and Precht 2001; Alvarez-Filip et al. 2009), much global attention is given to the impacts of elevated temperatures in driving the breakdown of symbiosis between scleractinian coral hosts and their photosynthetic zooxanthellae (Hoegh-Guldberg 1999; Kramer and Kramer 2000; Aronson et al. 2002; Sheppard 2003; Donner et al. 2005; De'ath et al. 2009; Cantin et al. 2010). However, acute and long-term temperature increases will also interact with other factors, such as habitat degradation, to affect other reef taxa (Przeslawski et al. 2008), and these effects remain largely unstudied.

Under natural conditions, it is likely that *D. antillarum* is afforded a degree of environmental protection from predation by the complex structure of the reef (Ogden et al. 1973). However, individuals living on flattened contemporary Caribbean reefs with low percent cover of hard coral are likely to be more heavily reliant on direct predator avoidance behaviours; a role fulfilled by movement of their longest spines which have defensive barbs directed towards the distal end (Randall et al. 1964). Here, *D. antillarum* predator avoidance behaviour (PAB) is defined as the percentage of long predatory spines that move in response to a shadow stimulus. Decreases in light intensity, indicating the potential presence of a predator, evoke an excitatory response in the spines, making the individual hard to capture (Millott and Yoshida 1960a; Raible et al. 2006; Ullrich-Luter et al. 2013). However, PAB has an energetic cost and should be reduced in the absence of a predation threat (Millott and Yoshida 1960b), therefore increases in light intensity have an inhibitory effect on spine movement (Millott and Yoshida 1960a).

The underlying physiological mechanism for this behaviour is well understood: a layer of melanin-containing photosensitive melanophores, which give

D. antillarum its characteristic black colouration, surrounds the test and enables changes in the light environment to be detected (Millott 1954; Millott and Yoshida 1959; Raible et al. 2006). This photic response is a direct result of interactions between light and the melanophore, as light stimuli cause expansion of the melanosomes, which in turn induces a nervous signal controlling spine movement (Yoshida 1956). However, melanin loses its structure at temperatures $>30.9^{\circ}\text{C}$ (Millott and Jacobson 1952; Sawhney 1994), suggesting elevated sea surface temperatures (SSTs) may cause a breakdown in these essential anti-predator light-detecting mechanisms.

Significant increases in SST are expected to occur on a decadal timescale and may reach values $>3.5^{\circ}\text{C}$ higher than current averages by 2100 (Collins et al. 2013). Additionally, the often catastrophic thermal anomalies of El Niño Southern Oscillation (ENSO) are also predicted to become biennial events of increasing severity by 2050 (Donner et al. 2005). With a lifespan of up to eight years (Randall et al. 1964), *D. antillarum* has relatively long generation times, and their capacity to adapt to both long-term gradual, and short-term acute, SST increases is likely to be limited. However, there is well documented phenotypic plasticity associated with *D. antillarum* melanin production (Millott 1954), and numerous ecological factors, such as wave exposure and water clarity, have been found to alter melanin distribution and concentration within an individual's test and spines (Kristensen 1964). This phenotypic plasticity may afford individuals with a degree of resilience to rising SST via up-regulation of melanin to counter breakdown associated with thermal stress.

Here, laboratory manipulations on natural populations are used to investigate how *D. antillarum* PAB is affected by increases in water temperature, and how this subsequently interacts with habitat and phenotype. Two separate populations from contrasting reef systems, representing both structurally complex and structurally

simple ‘flattened’ habitat types, are compared in order to address whether habitat complexity influences PAB. Given that *D. antillarum* colouration and light-detecting mechanisms are both controlled by phenotypically plastic melanin regulation, PAB variations driven by phenotype (black- and white-spined) and life-history stage (juvenile or adult) in relation to the individual’s site of origin were explored. White-spined individuals are defined as adult urchins whose complete complement of predatory defence spines are white in colouration. Theoretically, restoration of *D. antillarum* is an obvious conservation target, however, to date, no studies have investigated how they will respond to predicted environmental change. The results of this study will allow conservation managers to gain better understanding of the interactions between PAB and temperature, and make decisions on population restoration initiatives based on their future survival potential.

3.4 Materials and Methods

3.4.1 Study sites

Data were collected from Utila and Banco Capiro (Fig. 1.3). Banco Capiro (Fig. 3.1) has a mean scleractinian coral cover of 62%, which creates a structurally complex habitat that supports one of the highest contemporary *D. antillarum* population densities ever recorded. Utila (Fig. 3.2), by contrast, is a typical ‘flattened’ Caribbean reef system with low percentage scleractinian coral cover (15-20%) and consequently structural complexity is 25% less than at Banco Capiro (Bodmer et al. 2015; Chapter 5). Crucially, the abundance of key *D. antillarum* predators is similar between these two sites (Bodmer et al. 2015; Chapter 5).



Figure 3.1. Landscape photograph of Banco Capiro showing the high percent cover of hard coral and resultant architectural complexity. Photo credit: Dan Exton.



Figure 3.2. Landscape photograph of Utila showing 'typically' low hard coral cover and associated lack of habitat structure. Photo credit: Adam Laverty.

3.4.2 Future climate change predictions

In 2010, the Intergovernmental Panel on Climate Change (IPCC) described four new climate change scenarios, known as Representative Concentration Pathways (RCPs). Each RCP uses a different value of radiative forcing, dictated by the specific greenhouse gas (GHG) accumulation scenario being modelled, to predict the climatic changes that might occur by 2100 (Arora et al. 2011). Radiative forcing is measured in Wm^{-2} and is determined by the proportion of solar insolation that is trapped in the atmosphere relative to the energy radiated back into space and is, therefore, influenced by rates of GHG emission and accumulation (Van Vuuren et al. 2011). The four Representative Concentration Pathways (RCPs) are modelled on assumptions of socio-economic activity that are used to predict the extent of GHG accumulation in 2100, and they have been designed to represent a range of possible future climate change scenarios (Table 3.1).

3.4.3 Specimen collection and acclimatisation

Trials were run between March and August 2015. Thirty individuals in each of the three categories (black-spined adult, white-spined adult, juvenile) were collected from each site giving a total sample size of 180 urchins over the six-month sampling period. Juveniles were identified by their distinctive black and white banded spines, and their possession of a test diameter $<20\text{mm}$ (Randall et al. 1964). Four *D. antillarum* individuals were collected each day by a combination of snorkelling and SCUBA, and trials conducted on the same day. All individuals were returned alive to the reef within 24 hours of collection.

Table 3.1. Taken from table SM30-4, section 7 “Coral Reef Provinces”, row 1 “Caribbean Sea/Gulf of Mexico” (Hoegh-Guldberg et al. 2014).

Climate Change Scenario	Predicted near-term (2010-2039) increases in SST (°C)	Predicted long-term (2010-2099) increases in SST (°C)	Pattern of radiative forcing value increase	Likelihood of occurrence
RCP 2.6 (best-case)	0.48	0.68	<ul style="list-style-type: none"> • Mid-century peak at 3.1Wm⁻² • Decrease to 2.6 Wm⁻² by 2100 	<ul style="list-style-type: none"> • Unlikely • Requires immediate GHG emission reduction on a global scale
RCP 4.5 (stabilising)	0.64	1.43	<ul style="list-style-type: none"> • Rise to 4.5Wm⁻² by 2100 • No further increases 	<ul style="list-style-type: none"> • Moderately likely; radiative forcing peaks in 2040 and then plateaus • Would require immediate cooperation and coordination between the world’s governments
RCP 6.0 (stabilising)	0.61	1.87	<ul style="list-style-type: none"> • Rise to 6.0Wm⁻² by 2100 • No further increases 	<ul style="list-style-type: none"> • Most likely; radiative forcing peaks in 2080 and then plateaus • Pressure put on governments to address climate change issues will likely cause GHG emission reductions, but time is required to coordinate the effort
RCP 8.5 (worst-case)	0.83	3.14	<ul style="list-style-type: none"> • Rise to 8.5Wm⁻² by 2100 • Continue unabated into 22nd century 	<ul style="list-style-type: none"> • Unlikely • Requires GHG emissions to continue at current rates; concerted efforts are already being made to reduce them

Pseudoreplication was avoided by collecting from a different study site each day. When removing individuals from the reef, care was taken to ensure that minimal damage was caused to the spines and test. Once an individual was located, a 50 cm length of PVC pipe (outside diameter = 2.6 cm) was used to coerce them into the open. The PVC pipe was then used to lift the individual off the reef and into a container for safe storage.

In the laboratory individuals were placed in a 200 L plastic holding tank where they were allowed to acclimatise for a minimum of eight hours before trials were conducted. This short acclimatisation period was chosen to minimise stress and maximise survivorship to reduce adverse effects on populations of this key reef herbivore. Trials therefore tested the shock responses of *D. antillarum* to increased water temperature, and did not account for the possibility of potential short or long-term adaptation/phenotypic plasticity and results must be interpreted in that light.

3.4.4 Experimental setup and climate change scenarios

Experimental manipulations were conducted in three transparent 64 L plastic trial tanks. All tanks underwent 100 % water changes daily with fresh seawater collected from the specimen collection sites. Aquarium filters (Eheim Pick Up) were installed in the holding tanks to maintain water quality overnight, but were not included in trial tanks owing to the short time urchins were housed within them, and to ensure no external stimuli were present which may have influenced urchin responses. Aquarium heaters (Aquael Easy Submersible Aquarium Heater 150w) and digital thermometers (Aqua One ST-3 Electronic Thermometer) were used to achieve and maintain the required water temperature in each trial tank.

Trial temperatures were based on recently described climate change scenarios (Representative Concentration Pathways: RCP) from the Intergovernmental Panel on Climate Change (IPCC) and their respective predicted SST increases for the Caribbean Sea/Gulf of Mexico (Table 3.1; Arora et al. 2011, Hoegh-Guldberg et al. 2014). One trial tank was maintained as a control at 29.7 °C, the current annual mean peak SST (CSST) recorded off the Caribbean coast of Honduras (<http://www.seatemperature.org>). Experimental temperatures were then calculated by adding predicted SST increases to this CSST. The second trial tank was used to represent an intermediate/stabilising pathway (RCP 4.5; 31.1 °C), while the final tank was used to represent a worst-case pathway (RCP 8.5; 32.8 °C). (Collins et al. 2013).

Having access to *D. antillarum* from both Utila and Banco Capiro also enabled evaluation of whether the effects of rising SST are likely to be universal, or affected by the structural complexity of the population's site of origin. It is possible that temperature and site interact to affect PAB, which has major implications for *D. antillarum* restoration initiatives aiming to provide artificial reef structure to stimulate recovery.

3.4.5 Trial protocol

Trials were conducted in a laboratory at night to control for the confounding effects of daily fluxes in light concentration. The light environment was artificially maintained at an intensity of ca. 20 lm. The phenotype of each individual urchin was recorded and the total number of long defensive spines counted, along with individual weight (to the nearest mg) and test diameter (to the nearest mm) using long-jaw callipers. These measurements were recorded immediately after collection before individuals were placed in the holding tank to avoid inducing stress immediately prior

to the trials. The predation avoidance behaviour (PAB) of each individual was then tested under each temperature scenario. Individuals were acclimated to each temperature for at least 30 minutes before trials began, or until they had settled in a corner of the tank for a period of at least 10 minutes. This was done to ensure that urchins were adjusted to the heat shock and were therefore responding to the shadow stimulus and not the change in temperature.

At the start of each trial a GoPro Hero 3 underwater video camera was placed in the trial tank facing the urchin and set to record for the duration of the trial. Urchins were initially exposed to ambient light conditions for 30s. A shadow was then created over the urchin using an opaque wooden board to simulate the presence of a predator, and maintained for 30s before returning the urchin to ambient light. This was repeated three times for each urchin under each temperature scenario; urchins were exposed to two minutes of ambient light between each shadow exposure. The order in which individuals were exposed to the different temperature treatments was randomised ahead of each trial.

3.4.6 Quantifying predator avoidance behaviour (PAB)

Predator avoidance behaviour (PAB) is defined here as the percentage of an individual's total spines that move in response to a shadow stimulus, and quantified visually. Test diameter was measured in order to account for any confounding effect of body size on PAB. Only the movements of the longest spines were counted because the main function of these is known to be predatory defence whereas the shorter spines are used predominantly for feeding and locomotion (Randall et al. 1964).

Prior to their analysis, all 540 videos were renamed using RandomNames software. The video analyst was therefore unaware of the site of origin and climate

change scenario of the urchin they were processing, thus removing any potential observer bias from the data. Video recordings were replayed in slow motion allowing accurate counts of the number of long defensive spines that moved in response to the shadow stimulus. The PAB for each simulated ‘attack’ was calculated and the means of these PAB values were used for statistical analysis.

3.4.7 Statistical Methods

PAB data were normally distributed and their relationships with climate change scenario, site and phenotype were analysed using a three-way repeated measures ANOVA with urchin number nested within climate change scenario. PAB was the continuous dependent variable, site and phenotype were nominal, fixed effect between-subject variables, and climate change scenario was a nominal, fixed effect within-subject variable.

The relationship between *D. antillarum* body size (test diameter) and PAB was investigated to control for this as a potentially confounding variable, since smaller individuals are more vulnerable to predation, and predation threats are generally considered more relevant to juveniles than adults (Clemente et al. 2007; Jennings and Hunt 2010). All data were analysed using R v. 3.3.1 (R Core Team 2016) and RStudio v0.99.903 (RStudio Team 2015).

3.5 Results

3.5.1 Establishing a baseline PAB

The mean PAB of black-spined adult urchins at CSST on Banco Capiro (17.39 ±0.68%) is used as a baseline for comparisons of different combinations of climate change scenario (CSST, RCP 4.5, or RCP 8.5), site (Utila, or Banco Capiro), and

phenotype (black, or white). This is because black individuals on Banco Capiro are living in conditions that are most similar to those under which *D. antillarum* existed prior to the mass-mortality event, i.e. they are the most common phenotype, living within a dense population ($>2\text{m}^{-2}$) on a reef system with a high percentage cover of hard coral ($>60\%$). There is debate in the literature about the population densities under which *D. antillarum* evolved, and their relative importance as macroalgal herbivores over evolutionary timescales has been called into question (Jackson and Kaufmann 1987). However, countless studies conducted throughout the 20th century clearly document high *D. antillarum* population densities, and demonstrate the importance of this species for maintaining reef health on the overharvested Caribbean coral reefs of the Anthropocene.

3.5.2 *Effects of temperature, site and phenotype on PAB*

There was a significant negative relationship between PAB and urchin test diameter for juveniles ($F_1 = 4.993$, $p = 0.027$) but not for adults ($F_1 = 1.808$, $p = 0.18$) (Fig 3.3); therefore, all subsequent analyses dealt with these two groups separately. Juvenile analysis included test diameter as an independent variable while the analysis of adults did not.

Increasing water temperature caused a decline in PAB in both age categories of urchins (Fig 3.4; Juveniles $F_2 = 4.86$, $p = 0.0091$; Adults $F_2 = 15.37$, $p = 3.9 \times 10^{-7}$) and juvenile urchins had higher PAB than adults in all temperatures. Mean juvenile PAB declined from $24.54 \pm 1.28\%$ at CSST to $21.1 \pm 1.45\%$ under RCP 4.5 and $15.19 \pm 1.22\%$ under RCP 8.5. Repeated measures ANOVA revealed that there was no difference in PAB of juveniles between sites overall ($F_1 = 0.303$, $p = 0.58$) but the data for RCP 8.5 suggested lower PAB at Utila than Banco Capiro (Fig 3.4). Black-spined

adult PAB declined similarly to juveniles from 17.66 ± 0.76 % at CSST to 15.09 ± 0.9 % at RCP 4.5 to 10.80 ± 0.87 % at RCP 8.5. The percentage declines in PAB from CSST to RCP 8.5 were proportionately similar: 38.1 % for juveniles and 38.8 % for black-spined adults. Interestingly, PAB of juveniles under RCP 4.5 was still 21.33 % higher than that of black-spined adults under CSST.

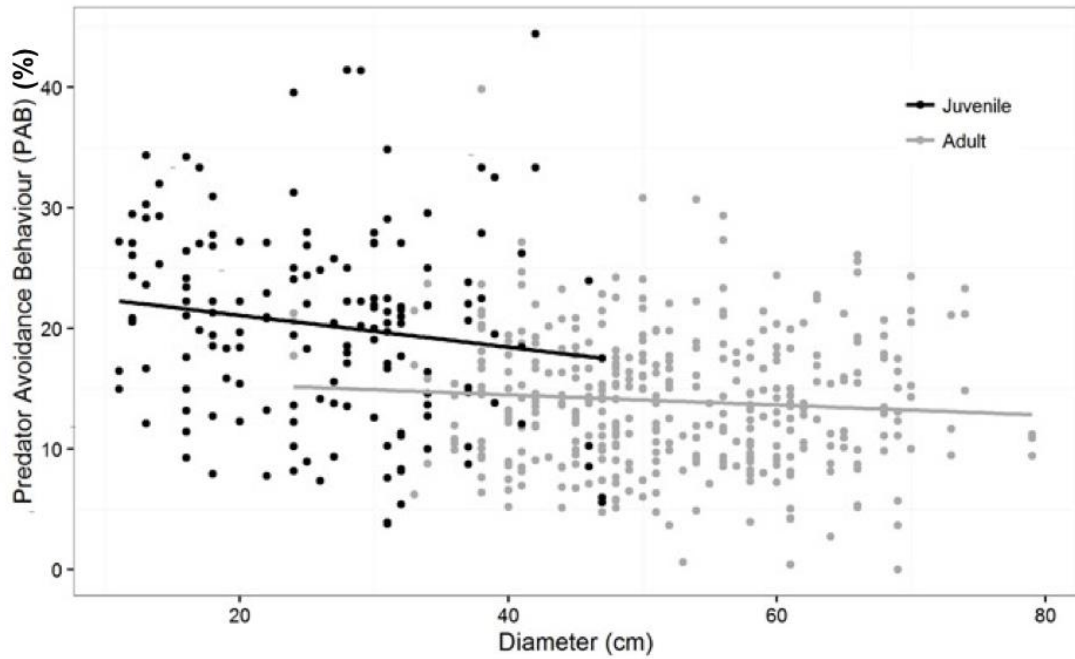


Figure 3.3. Relationship between urchin body (test) size and predator avoidance behaviour (PAB) in juvenile (black points) and adult (grey points) urchins. Plotted lines are least-squares regression lines.

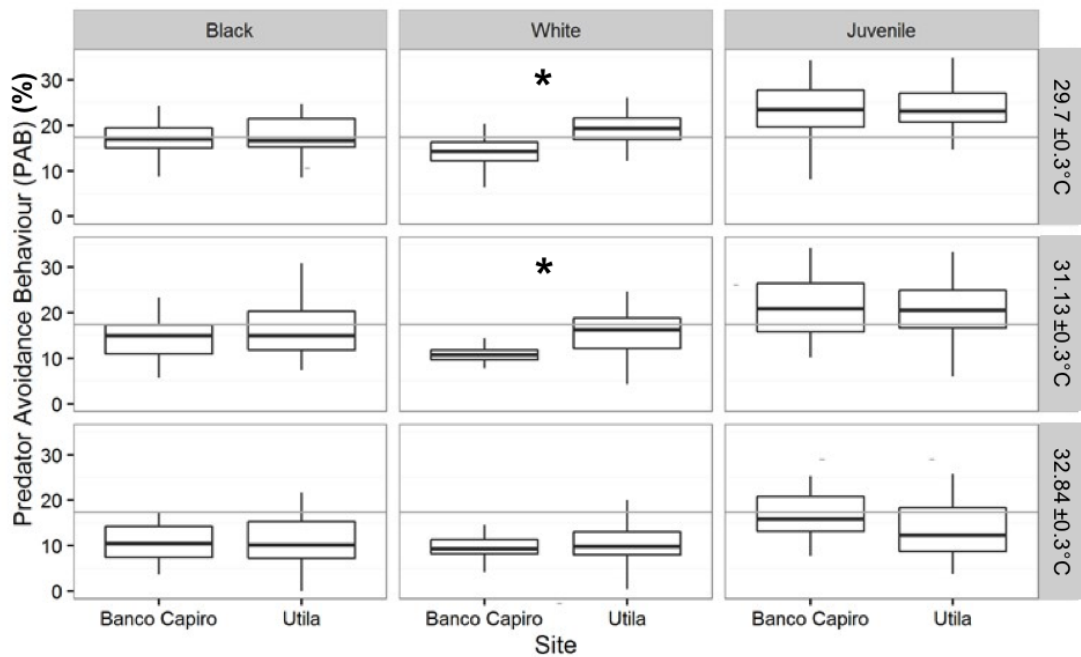


Figure 3.4. Predator avoidance behaviour (PAB) of *D. antillarum* of three categories (black-spined adult phenotype, white-spined adult phenotype and juvenile), across two sites (Utila: flattened reef and Banco Capiro: complex reef), under conditions simulating three different IPCC climate change scenarios (CSST = 29.7 °C, RCP 4.5 = 31.13 °C, and RCP 8.5 = 32.84 °C). Grey horizontal lines represent a baseline for comparison set as the mean PAB of black-spined adult *D. antillarum* on Banco Capiro under CSST. Vertical lines represent $\pm 1SE$. Asterisks denote where significant inter-site differences occur.

There was no evidence of between-site differences in PAB or its response to temperature for black-spined adult urchins but the pattern differed for white-spined adults, reflected by a significant interaction between phenotype and site ($F_1 = 8.96$, $p = 0.003$). White urchins from Banco Capiro (14.35 ± 0.58 %) displayed lower PAB than those from Utila (19.50 ± 1.34 %), and mean white urchin PAB on Banco Capiro (14.35 ± 0.58 %) was lower than that of their black counterparts (17.93 ± 0.68 %). However, the inverse was true on Utila, where mean white-spined adult *D. antillarum* PAB (19.50 ± 1.34 %) was higher than that of the black population (17.93 ± 0.84 %).

However, these differences were less apparent at RCP 8.5 (Fig 5). At CSST mean PAB of white-spined adults on Utila (19.50 ± 1.34 %) was almost 36 % higher than those on Banco Capiro (14.35 ± 0.58 %). This difference was maintained at RCP 4.5 (15.49 ± 0.91 %, and 11.20 ± 0.47 % respectively) but was roughly halved at RCP 8.5 (11.44 ± 0.92 %, and 9.70 ± 0.49 %). See table 3.2 for complete breakdown of results.

Table 3.2. Results of three-way repeated measures ANOVA for adult and juvenile *D. antillarum*. Degrees of freedom, F statistics and p-values are provided for all main factors (temperature, site, and phenotype), the interactions between these factors, and the potentially confounding factor of test diameter.

Life History Stage	Factor	Degrees of Freedom	F-statistic	P-value
Juvenile	Temperature	2	4.86	0.0091
	Site	1	0.30	0.58
	Test Diameter	1	4.99	0.027
	Temperature * Site	2	1.50	0.23
	Temperature * Test Diameter	2	0.30	0.74
	Site * Test Diameter	1	6.73	0.01
	Temperature * Site * Test Diameter	2	0.37	0.69
Adult	Temperature	2	15.37	3.91 x 10 ⁻⁷
	Site	1	21.29	5.46 x 10 ⁻⁶
	Phenotype	1	5.67	0.018
	Test Diameter	1	1.81	0.18
	Temperature * Site	2	1.71	0.18
	Temperature * Phenotype	2	0.83	0.44
	Site * Phenotype	1	8.96	0.003
	Temperature * Site * Phenotype	2	0.72	0.49

3.6 Discussion

3.6.1 Demographic influences on PAB

At CSST, mean juvenile PAB is 41.12 % greater than black-spined adults on Banco Capiro, and the higher PAB value is maintained even under moderate thermal stress (RCP 4.5). This is not surprising, as juvenile test diameters are typically smaller than the 40 mm predator escape threshold above which vulnerability is believed to decrease (Clemente et al. 2007; Jennings and Hunt 2010). The need for juveniles to maintain high PAB, even under physiological stress, is far greater than for their adult counterparts. This is supported by the negative relationship observed between juvenile body size and PAB magnitude; larger juveniles can partially relax PAB in favour of the energetic benefits associated with reduced spine movement (Millott and Yoshida 1960b). However, juveniles living within the complex structure of Banco Capiro still maintain similar PAB to those on the flattened reefs of Utila, despite potentially being able to gain energetic benefits from reducing PAB on a reef that provides individuals with environmental protection. The risk of death under any given attack is much higher for juveniles than adults, and thus the energetic benefits of reducing PAB on Banco Capiro are likely to be outweighed by the ultimate price of failing to respond to a potential predation threat.

On Banco Capiro, white-spined adult *D. antillarum* individuals have a significantly lower PAB than black-spined adults. One possible explanation relates to the developmental and environmental processes driving these phenotypic differences. Experimental manipulations have shown that adult *D. antillarum* will develop white spines if reared in low-light environments, while also favouring shaded areas of reef during adulthood (Kristensen 1964; Growns 1989). Due to reduced energy content in algae growing on shaded compared to light-exposed reef areas (Carpenter 1985;

McCook et al. 2001), white-spined adult sea urchins are likely to be nutrient-limited and may therefore be unable to invest in metabolically expensive melanin production. Whilst white-spined adults appear to be less sensitive to predation stimuli, their overall vulnerability may be unaffected by this decreased PAB ability because they favour shaded, and presumably more complex, habitats.

Conversely, juveniles develop black spines when reared in high-light environments (Kristensen 1964), typically when individuals settle on more exposed areas rather than within the complex coral framework. It is therefore likely that black-spined adult *D. antillarum* are grazing algae from light exposed reefs that have greater energy availability per unit area (Ogden and Lobel 1978) than their white-spined counterparts. Black-spined individuals may therefore be able to invest more heavily in melanin production. This investment in their light-detecting sensory systems is further justified in black-spined adults because their more exposed lifestyle leaves them vulnerable to predation.

For black-spined adults and juveniles the magnitude of PAB does not differ between sites, but for white-spined adults PAB is significantly greater on Utila. Unlike on Banco Capiro, white urchins on Utila are living in a flattened habitat and therefore lack abundant predation refugia. The major fish predators of *D. antillarum* (Ballistidae, Haemulidae and Labridae) all possess typical vertebrate visual systems comprised of image-forming eyes (Lamb et al. 2007), which rely, at least partially, on contrast for prey detection (Schuster et al. 2011). Against the darker backdrop of the reef, white individuals are likely to be more conspicuous to predators in a habitat where they are less able to hide. Therefore, while black individuals on Utila are less conspicuous to predation, and both adult phenotypes on Banco Capiro are afforded

environmental protection by the reef structure, white-spined adults on Utila must invest more heavily in the maintenance of their innate behavioural PAB.

3.6.2 *Elevated SSTs and their implications for restoration*

Across all combinations of site and phenotype, mean *D. antillarum* PAB was negatively affected by increases in water temperature, with the greatest reductions under the most extreme temperature trials (RCP 8.5). This suggests that *D. antillarum* is likely to become increasingly vulnerable to predation as climate change progresses, especially if ‘worst case’ temperature models arise. Subsequent increased predation vulnerability will further hinder population recovery from the 1983-84 mass mortality event, and potentially hamper current conservation initiatives as seas warm. Under RCP 8.5 conditions, *D. antillarum* PAB will be reduced between 32.44 % and 41.33 % relative to CSST. However, it is generally accepted that RCP 4.5 is a much more likely future temperature scenario (Masui et al. 2011; Thomson et al. 2011). According to the results, under RCP 4.5, smaller PAB decreases of between 14.55 % and 21.95 % will be seen; although this still represents a significant loss of anti-predation capability in such a threatened species.

Unfortunately, these results indicate that juvenile urchins will be similarly affected by rising SST as black-spined adults. Given that juveniles are more vulnerable to predation due to their small size below the predation threshold (Clemente et al. 2007; Jennings and Hunt 2010), it is likely that this decrease in PAB will translate into elevated mortality rates among younger cohorts. Previous research has already identified maturation as the key life history bottleneck to *D. antillarum* recovery (Williams et al. 2010 & 2011; Bodmer et al. 2015; Chapter 5), meaning any further reduction in juvenile survival will ultimately drive Allee effects and eventual

extinction. However, it is important to remember that this study has tested responses to sudden and acute thermal stress, using similar approaches to much other ecophysiology research, e.g. Eme and Bennett (2009), Eme et al. (2001) and Dabruzzi et al. (2013), and therefore the results do not account for phenotypic plasticity associated with the *D. antillarum* melanin-regulatory system (Millott 1954). This may serve to mitigate the negative effects of rising SST on PAB, meaning this study represents a worst-case scenario and not the end of the road for conservation efforts throughout the Caribbean.

It is also important to consider the temporal scale over which ocean warming will actually occur. Under the long-term water temperatures predicted by RCP 4.5 (CSST +1.43 °C), *D. antillarum* will likely be partially resilient with respect to the detection of, and reaction to, predators. With long-term temperature increases under RCP 4.5 greater than short-term increases under RCP 8.5 (CSST +0.83 °C), it can be assumed that *D. antillarum* will be resilient to near-term SST increases across the severity range. This suggests that, at least until 2039, incremental ocean warming is unlikely to negatively impact the success of *D. antillarum* restoration initiatives.

However, increases in the frequency and severity of El Niño anomalies means that long-term warming is not the only thermal threat to be faced. In winter 2016, average Caribbean SST was 0.5-1.5 °C higher than the 1981-2010 average (NOAA). Fortunately, the focus on acute temperature increases, similar to those experienced during El Niño, indicate that *D. antillarum* will be able to maintain PAB provided that sudden increases do not exceed ~3 °C. In general, the severity of El Niño in the Caribbean is less than other global coral reef hotspots, and this ~3 °C threshold falls outside the temperature anomalies previously experienced in the region (NOAA).

These results suggest that conservation interventions seeking to increase structural complexity will reduce the reliance of *D. antillarum* on innate behavioural PAB, and increase survivorship even in the face of worst-case scenario increases in SST. In essence, structural complexity may provide a buffer against the increased threat of predation caused by reduced PAB via melanin breakdown. Stakeholders can use this information to make informed decisions about strategies to increase the health of Caribbean coral reef ecosystems by focusing on this important species. This is in line with the IPCC's goal of "working with scenarios...in order to consider how robust decisions or options may be under a wide range of possible futures" (Moss et al. 2010). If *D. antillarum* is going to recover and aid the reversal of ubiquitous macroalgal phase shifts, they require urgent conservation attention to be buffered from climate change induced thermal stressors.

4 Chapter Four – Using an isolated population boom to explore barriers to recovery of *Diadema antillarum* populations

4.1 Thesis logic: part three

The previous chapters contain two pertinent messages for conservation managers aiming to preserve Caribbean coral reef health; (1) Augmentation of *D. antillarum* populations is likely to provide significant ecological, and therefore socio-economic, benefits, (2) *D. antillarum* are potentially resistant to future climatic changes, especially if conservation initiatives aim to enhance habitat structure, therefore investment in their restoration is worthwhile. It is widely acknowledged that successful biodiversity reintroduction requires all potential survival threats to be removed before populations are re-established, therefore the next step is to identify the factor(s) that may be operating to prevent wholesale *D. antillarum* recovery. Chapter 4 therefore explores the relationship between *D. antillarum* population density and numerous ecological factors that may be acting to suppress recovery.

4.2 Chapter summary

Recovery of *D. antillarum* populations poses one of the greatest challenges to Caribbean coral reef conservation, yet our understanding of the problem remains severely limited. While some recovery has been observed, this has been restricted to the shallows (≤ 5 m). The newly-discovered isolated population recovery on Banco Capiro, Honduras, represents the largest recorded post-mortality density beyond the shallowest environments (0.74 - 2.27 individuals m^{-2} at depths ≥ 10 m) alongside an unusually high mean percentage scleractinian coral cover of 49 - 62%. Evidence presented in Chapter 2 of this thesis suggests that this is no coincidence. Populations on the nearby island of Utila remain low with densities of 0.003 - 0.012 individuals m^{-2} and scleractinian coral cover of 12% at depths ≥ 10 m; 'typical' for a contemporary Caribbean coral reef. The three order of magnitude disparity in population density between sites separated by < 60 km presents a unique opportunity to investigate barriers preventing their region-wide recovery by simultaneously addressing a range of previously proposed hypotheses. Despite concerns over the impacts of asynchronous spawning in low-density populations, this study finds that recruitment is occurring on Utila, which suggests that, whilst Allee effects are likely to be a contributing factor, the major barriers suppressing recovery are instead impacting juvenile survival into adulthood. Similarly, variations in heterospecific echinoids, interspecific competitors and nutrient availability fail to account for population differences. Data presented here highlight that the lack of structural complexity on contemporary Caribbean reefs is limiting recovery by creating a dearth of juvenile predation refugia.

4.3 Introduction

To date, recovery from the 1983-84 *D. antillarum* mass-mortality has been extremely poor. Although some instances of recovery are reported, population densities remain low relative to pre-mortality levels, and these examples of recovery represent a small return on such large-scale loss. Most studies showing “recovered” populations have at least an order of magnitude lower density than prior to the mortality event (Chiappone et al. 2001; Edmunds and Carpenter 2001; Weil et al. 2005; Debrot and Nagelkerken 2006; Bologna et al. 2012). The most significantly recovered populations have maximum densities of 1.7-8.9 m⁻² (Carpenter and Edmunds 2006) and 16 m⁻² (Lacey et al. 2013), but these studies only survey shallow reefs (<5 m) and report absolute maximum values rather than local average, and there have been no reports of significant *D. antillarum* population recovery occurring beyond the shallows consistently across a reef system.

The lack of significant *D. antillarum* recovery observed throughout the Caribbean in the decades after the die-off is surprising. There is no consensus in the literature about the barriers that might be preventing wholesale *D. antillarum* recovery, but a variety of hypotheses have been postulated.

4.3.1 Hypothesised barriers to population recovery

A recent modelling study highlights the need for a shift in the balance between mortality and recruitment, estimating that either a 25 times increase in recruitment or a two order of magnitude decrease in mortality is required to achieve pre-mortality densities across a large spatial scale (Levitan et al. 2014). However, barriers preventing this necessary shift from occurring are not understood, and researchers are instead restricted to a handful of independent hypotheses, in particular (1) suppressed

recruitment resulting from natural asynchronous spawning behaviour, (2) immunosuppression leading to disease vulnerability, (3) increased competition from vertebrate reef herbivores, (4) predation pressure driving high mortality, (5) ecological interactions with heterospecific echinoids, and (6) loss of structural complexity removing microhabitat provision.

4.3.1.1 Asynchronous spawning

The asynchronous spawning behaviour of *D. antillarum* (Levitan 1988; Levitan 1991; Levitan et al. 2014) means that only 5% of a population will release their gametes at any one time (Iliffe and Pearse 1982). Naturally high population densities ensure fertilisation success, but mass-mortality has not only reduced the density of individuals, and thus the probability of multiple individuals spawning simultaneously, but has also increased average nearest-neighbour distances, meaning ejaculates are diluted in the water column and fertilisation success is significantly reduced (depensation; Pennington 1985).

4.3.1.2 Immunosuppression

D. antillarum immune systems are suppressed by the presence of lipopolysaccharides, which are an important component of Gram-negative bacteria (Beck et al. 2014). It is hypothesised that populations may have failed to recover, in part, because this immune deficiency has left them vulnerable to repeated infection. However, there are no reports of contemporary populations being affected by disease, meaning that this is probably not the most likely explanation.

4.3.1.3 Competition and predation

It has been suggested that a post-mortality increase in herbivorous fish has intensified interspecific competition with *D. antillarum* (Robertson 1991). This hypothesis is supported by data from Panama, where populations of herbivorous surgeonfish species increased by 0-250 % after mass-mortality (Robertson 1991). Increased competition may have reduced resource availability, meaning that the few remaining urchins have to allocate energy budgets to feeding rather than reproduction, thus reinforcing the aforementioned Allee effect (Black et al. 1982; Levitan 1989). It has also been suggested that the adoption of more generalist feeding strategies by predators of *D. antillarum* as a response to the mass-mortality event could have maintained predator abundances at levels that now suppress recovery (Carpenter 1984; Robertson 1987; Miller et al. 2007).

The echinoid, *Tripneustes ventricosus*, removes unpalatable mature macroalgae and clears substrata for the recruitment of juvenile macroalgae, which is the preferred food source of *D. antillarum* (Haley and Solandt 2001; Betchel et al. 2006). Another hypothesis therefore proposes that the increase in mature macroalgae since the *D. antillarum* mortality event exceeds the grazing ability of *T. ventricosus* that in turn suppresses their abundance and subsequently reduces nutrient availability for *D. antillarum* (Liddell and Ohlhorst 1986; Carpenter 2005; Macia et al. 2007).

D. antillarum and *Echinometra viridis*, another Caribbean echinoid species, behave aggressively towards one another (Shulman 1990) and, as such, their population sizes have been found to be negatively correlated (Williams 1981). It is therefore possible that competitive release following the mass-mortality of *D. antillarum* facilitated increases in *E. viridis* populations that now act to suppress their competitors. However, it appears that there was no increase in *E. viridis* populations

after the *D. antillarum* mass die-off (McClanahan 1999), and Lessios (1995) even found evidence to suggest that *E. viridis* actually facilitates *D. antillarum* recruitment because, similarly to *T. ventricosus*, they remove macroalgae and provide suitable larval settlement surfaces.

4.3.1.4 Structural complexity

Calcium carbonate skeletons laid down by reef building scleractinian corals are essential for provision of 3D complexity and living space (Alvarez-Filip et al. 2009). *D. antillarum* facilitate stony coral domination and therefore promote habitat structure (Lee 2006; Myhre and Acevedo-Gutierrez 2007; Ruiz-Ramos et al. 2011), which in turn provides juvenile urchins with predation refugia. It is therefore possible that the reduction in scleractinian coral cover that accompanied the loss of *D. antillarum* has created a feedback loop that is hampering urchin recovery (Lacey et al. 2013).

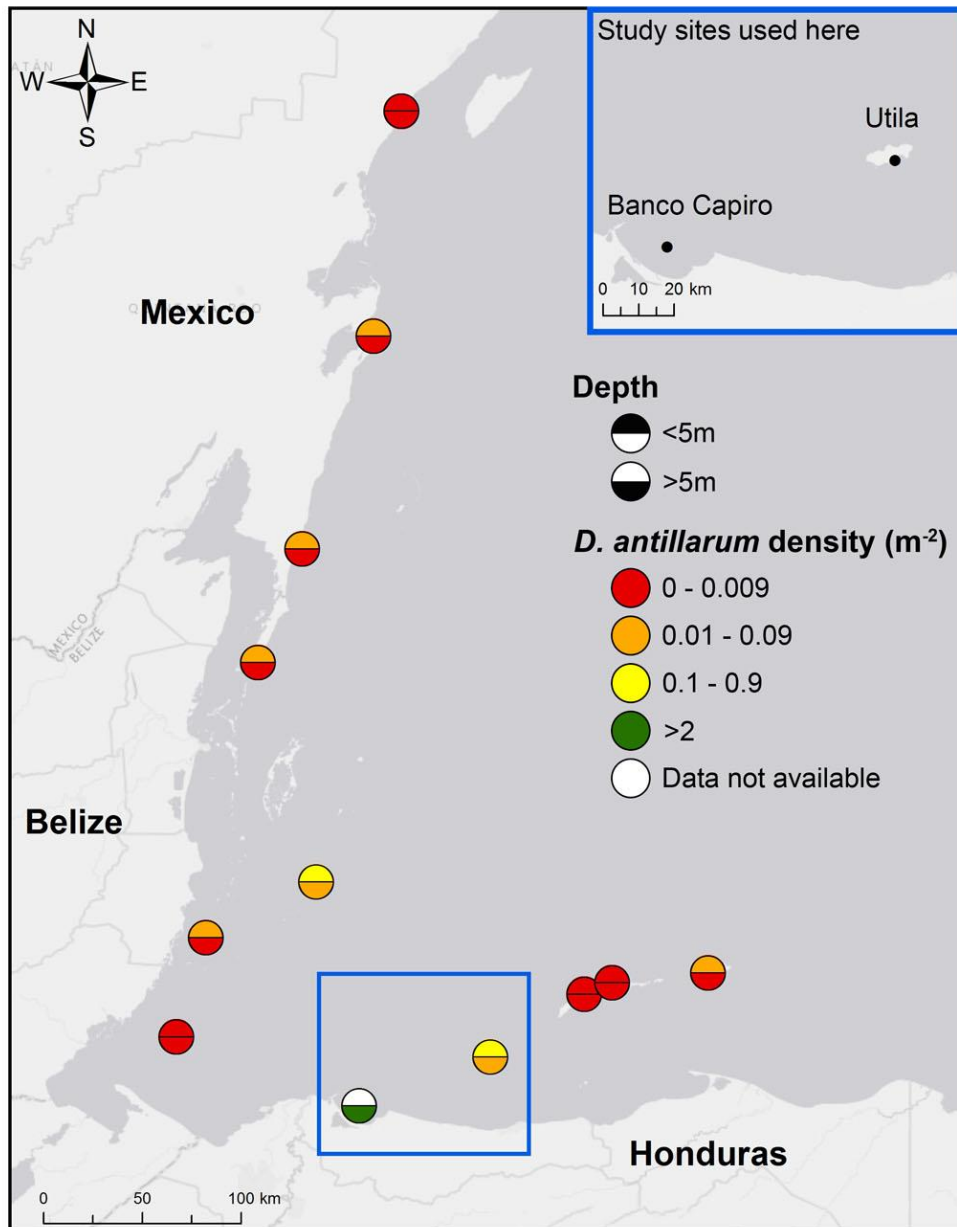


Figure 4.1. The current status of *D. antillarum* population densities throughout the Mesoamerican Barrier Reef system in shallow (<5 m) and deep (>5 m) coral reef environments. Data for Banco Capiro and Utila (Honduras, 2014) and Akumal (Mexico, 2013) were collected as part of this study. All other data shown are open access sourced from Atlantic and Gulf Rapid Reef Assessment (AGRRA, <http://agrra.org>) surveys conducted by Healthy Reefs Initiative (HRI, <http://healthyreefs.org>), using randomly placed 10m x 1m belt transects ($n = 6$ per depth and site) completed by SCUBA divers. Note that shallow data are not available for Banco Capiro due to the deep offshore topography of the site.

After a 30-year period of relative stasis, *D. antillarum* populations throughout the Caribbean are still struggling to recover. A summary of contemporary population densities (Fig. 4.1), based on a combination of data from this study and Atlantic and Gulf Rapid Reef Assessment (AGRRA) surveys, clearly demonstrates not only continued regional suppression, but highlights the previously unknown isolated population boom on Banco Capiro, Tela Bay. In this chapter, Banco Capiro is used as a model ‘recovered’ population to explore the barriers preventing large-scale recovery of *D. antillarum* by comparing it to the reefs of Utila, where *D. antillarum* densities and scleractinian coral cover are more typical of a contemporary Caribbean reef. Large disparities between these two populations, only 60 km apart, suggest that fundamental differences exist between the systems, and this unique comparison can be used to explore previously proposed barriers to *D. antillarum* recovery. A combination of assessment techniques is used to investigate echinoid population dynamics, biotic and abiotic benthic variables, and a quantification of predation and competition, to systematically address the mechanisms behind the continued widespread suppression of *D. antillarum* populations. The findings are used to suggest potential conservation management strategies that may help focus restoration efforts throughout the Caribbean.

4.4 Materials and methods

4.4.1 Study Sites

Three study sites were selected to represent as large a geographical range as possible along the Banco Capiro reef system: Kisci's Garden (N 15.51558 W 87.30068), Pinnacle (N 15.51509 W 87.30210) and The Fingers (N 15.51487 W 87.29429). Three study sites were selected along Utila's more accessible southern shore; Sturch Bank (N 16.05190 W 86.53464), Coral View (N 16.05179 W 86.54382), and Black Coral Wall (N 16.04583 W 86.55023) (Fig. 1.3).

4.4.2 In situ ecological surveys

All data were collected over two nine-week field seasons (June-August 2013 and 2014) using SCUBA along 50 m transects. The distribution of *D. antillarum* is known to vary with depth (Lessios 1988; Debrot and Nagelkerken 2006), so survey transects were carried out in triplicate at two depths, 10 m and 15 m. Additional study depths of 2 m and 5 m were surveyed on Utila, but not on Banco Capiro due to the site's naturally deep offshore topography. A randomly selected compass bearing was followed for 20 m from the base of the fixed mooring lines to set the starting point for each transect. The start of the transect line was placed on the reef whilst avoiding unnecessary damage to the substratum. This protocol was used to avoid pseudoreplication and to ensure that the largest possible area of each study site was surveyed to mitigate any bias associated with the aggregating behaviour of *D. antillarum*.

4.4.3 *Echinoid population status and D. antillarum morphometrics*

Belt transects of 2 m width were used, and all *D. antillarum* found within the survey area were recorded and life stage noted; juveniles have a test diameter of <20 mm (Levitan et al., 2014) and white bands on their spines (Randall et al., 1964). The abundances of *Echinometra viridis* (reef urchin) and *Tripneustes ventricosus* (West-Indian sea-egg) were also recorded.

4.4.4 *Benthic community assessment*

Benthic communities were assessed using the line-point-intercept method via underwater videography (GoPro Hero 3, 1080 HD, 60 frames per sec) with data points taken at 25 cm intervals. These data were used to determine (1) percentage cover of live scleractinian coral as a proxy for reef health, and (2) percentage cover of mature macroalgae. Habitat Assessment Scores (HAS), designed as an alternative to traditional chain-link rugosity measures, were also recorded four times along each transect following the protocol of Gratwicke and Speight (2005). HAS accounts for the fact that ‘habitat structure’ is a multifaceted phenomenon comprised of many different architectural components, each of which has its own idiosyncratic relationship with different aspects of ecosystem diversity and function. 1 x 1 m quadrats were placed haphazardly on the reef within the parameters of the belt transect and the following components of reef complexity were awarded a score from one to five; rugosity, variety of growth forms, height, refuge size categories, live cover, and substratum (Gratwicke and Speight 2005). Each quadrat was therefore awarded a HAS value out of 30; quadrats with values of six are the most architecturally simple whilst those with HAS approaching 30 are the most complex.

Abundances of juvenile coral recruits were also noted along the 2 m wide belt transects described earlier for echinoid surveys. A coral recruit is defined as a colony <4 cm across its longest dimension (Edmunds and Carpenter 2001).

4.4.5 Population abundance of selected fish families

To investigate the impact of predation and competitive herbivory on population recovery, the abundances of key fish families known to interact with *D. antillarum* were recorded using 5 m x 5 m underwater visual census (UVC) belt transects (Samoilys and Carlos 2000). Specifically, abundance data were collected for known *D. antillarum* predators; Ballistidae, Haemulidae and Labridae, and interspecific competitors; Acanthuridae, Scaridae, Chaetodontidae, and Pomacentridae.

4.4.6 Statistical analyses

Preliminary analysis of within-site variation indicated no significant differences in any variable measured, thus allowing study site data to be pooled leaving $n = 9$ for each depth. All data pertaining to the ecological variables of interest (echinoid abundances, predation, competition, nutrient limitation, and HAS) were non-normally distributed, therefore a series of non-parametric Kruskal-Wallis tests were conducted to investigate the differences in all factors between sites and depths, as well as between years. Data could not be transformed to normality and so relationships between each variable and *D. antillarum* population size were tested using Generalized Linear Models (GLM) that accounted for site and depth as potentially confounding variables. GLMs were performed using Poisson ANCOVA, with *D. antillarum* as the continuous response variable, ecological variables of interest

as continuous explanatory variables, and site/depth as discrete explanatory variables. Poisson ANCOVAs were also used to investigate the relationship between *D. antillarum* population size and three proxies of their ecological functions (juvenile coral recruitment, scleractinian coral cover and macroalgal cover) to assess whether they provide the same key services on these reefs as is documented elsewhere in the literature. All analyses were conducted using JMP (JMP, Version 7. SAS Institute Inc., Cary, NC, 1989-2007).

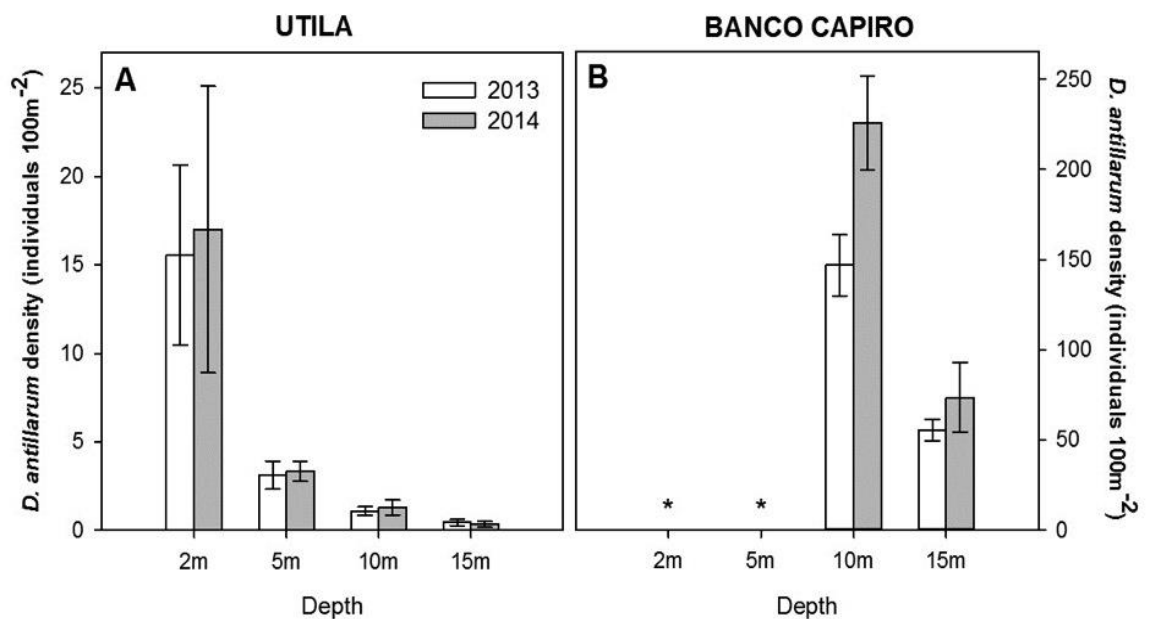
4.5 Results

4.5.1 *D. antillarum* population structure

D. antillarum population densities on Banco Capiro in 2014 were 225.67 ± 26.06 100m^{-2} (mean $\pm 1\text{SE}$) and 73.56 ± 19.11 100m^{-2} at 10 m and 15 m respectively. This was up to three orders of magnitude higher than on Utila, where densities were 1.22 ± 0.43 and 0.33 ± 0.17 100m^{-2} at the same depths (10 m: $H_1 = 12.95$, $p < 0.001$; 15 m: $H_1 = 13.340$, $p < 0.001$). At 10 m on Banco Capiro, *D. antillarum* population density increased by $>50\%$ between 2013 (146.89 ± 16.96 100m^{-2}) and 2014 ($H_1 = 4.31$, $p < 0.05$), while all other depths and sites showed no significant change between years. Mean *D. antillarum* densities were 17.00 ± 8.09 100m^{-2} and 3.33 ± 0.55 100m^{-2} at 2 m and 5 m on Utila (Fig. 4.2).

Reports of observed high population densities on Banco Capiro are supported by surveys conducted by the Atlantic Gulf Rapid Reef Assessment (AGRRA) in May 2011 (unpublished), which recorded mean *D. antillarum* densities ($n = 7$) of 156 ± 82 individuals 100m^{-2} . To further confirm the assumption that high *D. antillarum* population densities are a homogeneous characteristic across the Banco Capiro reef system, both temporally and spatially, surveys were conducted at two additional study

sites in 2014 (Mushroom Mountain: N 15.86497 W 87.49731; Rotonda: 15.86561 W 87.50680), recording mean densities of 178.00 ± 38.74 and 224 ± 25.54 individuals 100 m^{-2} respectively at 10 m depth. Three lines of evidence suggest these results represent the true status of *D. antillarum* populations, and are not simply a temporary phenomenon or an artefact of survey technique; *D. antillarum* population densities were similar (1) across three survey years (2011, 2013, 2014), (2) during two different seasons (spring, summer), and, (3) across the geographical extent of Banco Capiro.

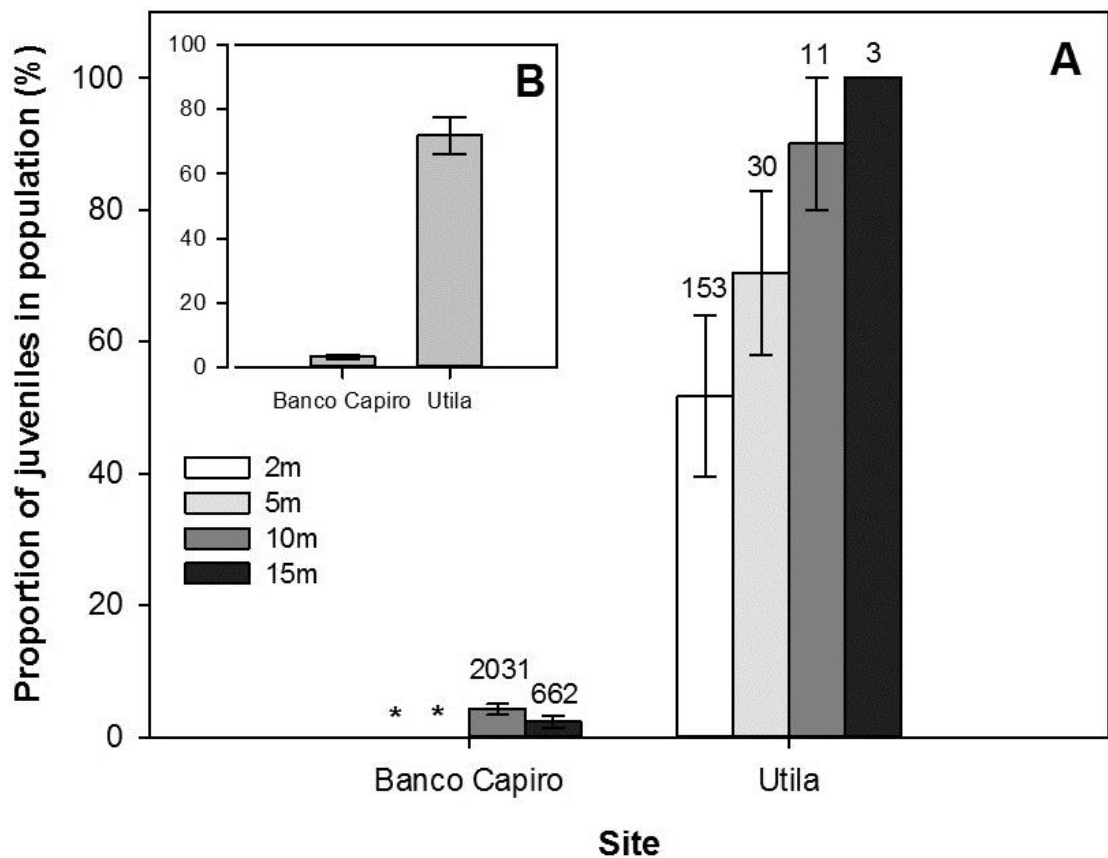


* Data for 2 m and 5 m on Banco Capiro were unavailable because of the topography of the site.

Figure 4.2. Population densities of *D. antillarum* at varying depths on the reef systems of Utila and Banco Capiro, including temporal variations between 2013 and 2014. Data shown are mean values \pm SE ($n = 9$), and were collected during June – August each year using 50 x 2m belt transects.

With all study depths combined (due to low sample size availability on Utila), the proportion of juveniles within *D. antillarum* populations was 22-fold higher on Utila than Banco Capiro ($H_1 = 16.37$, $p < 0.001$). On Utila 71.87 ± 5.77 % of all

surveyed *D. antillarum* were juvenile ($n = 197$), compared to just 3.35 ± 0.90 % on Banco Capiro ($n = 4541$). The proportion of juveniles did not significantly differ between depths. However, the number of juvenile *D. antillarum* 100m^{-2} was nearly 150 % greater on Banco Capiro (5.10 ± 1.15 100m^{-2}) than Utila (2.03 ± 0.36 100m^{-2}) ($H_1 = 4.26, p < 0.05$) (Fig. 4.3).



* Data for 2 m and 5 m on Banco Capiro were unavailable because of the topography of the site.

Figure 4.3. The proportion of juveniles within the overall *D. antillarum* population on the contrasting reef systems of Utila and Banco Capiro, shown (A) at individual study depths and (B) as a proportion of the total site population across depths. Data shown are mean \pm SE, and the total population size used to calculate proportions (n) are shown above each bar.

4.5.2 Investigating ecological function

There was a significant positive relationship between the density of juvenile coral recruits and *D. antillarum* population density, after controlling for the effects of site and depth ($F_1 = 27.49, p < 0.001$). Coral recruit density on Utila was 28.89 ± 2.96 and 23.22 ± 3.14 100 m^{-2} at 10 m and 15 m respectively, an order of magnitude lower than the 343.89 ± 23.53 and 185.89 ± 13.84 100 m^{-2} observed at the same depths on Banco Capiro (10 m: $H_1 = 12.80, p < 0.001$; 15 m: $H_1 = 12.80, p < 0.001$) (Table 4.1). Alongside the significant increase of *D. antillarum* population density at 10 m on Banco Capiro between 2013 and 2014 there was also an increase in juvenile coral recruitment at both 10 m and 15 m (10 m: $H_1 = 12.80, p < 0.001$; 15 m: $H_1 = 12.79, p < 0.001$). On Utila the abundance of juvenile coral recruits did not change significantly between 2013 and 2014.

Scleractinian coral cover on Utila was 12.17 ± 2.04 and 12.00 ± 1.73 % at 10 m and 15 m respectively, while cover on Banco Capiro was up to six times greater with values of 62.17 ± 6.61 and 48.72 ± 2.93 % at the same depths (10 m: $H_1 = 12.82, p < 0.001$; 15 m: $H_1 = 12.82, p < 0.001$) (Table 4.1). Urchin grazing facilitates expansion of existing coral colonies by removing competitive macroalgae and therefore drives the significant positive relationship between *D. antillarum* population density and percentage cover of scleractinian coral observed in this study ($F_1 = 4.16, p < 0.05$), although this relationship varies between sites ($F_1 = 4.07, p < 0.05$).

Mature macroalgal cover was up to 6.6 times greater on Utila (41.06 ± 3.55 and 46.72 ± 4.62 % at 10 m and 15 m respectively) than Banco Capiro (7.06 ± 1.46 and 23.06 ± 2.89 %) (10 m: $H_1 = 12.80, p < 0.001$; 15 m: $H_1 = 12.18, p < 0.001$) (Table 4.1); this is unsurprising given the large difference in *D. antillarum* population size and the important role that urchins have in removing primary productivity from the

reef. This assertion is supported by the observation that mature macroalgal cover decreased with an increase of *D. antillarum* population density on both Utila and Banco Capiro when controlled for site and depth ($F_1 = 17.69, p < 0.001$).

Ecological variable	Utila				Banco Capiro		P-values for differences in means between sites	
	2m	5m	10m	15m	10m	15m	10m	15m
<i>D. antillarum</i> population density (100m ⁻²)	17.00 ±8.09 ^a	3.33 ±0.55 ^{ab}	1.22 ±0.43 ^{bc}	0.33 ±0.17 ^c	255.67 ±26.06 ^d	73.56 ±19.11 ^e	<0.001	<0.001
<i>D. antillarum</i> biomass (100m ⁻²)	1429.7 ±680.78 ^a	280.33 ±46.49 ^{ab}	102.79 ±36.49 ^{bc}	28.03 ±14.01 ^c	17724.0 ±2046.90 ^d	5777.10 ±1500.10 ^e	<0.001	<0.001
Hard coral cover (%)	19.83 ±1.51 ^a	22.55 ±2.96 ^a	12.17 ±2.04 ^{ab}	12.00 ±1.73 ^b	62.17 ±6.61 ^c	48.72 ±2.93 ^d	<0.001	<0.001
Macroalgal cover (%)	33.78 ±2.51 ^a	36.00 ±5.56 ^a	41.06 ±3.55 ^a	46.72 ±4.62 ^a	7.06 ±1.46 ^b	23.06 ±2.89 ^c	<0.001	<0.0001
Predatory fish abundance (250m ⁻²)	35.78 ±9.11 ^a	9.11 ±4.12 ^{ab}	18.89 ±6.74 ^{ab}	9.11 ±3.03 ^{ab}	21.44 ±5.52 ^a	6.11 ±2.16 ^b	0.310	0.449
Herbivorous fish abundance (250m ⁻²)	102.89 ±11.34 ^a	93.89 ±11.34 ^a	61.00 ±6.05 ^{ab}	51.56 ±12.22 ^{ab}	78.11 ±6.96 ^a	53.11 ±5.51 ^b	0.078	0.507
Juvenile coral recruit density (100m ⁻²)	14.78 ±0.74 ^a	14.89 ±0.74 ^a	28.89 ±2.96 ^a	23.33 ±3.14 ^a	343.89 ±23.53 ^b	185.89 ±13.84 ^c	<0.001	<0.001
Habitat Assessment Score (HAS)	14.78 ±0.74 ^a	14.89 ±0.74 ^a	13.39 ±0.84 ^a	13.36 ±0.70 ^a	19.00 ±0.62 ^b	18.33 ±0.66 ^b	<0.001	<0.001
<i>E. viridis</i> abundance (100m ⁻²)	308.89 ±117.95 ^a	101.22 ±39.50 ^a	69.56 ±32.60 ^{ab}	15.22 ±9.13 ^b	67.89 ±21.74 ^{ab}	4.22 ±2.46 ^c	0.216	0.528
<i>T. ventricosus</i> abundance (100m ⁻²)	2.11 ±0.68 ^a	1.11 ±0.32 ^{ab}	0.00 ±0.00 ^{ab}	0.11 ±0.11 ^b	0.00 ±0.00 ^{ab}	0.00 ±0.00 ^{ab}	0.145	0.317
Proportion of juveniles in <i>D. antillarum</i> population (%) *			71.87 ±5.77 ^a			3.25 ±0.90 ^b		<0.001

*Data pooled across depths at each site due to the small sample size available on Utila.

Table 4.1. Echinoid population and broad ecosystem parameters at multiple depths on Utila and Banco Capiro. Data shown are mean values ±SE ($n = 9$). Superscript letters denote results of Steel-Dwass test (a non-parametric pairwise comparison) used because of non-normality of the distribution of all ecological variables. If the letters are the same there is no difference in the mean value of the variable between the corresponding depths/sites.

4.5.3 Barriers preventing population recovery

No significant difference was found between the abundance of fish predators of *D. antillarum* on Utila (21.44 ± 5.52 and 6.11 ± 2.16 250m^{-2} at 10 m and 15 m respectively) and Banco Capiro (18.89 ± 6.74 and 9.11 ± 3.03 250m^{-2}) (Table 4.1). There was also no significant relationship between predator abundance and *D. antillarum* population densities. Likewise, the abundance of herbivorous fish did not differ significantly between Utila and Banco Capiro at either depth. The mean abundance of herbivorous fish on Banco Capiro was 78.11 ± 6.96 and 53.11 ± 5.51 250m^{-2} at 10 m and 15 m respectively, and 61.00 ± 6.05 and 51 ± 12.22 250m^{-2} on Utila (Table 4.1). There was no relationship between herbivorous fish abundance and *D. antillarum* population size.

There was also no significant difference in the population density of *E. viridis* between Utila (69.56 ± 32.60 and 15.22 ± 9.13 100m^{-2} at 10 m and 15 m respectively) and Banco Capiro (67.89 ± 21.74 and 4.22 ± 2.46 100m^{-2}) (Table 4.1). Population densities of *E. viridis* and *D. antillarum* showed no significant relationship. However, when Utila was analysed independently, incorporating data from 2 m and 5 m, a significant positive relationship was observed between populations of these two echinoid species ($F_1 = 16.47$, $p < 0.001$). *T. ventricosus* were found to be present on the reefs of Utila, albeit at low population densities (0.11 - 2.11 individuals 100m^{-2}), whereas the species appeared to be entirely absent from Banco Capiro (Table 4.1).

HAS values on Banco Capiro were 19.00 ± 0.62 at 10m and 18.33 ± 0.66 at 15m, which were approximately 25% greater than the 13.39 ± 0.84 and 13.36 ± 0.70 recorded at Utila (10 m: $H_1 = 12.49$, $p < 0.001$; 15 m: $H_1 = 11.61$, $p < 0.001$) (Table 4.1). In the full Poisson ANCOVA model, no relationship between HAS and *D. antillarum* population densities was detected. However, when Utila was analysed in

isolation across all four depths, there was a positive relationship between *D. antillarum* population size and HAS ($F_1 = 22.34, p < 0.05$).

Temporally, mature macroalgal cover increased between 2013 and 2014 at both Utila (10 m: $H_1 = 11.56, p < 0.001$; 15 m: $H_1 = 10.41, p < 0.01$) and Banco Capiro (10 m: $H_1 = 8.04, p < 0.01$; 15 m: $H_1 = 10.99, p < 0.001$) (Table 4.1).

4.6 Discussion

4.6.1 Banco Capiro represents a unique contemporary reef system

Despite their close proximity, Utila and Banco Capiro have very different *D. antillarum* population densities, clearly demonstrating continued suppression of populations on Utila and augmentation of populations on Banco Capiro. Banco Capiro represents the highest reported post-mortality population density beyond the shallowest reef environments anywhere in the Caribbean. Crucially, these data also show that *D. antillarum* is fulfilling its expected role as a keystone species on both of these reef systems through a clear positive relationship between population density and both live scleractinian coral cover and juvenile coral recruit density, coupled with a negative relationship with macroalgal cover.

There are no pre-mortality data available for Honduran reefs and it is therefore possible that the *D. antillarum* populations of Banco Capiro were never impacted by the Caribbean-wide mass-mortality. However, given the ubiquity of the disease throughout the region, coupled with the fact Banco Capiro is located just 60 km away from Utila, where the low urchin densities allow one to assume that populations were impacted, it is highly likely that Banco Capiro was also left affected by the mass die-off.

Banco Capiro boasts a scleractinian coral cover of 48-62 %; impressive in a region where averages are estimated to be as low as 16.3 % (Jackson et al. 2014). The current dominance of corals of the genera *Agaricia* and *Undaria*, coupled with the increase in juvenile coral recruitment, suggests Banco Capiro is a reef system that is either (1) newly emerging, (2) in the process of regeneration, or, (3) transitioning to its likely future configuration (Aronson et al. 2004; Green et al. 2008; Côté and Darling 2010; Yakob and Mumby 2011; Darling et al. 2012; Garcia-Hernandez et al. 2017). *Agaricia* spp. and *Undaria* spp. are opportunistic plate corals with high reproductive outputs that recruit easily meaning they are often pioneers in the establishment of new reefs (Darling et al. 2012).

Although urchin populations on Banco Capiro increased between the two survey years, macroalgal abundance also increased. This finding is not unprecedented and mirrors those of a recent study in Puerto Rico, where the extent of macroalgal coverage was found to be uncorrelated with *D. antillarum* population size (Ruiz-Ramos et al. 2011). This result highlights the multifaceted nature of threats to coral reef ecosystems and shows that restoration of *D. antillarum* populations alone is unlikely to cause wholesale phase shift reversal. However, augmentation of *Diadema* populations and reintroduction of their associated ecosystem services may help to buy time to elucidate and mitigate other threats to coral reefs (Ghedini et al. 2015).

It is likely that recent increases in scleractinian coral cover, juvenile coral recruitment and *D. antillarum* population size have all occurred concurrently, and that a positive feedback loop has been established. The significant increases in *D. antillarum* population size and juvenile coral recruit abundance that occurred on Banco Capiro between 2013 and 2014 support this assertion. However, initiation of this positive feedback loop likely relies on Banco Capiro's release from a historical

barrier to *D. antillarum* recovery, initiating a population threshold to be exceeded that reinstates their ecosystem services. This barrier is likely to be related either to reproduction/recruitment dynamics, or to a change in the level of one or more ecological variables that have historically been suppressing population recovery.

4.6.2 Barriers preventing widespread population recovery

The spawning behaviour of, and volume of gametes produced by, *D. antillarum* before and after the mass-mortality event were similar (Lessios 1988), and experimental manipulations of *Strongylocentrotus droebachiensis* have demonstrated that when spawning adult sea urchins are separated by more than 2 m there is little chance of fertilisation success (Pennington 1985). Lessios (1988) therefore postulated that the observed lack of post-mortality juvenile recruitment might occur, not because of changes in reproductive dynamics, but because of gamete dilution caused by post-mortality increases in nearest-neighbour distance.

Even though the adult population is nearly 190 times greater on Banco Capiro than on Utila, the density of juvenile *D. antillarum* is only 150 % higher. This indicates that the rate of recruitment per individual is higher on Utila than on Banco Capiro. Whilst a potentially low level of juvenile *D. antillarum* recruitment on Utila is undoubtedly contributing to slow rates of population recovery, these data indicate the presence of a major ecological barrier that is suppressing recovery by operating to prevent juvenile survival into adulthood.

The time taken for juveniles to reach maturity is estimated to be roughly 12 months (Ogden and Carpenter 1987). However, despite the fact that in 2013 45 % of the Utilan *D. antillarum* population was juvenile, there was no significant increase in adult population size between 2013 and 2014. This fact, coupled with the observation

that the proportion of juvenile *D. antillarum* in the Utilan population increased from 45 % to 72 % between 2013 and 2014, indicates that at least low-level recruitment is occurring around Utila and that the resultant juvenile recruits are not surviving into adulthood.

On Utila there is a positive relationship between *E. viridis* and *D. antillarum* population densities that does not exist on Banco Capiro. This fact, coupled with the observation that *T. ventricosus* is entirely absent from Banco Capiro, suggests that Tela Bay might be a successional stage ahead of Utila or on a different ecosystem trajectory. In the initial stages of population recovery, a positive relationship between *D. antillarum* and both *E. viridis* and *T. ventricosus*, as seen on Utila, is expected as their generalist feeding habits clear areas of substratum for recruitment of palatable food resources for *D. antillarum* (Haley and Solandt 2001).

Competition from herbivorous fish fails to explain patterns of *D. antillarum* densities. Currently, densities of neither *D. antillarum* nor herbivorous fishes are sufficient for shared food resources to be a limiting factor. However, as *D. antillarum* (and fisheries) continue to recover on Banco Capiro competition will likely, at least partially, begin to regulate populations. With recently introduced fishing restrictions in Tela Bay, and improvements in fisheries management on Utila, the relationships between *D. antillarum* population and levels of competitive herbivory may change over time.

Banco Capiro is significantly more structurally complex than Utila but HAS only relates positively with *D. antillarum* density on Utila. This can be explained by the fact that Banco Capiro is highly homogeneous with lower variation in HAS than Utila, meaning that a significant relationship could be masked. Several studies highlight the importance of structural complexity for numerous echinoid species for

the facilitation of juvenile survival through the provisioning of shelter from predation (e.g. Andrew 1993; Hereu et al. 2005; Scheibling and Robinson 2008). Shelter enables urchins to develop until their test diameter is large enough to avoid predation when not hidden (Scheibling and Robinson 2008). While these results indicate predator abundance is not suppressing populations on Utila, observations of hiding behaviour suggest that urchins are reliant on shelter provided by the reef architecture as a key component of their ecology (Fig. 4.4).

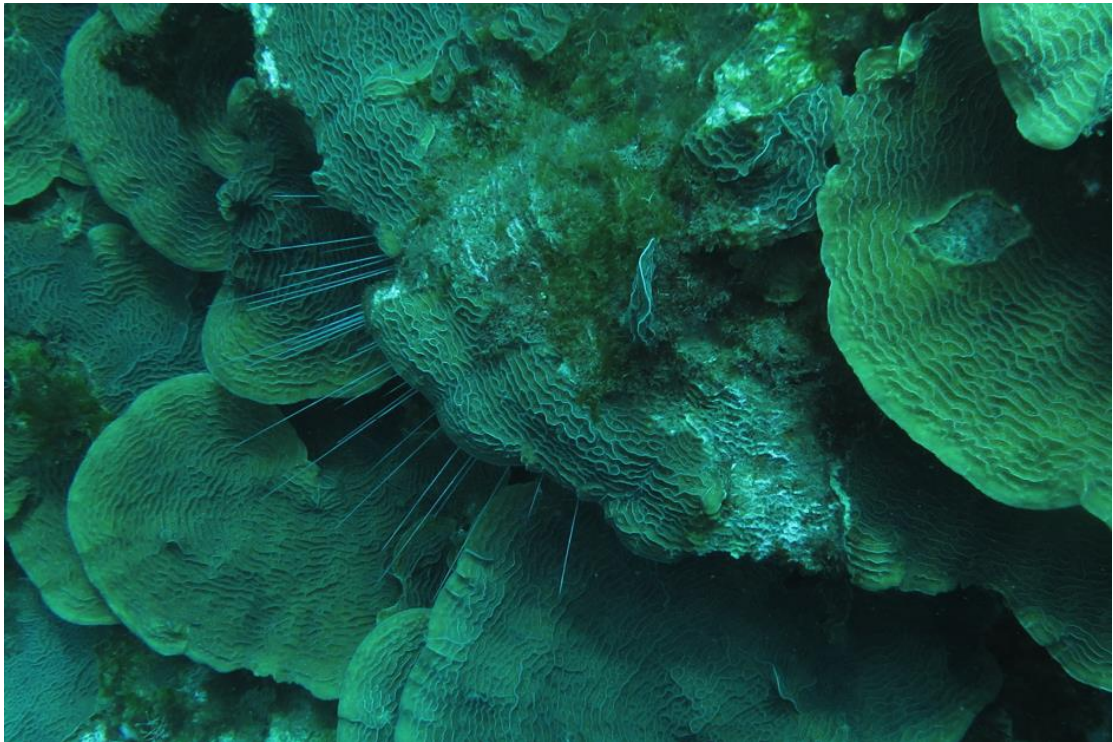


Figure 4.4. Photograph of adult *D. antillarum* exhibiting hiding behaviour on Banco Capiro by seeking shelter within a shelf created by a plate coral. This behaviour was commonly observed during data collection at this site. Photo credit: Alex Rogers.

The lack of relationship between *D. antillarum* and the abundance of predators on Banco Capiro may be elucidated by three, non-mutually exclusive, explanations: (1) the system is structurally complex enough that microhabitat availability still

outweighs demand, meaning predator avoidance is effective across the system. (2) Other predators not accounted for in this study, (e.g. *Panulirus argus*; spiny lobster), may affect *D. antillarum* population densities and explain the timid behaviour of the urchins. (3) There is a high proportion of juvenile urchins in Utila compared to adults suggesting that predation is acting on the population at this developmental stage, reducing numbers of mature individuals. If *D. antillarum* are most vulnerable to predation at this stage of their life-history it is possible that there is a link between habitat complexity and the provision of refugia from predation. Observations indicate that there is a positive relationship between *D. antillarum* population size and HAS on Utila. The low structural complexity of Utila's reefs may create a dearth of appropriate hiding places required by juveniles to develop test diameters that exceed the predation escape threshold.

Although AGRRA data used to create Figure 4.1 do not include a specific measure of habitat complexity (e.g. HAS), percentage cover of scleractinian coral can be used as a proxy for 3D structure because of the strong positive relationship that exists between these two variables (Lee 2006). All sites with *D. antillarum* population densities <1 individual m^{-2} represented in Figure 4.1 (i.e. all sites excluding Banco Capiro) had low mean scleractinian coral cover of 7-25 %. This means that Banco Capiro, the only site exhibiting *D. antillarum* densities >1 individual m^{-2} , is also the only site with scleractinian coral cover >25 % (10 m average of 62%). This strengthens the proposal that a lack of structural complexity across the MBRS may be a key-contributing factor to the near ubiquitous lack of *D. antillarum* population recovery, and that continued 'reef flattening' is likely to exacerbate this problem.

With this in mind, it is possible that adult *D. antillarum* populations could be augmented through the use of artificial reef systems designed specifically to protect

juveniles from predation. Doing this would enable *D. antillarum* ecosystem functions to be reinstated, which in turn would lead to increased stony coral cover and habitat complexity that would provide shelter for future generations of *D. antillarum* recruits. Enhancing *D. antillarum* population densities in this way would also help populations to overcome problems associated with low levels of juvenile recruitment, which is almost certainly an underlying barrier to recovery. High adult *D. antillarum* densities will lead to decreased nearest-neighbour distances, which in turn will increase fertilisation success rates and reduce the extent to which recruitment failure contributes to population suppression.

Future research efforts should focus on the relationship between reef structural complexity and survival of *D. antillarum* to the adult stage. Reduced habitat complexity may increase the impact of predation, thus increasing mortality rates amongst juvenile *D. antillarum*, and driving the barrier to maturation. If widespread population increases can in fact be stimulated via conservation interventions, Utila and Banco Capiro could provide a model for a wider-scale improvement of coral reef health throughout the Caribbean and sustain, if not improve, the socioeconomic circumstances of the millions of people who rely on its reef systems for survival.

5 Chapter Five – Provision of artificial habitat complexity drives recovery of *Diadema antillarum* and subsequent phase shift reversal on a degraded Caribbean coral reef

5.1 Thesis logic: part four

Now that a lack of reef structure has been identified as a potential barrier to *D. antillarum* population recovery, it is necessary to consider how this information can be used to stimulate region-wide restoration. Chapter 5 begins by using new 3D modelling technologies to further assess the importance of habitat complexity for *D. antillarum*. It continues by extending the work presented in Chapter 3 to experimentally evaluate the suggestion, previously based on ecological correlations, that provision of artificial structure may facilitate *D. antillarum* survival in a warming world. These data are used to justify the deployment of a series of experimental artificial reefs on La Ensenada, a degraded reef system in the southeast corner of Tela Bay. The ecological consequences of enhancing underlying reef complexity, on both urchin population status and common metrics of reef health, are investigated, and the use of artificial reefs as a future *D. antillarum* restoration strategy is evaluated.

5.2 Chapter summary

When populations of the Caribbean long-spined sea urchin, *Diadema antillarum*, are stable at high densities, their grazing facilitates scleractinian coral dominance. Today, populations remain suppressed after a pathogen-induced mass-mortality in 1983-84 caused a loss of their ecosystem functions, and led to rapid, widespread declines in ecosystem health. Using 3D habitat models generated with structure from motion and controlled behaviour experiments, this chapter demonstrates that urchins preferentially inhabit areas of higher than average reef complexity at spatial scales relevant to their ecology, and habitat structure helps to protect individuals against the negative fitness consequences of ocean warming. These findings justified deployment of a network of simple and cost-effective artificial structures on a heavily degraded reef system, which stimulated significant *D. antillarum* population recovery and phase shift reversal over a 24-month period. This study provides multiple lines of evidence to support the use of artificial reefs as a viable strategy for restoration of *D. antillarum* ecosystem functions and reversal of coral reef phase shifts.

5.3 Introduction

Efforts to restore *D. antillarum* have had mixed success, but reintroductions have been associated with increased abundances of mature and juvenile scleractinian coral, and decreased macroalgae cover (Nedimyer and Moe 2003; Macia et al. 2007; Rodriguez-Barreras et al. 2015a; Williams 2017). However, restoration attempts have largely failed due to high levels of post-introduction mortality (Miller et al. 2006; Leber et al. 2008). Researchers agree that high mortality rates, among juveniles in particular, can be linked to low complexity habitats failing to provide predation refugia. If restoration is going to be successful, the factors preventing natural population recovery must first be removed (Miller et al. 2006).

The ecological importance of reef architecture to *D. antillarum* is well understood, and population size is positively correlated with habitat complexity (Miller et al. 2006; Bodmer et al. 2015; Chapter 5). Complex habitats not only create a greater volume of living space, but they also provide individuals with refuge from predation (Haley and Solandt 2001; Tuya et al. 2004; Betchel et al. 2006; Bohnsack 2012; Chiappone et al. 2013). It is therefore likely that *D. antillarum* mass-mortality stimulated a self-reinforcing feedback loop that continues to suppress populations today. Scleractinian corals lay down hard calcium carbonate skeletons that provide structure (Heck and Wetstone 1977; Lee 2006; Alvarez-Filip et al. 2009; Graham and Nash 2013), and the large decreases in coral cover associated with the functional extinction of *D. antillarum* (Bak et al. 1984; Chiappone et al. 2002) have therefore led to region-wide reef flattening (Gardner et al. 2003; Alvarez-Filip et al. 2009). In turn, reef flattening has created a dearth of refugia that leaves *D. antillarum* vulnerable to predation (Scheibling and Robinson 2008; Pomory et al. 2014), and populations subsequently remain at ecologically irrelevant densities.

As we progress further into the Anthropocene, suppression of *D. antillarum* populations by reef flattening is likely to be exacerbated by the negative impacts of ocean warming on their innate, melanin-mediated, predator avoidance behaviours (PAB; Millott and Yoshida 1960; Chapter 3). Urchins living on flattened reefs are therefore likely to become increasingly vulnerable as the efficacy of their secondary line of predatory defence is reduced by ocean warming. As was demonstrated in Chapter 3, the impacts of rising SST on *D. antillarum* survivorship may be less keenly felt on high complexity reefs as individuals are afforded a degree of environmental protection from predation.

Provision of artificial structures on degraded Caribbean reefs may therefore, in theory, aid restoration of *D. antillarum* populations. Not only could structure help to reverse the positive feedback loop currently operating to suppress populations, but it may also play a protective role against the effects of climate change. Opinions surrounding the efficacy of artificial reefs vary hugely, with many researchers finding that they have positive effects on diversity and abundance (Carr and Hixon 1997; Clark and Edwards 1999; Sherman et al. 2002), while others question their efficacy stating that 50% of the time they fail to meet their initial objectives (Baine 2001).

Several studies looking at the effects of AR deployment on fish populations have shown that community composition and species richness are rarely as high as on neighbouring natural reefs (Carr and Hixon 1997; Perkol-Finkel et al. 2006; Walker and Schlacher 2014), they are too expensive to be deployed on a meaningful scale (Pickering et al. 1998), and, if the wrong materials are used, they can have detrimental effects on nearby reef communities (Brock and Norris 1989). However, using ARs to restore *D. antillarum* populations is much more likely to be successful, because they work best when targeted towards a single species (Seaman 2000). Artificial reefs of

varying size, shape and material are deployed on coral reefs for numerous purposes, but a single unifying factor is their use to create complex habitat that can be used as predation refugia (Sherman 2002; Bohnsack 2012).

This study uses a combination of *in situ* field-based surveys and *ex situ* laboratory manipulations to demonstrate the critical nature of habitat complexity in supporting *D. antillarum* survival since the mass-mortality event. Novel 3D modelling was used to explore the spatial distribution of surviving *D. antillarum* in relation to habitat complexity at an ecologically relevant scale on a ‘typical’ contemporary reef system. Controlled behavioural experiments were then used to experimentally assess the suggestion made in Chapter 3 that the provision of habitat complexity will provide energetic benefits by mitigating the effects of rising SST on natural predator avoidance behaviour. Finally, a network of simple and cost-effective artificial reefs on a macroalgae dominated reef system were surveyed over a 24-month period to explore whether the provision of artificial habitat complexity can be used to stimulate *D. antillarum* recovery, restore their ecosystem function and reverse macroalgae phase shifts in Caribbean reef systems.

5.4 Methods

5.4.1 *In-situ* *D. antillarum* habitat preferences

D. antillarum habitat preference on reefs around the island of Utila were studied. Utila can be considered ‘typical’ of a contemporary Caribbean coral reef, and it therefore provided a representative *in situ* post-mortality *D. antillarum* population to investigate the relationship between reef 3D complexity and reef use.

Measuring structural complexity of natural systems is challenging and a variety of field methods and analytical tools have been used to derive measures with

varying levels of success. Risk's chain method attempts to quantify rugosity by creating a ratio between the known length of a chain laid over the reef and its extent when allowed to follow the underlying reef contours (Risk 1972; Luckhurst and Luckhurst 1978), and the Habitat Assessment Score (HAS) is a more subjective measure that aims to provide visual estimates of six different components of reef complexity (Gratwicke and Speight 2005). Both methods have provided key insights into the role of structure on coral reefs, but their methodological limitations restrict their utility. Recently, Young et al. (2017) have shown it is possible to build 3D models of coral reefs using simple cameras and structure-from-motion. Their approach was used to model complexity on target reef systems in this study, and fractal dimension (D) was selected as the appropriate metric to assess complexity. D allows structural complexity to be measured within defined resolution boundaries (Zawada and Brock 2009), making it ideal when focusing on a single study organism as it allows complexity which is ecologically relevant to that species to be quantified in isolation. Complexity was assessed at 1-5 cm, 5-15 cm, 15-30 cm, 30-60 cm and 60-120 cm size intervals to give a broad overview of habitat complexity. Between 5-15 cm was identified as the likely size category of *D. antillarum* refugia based on variation in the size of the test (the hard, calcareous endoskeleton; Bodmer et al. 2017; Chapter 3). D provides a value between two and three for each size class, with a higher number indicating greater complexity. The five size categories were ultimately used to plot complexity signatures, providing a visual representation of how complexity changes across spatial scales between data sets.

3D models were built based on video scans of 2m x 2 m quadrats following Young et al. (2017). The 3D modelling protocol is sensitive to moving objects within the quadrat, therefore survey areas excluding octocorals and moveable sponges were

selected. Each quadrat was filmed from a birds-eye perspective with the camera (GoPro Hero 4 Black) approximately 50 cm above the substrate. The quadrat was swept by a diver carrying the camera and using a lawnmower pattern (Young et al. 2017). Once the first pass was completed, the camera's trajectory was turned 90° (without rotating the camera itself) and the pattern repeated. Each video was approximately 2.5 to 3 minutes long, camera movement was minimised as much as possible, and care was taken to ensure that the edges of the quadrat were filmed on each pass. Videos were converted to images using QuickTime Player v.7.6.6 (1709) (QuickTime 1989-2010) at an extraction rate of three frames per second, which generated 450 to 540 still images per quadrat. These images were uploaded to PhotoScanPro v.1.3.2 build 4205 (64 bit) (Agisoft PhotoScan Professional 2017) and 3D models were created. Resultant PhotoScan files (.psx) were converted to object files (.obj) and imported into Rhinoceros 5.3.2 (5D197) (Rhinoceros 1993-2017), where the models were analysed and fractal dimension values were extracted using Python script provided by Young et al. (2017).

Background reef complexity was assessed by generating 35 models based on 2 m x 2 m quadrats on six reef sites around Utila at depths of 8-10 m. Quadrats were placed to ensure no *D. antillarum* were found within them. These were compared with a further five models produced from quadrats intentionally positioned on reef areas inhabited with urchins. The uneven sample sizes, a result of the dearth of *D. antillarum* on study reefs, were accounted for in the statistical analyses.

5.4.2 *Ex-situ impacts of structural complexity on D. antillarum predator avoidance behaviour*

Modified temperature trials, based on those conducted in Chapter 3, were used to experimentally test the hypothesis that provision of artificial structure may ameliorate the negative effects of rising SST on *D. antillarum* PAB. The temperature treatments were selected to reflect the current mean SST in the Caribbean ($29.7 \text{ }^{\circ}\text{C} \pm 0.3 \text{ }^{\circ}\text{C}$; <http://www.seatemperature.org>) and to reflect lower ($31.6 \pm 0.3 \text{ }^{\circ}\text{C}$) and upper ($34.6 \pm 0.3 \text{ }^{\circ}\text{C}$) potential increases by 2100 (Hoegh-Guldberg et al. 2014). The Uta-Banco Capiro site comparison was removed, and a complexity factor, comprised of three different levels ('flat', 'low' and 'high'), was added. For 'flat' treatments no reef material was provided, for 'low-complexity' treatments breezeblock fragments lined the bottom of the tank, and for 'high-complexity' treatments tanks were enriched with a whole breezeblock. One hundred and eighty black adult urchins from Banco Capiro were tested under nine different experimental treatment combinations ($n = 20$ for each combination) in a fully-factorial design. Each urchin was used for a single trial only to remove the need for a repeated measures statistical design.

The sample collection and acclimation protocol was the same as that described in Chapter 3, therefore treatments were acute and represent a worst-case scenario: it is probable *in situ* that some level of adaptation would occur even to rapid, acute warming events (such as El Niños) where warming occurs over a period of months.

For each trial an individual *D. antillarum* was placed in the trial tank and allowed to settle for 30 minutes. Urchins naturally seek shelter, therefore, in treatments where it was available, they quickly moved towards the structure in the tank. After the settling period, a GoPro Hero 4 was set to record, placed in the tank and positioned to focus on the urchin.

Presence of a predator was simulated by creating a shadow over the tank following Bodmer et al. (2017; Chapter 3). Predator avoidance behaviour (PAB) was defined as the number of spines that move in response to the shadow stimulus as a percentage of the total number of long defensive spines visible in the video. This effectively standardises the measure between urchins and negates the problem that some long spines may be obscured by structures in the tank. Videos were analysed in a random order to avoid observer bias.

5.4.3 Deployment of artificial reefs to aid *D. antillarum* recovery and reef restoration

A trial restoration using artificial reefs was conducted at La Ensenada, a shallow patch reef (3-10 m) located in the southeast corner of Tela Bay, Honduras, approximately 12 km from the Banco Capiro reef system. Initial diver observations indicated a highly degraded and flattened reef system with scleractinian coral cover well below the 10 % threshold for active accretion to occur (Perry et al. 2012), macroalgae cover as high as 50%, and *D. antillarum* population densities less than the 1 m⁻² required for their ecosystem functions to be effective (Mumby et al. 2006). La Ensenada was selected as an ideal site for artificial reef (AR) deployment because (1) its high level of degradation makes it a good target for *D. antillarum* reintroduction, and (2) the high cover of sandy substrate facilitates deployment of artificial structures (Bohnsack 2012).

In summer 2015, 30 experimental ARs were deployed on La Ensenada. Each AR was constructed from 16 locally available breezeblocks (41 x 20 x 20 cm each) with three holes of 10 x 10 cm diameter (Fig. 5.1). Since the majority of artificial reef initiatives are considered to fail because they are too expensive (Pickering et al. 1998),

breezeblocks were used, not only because concrete has been identified as the best material (Fitzhardinge and Bailey-Brock 1989; Baine 2001), but also because they are inexpensive to produce and widely available. This cost-effective approach is essential if region-wide *D. antillarum* population recovery is going to be stimulated in a stepwise manner using non-expert contributors.



Figure 5.1. 3D image of an example artificial reef. Image credit: Shannon Cameron.

5.4.3.1 Artificial reef deployment

Three sites were selected at La Ensenada, and ten ARs were constructed at each site; Palm View 01 (N 15.80337 W 087.43922), Palm View 02 (N 15.80336 W 8743955), and Becky's Choice (N 15.80494 W 87.43955). ARs were separated by a minimum distance of 30 m. Divers descended to the base of the mooring buoy, tied off a transect tape and swam 30 m on a pre-arranged compass heading. The divers then

agreed upon a suitable area of reef with a large sand patch and deployed a Surface Marker Buoy (SMB) to alert the surface team to their position. Two lift bags were attached to a heavy-duty plastic crate, and used to lower the breezeblocks to the seafloor. Once all breezeblocks had been lowered, the dive team constructed the AR by creating a two-layered square structure on the benthos with holes facing outwards/inwards.

All ARs (Fig. 5.1) were placed in a 30 m arc around the mooring buoy, which was essential for ensuring future location and identification. This process was repeated until 10 ARs had been established at each study site within La Ensenada.

5.4.3.2 *Ecological assessments*

Immediately after deployment of the ARs in 2015, a t_0 ecological assessment was carried out around each structure to provide the baseline data to which future years could be compared. The same protocols were carried out in summer 2016 (t_1) and summer 2017 (t_2). Ten randomly placed 1 x 1 m quadrats were used to quantify the benthic community within a 5 m radius of each AR; 300 quadrats were surveyed each year, totalling 900 over the three-year study period. Each quadrat was photographed using a GoPro Hero 3+/4, and *D. antillarum* and juvenile coral recruit abundances were recorded *in situ*, while relative abundances of mature scleractinian coral, macroalgae, and rock were estimated using CoralPointCount (CPCe) software with 100 points overlaid on each image. Juvenile coral recruits are defined as coral colonies <40 mm in their longest dimension (Edmunds and Carpenter 2001). *D. antillarum* life-history stage of all encountered individuals was also noted; juvenile *D. antillarum* are identifiable by the distinctive black and white striped pattern of their spines (Randall et al. 1964).

Control data were collected using protocols outlined in Bodmer et al. (2015; Chapter 5), to ensure that any observed inter-year differences were associated with AR deployment and not natural changes in the system. Randomly placed 50 x 2 m belt transects created a 100 m² survey area in which *D. antillarum* and juvenile coral recruit abundances were recorded, and benthic percentage cover estimates were obtained using filmed line-point-intercept transects. Two transects were carried out on control reefs located at least 100 m away from any of the ARs at each site at La Ensenada ($n = 6$) in all three survey years.

5.4.4 Statistical methods

5.4.4.1 Habitat preference

Mann-Whitney U tests (selected because they are robust to unbalanced survey designs) were used to compare D values of the background complexity quadrats to the urchin-inhabited quadrats separately at each of the five spatial scales.

5.4.4.2 Predator avoidance experiments

Exploratory analysis showed that the data conformed to all the assumptions of simple linear regression. Two-way ANCOVA was therefore used to explore interactions between temperature treatment and complexity, and the *D. antillarum* PAB. Model selection was performed using the hypothesis testing approach (Zuur et al. 2007) until an appropriate model was identified. Post-hoc Tukey-Kramer analyses were used to identify where differences between treatments occurred.

5.4.4.3 Artificial reefs

Annual changes in the following metrics of reef health were assessed: juvenile and adult *D. antillarum* population sizes, percentage covers of macroalgae and scleractinian hard coral, and abundance of juvenile coral recruits. A series of repeated-measures Poisson, quasi-Poisson and negative binomial GLMs were conducted to identify differences in the means of each response variable between survey years (2015, 2016 and 2017) and treatment type (control and AR). All metrics were initially tested using Poisson GLMs and these were accepted if dispersion values were <1.5 . If dispersion values were between 1.5 and 5 for any given variable the GLM was rerun using a quasi-Poisson distribution, and if dispersion exceeded five, a negative binomial GLM was conducted (Zuur et al. 2007). Thirty ARs were deployed in 2015, but one was unable to be located in 2017 and has been removed from the analyses; therefore, $n = 29$.

All analyses were conducted using R v. 3.3.1 (R Core Team 2016) and RStudio v0.99.903 (RStudio Team 2015).

5.5 Results

5.5.1 *In-situ D. antillarum* habitat preferences

Across the five spatial scales tested, significant differences in habitat complexity between areas with surviving *D. antillarum* and the background reef average only occurred at 5-15 cm, the range identified as ecologically relevant to *D. antillarum*. Within this size category, Utila's reefs showed a background average fractal dimension (D) of 2.14 ± 0.01 (mean ± 1 SE), while *D. antillarum* were found in areas with an average of 2.22 ± 0.04 ($W = 38$, $p = 0.049$) (Fig. 5.2). There were no significant differences found across the remainder of the two complexity signatures.

At spatial scales >15 cm, there were no differences in D between urchin inhabited areas and the background average (15-30 cm: $W = 98$, $p = 0.61$; 30-60 cm: $W = 80$, $p = 0.86$; 60-120 cm: $W = 94$, $p = 0.73$).

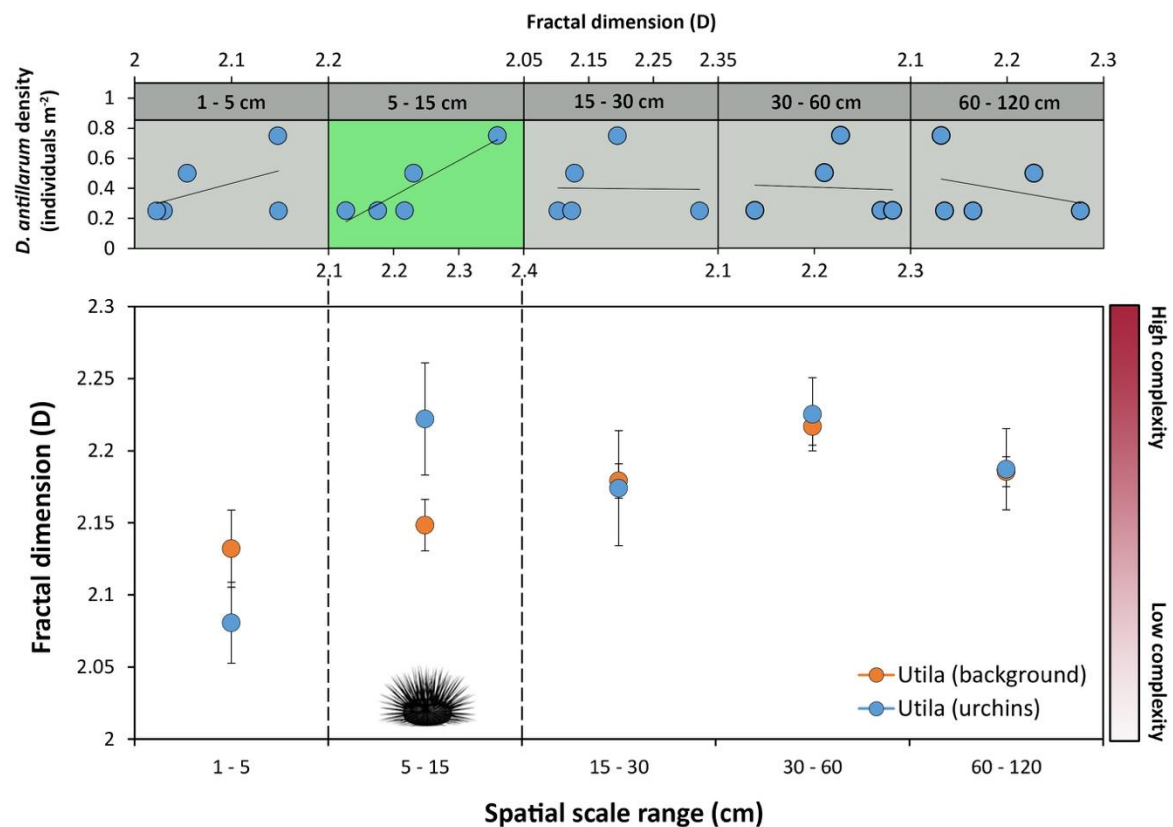


Figure 5.2. Complexity signatures of Utilan reef areas devoid of *D. antillarum* (orange, $n = 35$), and areas inhabited by *D. antillarum* (blue, $n = 5$). Data shown in the main panel are mean $\pm 1SE$ fractal dimension (D), shown at: 1-5 cm, 5-15 cm, 15-30 cm, 30-60 cm and 60-120 cm. The top panel shows relationships between *D. antillarum* population density and D at corresponding spatial scales..

5.5.2 *Ex-situ impacts of structural complexity on D. antillarum PAB*

Temperature and complexity interacted significantly to affect PAB magnitude ($F_2 = 11.73$, $p = 2.96 \times 10^{-8}$) (Fig. 5.2). Under current SST and with no structural complexity (i.e. ‘flat’ treatment) mean PAB was 54.94 ± 2.42 %. PAB decreased by 27.3 % in medium (39.89 ± 2.03 %) and 49.9% at high (27.51 ± 2.18 %) temperature scenarios ($F_2 = 46.86$, $p = 2.49 \times 10^{-16}$). With low structural complexity, these effects reduced significantly ($F_2 = 106.20$, $p < 2.00 \times 10^{-16}$). Enrichment of trial tanks with a low complexity environment reduced PAB at current SST (41.49 ± 1.67 %), and medium (43.22 ± 1.74 %) temperature scenarios, and mitigated the PAB reduction observed between these treatments in the absence of reef material; PAB reduction between control and high (28.21 ± 1.31 %) trials remained at ca. 30 % (Fig. 5.3). However, when individuals were provided with high complexity habitat the negative relationship between PAB and temperature was almost entirely negated; control = 24.32 ± 1.31 %, medium = 22.53 ± 1.70 %, high = 19.27 ± 1.49 % (Fig. 5.3).

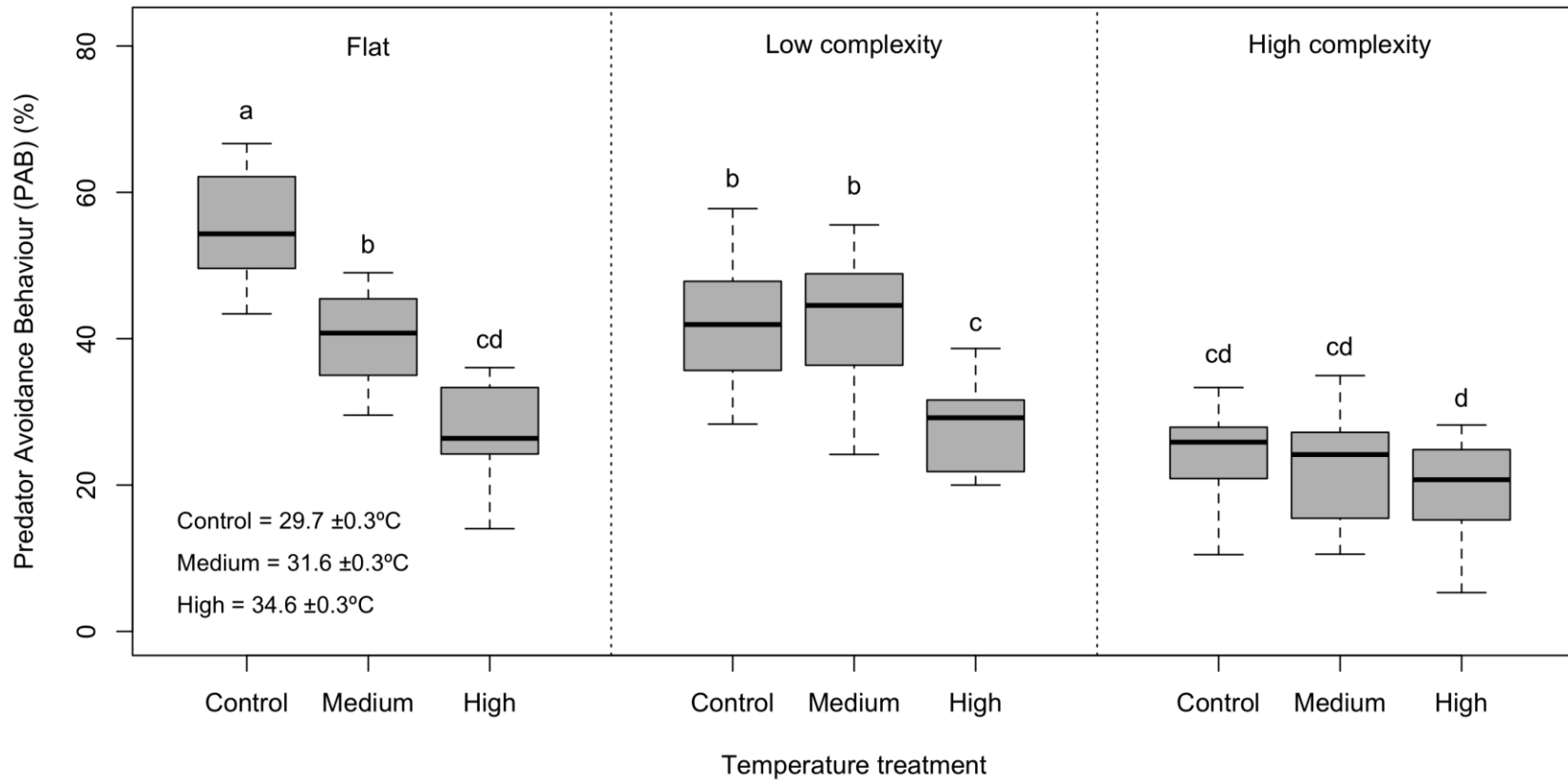


Figure 5.3. Impacts of water temperature and habitat structure on the predator avoidance behaviour (PAB) of *D. antillarum*. The study was fully factorial and $n = 20$ for each treatment. The bold horizontal line on each boxplot represents the mean, the box itself shows the interquartile range and the whiskers delimit the full range of the data.

5.5.3 Artificial reefs as a tool for *D. antillarum* population restoration

Prior to AR deployment, control reefs in La Ensenada exhibited mean scleractinian coral cover of 5.04 ± 0.73 %, macroalgae cover of 21.58 ± 0.50 %, *D. antillarum* densities of 0.14 ± 0.06 m⁻² and juvenile coral recruit densities of 3.38 m⁻². On the control reefs, the abundance of juvenile coral recruits decreased by 50 % in the first year, and by a further 47 % in the second year ($F = 70.06$, $p = 3.07 \times 10^{-7}$), and the juvenile *D. antillarum* population doubled ($F = 4.54$, $p = 0.05$). This supports the classification of La Ensenada as a degraded, macroalgae dominated reef system making it ideal for experimental restoration treatments. By contrast, within a 5 m radius of the ARs, adult *D. antillarum* densities increased nearly threefold in the first year (from 0.052 ± 0.01 to 0.179 ± 0.02 m⁻²), and by a further 15 % in the second year to 0.207 ± 0.04 m⁻² ($F_2 = 25.82$, $p = 1.28 \times 10^{-11}$) (Table 5.1). Changes in juvenile populations in the first year mirrored those of their adult counterparts (0.079 ± 0.02 to 0.121 ± 0.02 m⁻²), but a six-fold increase in population size observed in the second year (to 0.679 ± 0.07 m⁻²) indicates a faster rate of recovery ($F_2 = 119.08$, $p < 2.2 \times 10^{-16}$) (Fig. 5.4).

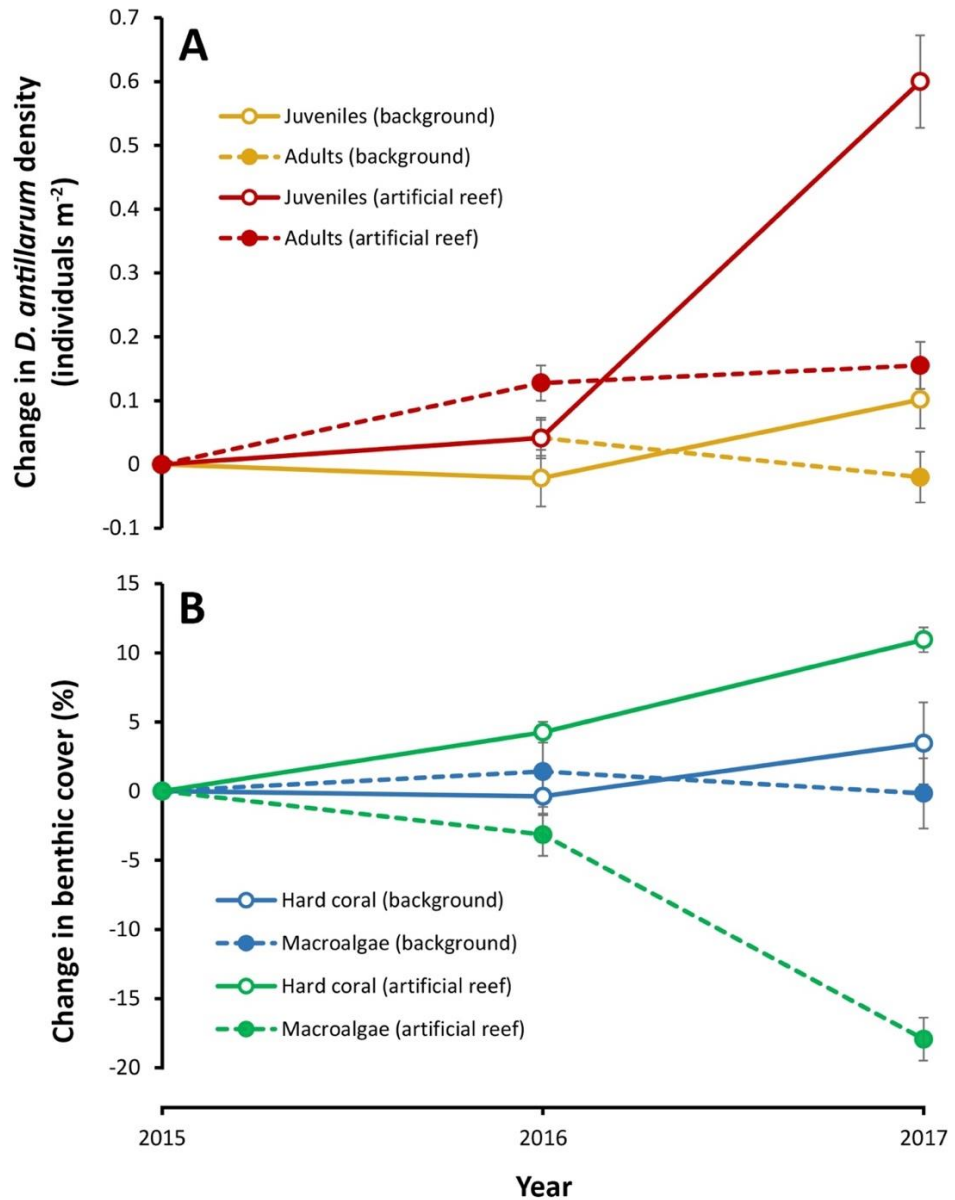


Figure 5.4. (A) changes in mean juvenile and adult *D. antillarum* populations from the point of artificial reef (AR) deployment in 2015 until 2017, showing mean values $\pm 1SE$ for control reefs (yellow), <5 m radius of artificial reefs (ARs, red), juvenile *D. antillarum* (solid) and adults (dashed). (B) absolute percentage changes in benthic community structure over the same study period, showing mean values $\pm 1SE$ for control reefs (blue), <5 m radius of ARs (green), scleractinian hard coral (solid) and macroalgae (dashed). For all variables, 2015 is the baseline year to which changes in population/benthic structure are compared. Mean $\pm 1SE$ of variables in 2016 and 2017 show changes in raw values relative to this 2015 baseline.

Significant improvements in benthic community composition accompanied the observed increases in urchin population density. Macroalgae cover decreased from 56.07 ± 1.19 to 52.92 ± 1.04 % in the first year, and again to 38.13 ± 0.91 % in the second year ($F_2 = 74.19$, $p < 2.2 \times 10^{-16}$), representing a 17.94 % decline in actual percentage cover (Fig. 5.3). Scleractinian coral cover doubled in year one (4.03 ± 0.41 to 8.29 ± 0.59 %), and then increased by a further 80 % in year two (to 14.97 ± 0.74 %) ($F_2 = 58.41$, $p < <0.001$); an overall increase of 10.94 % in actual percentage cover (Fig. 5.4). There was no significant change in the abundance of coral recruits throughout this time period, despite the significant decline on the nearby control reefs (Table 5.1).

Table 5.1. Mean (SE) values of *D. antillarum* population size and common ecological metrics of reef health for control and artificial reefs in La Ensenada surveyed in 2015, 2016 and 2017. *F* values correspond to GML statistical tests used to compare mean values across survey years, and corresponding *p* values are provided.

Control Reefs					
	2015	2016	2017		
Ecological factor	Mean (SE)	Mean (SE)	Mean (SE)	<i>F</i>	<i>p</i>
Adult urchins (m ⁻²)	0.07 (0.02)	0.11 (0.03)	0.05 (0.03)	0.22	0.64
Juvenile urchins (m ⁻²)	0.08 (0.04)	0.06 (0.01)	0.18 (0.04)	4.54	0.05
Total urchins (m ⁻²)	0.14 (0.06)	0.16 (0.04)	0.23 (0.05)	1.46	0.24
Macroalgae (%)	21.58 (0.50)	23.00 (2.53)	21.42 (2.36)	0.003	0.95
Coral cover (%)	5.04 (0.73)	4.67 (1.44)	8.50 (3.22)	1.38	0.26
Coral recruits (m ⁻²)	3.38 (0.28)	1.67 (0.22)	0.87 (0.15)	70.06	<0.05
Artificial Reefs (ARs)					
	2015	2016	2017		
Ecological factor	Mean (SE)	Mean (SE)	Mean (SE)	<i>F</i>	<i>p</i>
Adult urchins (m ⁻²)	0.05 (0.01)	0.18 (0.02)	0.21 (0.04)	25.82	<0.05
Juvenile urchins (m ⁻²)	0.08 (0.02)	0.12 (0.02)	0.68 (0.07)	119.08	<0.05
Total urchins (m ⁻²)	0.13 (0.03)	0.30 (0.04)	0.89 (0.08)	85.01	<0.05
Macroalgae (%)	56.07 (1.19)	52.92 (1.04)	38.13 (0.91)	74.19	<0.05
Coral cover (%)	4.03 (0.41)	8.29 (0.59)	14.97 (0.74)	58.41	<0.05
Coral recruits (m ⁻²)	4.32 (0.19)	3.47 (0.29)	4.01 (0.20)	4.38	0.10

5.6 Discussion

D. antillarum populations are failing to recover because processes of reef flattening (Gardner et al. 2004; Alvarez-Filip et al. 2009) have reduced complexity and left individuals vulnerable to predation (Scheibling and Robinson 2008; Pomroy et al. 2014; Bodmer et al. 2015; Chapter 5). The data show that, at a spatial scale ecologically relevant with regards to suitable predation refugia, *D. antillarum* inhabits areas of reef with disproportionately high habitat complexity compared to the surrounding reef average, and population size positively correlates with underlying reef structure at this scale. This suggests either active preference towards complexity at this spatial scale, or passively increased survival potential because of inhabiting these reef areas. The impacts of habitat structure and predation on *D. antillarum* population dynamics are well-documented (e.g. Tuya et al. 2004; Miller et al. 2006; Chiappone et al. 2013), but this study is the first to show how the species-specific importance of structural complexity varies according to the spatial scale of the observation.

D. antillarum test diameter ranges from 10-130 mm (Randall et al. 1964), and therefore it is logical to assume their population dynamics are largely determined by structural elements and predatory forces occurring at spatial scales <15 cm. At scales >15 cm the results demonstrate that the benefit of increased habitat structure is likely diminished because refugia no longer exclude predators, and further increases in structural complexity will not afford more protection. At the other end of the spectrum, complexity at a scale <5 cm also has no impact on *D. antillarum*, undoubtedly because individuals are simply unable to fit into refugia of this size and the space is therefore unusable. These findings support the assertion that a lack of suitable habitat complexity on contemporary Caribbean reefs is acting as a barrier to widespread

survival and recovery in *D. antillarum* populations (Lacey et al. 2013; Bodmer et al. 2015; Chapter 5), which will likely be exacerbated by continued reef flattening.

The *ex situ* laboratory trials show that structure is not only important for providing shelter from predation, but also potentially has a protective effect against the negative impacts of ocean warming on *D. antillarum* fitness. In the absence of reef material, *D. antillarum* PAB decreased in response to elevated water temperature, which agree with previous findings (Bodmer et al. 2017; Chapter 3). This relationship has the potential to further hinder *D. antillarum* population recovery due to the simultaneous occurrence of the phenomena of ocean warming and reef flattening (Alvarez-Filip et al. 2009); as reef complexity decreases, urchins become more reliant on PAB for survival, but as SST increases, PAB is reduced. However, the negative relationship between SST and PAB is shown to be attenuated by the provision of habitat complexity.

Under control temperature treatments, there is a stepwise reduction in PAB associated with increasing levels of structural complexity. Addition of habitat structure enables individuals to gain fitness benefits associated with reduced energy expenditure without incurring the fitness costs associated with increased predation pressure (Millott and Yoshida 1960). In the absence of reef material, PAB in the medium temperature treatment was lower than that observed at the control temperature, but this difference disappeared when urchins were provisioned with low complexity habitat. In the high-temperature-low-complexity treatment, PAB was significantly lower than under the low-complexity treatments of either of the other two temperature scenarios, which indicates that the mitigating effect of low complexity reef architecture may not occur if the most severe climate change predictions come to fruition. However, regardless of the temperature scenario, *D. antillarum* PAB was

similar across all high complexity treatments, which implies that complex reef structures may help facilitate *D. antillarum* survival in a warming world by providing a secondary line of predatory defence and reducing reliance on innate predator avoidance behaviours that will be negatively impacted by rising SST.

The *in situ* habitat complexity preference results, coupled with the *ex situ* laboratory trials, support the assertion that deployment of ARs is a suitable strategy for restoration of *D. antillarum* populations and their ecological benefits to ecosystem health and resilience. Enhancement of habitat complexity at the 5-15 cm spatial scale will not only provide *D. antillarum* with suitable predation refugia, but will also buffer them against the negative effects of future climatic changes. For artificial reefs to be successful in achieving their conservation goals, materials must be cheap and readily available (Fitzhardinger and Bailey-Brock 1989; Seaman 2000; Baine 2001). Concrete breezeblocks were an obvious candidate, not only because of their ubiquity throughout the Caribbean, but also because their openings have standard dimensions of ca. 10 x 10 cm. The complexity signature of a breezeblock is similar to *D. antillarum*'s *in situ* habitat preference, and therefore provides structure at the spatial scale required for size-specific protection against predation at all life-history stages.

The threefold increase in *D. antillarum* population size and significant benthic recovery observed around 29 ARs on a highly degraded macroalgal dominated reef system over a 24-month period provides strong evidence that deployment of ARs is a viable restoration strategy at the ecosystem level. Given *D. antillarum*'s important role as a macroalgal grazer (Carpenter 1984; Haley and Solandt 2001; Mumby et al. 2006; Chiappone et al. 2013), it is unsurprising that urchin population growth was associated with decreases in macroalgae cover and increases in hard coral cover.

It must be noted that the observed increase in the means of both *D. antillarum* population size and percent cover of scleractinian hard coral between 2015 and 2017 is accompanied by an almost threefold increase in standard deviation. This may indicate that, while there have been significant improvements in urchin population status and metrics of reef health, *D. antillarum* recovery, and therefore reinstatement of its associated ecosystem functions, has been patchy.

Many studies show a positive correlation between *D. antillarum* population density and abundance of juvenile coral recruits (e.g. Edmunds and Carpenter 2001; Idjadi et al. 2010). Coral recruit abundances decreased by 74 % between 2015 and 2017 on the control reefs at La Ensenada, possibly because high levels of sedimentation and macroalgae in the area have created suboptimal settlement conditions (Rogers 1990). However, the stability of the juvenile coral recruit community around the ARs suggests that reinstatement of *D. antillarum* grazing has acted to protect the reef from environmental/ecological factors driving declines observed elsewhere.

The benefits associated with deployment of artificial reefs appear to be highly localised, as control reefs in La Ensenada located just 100 m away from the structures saw no change in urchin population size or metrics of reef health throughout the study period. Conservationists attempting region-wide restoration will need to account for this by designing strategies that facilitate recovery in a stepwise manner. It is hypothesised that population recovery is density-dependent (Rogers and Lorenzen 2016), and will initially occur in high quality (i.e. complex) habitats. Once populations in optimal habitats reach carrying capacity, intraspecific competition will force individuals into adjacent suboptimal reef areas. These lower complexity reefs will benefit from *D. antillarum* grazing as macroalgae cover decreases and scleractinian

coral cover increases to enhance the structure of the environment, and promote further augmentation of urchin populations. Provision of strategically placed artificial reef structures over larger geographical areas may stimulate this cycle of localised recovery and spill-over, and ultimately enable *D. antillarum* to create new complex habitat that will reinforce its own recovery. Numerous studies addressing the SLOSS (single large or several small) question in marine environments conclude that conservation of small areas can have far-reaching benefits, both spatially and temporally, as a result of spill-over effects (Jones et al. 2007). The small-scale intensive management intervention proposed here is therefore based on a tried and tested approach to marine conservation.

The manpower required to stimulate the recovery of *D. antillarum* will be huge, and conservationists will need to look beyond the scientific community for help. A major advantage of artificial reefs is that the theory behind their use is easy to understand, and the simple and inexpensive nature of this design means they could be deployed by interested non-experts (Seaman 2000) such as the recreational dive industry. In theory, artificial structures only ever need to be deployed once on any given local reef system because they will catalyse the occurrence of a positive feedback loop; restoration of *D. antillarum* ecosystem services will lead to increased hard coral cover and structural complexity, which will stimulate further increases in urchin population size. Using a combination of reef surveys, ex-situ behavioural trials and field-based experimental manipulations this study has demonstrated that deployment of artificial reefs, constructed from cheap and readily available materials, is a viable conservation strategy for the restoration of *D. antillarum* in the Caribbean, and may even serve to give some protection to populations against the negative impacts of climate change.

6 Chapter Six – Discussion

6.1 Major findings and conservation implications

The ubiquity of macroalgal phase shifts throughout the Caribbean means that the region is in need of urgent conservation attention. Most local threats in the Caribbean operate to reduce herbivory either directly, as a result of overfishing and disease (Hughes et al. 2007), or indirectly, e.g. through stimulation of trophic cascades caused by the introduction of the invasive lionfish (Lesser and Slattery 2011). Enhancement of herbivore populations is likely to aid phase shift reversal, but because the mechanisms by which this functional group is being suppressed are so many and varied, and conservation resources are so limited, managers are unable to simultaneously ameliorate all potential threats. They are therefore left in the unenviable position of having to prioritise among numerous potentially beneficial strategies.

Echinoids and herbivorous fish are the major Caribbean reef herbivores (Roff and Mumby 2012), and there is debate in the literature surrounding the relative merits of targeting each of these groups for conservation. Chapter 2 demonstrated that, respectively, fish-grazing and urchin-grazing create low-abundance-high-diversity and high-abundance-low-diversity coral communities; neither configuration is ideal as low coral abundance reduces structural complexity and living space (Lee 2006; Alvarez-Filip et al. 2009), whilst low diversity is likely to reduce resilience and leave the system vulnerable to catastrophic collapse (Bellwood et al. 2004). Data from Chapter 2 supports the prediction that the coral community on a fully-grazed reef will be high-abundance-high-diversity, and therefore a mixed conservation approach aimed at augmentation of both echinoids and fish is likely to be the most effective strategy, although also the most challenging to implement. However, the degraded

state of coral reefs in the region, made it impossible to directly survey benthic structure and diversity metrics on a fully-grazed Caribbean coral reef to verify this prediction.

Future work focussed on herbivore restoration should attempt to evaluate the above hypothesis through assessment of naturally occurring reef systems with herbivore biomasses that exceed their thresholds for ecological relevance. However, while there are isolated reports of post-mortality *D. antillarum* populations exceeding 1 m^{-2} , Banco Capiro appears to be the only reef system with consistently high urchin numbers across a large geographical area, which makes this aim difficult to achieve. Assessment of a mixed conservation strategy may therefore only be possible once efforts to restore *D. antillarum* populations have been made on naturally fish-grazed reefs.

The 18 g m^{-2} fish herbivore biomass threshold used throughout this thesis is based on estimations made by Williams et al. (2001) from a healthy reef on Ambergris Caye, Belize, and the 1 m^{-2} *D. antillarum* density threshold is extracted from a simulation modelling study conducted by Mumby et al. (2006). The herbivorous fish threshold was chosen because the coastal waters of Belize and Honduras are both located within the Mesoamerican Barrier Reef system and are therefore geographically related, whereas the *D. antillarum* threshold was used simply because it is the best estimate available in the literature.

When investigating the impacts of grazer identity on benthic community composition in Chapter 2, data were only collected from three reef sites, therefore the sample size of each grazing scenario was one. Whilst 20 replicate transects were carried out at each site, these repetitions may be considered pseudoreplicates. Logistical and monetary restrictions associated with data collection, coupled with the

rare occurrence of urchin-grazed reefs throughout the Caribbean today, made it impossible to increase the sample size.

The low sample size means that the results presented in Chapter 2 may be spatially confounded, and any conclusions drawn about their wider applicability must be considered within this context. Whilst Utila, Roatan and Banco Capiro are all located within 100km of each other, and are therefore closely geographically related, it is possible that there are unaccounted for differences in the abiotic environment that may, at least partially, drive the observed composition and diversity patterns. Whilst Chapter 2 provides a good case study of the potential impacts of fish versus urchin grazing, researchers must endeavour to identify other systems within the tropical Western Atlantic that meet the threshold limits of fish-grazed, urchin-grazed, under-grazed, and even fully-grazed reefs, if we are to fully understand how herbivores shape Caribbean coral reef communities.

The Atlantic Gulf Rapid Reef Assessment (AGRRA) is a collaboration of researchers working in the tropical Western Atlantic that aim to monitor reefs throughout the entire extent of the Caribbean. The AGRRA database contains thousands of transects from hundreds of reef sites throughout the Caribbean across a gradient of herbivory. Future research should use their open access database to increase the sample size of the experimental treatments and ascertain how grazer identity impacts benthic structure on a regional scale. Accessing the AGRRA database could also help to ascertain herbivore biomass thresholds that are (1) applicable to a wider geographical range extending beyond the MBRS, and, (2) based on real world datasets rather than modelling studies. Using these data will better enable conservationists to gauge the applicability of this thesis' findings to a wider range of reef sites throughout the Caribbean.

Whilst a mixed strategy may be ideal, protection of herbivorous fish populations in MPAs has had only limited success because of high levels of non-compliance and difficulties associated with rule enforcement in socio-economically deprived regions of the world (Edgar et al. 2007; Gill et al. 2017). *D. antillarum* restoration studies are less common than those assessing the efficacy of MPAs, but this thesis has identified that localised deployment of artificial reefs may be a cheap and easy strategy to not only augment urchin densities, but also reverse the effects of macroalgal phase shift. Threats in the Caribbean are acute and immediate therefore combative action needs to be taken now, and, whilst reefs dominated by urchin-grazing may have reduced diversity and long-term resilience, population enhancement is likely to prevent further macroalgal overgrowth and enhance coral domination in the short-term.

Successful conservation will only occur if managers design strategies within the context of future reef configurations; it is predicted that the numerous anthropogenic threats occurring in the Caribbean will promote growth of fast-growing agaricids (Côté and Darling 2010; Darling et al. 2014; Garcia-Hernandez et al. 2017), and data from Chapter 2 indicates that urchin-grazing may also aid the expansion of this coral group. Restoration of *D. antillarum* on a local-scale is not a silver-bullet for Caribbean coral reef conservation, but if implemented immediately, it may facilitate the predicted *Montastrea/Orbicella* to *Agaricia/Undaria* transition, which will, in turn, capture diversity and confer a modicum of short-term resilience whilst longer term management solutions are sought.

Having identified *D. antillarum* population restoration as an important conservation strategy, it was necessary to assess its viability in the context of future predicted climatic changes. Conservation of any species will require large time and

financial investment, therefore the target species' future survivorship must be evaluated to ensure minimal wastage of already scarce resources; in the light of unprecedented rates of climate change, assessment of 'future-proofness' has never been more important. Chapter 3 is the first study to address *D. antillarum* temperature tolerances, and discuss how they may potentially impact the design of restoration initiatives. The finding that the magnitude of innate predator avoidance behaviours (PAB) is negatively impacted by rising temperature is worrying when considered alongside the large-scale reef flattening currently occurring around the Caribbean (Gardner et al. 2003; Alvarez-Filip et al. 2009). As coral is lost and reef structure is diminished, individuals are left without predation refugia and become increasingly reliant on their innate anti-predator responses for survivorship. Ocean warming and reef flattening may operate synergistically to reduce the probability of long-term *D. antillarum* survivorship; rising SST causes coral bleaching and mortality (Roth 2014), and reduction of reef complexity. This increases individuals' reliance on PAB, which, in turn, is also reduced at elevated water temperatures. Ocean warming therefore has the capacity to damage both lines of predatory defence available to *D. antillarum* (i.e. environmental and behavioural), which could lead to further suppression of already struggling populations.

At first glance, these results appear damning for advocates of *D. antillarum* restoration as reinstatement of ecosystem functions is unlikely to persist beyond the end of the century. However, idiosyncrasies in the data indicate that long-term survival prospects may be less severe than initially thought. PAB reductions under medium severity climate change scenarios are small in comparison to those observed under worst-case scenarios. Given the pressure being put on governments to reduce greenhouse gas emissions, the IPCC predicts that medium severity scenarios are the

most likely to come to fruition (Masui et al. 2011; Thomson et al. 2011). Whilst medium severity temperature increase does lead to small PAB reductions, the survival impacts may be minimal as the magnitude of the PAB response should still provide protection against predation. The extent to which reductions in PAB lead to increases in predation is an important area for future research.

The near-term (by 2039) water temperature increase predicted by the IPCC under a worst-case scenario (30.53°C) is lower than the long-term (by 2100) temperature predicted under the medium severity scenario (31.1°C) at which PAB was tested. Therefore, even under worst-case scenario conditions, *D. antillarum* is likely to be resilient to near-term increases in water temperature. If a concerted effort is going to be made to restore *D. antillarum* immediately to buy time for development of longer-term strategies, then initiatives aimed at population augmentation will remain worthwhile even in a worst-case climate change situation. Since the studies presented here were unable to examine longer-term adaptation of *D. antillarum* to temperature increases, it may be that the impacts suggested will not be so severe in reality.

The scope of this thesis only allowed the potential impacts of ocean warming to be assessed, and the effects of ocean acidification, often known as ‘global warming’s evil twin’, were unable to be evaluated. As a calcium carbonate-based organism, *D. antillarum* is likely to be vulnerable to chemical changes driven by decreasing pH, and data pertaining to their likely responses should therefore be gathered and factored into predictions of future survivorship. Having said this, assessment of the impacts of rising SST is more urgent as tropical water temperatures are already rising, whereas the extent of ocean acidification is anticipated to be worse in temperate marine environments than on coral reefs (Fabry et al. 2008). One must also consider that, by the time decreases in pH affect *D. antillarum* survival, it is likely

that ocean acidification will have negatively impacted a plethora of other reef-dwelling organisms and disrupted normal ecosystem functioning, meaning that the battle to save Caribbean coral reefs may already be lost.

Successful species restoration can only occur *in-situ* if survival threats are mitigated (Miller et al. 2006). Having confirmed that *D. antillarum* restoration is not only likely to be beneficial to Caribbean coral reef health, but is also viable in the face of climate change, it was therefore necessary to think about the mechanisms operating to suppress population recovery. *D. antillarum* population densities on Utila are typical of a contemporary Caribbean coral reef, and its ecological dynamics were therefore compared to those of nearby Banco Capiro, which may be home to the healthiest post-mortality urchin population found in the region, to identify the ecological barriers operating to suppress recovery.

Findings from Chapter 4 were congruent with numerous studies highlighting the importance of habitat structure for *D. antillarum* (Lee 2006; Myhre and Acevedo-Gutierrez 2007; Ruiz-Ramos et al. 2011), and it was proposed that their own functional extinction in the early 1980s established a positive feedback loop that continues to hamper populations to this day. Loss of *D. antillarum* ecosystem functions causes decreases in coral cover (Solandt and Campbell 2001; Chiappone et al. 2013), which leads to a reduction of habitat complexity (Heck and Wetstone 1977). The deficit of predation refugia created in low complexity environments leaves individuals, and juveniles in particular, vulnerable to predation (Hereu et al. 2005; Scheibling and Robinson 2008), and reduces survival into adulthood; populations remain low and reef structure and survivorship become worse with every cycle of the feedback loop.

Evidence from Chapter 4 was therefore used to propose that augmentation of reef complexity using artificial structures may reverse the ecologically damaging

positive feedback loop, and lead to establishment of an ecologically beneficial positive feedback loop; ultimately stimulating a self-reinforcing cycle of recovery. Deployment of artificial reefs would provide individuals with shelter from predation and increase juvenile survival into adulthood, and densities will subsequently be able to surpass the ecologically relevant threshold needed for reinstatement of their ecosystem functions (Mumby et al. 2006). Coral cover and structural complexity will increase thus providing more predation refugia to stimulate further recovery.

The other previously hypothesised major barrier to recovery is the fact that large nearest-neighbour distances associated with low density populations have led to an Allee effect (Levitan et al. 2014). External fertilisers, such as *D. antillarum*, must live at high densities to ensure fertilisation success as ejaculates are significantly diluted over even very small spatial scales (Pennington 1985). Enhancement of reef complexity would not only serve to create predation refugia, but would also facilitate aggregation thereby offering a solution to both major barriers to population recovery.

Findings from the previous three chapters were coupled with *in-situ* habitat preference and *ex-situ* lab-based studies, to justify the deployment of experimental artificial structures on the degraded reef system of La Ensenada located in the southeast corner of Tela Bay, and the efficacy of this approach was evaluated in Chapter 5. For the first time, novel 3D modelling technologies (Young et al. 2017) were used to confirm the importance of habitat structure for *D. antillarum*; at the spatial scale most relevant to their ecology, they were found to preferentially inhabit areas of higher complexity than the background average. Further exploration of the relationship between *D. antillarum* PAB, water temperature and habitat structure provided experimental evidence to support the hypothesis, proposed in the discussion

of Chapter 3, that reef structure may help mitigate against the negative fitness effects of rising SST.

The data suggest that provision of artificial habitat structure is a cost-effective and viable management solution for the restoration of *D. antillarum* populations on a local-scale. Over a 24-month period, significant increases in urchin population size were accompanied by augmentation of scleractinian coral cover and decreased macroalgae abundance, indicating that facilitation of *D. antillarum* recovery can lead to macroalgal phase shift reversal. Unsurprisingly, juvenile urchins seemed to gain the most benefit from deployment of the reefs, which provides a further line of evidence to support the hypothesis that population recovery is limited by the previously outlined positive feedback loop.

6.2 The importance of reef architecture

The unifying theme that has emerged from this thesis is the pivotal role that habitat structure plays in the maintenance of healthy Caribbean coral reef ecosystems. Most conservationists highlight the importance of protecting diversity within functional groups as a means of maintaining redundancy and resilience (e.g. Elmqvist et al. 2003; Mumby et al. 2006; Graham 2014; Micheli et al. 2014), but data presented here indicate that preservation of underlying reef architecture may be even more fundamental.

Most MPAs aim to protect diversity and ecosystem function by legislating against overharvesting and other destructive human activities within the boundaries of the park (Edgar et al. 2007), but concerted efforts to preserve structure are rarely made. Reef flattening can largely be attributed to loss of herbivory and coral mortality caused by rising SST (Alvarez-Filip et al. 2009; Graham 2014). Whilst MPAs with effective

enforcement may aid recovery of herbivore populations, they will never mitigate against the negative structural consequences of ocean warming. The ultimate aim of all protected areas, marine or terrestrial, should be to capture diversity and function to provide ecosystem resilience, but unless efforts to preserve remaining structure, and restore lost structure, are integrated into current conservation strategies, this aim will not be achieved. Protection of reef architecture is more fundamental than protection of diversity, but, because structure begets diversity and diversity begets resilience (Graham and Nash 2013; Graham 2014), collateral benefits will help conservationists achieve the ultimate aim of maintaining ecosystem function.

The ecological importance of habitat structure is well-documented in a variety of ecosystems. The mechanisms by which 3D complexity influences species ecology nearly always mirror the dynamics observed on coral reefs, as habitat structure interacts to attenuate predator-prey dynamics. In mangrove forests, juvenile fish abundance and diversity is always highest in the most complex root systems (Laegdsgaard and Johnson 2001), and structured environments are especially important for avoiding nocturnal predators (Verweij et al. 2006). In desert-dwelling baboons, the best determiner of distribution and behaviour is habitat structure, and they will preferentially forage in areas of poor food quality if the level of environmental protection afforded against predation is greater than in areas with higher quality resources (Cowlshaw 1997).

Mostly, species prefer to live in complex habitats to avoid predation, but there are examples of the predator-prey-complexity interaction that lead to preferential inhabitation of low complexity environments. The distribution of large herbivore populations in African grasslands is determined by predation risk and habitat availability, but rather than seeking high complexity habitats like urchins, fish or

baboons, they seek low complexity areas to minimise the efficacy of ambush hunting by lions (Valeix et al. 2009). Similarly, there is an ‘anti-refuge’ relationship between microinvertebrate abundance and habitat structure in freshwater ponds, as enhanced structure provides shelter for predators and therefore negatively impacts zooplankton population size (Klecka and Boukal 2014).

The universality of the importance of habitat structure throughout myriad ecosystems highlights the need for conservationists to put these ideas at the forefront of their proposed management strategies. There is a catch-22 that exists on Caribbean coral reefs; *D. antillarum* is essential for promoting habitat structure, and therefore diversity and resilience, but the urchins themselves are currently functionally extinct because of a *lack* of habitat structure in the ecosystem, which is, at least partially, attributable to their own population crash. Enhancement of habitat structure through construction of ARs will enable reinstatement of *D. antillarum* ecosystem functions. This will create a more structured environment, which will not only facilitate further increases in urchin populations, but will also promote diversity, functional redundancy and resilience.

6.3 Scaling-up

A potential solution to the problem of *D. antillarum* population restoration has been found. However, it is now necessary to consider how this locally successful approach may be scaled-up to a regional level so that populations throughout the Caribbean can benefit. It is hypothesised that recovery will be density-dependent and occur in a stepwise manner (Rogers and Lorenzen 2016); as populations reach carrying capacity in optimal habitats, they will spill-over into adjacent suboptimal habitats and reengineer them into more suitable reef areas. When carrying capacity is reached in

these newly optimal patches, the process will repeat thus eventually facilitating widespread population increases through multiple localised recovery events.

The major limitation of this thesis is the small geographical extent over which data were collected. It has been shown that *D. antillarum* population restoration is possible, and ecologically beneficial, on a highly degraded reef system off the north coast of Honduras, but it remains to be seen if these findings can be replicated elsewhere in the Caribbean. This thesis provides proof of concept that artificial reefs can facilitate *D. antillarum* restoration and subsequent phase shift reversal locally, so the next step is to assess whether the strategy proposed above can be used to scale-up restoration to a regional-level.

Deployment of ARs will likely stimulate this chain of recovery, but for populations to increase throughout the entire Caribbean they will need to be constructed at a large number of reef sites across a huge geographical range. Using a team of six people, it took two weeks to construct just 30 ARs on La Ensenada in 2015, therefore the manpower required to stimulate regional population recovery using this model will be huge. By making simple structures from cheap and widely available materials, i.e. breezeblocks, conservationists can look beyond the scientific community for help. Fortunately, it is estimated that there are ca. six million active SCUBA divers worldwide (Sfia.org 2017), and increasing awareness of environmental issues means that many of these have already shown willingness with regards to assisting with the establishment and development of marine conservation initiatives (Hammerton et al. 2012).

There are numerous conservation organisations that aim to exploit the SCUBA diving community to protect marine environments. Project AWARE is an NGO established by the Professional Association of Dive Instructors (PADI) in 1989 with

the aim of increasing public awareness of marine conservation issues. It currently has >180,000 members from 182 countries and, to date, they claim this network has taken 174,014 conservation actions (Projectaware.org 2016). AGRRA uses networks of high-level scientists and interested non-experts to collect ecological monitoring data from around the tropical Western-Atlantic, and, since its establishment in 1997, the network has conducted >2,300 surveys in 26 different countries (Agrra.org 2017). The Healthy Reefs for Healthy People Initiative, established in 2004, works with a large number of volunteer-led research organisations and dive centres throughout the MBRS to track key indicators of reef health. Their ultimate aim is to influence conservation management policy in the MBRS to ensure that practices are not only ecologically advantageous, but are also socioeconomically beneficial (Healthyreefs.org 2017). There is an appetite for active involvement in conservation amongst SCUBA diving communities, and, if a sufficient number of ARs are going to be deployed across the entire 3.5 million km² area of the Caribbean (Lessios et al. 1984a), this is a resource that will need to be tapped into.

A source of manpower has been identified, so it is now important to consider the economics of region-wide AR deployment. The raw materials required to create a single AR amount to ~US\$30; individual costs are low but when scaled up to the regional level large financial investment will still be required to achieve success. However, as part of their further education programmes many of the major dive certification agencies, including PADI, the National Association of Underwater Instructor (NAUI) and SCUBA Schools International (SSI) run distinctive speciality courses, which can be written and conducted by any SCUBA diving professional. Dive centres throughout the Caribbean could sell an ‘Artificial Reef Building’ diver speciality course at a price that not only covers their overheads, but also creates a

profit. Dive centres are financially incentivised and become responsible for providing resources and training to customers, who participate in the construction of an artificial structure on a local reef.

If these specialities are adopted widely enough it could help stimulate the stepwise recovery of *D. antillarum* throughout the region. This approach is more sustainable than relying on grant money for AR deployment, and has the added advantage of using the manpower provided by the large, and environmentally aware, SCUBA diving community. There is also a precedent for this approach to coral reef conservation; PADI's Project AWARE already runs a number of conservation-focussed speciality dive courses including, Shark Conservation, Invasive Lionfish Tracker, and Sea Turtle Awareness; SSI offers Marine Ecology/Underwater Naturalist, Shark Ecology, Sea Turtle Ecology, Coral Identification and Fish Identification specialities; and NAUI provides educational courses on the physical and biological aspects of underwater environments, and an Underwater Ecologist: Coral Reef speciality.

Before this approach can be adopted throughout the Caribbean, it is necessary to conduct a small-scale study to assess its viability. This may be achieved by using contacts in the Roatan Marine Park (RMP) made throughout the PhD process. The RMP is well-respected by the twenty local dive operators found around Roatan, and initial contact indicates that many of them might be willing to partake in a trial study designed to assess the efficacy of the 'Artificial Reef Building' dive speciality. Regular monitoring of customer-deployed artificial reefs will provide key data needed to evaluate the efficacy of the proposed strategy and, if successful, will justify its use throughout the Caribbean.

This thesis attempts to provide conservation scientists and managers with important information, currently missing from the literature, needed to aid *D. antillarum* population conservation efforts in the Caribbean. A combination of traditional and novel ecological survey techniques, coupled with lab- and field-based experimental manipulations, demonstrate that restoration of this keystone herbivore is not only worthwhile, but is also feasible even in the context of unprecedented rates of climatic change. If the management strategies proposed throughout this body of work can be scaled-up, there is a very real possibility that significant improvements to Caribbean coral reef health can be made.

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