

The Role of Marine Protected Areas in Coral Reef Ecosystem Resilience in Response to Increasing Sea Surface Temperatures.

A case study; Napantao Marine Protected Area, Southern Leyte and El Nino Southern Oscillation 2015.

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in collaboration with Coral Cay Conservation ©



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Declarations

This dissertation is the product of my own work and does not infringe the ethical principles set out in the University's Handbook for Research Ethics. I agree that it may be made available for reference via any and all media by any and all means now known or developed in the future at the discretion of the University.

Abbie Dosell, 2017.

Abstract

1. Marine Protected Areas (MPAs) are created with the intention of protecting coral reefs from external anthropogenic pressures; this protection is hypothesised to increase coral health and in turn increase coral resilience and tolerance to bleaching as a result of increased SST.
2. This study examines data from inside and outside Napantao MPA, Philippines, studying the response of benthic organisms and reef fishes from 2013 through to 2016 over the period of the 2015 El Nino warming event.
3. This report concludes that coral and coral dependent fish species within the MPA showed stronger declines, than outside the MPA beginning around the El Nino period of late 2014; this is likely to be attributed to originally higher densities commonly associated with long-term MPAs. However, trends of recovery were found to be stronger within the MPA, while signs of recovery in both coral and fish species abundance outside the MPA were observed to be minimal or non-existent.
4. Change in the percentage of coral population bleaching over the study period (2013 - 2016) was found to be significantly higher ($P = 0.002$) outside the MPA. Abundance of obligate corallivore species *Chaetodon lunulatus* were found to be significantly affected by MPA or non MPA location, ($P = 0.0001$) likely to be attributed to levels of coral cover. Abundance of *Chaetodon baronessa* was found to be highly significantly affected by year ($P = 0.0001$), which can be linked to El Nino effects.
5. This study also identifies a strong link between patterns of macro-algal colonised corals and herbivore biomass; recognising a spike in herbivore biomass outside the MPA beginning in early 2016; occurring at a similar time to a spike in macro-algal colonised corals occurring outside the MPA at the end of 2015.
6. Both inside and outside the MPA, similar levels of decline were seen in most study species, however, data from this study does corroborate the hypothesis that MPAs can strongly improve coral reef ecosystem recovery rates.

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1. Introduction

1.1 The Importance of Coral Reefs

Coral reefs cover less than 0.1% of the ocean floor, but provide habitat for approximately 25% of all marine species, around 830,000 species on reefs worldwide. (Fisher et al. 2015). More than 500 million people across at least 90 countries depend on coral reefs for food, storm protection, jobs and recreation. The asset value of coral reefs has been estimated as close to USD \$1 trillion, with the value of economic ecosystem services coming from coral reefs reaching USD \$375 billion annually (Hoegh-Guldberg et al. 2017). However, according to the Status of Coral Reefs of the World: 2015, 70% of the world's coral reefs are threatened or destroyed and 20% of those are damaged beyond repair; coral reefs have been identified as one of the ecosystems most vulnerable to climate variation and change (Graham, et al. 2008). The ecosystem goods and services provided by healthy coral reefs are a key component in the economic, social, and cultural fabric of many tropical maritime countries (Wilkinson, C. 2004).

1.2 Threats to Coral Reef Ecosystems

With a growing global population and rapid economic development, coral reef ecosystems are facing a number of serious threats, including overfishing, marine pollution, land alteration and climate change (Post, 2016). Stressors including land alteration and marine pollution - which are often already very high and poorly regulated – are only expected to increase due to growing populations (Post, 2016). Projected increases in CO₂ and temperature over the next 50 years exceed the conditions under which coral reefs have flourished over the past half-million years (Hughes et al. 2008). Coral bleaching is one of the most severe threats facing coral reef ecosystems; it can be triggered by a number of stresses, such as UV radiation, bacterial infection or reduced salinity (Baird & Marshall 2002). However, large-scale coral bleaching is most commonly associated with elevated sea surface temperatures, particularly recurrent ENSO (El Nino Southern Oscillation) events (Hughes et al. 2008).

Zooxanthellae are symbiotic dinoflagellates of the genus *Symbiodinium* living inside coral's tissues; it is this symbiosis that is key to the success of Scleractinian corals. The symbiosis is highly efficient and provides up to 90% of the corals nutritional requirements (Muscatine and Porter 1977). However, this interaction is under threat due to unprecedented levels of thermal stress occurring over the last century (Lough 2000). Rising sea surface temperatures (SST), as a result of climate change, cause coral to expel the symbiotic zooxanthellae found within their tissue. The elevated temperatures reduce the photosynthetic, oxygen assimilating, ability of zooxanthellae, often resulting in the formation of dangerous oxygen radicals that can cause damage to the tissue of the coral (Reid et al. 2009); if bleaching is prolonged, many corals may die. The frequency and

severity of bleaching events has risen sharply in recent years, and most projections of SST increases under climate change, estimate that devastating coral bleaching events will become more and more frequent (Reid, et al. 2009; Hughes et al. 2008). Climate driven coral bleaching has emerged as one of the greatest threats to coral reef ecosystems (Hoegh- Guldberg 1999). The popular model (Fig. 1) shows an invariant bleaching threshold at $\sim 1^{\circ}\text{C}$ above global mean summertime maximum temperatures. It is inevitable that this threshold will be exceeded as SST rise over the next 50-years, leading to predictions of massive losses of corals (Hughes et al. 2008).

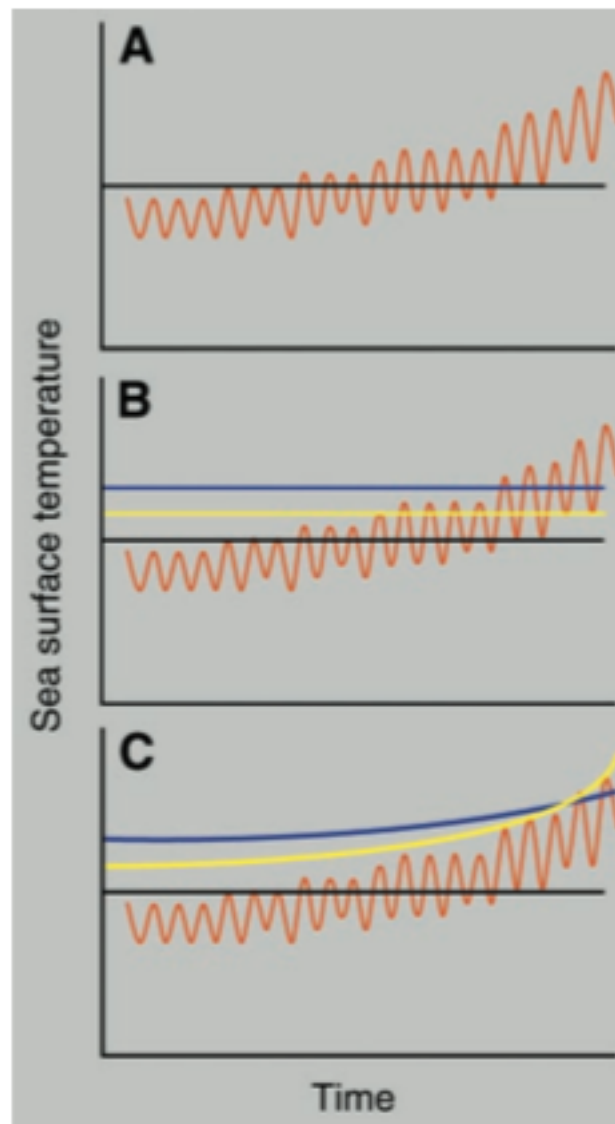


Figure 1- A model showing a constant coral bleaching threshold (black line), which is likely to be chronically exceeded in the future by rising SST (orange line). Source: Hughes et al. 2003.

Marine ecosystems are in global decline, this decline is then magnified by direct and indirect human effects (Hughes et al. 2003). Direct human effects consisting of activities such as fishing, the curio trade and indirect effects such as an increase in anthropogenic CO_2 , resulting in ocean acidification and climate change (Hughes et al. 2003). Reefs worldwide have suffered severe declines in health due to poor land-use practices, rapid coastal development, overfishing and

destructive fishing techniques, including the use of dynamite and cyanide; there are only a few areas remaining of high fish diversity and biomass, usually in large MPAs (Post, K. 2016).

This decline in overall ecosystem health makes coral reefs far more susceptible to bleaching events and reduces the coral reef's ability to recover (Carilli et al. 2009). Recovery potential relates to the coral community's capacity to maintain or recover its structure and function in spite of coral mortality; this capacity often relies on the surrounding reef ecosystem being healthy, diverse and non-depleted (Hughes et al. 2008). These properties at the coral colony and coral community level are termed 'resistance' and 'resilience' (West and Salm 2003). Similarly, Holling's (1973) definition of resilience is 'the magnitude of the disturbance that a system can absorb without fundamentally changing.' Reef resilience is eroded by chronic human impacts that cause persistently elevated rates of mortality and reduced recruitment of larvae (Hughes et al. 2008).

The massive scale of the 1997 - 1998 El Nino associated coral bleaching event underscores the need for strategies to mitigate biodiversity losses that result from temperature-induced coral mortality (West et al. 2003). The ecological attribute of 'resilience' in reef populations and ecosystem function is increasingly identified as a key goal for management of coral reefs (Done et al. 1996, Wilkinson 2004). A strong focus on reducing pollution, protecting food webs, and managing key functional groups (such as reef constructors, herbivores, and bio-eroders) is essential as insurance for reef sustainability (Hughes et al. 2008). Should an ecosystem experience a disturbance, biodiverse fish communities can compensate for a loss of a certain species through functional redundancy, a characteristic in which one species may substitute another to contribute the same ecosystem functions. However, functional redundancy is only possible when fish stocks are diverse and abundant.

1.3 Napantao Marine Protected Area, Southern Leyte, Philippines.

Napantao Marine Protected Area (MPA) is located in Sogod Bay, on the Panaon Island south of Southern Leyte (Fig.2) in the Visayas region of the Philippines; the Philippines is widely recognised as a global priority for marine conservation (Roberts et al. 2002; Bundy 2004; Lowry, White and Christie 2009; Weeks et al. 2009). The Philippine archipelago boasts some 499 hard coral species (Chou 1998) and more than 2500 fish species (Lieske and Myers 2001). The coastline is covered by approximately 27,000km² of coral reefs; around 10% of the total land area of the archipelago. (Philippine Statistics Authority 2015). As part of the coral triangle, the Philippines boasts high levels of biodiversity across all marine taxa; highlighting the need for protection of these highly diverse ecosystems. This is further amplified by the high dependence on fishing in the Philippines for food and the local economy; marine ecosystem services are an essential part of the Philippine economy. As of 2015, the commercial fisheries volume of production of the top 31 fish species was 1,084,624.70 metric tons, producing an overall value of P71,717,976,27 with a value of P476,156 generated in Southern Leyte alone (Philippine Statistics Authority 2015). A Study conducted by

Newton et al. (2007) concluded that the average annual fish yield in fishing towns across the Philippines was nearly three times higher than the maximum sustainable yield in the area. These high levels of exploitation of natural resources throughout the Philippines increases the necessity for more intensive management implementation in order to prevent ecosystem collapse. In order to ensure successful coastal resource management throughout the Philippines, MPAs must account for 56% of municipal waters (Muallil et al. 2014).



Figure 2 - Map of Napantao MPA and the surrounding waters (highlighted in red).

Sogood Bay reaches depths of approximately 1,400m in the central channel, it is also an important fishing ground and is rich in Tuna, Flying Fish, Herring, and Shell-Fish (CCC, 2012). The bay has been historically targeted by the Fisheries Sector Program of the Department of Agriculture as one of the country's ten largest bays in need of assessment and management (Calumpong et al. 1994). Sogod Bay is surrounded by 131.67km of coastline, bordered by 11 municipalities, with Napantao MPA being located in the Municipality of San Francisco. The bay typically consists of naturally limited mangrove areas, narrow coral reefs, limited seagrass beds and narrow intertidal areas (Calumpong et al. 1994).. Sogod Bay has been highlighted as an area hosting important species and habitats (Alino et al. 2002), as seen highlighted in Fig. 3 under area MP25.

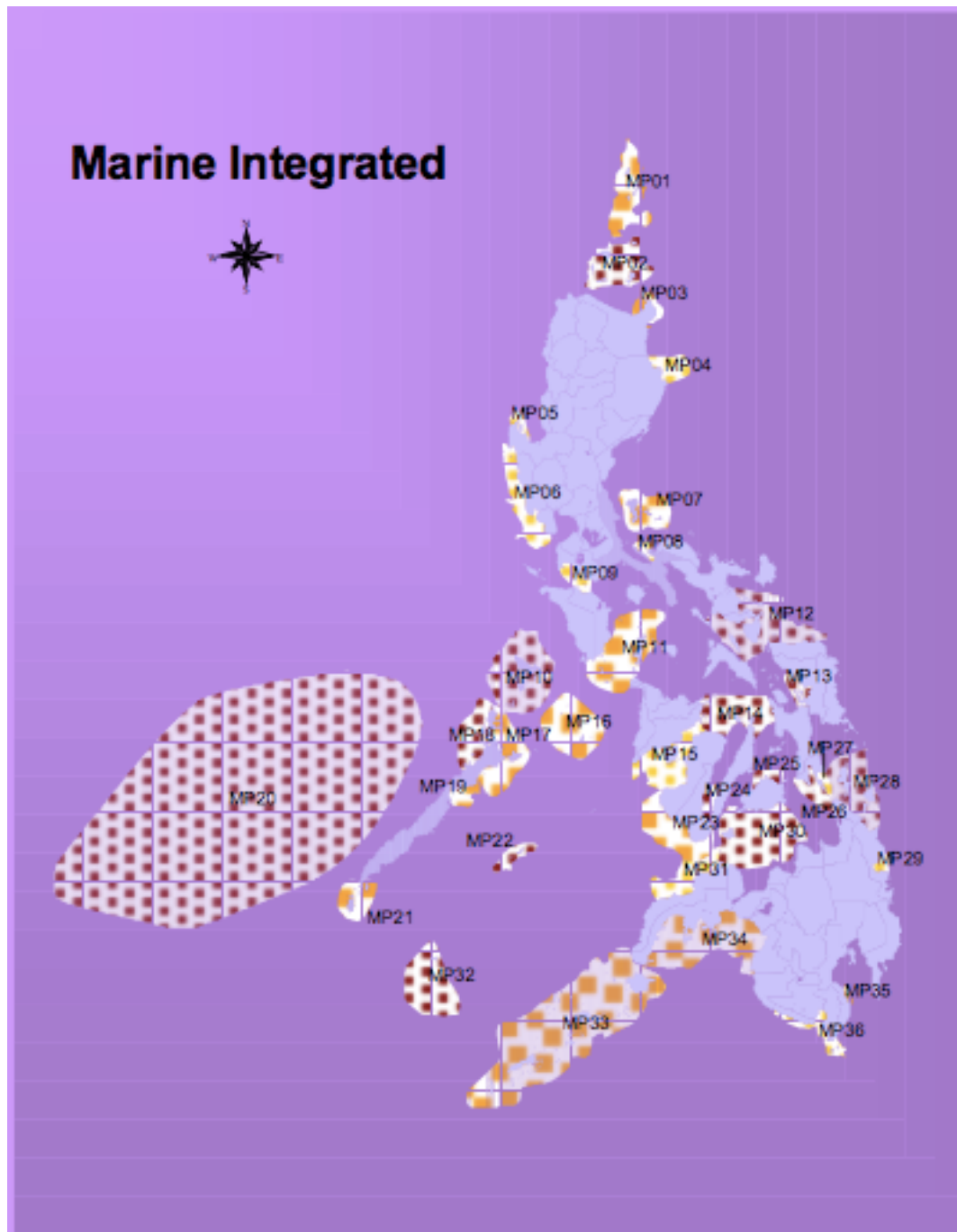


Figure 3 - Integrated map of important marine species and habitats. Source: Alino et al. 2002.

Koch (1993) conducted one of the earliest studies of marine resources in Sogod bay, marine surveys concluded that the coral reefs of the area were extensively damaged; with an estimated 50% of the coral reefs completely destroyed and less than 25% of the corals remaining. Koch attributed this to anthropogenic impacts and strongly recommended the implementation of MPAs throughout the bay to prevent further damage and encourage coral reef recovery.

Napantao MPA has been established since 1996 and covers 5 hectares, it is managed by a committee of representatives from the local Barangay (village) and Municipal Government. It consists of an inner no-take zone, and a buffer zone which permits minimal fishing under restrictive

guidelines; this is a multiple use MPA, which balances social, economic and ecological goals to create a practical and long-term sustainable protected area.

Coral Cay Conservation (CCC) is an NGO, established in 1989, working on the reefs of Sogod Bay, in particular, Napantao MPA; assisting with management through technical support, scientific recommendations and continued scientific monitoring. The methodology used for MPA monitoring conducted by CCC is consistent with the methodology of Reef Check; a global coral reef monitoring program, designed to meet the need for a simple, rapid monitoring protocol that can be used to measure the health of coral reefs on a global basis (Hodgson, 1999). A large majority of the world's coral reefs are located in developing countries with low resources and capacity available for monitoring (Obura & Grimsditch, 2009), this highlights the need for a low resource, effective monitoring methodology that is possible to maintain for long periods of time in such economies; such as the Reef Check methodology. This methodology is used widely throughout the Philippines to monitor coral reef health, including the continued long-term monitoring of Apo Island Marine Reserve by Silliman University (Raymundo, L). CCC has enhanced the Reef Check methodology in order to account for the high levels of biodiversity in the area by adding extra target species (see Appendix A, B & C for full species lists). This methodology was used widely to document the global extent of the 1998 El Nino bleaching and mortality event that devastated tropical reefs (Hodgson, 1999), thus it is a well-suited methodology to examine any changes to reef health throughout the 2015 El Nino event.

1.4 MPAs as a Management Tool

Marine Protected Areas (MPAs) are a key management strategy in addressing and rectifying the current condition of coral reefs worldwide (Hughes et al. 2007); MPAs have been identified as one of the key methods of mitigating human impacts on reefs (Hughes et al. 2008). As defined by the World Conservation Union (IUCN 2008), an MPA is 'a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values'; currently, only 2.8% of the world's oceans are protected through MPAs (IUCN and UNEP-WCMC 2013).

Creating an MPA requires implementation of legislation regarding practices such as fishing, tourism, land alteration, scuba diving, etc.; this is with the aim of protecting the coral reefs through reducing external pressures. A fundamental question in coral reef ecology is whether chronic local stress reduces coral resistance and resilience from episodic stress such as bleaching, or alternatively promotes acclimatisation, potentially increasing resistance and resilience (Carilli et al. 2009). However, most studies suggest that coral colonies experiencing higher chronic anthropogenic stress show less resilience and slower recovery times after a major bleaching event. (Carilli et al. 2009; Mumby & Harbourne 2010). An investigation into the growth rate of the Massive

coral, *Montastraea faveolata* following a major bleaching event, found that growth rates at sites with higher local anthropogenic stressors remained suppressed for at least 8 years, while coral growth rates at sites with lower anthropological stressors recovered to previous levels within 2-3 years (Carilli et al. 2009).

In a study into the effect of MPAs in preventing coral loss, Selig et al. (2010) found that MPAs have a positive effect in the reduction of coral loss; across all reefs that were surveyed, there was no change in coral cover within MPAs over 28-years, compared to coral cover on unprotected reefs showing a continued decline throughout the 28-year period. However, this is more likely to be attributed more directly to reductions in destructive fishing practices alongside other directly damaging actives such as excessive tourism and boat damage; in turn, this direct reduction in coral damages and stressors is likely to be improving the corals ability to adapt and recover in response to increasing thermal stress. MPAs commonly introduce restrictions on various fishing and tourism practices; this in turn has had proven positive effects on fish and invertebrate populations. In particular no-take MPAs, can increase size, abundance and diversity of ecologically and commercially important species (Richards et al. 2012). The success of MPAs in protecting fish populations has led to optimism that they may also have positive, direct and indirect effects on corals (Hughes, et al. 2003).

A coral reef relies on numerous symbiotic relationships in order to maintain a healthy and functioning ecosystem; hard corals, benthic animals, herbivorous fish and carnivores all ensure the health of the reef, each with individual functional traits (Reid et al. 2009). It is when the key groups are lost that the supporting framework becomes so weakened that a single large-scale event is enough to push a reef beyond its tipping point (Reid et al. 2009). MPAs may not dramatically reduce direct bleaching impacts, as rising SST is a much more widespread issue, requiring a more complex solution. However, studies show (Carilli et al 2009; Micheli et al. 2012; Hughes et al. 2007) that the protection offered to a reef by an MPA may significantly improve coral recovery times after a bleaching event by protecting other key taxonomic groups within the ecosystem. One strategy in combating coral mortality is to identify reef areas where environmental conditions are likely to result in maximum recovery after bleaching has occurred (West et al. 2003). Predicting and preparing an ecosystem for climate change induced events such as bleaching, coupled with additional external stressors on a reef such as fishing adds further complexities. Models of predicted population responses to climate change become more sporadic when additional external pressure and exploitation is included (Fig.4).

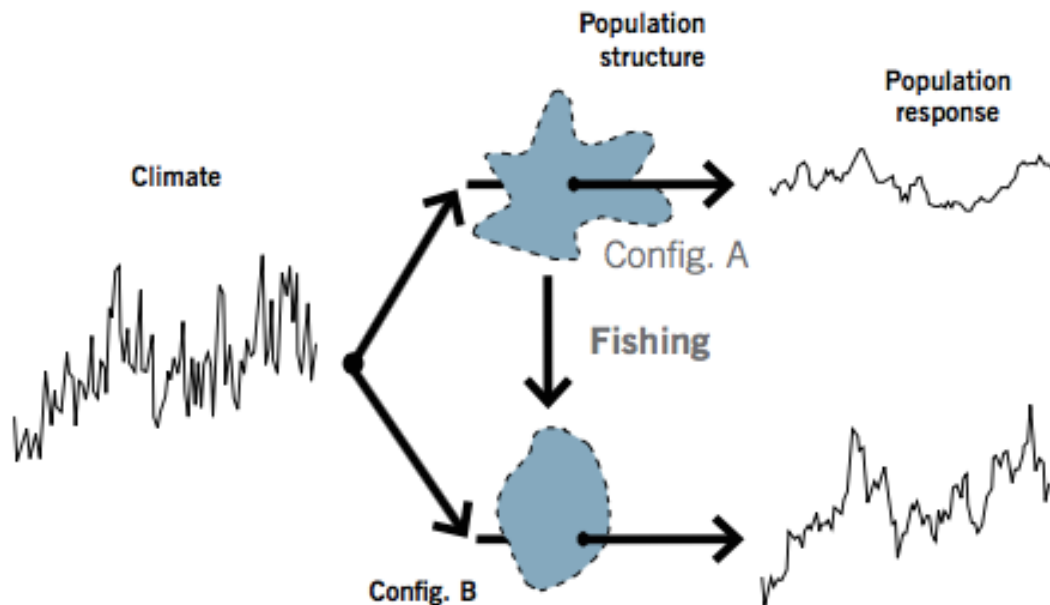


Figure 4 - A schematic representation of the increased vulnerability of a population to climate change effects when also affected by exploitation. Source: Perry et al. 2010.

Previous studies into the effects of MPAs have often found that one significant benefit of NTAs and the improvement found inside the MPA boundary is the presence and size of commercially important fish such as Parrotfish (*scaridae*) and Grouper (*epinephelinae*). This is likely to be attributed to decreased direct fishing pressures upon these commercial species. These more intact communities could prevent outbreaks of coral predators and may limit the coverage of macroalgae by restoring grazer populations, which in turn could facilitate coral recruitment (Mumby, 2007). Management of fish stocks is a key component in preventing phase shifts on reefs and managing reef resilience (Hughes et al. 2007). The exclusion of large, herbivorous fish, profoundly erodes the resilience of coral reefs and their ability to regenerate after bleaching (Hughes et al. 2007). Similarly, marine communities with reduced species diversity and depleted population sizes are less resilient to potentially disturbing or perturbing forces (Jones, 2014). MPAs and fishery closures are seen by many as the main way to mitigate the effects of climate change and to enhance recovery of corals often believed to be lost (McLanahan et al. 2011).

There are two inter-related ways in which diversity is recognised as conferring resilience:

1. Functional redundancy: whereby different species within a functional group can adopt each other's ecological role should one species become depleted by overfishing, predation, disease, ect.
2. Response diversity: whereby different species within a functional group display different responses to different environmental conditions, providing for adaptation to changing conditions (Bellwood et al. 2004; Elmqvist et al. 2003).

There is an urgent need for assessing and mapping resilience in coral reefs in order to better inform resilience-based management practices in a rapidly changing oceanic climate. This study assesses the role and impact of coral reef conservation and management in protection against global climate change. Although there are expectations that MPAs and NTAs promote faster recovery from climate disturbance, some previous site-specific studies have found that this is not the case, thus the effectiveness of such management needs to be assessed more thoroughly in coming years (Graham et al. 2008).

1.5 Aims of this study

This report examines data from both inside and outside Napantao MPA, from before and throughout the duration of El Nino Southern Oscillation 2015, examining data from 2013, 2014, 2015 and 2016. This study investigates any effect the rising SST, as a result of ENSO 2015, has had on the coral reef in terms of reef health, by considering key indicator fish species such as Butterflyfish (*chaetodontidae*), Angelfish (*pomacanthidae*) and Parrotfish (*scaridae*) alongside a number of species that play key ecosystem roles such as Giant Clams (*Tridacna gigas*) and Long Spine Sea Urchins (*Diadema antillarum*) (See Appendix for full species lists) This study also examines the presence and abundance trends of key coral species (*Acropora* spp.) and impact surveys that record levels of bleaching. Furthermore, I then examine whether the coral reef within the MPA boundaries has demonstrated reduced signs of stress, bleaching and decreases in fish abundance, and, if a stress and bleaching is observed, whether there has been less recovery time for the ecosystem within the MPA boundary. This study aims to establish if and how the MPA is protecting the coral reef ecosystem from potentially devastating climatic events, in order to better inform management techniques and target areas in light of future climatic changes.

2. Methodology

The data used in this report are secondary data collected by CCC; data is collected by a combination of CCC staff and volunteers in a highly trained citizen science approach. CCC conduct 2-weeks of training alongside numerous written and in-water examinations before volunteers can contribute to data sets, to ensure a high standard of accuracy and reliability in their data.

CCC's Napantao surveys consist of six 100m transects across the site at 12m, three transects within the MPA boundary, and three outside (Fig. 5). These transects are re-surveyed twice a year, in March and October to monitor reef health and any possible ecological changes to the MPA and its biodiversity. The transects are permanent and are kept in the exact same location every year, marked by stakes. This is beneficial for long-term monitoring as it allows for consistent, reliable data that is comparable between years; it also eliminates the possibility of transect location accounting for changes identified in data sets. The 100m transect lines run parallel to the shore and are split up into four 20m replicates with 5m spaces between to allow for independent statistical analysis. The sample size for one complete survey is 800m² each for the fish and the invertebrate transects, plus 320 point samples along 160m of transect for the substrate survey.



Figure 5 – Map of the six permanent transect locations located inside and outside Napantao MPA boundary.

Before commencing a survey dive, the center-point of the transect was marked and checked against the GPS, the surface boat activity, weather and air temperature was recorded prior to the commencement of the dive. Once the dive has begun, the leader of the dive recorded the water temperature (°C) at the surface, at 4m during the decent and at the depth of the transect -

however, this is a snapshot temperature, not an average, and often more representative of daily weather conditions rather than overall temporal changes indicative of rising SST.

2.1 Invertebrates and Impacts

Diversity and abundance of target invertebrate species were recorded using a belt transect method across 50m of the 100m transect in one dive. Target species are key species used in the food and souvenir trades, but also hold high ecological value to the coral reef ecosystem; see Appendix A for a complete list of target species. Giant Clams (*Tridacna gigas*) were recorded into size categories of 0-10cm, 11-20cm, 21-30cm, 41-50cm and > 60cm. Divers swam in an 'S' shaped pattern to 2.5m out from the transect line on each side (Fig. 6), recording abundance of all target species sighted. Divers paid careful attention to checking underneath overhangs and in crevices for such species as sea urchins, and various target crustaceans.

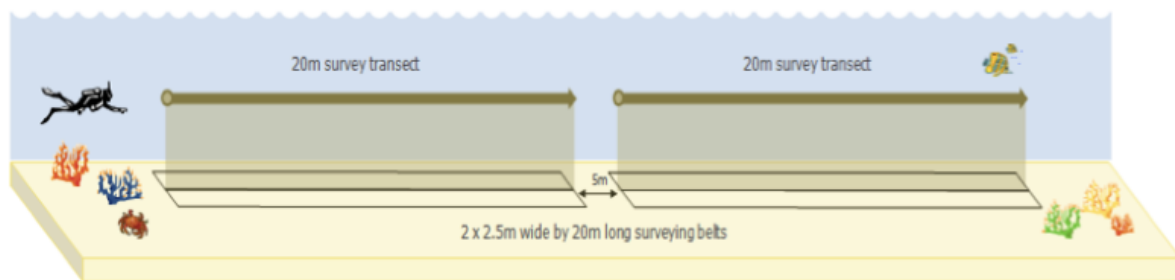


Figure 6 – Invertebrates and impacts transect survey methodology used by CCC, demonstrating two of the four 20m replicates completed one 100m transect. Taken from: Coral Cay Conservation MPA assessment report – Cuasi 2016.

During this transect, divers also recorded any visible impacts on the reef; these impacts consist of trash (fishing or other), damage (boat / anchor, dynamite, or other), coral disease, coral bleaching, and coral predation. Coral bleaching was estimated to a percentage of the population, alongside a percentage of individual coral colonies. Trash and damage were recorded on a categorical scale from 0-3, 0 = none, 1 = low, 2 = medium and 3 = high. Divers stopped recording after the first 20m replicate, swam through the 5m gap and begun replicate 2 with the data recorded separately. A total of 29 species / families of invertebrates was recorded and 10 impacts (Appendix A).

Sea urchins (*Echinoidea*) are known to show preference to fleshy turf algae as a food source, algae that often colonizes upon bleached and dead corals, preventing any possible recovery (McLanahan et al. 2005). It is this relationship between macro-algae and the Long Spine Sea Urchin (*Diadema antillarum*) that identifies this species as an area of interest when examining possible bleaching and recovery. Giant clams are also an area of interest within this study due to their ability to host zooxanthellae and excrete excess zooxanthellae in fecal pellets; which is then available for uptake by already bleached corals. It is common that Giant Clams are more thermally tolerant than scleractinian corals (Bruno et al. 2001), thus they are a key tool in re-colonisation of

zooxanthellae by corals and can drastically improve reef recovery rates, thus highlighting these invertebrate species a key area of interest within this study.

2.2 Fish

A belt transect method was also used to measure fish abundance and diversity. After divers had descended to the start of the transect line, there was a 3 minute 'cooling off' period before any recording began, this was to ensure minimal disturbance to the fish from the divers decent and to allow for normal behaviour to resume, for accurate recording. Both divers then swam slowly, smoothly and with correct buoyancy along the transect line on either side, recording all target species seen at a distance of 2.5m to each side of the transect and 5m above. Divers paused along the transect for 1 minute at each 5m marking on the line, and continued to record species during these pauses. Particular attention was paid to ensure no double recording, as certain species of reef fish such as Butterflyfish (*chaetodontidae*) tend to stay in a small area but swim inside and outside the boundary of a transect numerous times. After the first 20m replicate, there was a 5m gap before the next replicate and another one minute cooling off period with no recording before the transect begins, in keeping with Reef Check methodology. Three commercially important fish species: Parrotfish (*scaridae*), Snappers (*lutjanidae*) and Groupers (*epinephelinae*) were recorded but also classified into size classes of 0-10cm, 11-20cm, 21-30cm, 31-40cm, 41-50cm and > 60cm to create a more accurate representation of maturity levels.

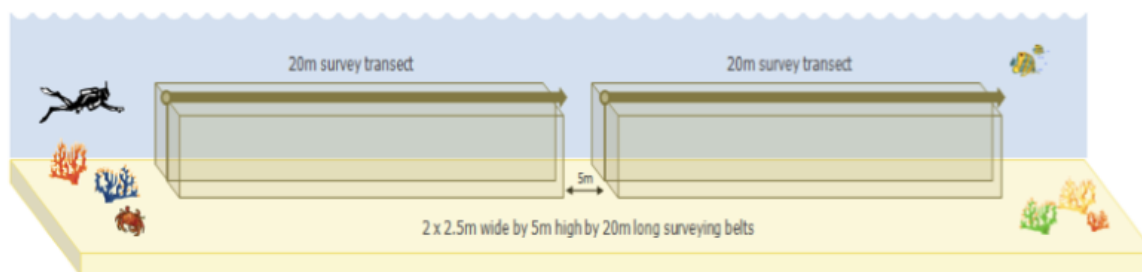


Figure 7 – CCC's fish transect survey methodology showing two 20m replicated with a 5m no recording gap between. Taken from: CCC MPA Assessment - Cuasi 2016.

A total of 45 fish species were recorded (See Appendix B), including similar indicator species used in previous studies by Hodgson (1999) and Samoilys et al. (2007), such as Butterflyfish (*chaetodontidae*) and Surgeonfish (*acanthuridae*). Monitoring using indicator species often allows a sensitive and accurate assessment of the extent of an environmental impact which might not be possible using more direct methods (Roberts et al. 1988).

2.3 Substrates

The benthic diversity of the survey area was measured using a 'point-intercept' transect method using a plumb line to avoid bias, recording biotic and a-biotic substrate categories. Substrates and benthic organisms were recorded at 50cm intervals along the transect line by dropping a plumb line at every 50cm marker and recording the substrate that it lands on into various categories. Survey categories consist of: rock (RK); rubble (RB); sand (SD); silt / mud (SI); recently killed coral (RKC); sponge (SP) nutrient indicator algae (NIA) soft coral (SC) and hard coral (HC). Hard coral is then identified to life form and certain species level (*Acropora* spp.), see Appendix C for exact categories.

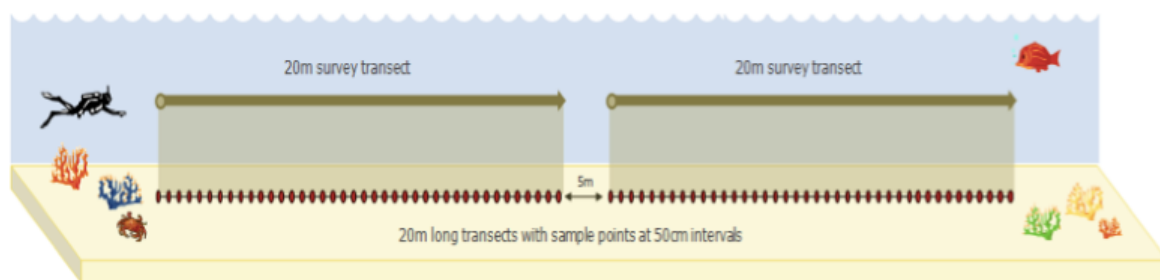


Figure 8 – CCC's substrates point-intercept transect methodology; both abiotic substrates and biotic benthic organisms are recorded at each 50cm point along the replicate. Taken from: CCC MPA Assessment – Cuasi 2016.

Acropora spp. is a highly thermally sensitive coral species and bleaches relatively easily in comparison to other scleractinian coral species (Guest et al. 2010, Baird et al. 2002); this highlights this species as a key species to examine separately to hard corals as a whole, as it is likely to show a different, more severe response to higher SST; giving a more in-depth analysis than examining hard corals overall as one category.

2.4 Statistical Analysis

Mann-Whitney U

Due to the number of rarely sighted target species, resulting in a high number of 0 values in CCC's data, to accurately analyse the data, non-parametric tests were employed. To establish any initial differences in species abundance inside and outside of the MPA, a Mann-Whitney U test was used, this was not investigating any change across the study period or focusing on a particular year, it was used to initially establish the difference between the study sites of inside and outside the MPA.

2-Part Pearson's correlation and T-test

To correctly analyse changes in abundance from 2013 – 2016, a two-part analysis was used. Firstly, a Pearson's correlation was calculated for each set of data from every year for each 20m replicate of each transect. These correlations were then put into a T-test, analysing for any significant difference between correlations inside and outside the MPA for each individual species recorded. To ensure a certain level of reliability, this test must be done on a large amount of data, thus correlations for each 20m replicate were calculated separately, as opposed to combining data into whole transects; this should ensure a higher level of reliability in the analysis.

Multiple Linear Regression

The Multiple Linear Regression (MLR) focuses on a particular species or group, and examines environmental factors significantly affecting changes in levels of abundance. 35 environmental variables were entered into the MLR, including all substrate categories, using the stepwise method, these variables were then compared against an individual species abundance. Particular species of interest were chosen to enter into the MLR, e.g. *Chaetodon lunulatus* for the species' close dependency on hard corals (Cole et al. 2008), see Table 1 for complete list of all species entered into the MLR.

Species	Reason of Interest
Redfin Butterflyfish	Obligate Coralivore - 1:1 relationship with food source
Eastern Triangle Butterflyfish	Obligate Coralivore - 1:1 relationship with food source
Parrotfish	Algal Herbivore - Presence could be indicative of macro-algal levels. Presence also contributes to macro-algal control
Surgeonfish	Algal Herbivore - Presence could be indicative of macro-algal levels. Presence also contributes to macro-algal control
Angelfish	Highly disturbance sensitive species
COTs	Species often known to colonise areas of disturbance - abundance can be correlated with nutrient input.
Drupella	Coral Predator
Rabbitfish	Herbivore

Table 1 – A list of all individual species / families entered into the MLR for investigation into relationship between species abundance and environmental factors; and the reasons for choosing each species.

Discriminant Function Analysis

In order to investigate factors driving change in abundance or species assemblage, a discriminant function analysis (DFA) model was used. The model used data from an individual year and attempts to correctly classify each individual case into either inside or outside the MPA. The stepwise method was then used to identify the factors driving correct classification into either inside or outside MPA categories, thus highlighting the factors that show greatest identifiable change inside or outside the MPA. This process was repeated for all 4 target years individually, from 2013 – 2016.

3. Results

An initial Mann-Whitney U test was conducted on all species and substrate data, making a direct comparison between levels of abundance inside and outside of the MPA, results are displayed in Tables 2, 3 and 4 with significant differences in species abundance highlighted (Appendix D).

However, a direct comparison of inside MPA and outside MPA data may not provide an accurate representation of possible benefits provided to a reef from an MPA. It is likely that originally the MPA was established around the most biodiverse and ecologically valuable area of reef, thus it is possible that the contrast between inside and outside can be attributed to natural formation. To establish effects of MPA protection, one must examine the trends of data between inside and outside over a period of thermal stress. Key points of interest in this study are trends and declines in herbivore and corallivore abundance, trends of macro-algal levels, benthic data and presence of thermally sensitive coral species.

There are many species features in Tables 2, 3 and 4 that will not be analysed in further detail; It is essential to extract key elements from the data sets that indicate effects of thermal stress on the reef whilst discarding some of data that is more reflective of general biodiversity and ecosystem health.

3.1 Corallivores

The key target obligate corallivores in CCC's data sets are Eastern Triangle Butterflyfish (*Chaetodon baronessa*), and Redfin Butterflyfish (*Chaetodon lunulatus*) (Cole, et al. 2008); within Napantao surveys, both these species are abundant. As highlighted as species of key interest, a number of statistical analysis were conducted upon both of these species. A multiple linear regression with a stepwise method, comparing all recorded environmental factors against abundance of Redfin Butterflyfish, found that the most influential environmental factors affecting Redfin abundance were; Site Type (Inside or outside MPA) ($P = 0.0001$, $R^2 = 0.199$) and General Trash ($P = 0.021$ $R^2 = 0.221$). General trash levels are likely to be attributed to whether or not a site is protected through an MPA, so both factors are strongly related. The same MLR conducted upon Eastern Triangle Butterflyfish data found that the most influential environmental factors affecting abundance were; presence and levels of sand ($P = 0.0001$, $R^2 = 0.177$); levels of coral damage ($P = 0.0001$ $R^2 = 0.234$) and year ($P = 0.0001$ $R^2 = 0.361$).

A DFA based on 2013 fish abundance correctly classified 89.6% of all cases to inside or outside the MPA, the stepwise method identified Redfin Butterflyfish as a key species in correct classification. Redfin were again identified, alongside Rabbitfish (*iganidae*) and Unicornfish (*Naso*) by the stepwise method in the 2016 discriminant function analysis which correctly classified

87.5% of cases into inside or outside MPA data; however, Redfin were not a key identifying factor within the model for 2014 or 2015. A two-part analysis based upon Pearson's correlations was conducted to establish changes in abundance over the study period and create comparable values of change for inside and outside the MPA. Using Pearson's correlation, followed by a T-test, the correlation of Redfin Butterflyfish was found to be significantly different ($P = 0.0001$, $F = 16.094$, $DF = 35.635$) outside the MPA, with a positive mean correlation of $R = 0.0066$ inside the MPA, and a negative mean correlation of $R = -0.033$ outside the MPA. Showing a significant increase in Redfin abundance inside the MPA from 2013 to 2016, with a significant decrease in abundance outside Napantao MPA.

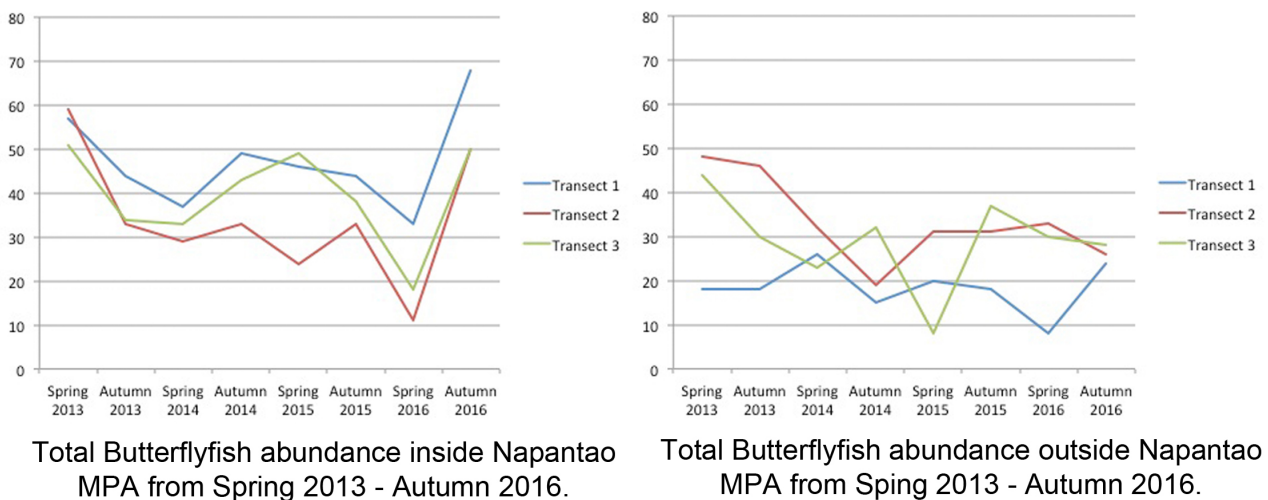


Figure 9 - Line graph showing total abundance for all recorded *chaetodontidae* species both inside and outside Napantao protected area throughout the study period.

The 2-part Pearson's correlation T-test found a highly significant difference ($P = 0.009$, $F = 7.555$, $DF = 40.765$) in the change in abundance of Moorish Idol (*Zanclus cornutus*) between inside and outside the MPA across the study period. Both inside and outside correlations are negative, showing declines in abundance however the decline is greater within the MPA with mean correlations of $R = -0.014$ outside and a stronger decline of $R = -0.599$ within the MPA. The same test also identified a significant difference in changes in abundance of Longnose Butterflyfish (*Forcipiger flavissimus*) inside / outside the MPA ($P = 0.0001$), with a mean correlation of $R = 0.5$ within the MPA and 0 outside the MPA.

Inside the MPA, overall levels of abundance of all recorded species of Butterflyfish (*chaetodontidae*) show decline as early as 2013 (Fig.9), and occurring again in 2015, coinciding with predicted elevated, El Nino induced, SST. However, the most drastic declines are occurring in Spring 2016, followed by a sharp increase in abundance in Autumn 2016, returning to near pre - El Nino abundance levels and above. However, outside MPA abundance data shows more sporadic declines beginning as early as Autumn 2013, followed by repeated peaks and declines with no key time frame identifiable as a specific time of decline. An essential aspect of these trends to note is

the lack of increase in abundance or recovery displayed at the non-MPA site; some transects appear to still display declines through late 2016 while others (transect 1) show a slight increase, but without demonstrating the same level of population recovery as seen within the MPA.

Trends of total abundance from 2013 - 2016 for both Redfin and Eastern Triangle Butterflyfish are displayed in Fig. 10 alongside two other corallivore families; Triggerfish (*balistidae*) and Pufferfish (*tetraodontidae*) in Fig. 11. All trends show dramatic decreases in abundance beginning in Spring 2015 - in keeping with El Nino driven elevated SST. Triggerfish (*balistidae*) show further increase and decrease throughout the remainder of 2015 and through 2016, with overall abundance showing signs of improvement by Autumn 2016 although drops in abundance are still present on some transects inside the MPA by late 2016. However overall abundance is still distinctly higher inside the MPA than outside and increases in abundance post-2015 are stronger within the MPA. The 2-part T-test found the difference in changes inside or outside the MPA in abundance of both Triggerfish and Pufferfish to be insignificant ($P = 0.6$ and $P = 0.1$).

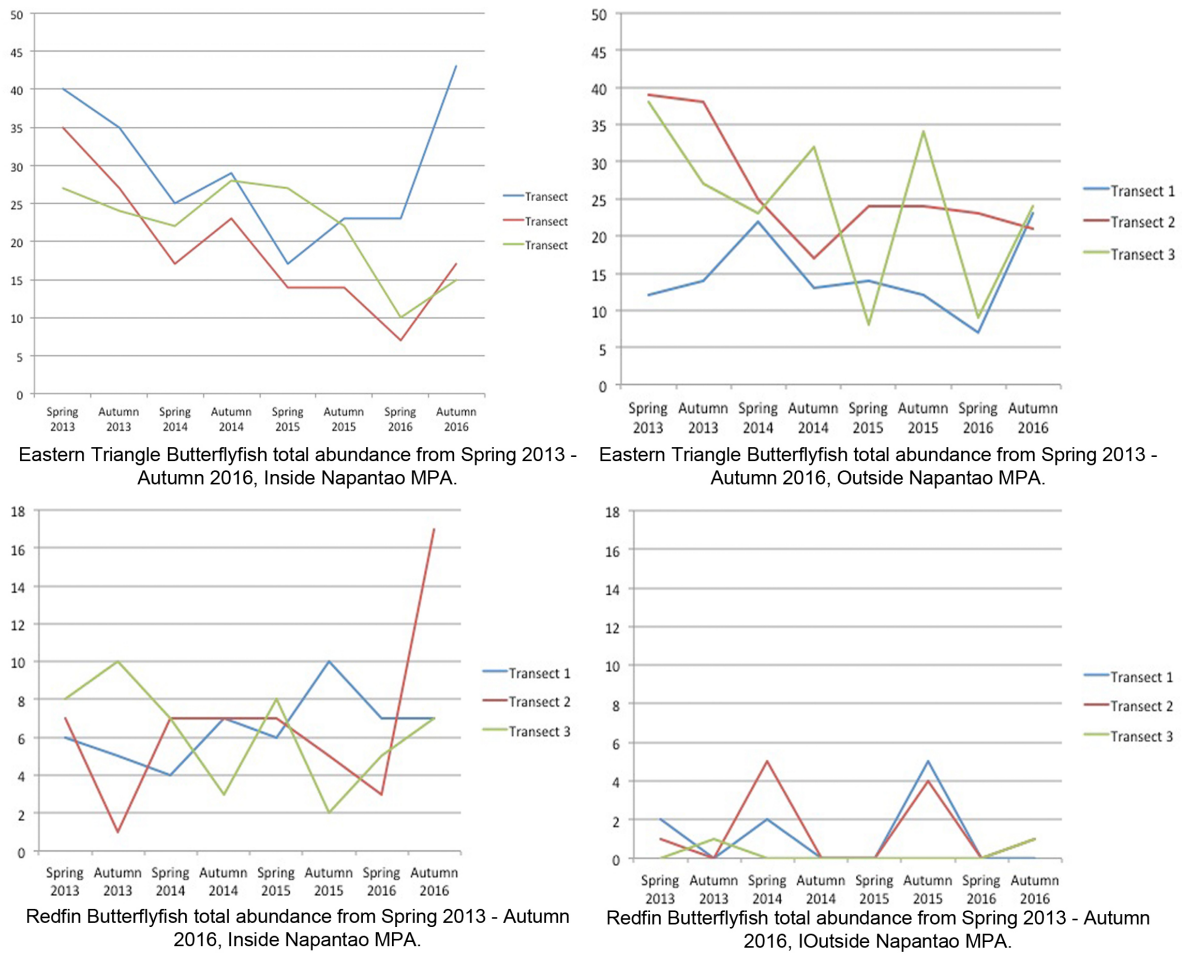
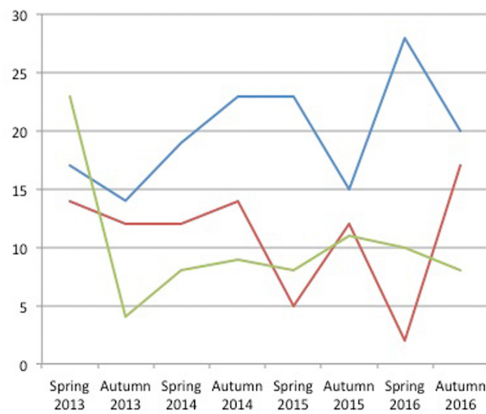
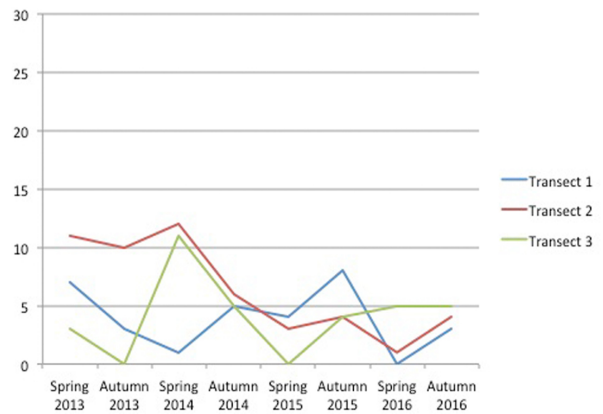


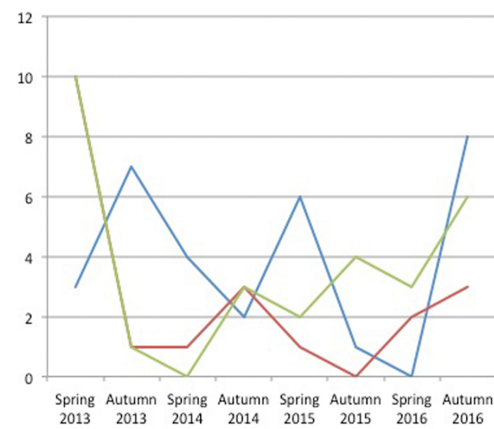
Figure 10 - Line graphs showing total abundance trends of Eastern Triangle Butterflyfish (*Chaetodon baronessa*) and Redfin Butterflyfish (*Chaetodon lunulatus*) inside and outside the protected area, across the study period.



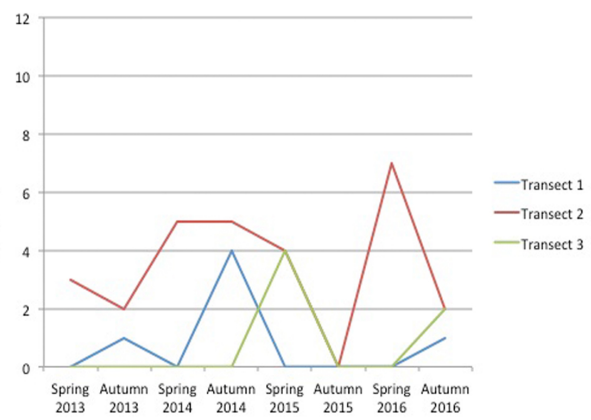
Triggerfish total abundance from Spring 2013 - Autumn 2016, Inside Napantao MPA.



Triggerfish total abundance from Spring 2013 - Autumn 2016, Outside Napantao MPA.



Pufferfish total abundance from Spring 2013 - Autumn 2016, Inside Napantao MPA.



Pufferfish total abundance from Spring 2013 - Autumn 2016, Outside Napantao MPA.

Figure 11 - Line graphs showing total abundance trends of Triggerfish (*balistidae*) and Pufferfish (*tetraodontidae*) inside and outside the protected area, across the study period.

3.2 Herbivores

The trends of total abundance of the herbivorous fish family Parrotfish (*scaridae*) from Spring 2013 through the El Nino year of 2015, through to Autumn 2016 are seen in figure 12. Both data sets (inside and outside MPA) show increases in *scaridae* abundance in 2016 after the elevated SST as a result of ENSO 2015, however inside the MPA this increase is weak, as opposed to a dramatic spike in numbers of Parrotfish recorded on the transects located outside the MPA. An MLR conducted on Parrotfish abundance comparing all environmental variables concluded that the main driving factor affecting Parrotfish abundance was coral damage ($P = 0.0001$, $R^2 = 0.109$).

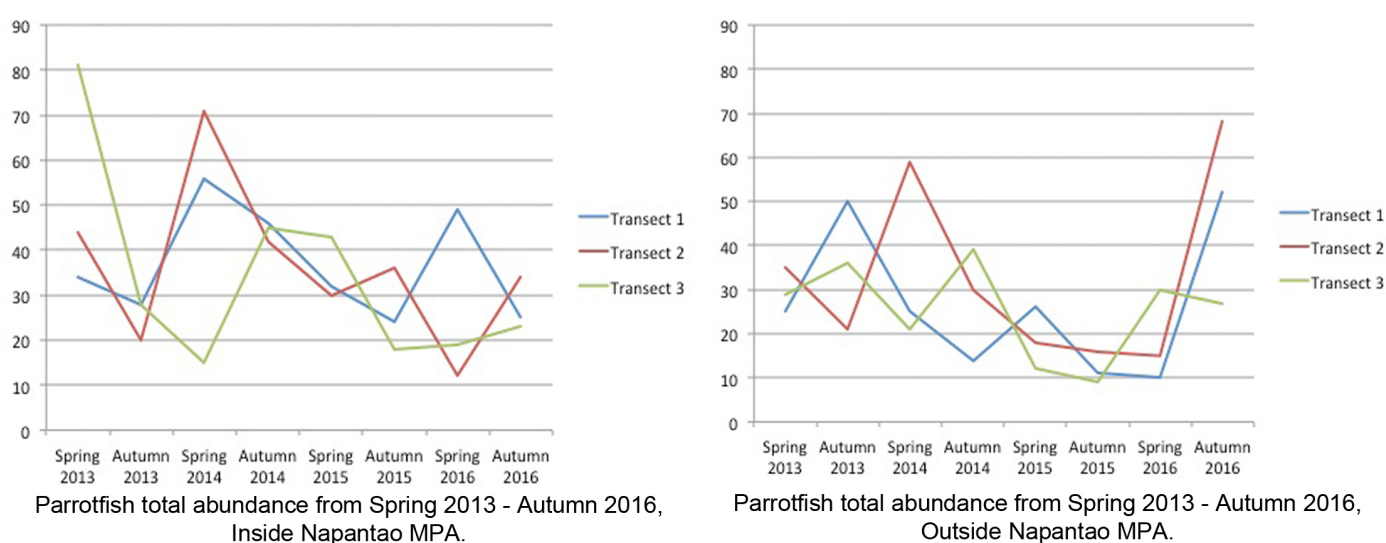


Figure 12 - Line graphs showing trends of total abundance of Parrotfish (*scaridae*) from both inside and outside the protected area across the study period.

The two-part T- test, conducted on Pearson's correlations, found the change in Rabbitfish (*siganidae*) abundance to be significantly different ($P = 0.002$, $F = 10.833$ $DF = 39.935$) inside and outside Napantao MPA, with a positive mean correlation of $R = 0.290$ inside and a negative correlation of $R = - 0.167$ outside.

3.3 Invertebrates

Giant Clams

T-tests based on Pearson's correlations found a significant difference in the change in abundance inside and outside the MPA, of Giant Clams (*Tridacna gigas*) 0 - 10cm ($P = 0.034$, $F = 4.768$, $DF = 40.097$); Giant Clams 31cm - 40cm ($P = 0.006$, $F = 8.302$, $DF = 25.657$) and Giant Clams 41cm - 50cm ($P = 0.001$, $F = 7.266$, $DF = 23$), with abundance of all three size categories greater outside the MPA than inside.

Sea Urchins

The overall trend of abundance data for the Long Spine Sea Urchin (*Diadema antillarum*) (Fig. 13) within the MPA is declining, with some spikes or declines occurring sporadically. These sporadic patterns could be attributed to seasonal changes, or to changes in the individual recording the data in the field; as identifying Sea Urchins in an invertebrate survey requires more searching than other species due to their location within the reef matrix. As opposed to the inside MPA data, the trends in abundance outside the MPA show varied decline up until Autumn 2015, then sharp increases beginning in 2016, with 2 out of 3 transects remaining relatively high throughout 2016.

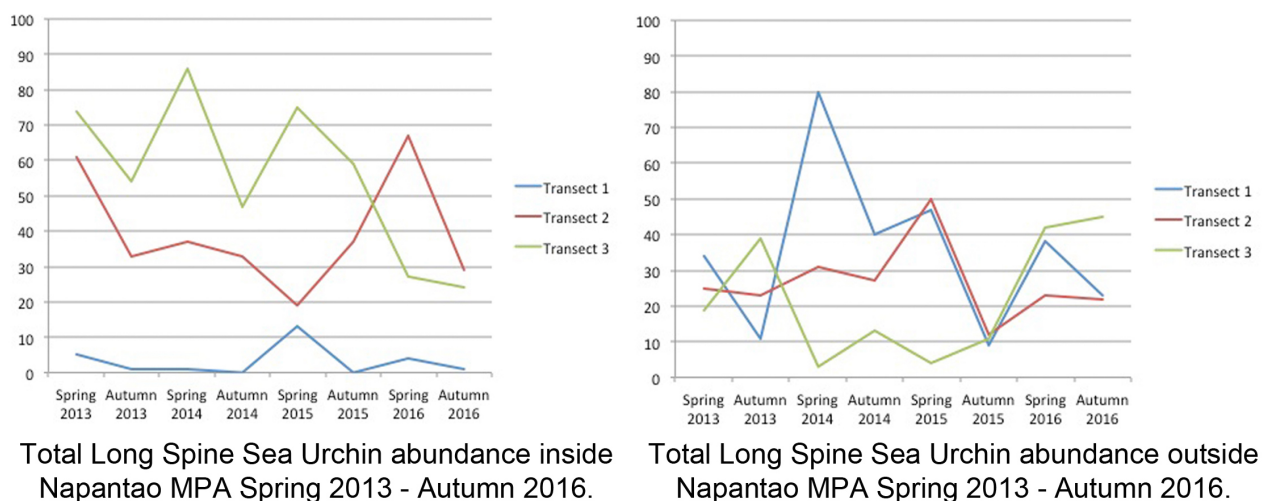


Figure 13 - Line graphs showing trends of total abundance of the Long Spine Sea Urchin (*Diadema antillarum*) from both inside and outside the MPA across the study period.

Gastropods

The two-part T-test based on Pearson's correlation values found a highly significant ($P = < 0.000$, $F = 17.445$, $DF = -36.741$) difference between changes in Other Gastropod populations inside and outside the MPA; with a mean correlation of $R = -0.158$ outside the MPA and $R = 0.243$ inside.

3.4 Substrates

Hard Coral

Declines in overall scleractinian coral abundance is observed beginning at the end of 2014 leading into early 2015 (Fig. 14) however, these declines are not severe and there are signs of recovery towards to end of 2016. Overall abundance of hard coral species is lower outside the MPA as to be expected. As discussed early, it is not accurate to attribute this difference in abundance to MPA protected as it is likely to be naturally occurring and the MPA boundary was established around the area of higher coral cover and biodiversity.

This is a combined overlook of all scleractinian corals recorded on the survey transects; overall it shows slight decline around 2015 but nothing that warrants particular concern as there are positive signs of recovery post-2015. To gain a more in-depth view of benthic changes over the El Niño period it is essential to look more closely into particular species and life forms.

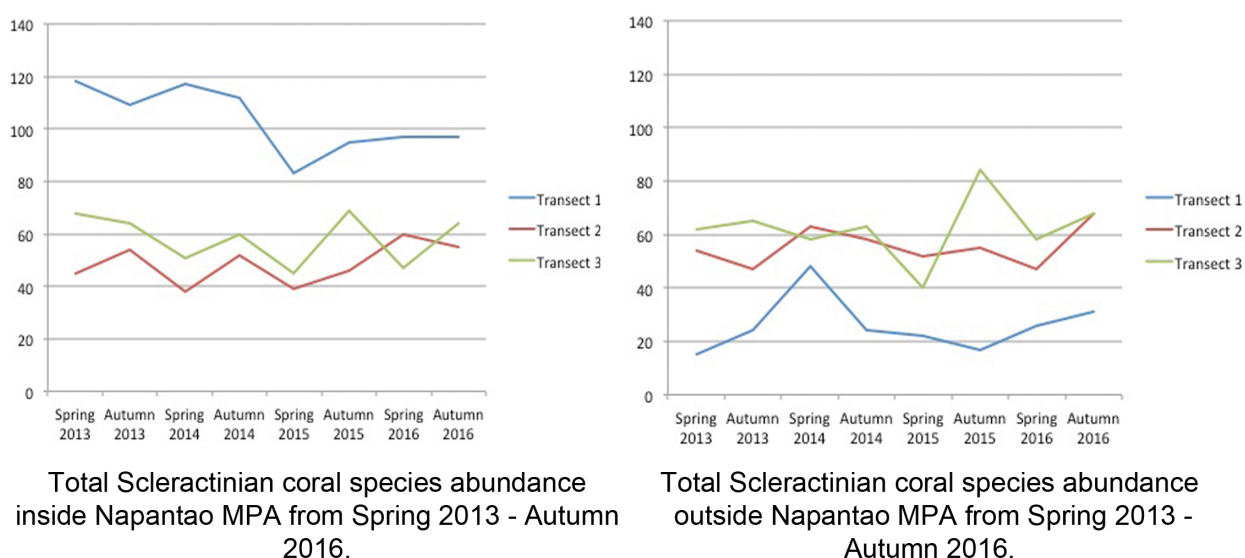


Figure 14 - Line graphs showing trends of total abundance of all hard-coral species from both inside and outside the protected area across the study period.

Encrusting Scleractinian Corals

Encrusting corals, or corals in the early stages of development showed a negative mean correlation outside the MPA of -0.008, and a positive correlation inside the MPA of 0.044, however this was not significant ($P = 0.870$).

Branching Scleractinian Corals

Mean Pearson's correlations for branching scleractinian corals were positive for both outside and inside the MPA, although this correlation was weak. The mean correlation inside the MPA was $R = 0.115$, and outside $R = 0.06$; both of these values show weak positive correlations but with a stronger correlation inside Napantao MPA. When these values were tested through a T-test, they were not significantly different from one another ($P = 0.922$).

Solitary Corals

A discriminant function analysis (DFA) based on both 2015 and 2016 substrate data correctly classified 79.2% of all cases to inside or outside the MPA, with the stepwise method identifying Solitary / Mushroom corals as the main classifying factor for correct identification with a significance of $P = 0.012$.

Acropora spp.

Acropora spp. has been examined individually from scleractinian corals due to its high thermal sensitivity. The trends of total abundance of all *Acropora* spp. surveyed by CCC from spring 2013 to the end of 2016, both inside and outside the MPA, are displayed in figure 15. Strong declines within the MPA beginning in Spring 2015 are observed, in keeping with the predicted El Nino effects; followed by weak increase throughout the remainder of 2015 with stronger increase in abundance beginning in 2016. Outside the MPA trends are far more sporadic with regular drops in abundance, however, similarly to inside the MPA, the strongest declines are observed in Spring 2015.

A DFA correctly classified 81.3% of all 2013 substrates into the correct study site (inside / outside MPA), with the stepwise method identifying branching *Acropora* spp. as the top significant identifying variable ($P = 0.0001$). The same model based on classifying substrate data from 2014, again correctly classified 81.3% of cases and also highlighted branching *Acropora* spp. as the initial significant identifying variable ($P = 0.001$). However, by 2015 the same DFA model no longer recognises *Acropora* spp. as a significant identifying variable. This is likely to be as a result of *Acropora* spp. levels within the MPA declining to similar levels to outside the MPA, thus no longer being an effective identifying variable within the model.

The 2-part T-test also found a significant difference ($P = 0.017$, $F = 6.181$, $DF = 41.49$) between the change in abundance of *Acropora* (branching) inside and outside the MPA, with mean correlations of $R = 0.454$ outside the MPA and 0.003 inside, this is an average correlation and it is likely that the severe drops in *Acropora* spp. inside the MPA beginning in Spring 2015 have

lowered this average to be lower than the outside MPA data. It is expected that areas with higher coral density, such as inside the MPA will show higher declines in coral cover as a result of elevated SST; this is where it is essential to look at recovery patterns to establish the resilience of a coral reef.

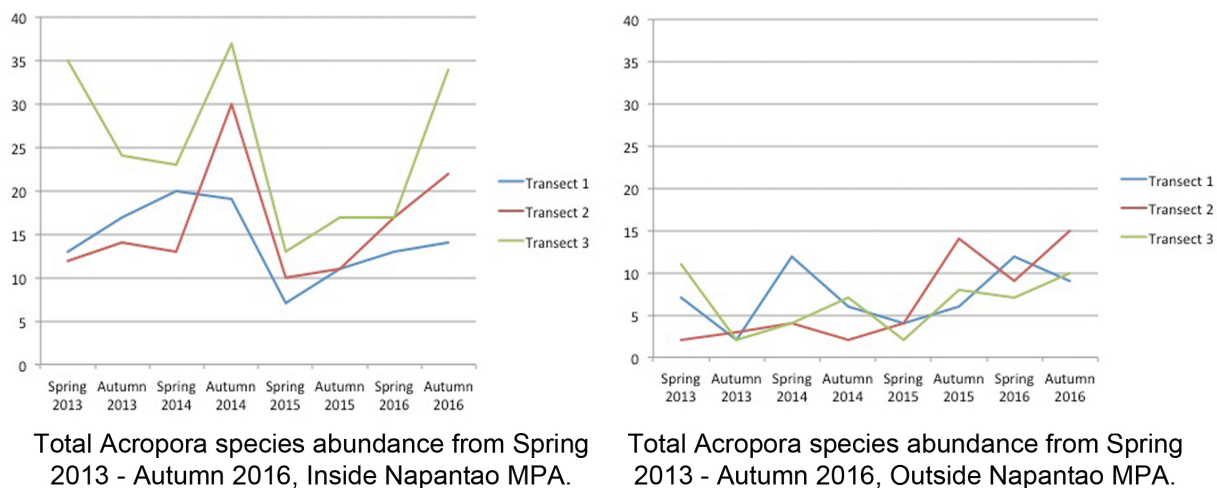


Figure 15 - Line graphs showing trends of total abundance of all *Acropora* species from both inside and outside the protected area across the study period.

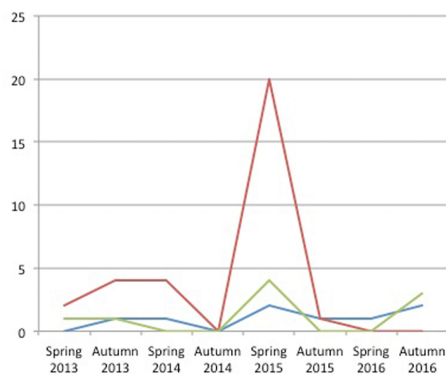
Coral Bleaching

T-tests, conducted on Pearson's correlations, found a highly significant difference ($P = 0.002$, $F = 10.268$, $DF = 36.4$) between population coral bleaching trends inside the MPA and outside; with mean bleaching correlation inside the MPA staying consistent across all 4 years ($R = 0$), while correlations outside the MPA show a significant increase ($R = 0.35$).

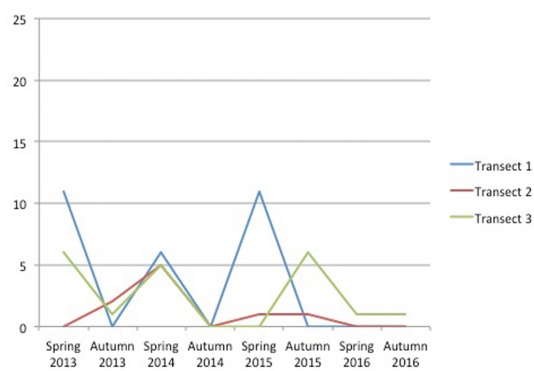
Recently Killed Coral

Recently killed coral (RKC) is classified by CCC as over 5mm of algal growth upon a bleached coral, it is at this point that the macro-algae prevent the re-colonisation of zooxanthellae and thus the coral is recorded as recently killed and no longer bleached. RKC abundance across the study period on both sites is displayed in Fig. 16. As predicted, both sites show dramatic increases in RKC throughout 2015; although inside MPA data shows a more dramatic increase with a total abundance of 20 areas of RKC occurring in one transect, as opposed to 11 outside the MPA. Levels then revert back to > 5 by early 2016 within the MPA however levels of RKC outside Napantao MPA are less consistent, again, there is an obvious peak in abundance throughout 2015 but there is a somewhat unpredictable reoccurrence of smaller peaks throughout the remainder of the study period. This could be attributed to other external pressures causing corals to bleach, such as anthropogenic damage from boats etc and a lack of recovery from bleaching events. It is possible that this trend could also be seasonal, with increases in abundance more likely to occur in

spring, and drop again by august, similar to seasonal increased in eutrophic waters observed worldwide. However, this would have to be examined over a greater time period to draw any accurate conclusions.



Total RKC abundance inside Napantao MPA from Spring 2013 - Autumn 2016.



Total RKC abundance outside Napantao MPA from Spring 2013 - Autumn 2016.

Figure 16 - Line graphs showing trends of total abundance of recently killed coral from both inside and outside the protected area across the study period.

4. Discussion

4.1 Coral and Benthic changes

Branching Corals

Both Pearson's correlations for internal and external MPA data show minimal, but positive correlations of branching corals, with a stronger positive correlation within the MPA. Previous studies in the Indo-Pacific have found that branching forms of coral are frequently the first to bleach and die, during coral bleaching events (Brown and Suharsono 1990; Gleason 1993; Hoegh-Guldberg and Salvat 1995); however, this is not the case with the data within this study. This is indicative that, although branching corals are identified as one of the least bleaching-resilient coral lifeforms, both inside and outside the MPA, throughout the ENSO study period, branching coral cover is not declining overall. As hypothesised, the increase in mean abundance from 2013 - 2016 is higher, although not significantly, within the MPA; likely to be as a result of more suitable conditions for coral recruitment and growth which can be partially attributed to the protection granted by the MPA.

Acropora spp.

As a result of high respiration rates, *Acropora* spp. are thought to have a low thermal tolerance, thus a high susceptibility to thermal bleaching (Jokiel & Coles 1990). However, *Acropora* spp. is also fast growing and often demonstrates a rapid recovery post-bleaching (Baird & Marshall 2002). It is likely that this pattern of rapid increase post-spring 2015 followed by further decrease again, recorded outside the MPA seen in Fig. 15, can be attributed to this fast recovery trait of the species. The following decrease observed shortly afterwards is likely to be attributed to unfavourable environmental factors making the permanent establishment of new coral recruits problematic. Larval dispersal is likely to be similar between both sites due to their close proximity, however despite recruitment occurring post-bleaching at both sites, further growth from the preliminary life stages of *Acropora* is hindered outside the MPA due to unstable ecosystem conditions; the early reproductive output of *Acropora* is more susceptible to bleaching than many other scleractinian corals (Baird and Marshall 2002). It is clear that the environment outside the MPA capable of new coral recruitment but not able to support a stable *Acropora* community. It is likely that the protection offered to the ecosystem within the MPA has resulted in a faster recovery and stable re-establishment of coral community; without this protection, the ecosystem remains unstable and unable to further support coral development. The response to elevated SST over the El Nino year of 2015 and recovery patterns shown by *Acropora* spp. outside Napantao MPA seen in fig. 13 show a similar response pattern as predicted by Perry et al. (2010) when modelling a marine population variable's response to climatic change when that population is also strongly influenced by added external stressors (Fig.4).

The growth and recovery rate of *Acropora* spp. is largely variable and dependent upon the severity of bleaching (Baird and Marshall 2002). Thus, it is possible that *Acropora* outside of Napantao MPA experienced more severe bleaching, not as a result of higher SST but as a result of a lower resilience, which could also be causing the sporadic and unstable recovery. It is possible that the *Acropora* outside of the MPA was more susceptible to potential bleaching during 2015 due to immediate external pressures that will not affect corals inside the MPA, such as excessive fishing, high levels of anthropogenic disturbance and pollution such as trash etc. Mumby & Harboure (2010) found similar results that marine reserves can increase the post-disturbance recovery rates of some corals. Additional external stressors may be enough to lower the thermal tolerance of already susceptible recovering *Acropora* colonies during a period of elevated SST, thus resulting in secondary declines in abundance as seen in Fig. 13.

The DFA identifies *Acropora* as a key identifying factor when correctly classifying data into inside / outside MPA for 2013 and 2014. However, by 2015 the model now identifies Solitary or Mushroom corals as the main factor influencing correct classification. This is likely to be because of elevated SST reducing abundance of *Acropora* spp. to similar levels both inside and outside the MPA, thus rendering it a less effective factor in classification. Solitary corals however, are often the first scleractinian coral to colonise an area post-disturbance (Chadwick-Furman & Loya 1992), this is likely to be why these species have been identified as a key classifying factor post 2015 disturbance.

Coral Bleaching

Coral bleaching data sets indicate that throughout the study period, levels of coral population bleaching were significantly higher outside the MPA than inside; this data may corroborate the hypothesis that MPAs increase thermal resilience of coral reefs. This increased resilience could be attributed to a number of factors; it is possible that the coral species composition within the MPA consists of more naturally thermally resilient corals than outside the MPA, for example, massive corals such as *Porites* and *favidae* that are thought to be more thermally tolerant (Marshall & Baird 2000, Loya et al. 2001). Jones et al. (2000) suggested that poritids and faviid corals can withdraw their polyps into deeper shaded regions, thus protecting algae from further light and heat exposure, possibly reducing bleaching susceptibility. Massive corals are often subject to anthropogenic damage from boats or being mistaken for rocks and stood on by tourists and fishermen. Such stressors are less likely to occur within the MPA, making the establishment and survival of such corals more successful; Carpenter et al. (2010) found that local anthropogenic impacts reduce the resilience of corals to withstand global threats. Well managed MPAs reduce these threats to reefs, thus hypothetically, increasing a coral reef's ability to withstand elevated SST with lower levels of coral bleaching. These reduced external anthropogenic stressors, as a result of the implemented

MPA, may be another factor contributing to the significant difference in population bleaching inside and outside the MPA.

Recently Killed Coral

Mclanahan et al. (2003) found turf algae to be negatively associated with coral mortality, algal competitive superiority is often due to reduced herbivory or increased nutrient input (McCook et al. 2000). Similarly, Done et al. (1992) concluded that the cover and biomass of benthic macro-algae increased concurrently with coral loss. Widespread replacement of corals by algae may often indicate coral mortality due to external disturbances, rather than competitive overgrowth, but may lead to competitive inhibition of coral recruitment, with consequences for reef recovery (McCook et al. 2001).

Pre-2015 data suggests that there are seasonal trends in levels of RKC, typically peaking in Spring and dropping again by Autumn, this trend is observed more outside the MPA than inside. It is likely to be that the no-take regulations of the MPA ensure a stable herbivorous population within the MPA, that in-turn, prevent spikes in macro-algal colonisation of corals similar to those seen outside the MPA. This stable herbivorous population prevents coral overgrowth from algae and other coral competitors through the continued grazing of the substrate. Similarly, Mumby et al. (2006) found a greater biomass of parrotfishes and thus, less macro-algae inside a no-take reserve as a result of fisheries management.

Inside the MPA from 2013 through to the end of 2014 levels of RKC are low, and relatively consistent, representative of a stable ecosystem; as expected, there is a large spike in abundance of RKC throughout 2015, indicative of higher levels of coral bleaching, in keeping with the predicted effects of the El Nino. This increase is dramatic on some transects but others only show a slight increase. Due to the higher abundance of scleractinian coral inside Napantao, as opposed to outside, it is predicted that the amount of RKC during this period would be higher inside the MPA, due to the initial higher abundance of coral. By the end of 2015, abundance of RKC had decreased and returned to pre-El Nino levels; the healthy herbivorous fish stocks inside the MPA, as a result of the no-take zone, are a contributing factor to this algal control, rapid recovery and return to pre-El Nino state. Outside the MPA a decline in levels of RKC is observed at the end of 2015 (Fig.13). Different to all previous years, this lower level of abundance has remained low throughout 2016 as opposed to peaking again in Spring as previous years have demonstrated. This prolonged period of low levels of RKC coincides with record high numbers of herbivorous species found in the same time period, along the same transects. It is likely that these consistently low levels of RKC, are attributed to low levels of macro-algal colonisation as a result of increased herbivorous grazing. Similarly, Hughes et al. (2007) found that where herbivorous fishes were abundant, algal abundance remained low and controlled.

4.2 Fish Assemblage

Herbivores

The presence and abundance of herbivorous fish species can be an indicator of various ecological conditions, in order to maintain coral reefs in a coral dominated state and prevent phase-shifts, herbivores are essential. The analysis of abundance trends of herbivores during a period of elevated SST may be indicative of macro-algae colonising bleached corals upon a reef (McLanahan et al. 2001). However, an increase in herbivores, although possibly indicative of raised algal levels, may also prove positive as this abundance could result in control of algal-domination, preventing a phase-shift (Graham et al. 2008).

Grazing by herbivores, by creating space for coral and invertebrate larval settlement, is thought to be key to maintaining reefs in a coral dominated state (Hughes, 1994, Mumby & Harbourne 2010). Overfishing can drastically diminish numbers of herbivores and create imbalance within an ecosystem. This imbalance leaves an ecosystem vulnerable to climatic events, reducing the ability to adapt and recover; possibly resulting in phase shifts from a coral dominated, to algal dominated ecosystem. (Hughes et al. 2007; Cheal et al. 2010). Herbivores rapidly graze the reef substratum removing up to 90% of the net algal production (Polunin and Klumpp 1992; Ferreira et al. 1998). Such intense herbivory inhibits the proliferation of algal biomass and minimises algal–coral competition (Hughes et al. 2007;) thereby promoting the recovery of coral assemblages following disturbance (Bellwood et al. 2004; Mumby and Steneck 2008). It is clear that the successful establishment of more resistant coral populations from newly settled spat or small remnants is heavily reliant upon the existence of recovery conditions at damaged sites that ensure the substrate is kept free of algal carpets. (Wooldridge et al. 2005). Theory predicts that maintenance of greater biomass, density and size of herbivorous fishes by MPAs, should promote coral recovery, thus providing spatial resilience in the form of populations that can re-seed depleted areas (Nystrom & Folke 2001; Hughes et al. 2003). It is likely that the consistently, significantly higher herbivorous fish stocks within Napantao MPA as a result of fishing restrictions, are a strong contributing factor to the rapid recovery of both coral species and coral dependent species seen within the MPA during 2016.

McLanahan et al. (2001) found that using herbivore bio-mass can be used as a reliable way to estimate fleshy-algal colonisation of a bleached reef during the 1 year post-bleaching period, due to a strong correlation between herbivore abundance such as *scaridae* and algal abundance. The results from Napantao data suggest a similar pattern, the outside MPA transects show a sharp increase in Parrotfish (*scaridae*) abundance beginning in 2016, likely to be as a direct result of increased macro-algal colonisation of bleached corals following elevated SST. The inside Napantao MPA data, does not show such a sharp increase, and numbers at the end of 2016 had

not risen as extremely as outside the MPA. It is possible that this is indicative of lower levels of macro-algal colonisation; possibly as a result of corals recovering at a faster rate and prohibiting vast colonisation of algal matter. It is also likely to be attributed to healthy herbivore stocks within the MPA controlling the level of macro-algae; the protection of herbivores could assist the recovery of corals from climate change disturbances (Mumby and Harborne, 2010).

Overall, managing of fish stocks is an essential factor in managing and increasing reef resilience, local stewardship of fishing effort is a tractable goal for conservation of reefs, and this local action can also provide some insurance against larger-scale disturbances such as mass bleaching, which are impractical to manage directly (Hughes et al. 2007). Using the hypothesis that spikes in herbivore abundance is an indicator of bleaching and macro-algal levels, this data could provide evidence that MPAs do have a positive effect on coral bleaching recovery times and overall reef resilience, as only the outside of the MPA shows such sharp increases in abundance indicative of an increase in macro-algae and bleached corals, however, this relationship does require further investigation.

Although also herbivorous reef fish, it is suggested that rather than playing a key role in algal removal on a coral reef, Rabbitfish (*iganidae*) display a more mixed diet with some species feeding entirely on sponges (Hoey et al. 2013); Rabbitfish are thought to perform a role that is complementary to the more algal-focused role of Parrotfish and Surgeonfish (Hoey et al. 2013). A study of three species of rabbitfish revealed that they fed to a greater degree on benthic organisms within crevices than species of Parrotfishes or Surgeonfish (Fox and Bellwood 2013), removing their reliance on algae for food. The T-test based on Pearson's correlations found a significant difference between changes in *iganidae* abundance inside and outside the MPA. A weak negative correlation of *iganidae* abundance was identified outside the MPA, while there was a weak positive correlation of abundance inside the MPA. It is likely that this family shows a different pattern to Parrotfish, with no sharp increase in abundance relating the macro-algal levels outside the MPA as a result of a lower dependence on algae as a food source, and a higher reliance on the reef matrix to provide alternative food sources such as sponges and benthic organisms. Hoey et al. 2013, found that Rabbitfish abundance on the Great Barrier Reef was markedly higher on the reef flat, and inner shelf reefs than the outer reefs. The overall positive correlation of Rabbitfish abundance within the MPA, contrasted with the negative correlation outside the MPA could be indicative of coral cover or food availability.

Coralivores

Reese (1977) chose to use coral predators as indicators of the 'health' of the coral community. He reasoned that stressed corals would provide a less adequate food source and that this would affect the abundance and or behaviour of corallivores. (Reese, 1977, 1981). Graham et al. (2008) identified a 1:1 linear relationship between coral loss and obligate corallivore decline, suggesting a clear link between their survival and coral cover; this group of species is clearly a key indicator of coral cover and coral health. Bell and Galzin (1984) found similar results, that species richness of the chaetodontidae, pomacentridae, abridae, scaridae, acanthuridae and gobiidae rose with increasing live coral cover, and changes in live coral cover as small as 0% - < 2% produced significant increases in number of species and number of individuals.

The short-term impacts of bleaching on fish are mainly manifested in species that specialise on live coral for diet, shelter or as a recruitment habitat (Wilson et al. 2006). Both Redfin Butterflyfish (*Chaetodon lunulatus*) and Eastern Triangle Butterflyfish (*Chaetodon baronessa*) are obligate corallivores with a high dependence on *Acropora* spp. in their diet (Cole et al. 2008). Trends of both species show dramatic declines beginning in Spring 2015, in keeping with the rising SST effects of El Nino. Inside Napantao MPA, *C. baronessa* abundance begins to decline in Spring 2015, with continued declines through to Spring 2016, where abundance begins to show signs of rapid recovery with 2 out of the 3 transects returning to pre - 2015 numbers by Autumn 2016. However, outside the MPA, both obligate corallivore species mimic the *Acropora* trends with drastic declines in Spring 2015, followed by rapid increases and decreases again, these trends within both species are likely to be attributed to the strong correlation between obligate corallivores and their food source which is in this case is *Acropora* spp. Graham et al. (2007) found striking declines in abundance of corallivores, strongly associated with a similar pattern of decline in their preferred corals. Both patterns, outside and inside the MPA are accurate representations of not only the species populations but the condition of the corals that these species depend so heavily on.

Although not always obligate, nearly all species of Butterflyfish are corallivores and are highly dependent on the coral reef matrix for both food and protection from predation (Munday & Jones 1998). Trends of all recorded Butterflyfish species throughout the study period are displayed in figure 6. Within the MPA, there is a delay in the expected drop in abundance likely to be as a result of ENSO; with the majority of decline being observed in late 2015 and Spring 2016. It is possible that this is a 'lag effect' (Graham et al. 2010) as a result of lower food availability caused by raised levels of coral bleaching and coral mortality, that has then had a knock-on effect upon population levels in 2016. As this data focuses on all species of *chaetodontidae* not just obligate corallivores, coral polyps only contribute to many species' diet. It is likely that the effects are not as evident immediately due to an overall lower dependence on coral as a food source within this group. Since

a loss in structural complexity of the reef framework, which can take > 5 years (Wilson et al. 2006), is likely to affect small individuals, and since these may take some time to recruit to the fishery, a lag effect may exist before the full impact of coral bleaching on reef fisheries is realised (Graham. 2007).

It is expected that abundance within the MPA will demonstrate sharper declines than outside, as a result of higher abundance of both butterflyfish species and their food sources previously to the bleaching event. Corallivores often demonstrate striking declines in numerical abundance which are greatest in MPAs, and associated with a similar pattern of decline in their preferred corals (Graham et al. 2007).

Triggerfish (*balistidae*) and Pufferfish (*tetraodontidae*) are also corallivores depending highly on the reef matrix (Cole et al. 2008). Within the MPA, the total abundance of Triggerfish begins to decline around Spring 2015, which is expected as a response to predicted coral bleaching resulting in a lack of available food sources. This decline is present in both inside and outside MPA data, however it is much more severe within the MPA. Similar results have been found in other studies into the response of corallivores to bleaching related to MPAs. This greater decline is associated with the greater cover of the complex coral category in the MPAs prior to the bleaching event, which is the preferred habitat of many specialist fish (Munday 2004; Pratchett 2005).

Pufferfish (*tetraodontidae*) abundance both within the MPA and outside show similar declines however some begin as early as Autumn 2014 and continue to increase and decrease again sporadically throughout 2015, thus accurate conclusions are somewhat difficult to draw from this data. However, in Spring 2016 all 3 transects within the MPA show signs of recovery and drastic increases in abundance, overtaking some pre-El Nino recordings, this pattern of recovery is not mimicked outside of the MPA, with some transects showing marginal increases in abundance while others show a continued decline. It is possible that this increase in Pufferfish abundance in Spring 2016 within Napantao MPA indicates coral recovery; recovery that is not occurring to the same extent outside the MPA.

Mclanahan et al. (2005) identified a heavy dependency on coral in the Moorish Idol (*Zanclus cornutus*)'s diet, highlighting this species as an essential indicator of coral abundance and health. The Pearson's correlation T-test identified a highly significant difference ($P = 0.009$) between abundance correlations from 2013 - 2016 inside and outside the MPA. Both study sites show a mean negative correlation, however the decline is stronger within the MPA. As Graham, et al. (2007) identified, this stronger decline within MPAs is not unusual, associated with higher pre-disturbance abundance and coral cover. This greater decline within an MPA is seen frequently throughout the examination of corallivore populations in this study, however to examine this pattern more accurately, these declines should be assessed as a percentage of a population to create more comparable values.

4.3 Invertebrate populations

Sea urchins, in particular, the Long Spine Sea Urchin (*Diadema antillarum*) feed on fleshy turf algae that colonises on bleached and dead corals, thus preventing possible post-bleaching recovery; abundance of sea urchins can prevent this colonisation and promote coral recovery (McLanahan et al. 2011). Similar to algal herbivores, abundance of the Long Spine Sea Urchin can be used as an indicator of macro-algal levels, which in turn could be indicative of levels of bleached corals. The overall trend of abundance of *Diadema antillarum* within the MPA is negative, showing a weak and somewhat sporadic, but overall decline in abundance. The opposite of this is seen in the data outside of the MPA, with an increase in abundance being recorded at the end of 2015 and remaining high throughout 2016. It is likely that similarly to Parrotfish, this increase in abundance could be attributed to availability of macro-algae to feed on. Should this be the case, these abundance trends demonstrate an increased level of bleached corals being colonised by algae outside the MPA, that does not occur to the same extent within the MPA.

A complex coral reef matrix is essential for Gastropod (*Gastropoda*) survival, many species rely heavily on the reef for protection from predation pressures and food availability (McLanahan 1990). The significant difference in changes in gastropod abundance, with a negative correlation outside the MPA and a positive correlation inside is a positive indicator for benthic condition within the MPA, while demonstrating a decline in benthic quality, in particular, hard coral cover, outside the MPA.

Giant Clams (*Tridacna gigas*) contribute greatly to the coral reef matrix; with their calcium carbonate shells, they act in a similar way to hermatypic corals and improve the structural complexity of a reef. Similar to hermatypic corals, Giant Clams also rely on a symbiosis with zooxanthellae, dinoflagellates of the genus *Symbiodinium*; this can prove vital in bleaching events as an aid to re-colonisation of zooxanthellae by bleached corals. Giant Clams act as a reservoir for zooxanthellae, they host numerous types of the *Symbiodinium* (Neo et al. 2015), they then release large numbers of zooxanthellae in fecal pellets into the water column (Maruyama and Heslinga 1997). These symbionts become available for other species, in particular corals, to 'take up' if necessary (Neo et al. 2015). Giant Clams are also more thermally tolerant and typically bleach later than corals and only during very extreme events (Bruno et al. 2001) thus making them a valuable asset in maintaining a thermally resilient reef. It is possible that in bleaching events that only affect corals, giant clams may accelerate the recovery of nearby bleached corals by making live symbionts available to the corals (Frias-Torres 2017). Abundance of Giant Clams in three size categories (>10cm, 11cm -20cm & 31cm – 40cm) is significantly higher outside the MPA ($P = 0.035$, $P = 0.030$, $P = 0.017$) retrospectively. This higher abundance outside the MPA may be a

contributing factor the fast, although somewhat unstable recovery displayed by various coral species. However, the geographical distance between both study sites is minimal and there is a regularly occurring south-ward current that will disperse zooxanthellae in the water column across both study sites. Although there may be a higher abundance of Giant Clams outside the MPA, this abundance is likely to be improving post-bleaching recovery rates across both study sites regardless of whether bleached corals are situated inside or outside the MPA boundary.

4.4 MPAs - Design and Management

The Fisheries Code of 1998 set the target of 15% of Philippine coastal municipal water to be within no-take MPAs; this may be an explanation for the rapid increase of the establishment of MPAs around the Philippines within the last decade. It has been suggested that as 15% of municipal waters is almost twice the total coral reef area in the Philippines, and it is likely that this target may not have come from scientific reasoning (Weeks et al. 2009); over 400 MPAs have now been recorded within the Philippines (Fig. 17) (Alino et al. 2002).

The benefits that MPAs can deliver are strongly related to the effectiveness of the management of the MPAs (Christie et al. 2007; Cicin-Sain and Belfiore 2005). However, once established, it is common for management techniques to not be enforced to the necessary extent needed to make significant impact upon the ecosystem. The number and area of MPAs can be misleading indicators of conservation effectiveness if MPAs are not well managed and enforced (McClanahan, 1999). Edgar et al. (2014) states that more emphasis and guidance is needed in regard to MPA design and management in order for MPAs to achieve their desired conservational value. Selig and Bruno (2010) found that the positive MPA effects in the Caribbean were found for closures with > 14years of protection, Napantao MPA has been protected the reef since 1998, therefore it does comply with Selig and Bruno's criteria.

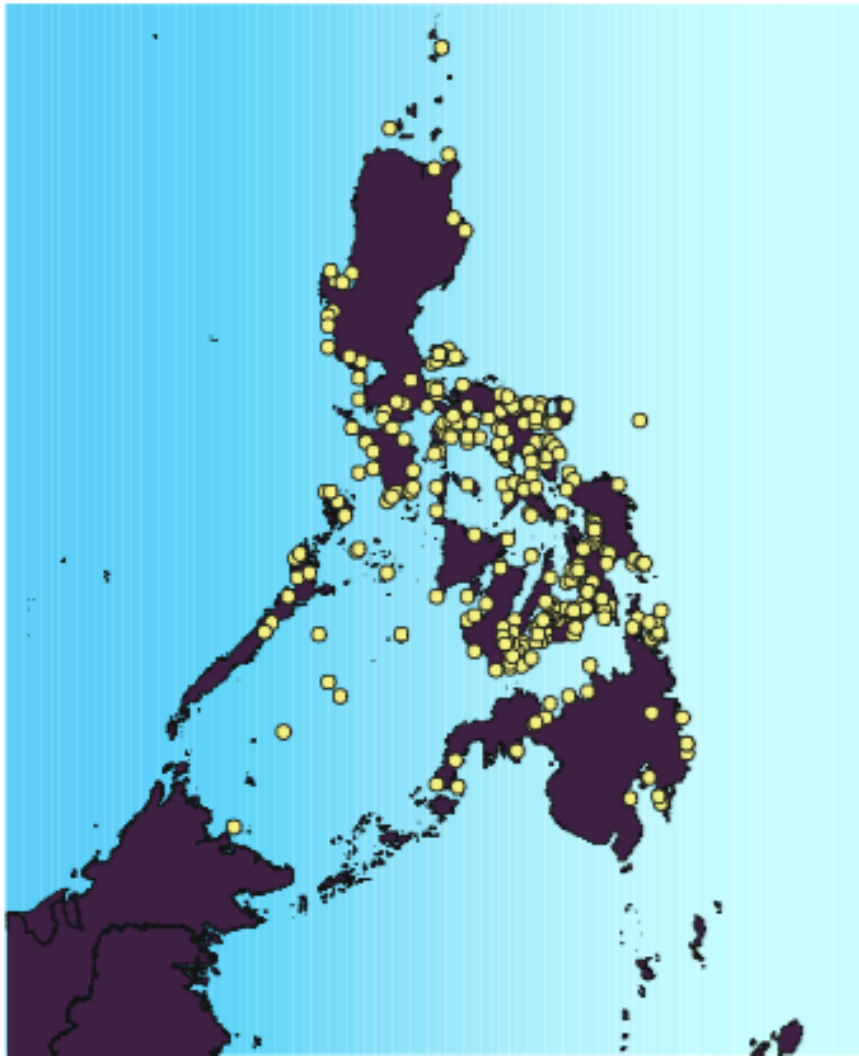


Figure 17 – Map of the location of MPAs within the Philippine archipelago (marked in yellow). Source: Alino et al. 2001.

A study into the effectiveness of MPAs within the Philippines specifically, concluded that marine corridors were not well represented by current MPAs, as four of the nine essential corridors did not contain MPAs (Weeks et al. 2009). The study also found that 90% of all MPAs of which spatial data was available, had a total area of < 1km². However, one of the key features identified for MPAs to reach global conservation outcomes is to be > 100km² (Edgar et al. 2014). It has been concluded that the current extent, size and distribution of MPAs across the Philippines is inadequate in order to achieve conservation objectives (Weeks et al. 2009). Edgar et al. (2014) also suggests that in order for MPAs to achieve conservation goals an MPA must be no take; well enforced, old (>10 years), large (>100km²) and isolated by deep water or sand. Nevertheless, in the context of the Philippines, widespread increases in the no-take area of MPAs are unlikely because of socioeconomic constraints imposed by the high dependence of local communities on marine resources and low spatial mobility of fishers.

MPA Networks



Figure 18 – Location of MPAS in Sogod bay, around Panon Island.

Connectivity between MPAs is essential in order to achieve thriving and healthy marine ecosystems. MPA networks are essential as when used in isolation, small MPAs may not support populations that are large enough to sustain themselves. As social and economic constraints often

limit the size of MPAs, networks between smaller MPAs is an effective way of ensuring conservation success. An MPA network can include several MPAs of different sizes, located in critical habitats, containing components of a particular habitat type or portions of different kind of habitats and interconnected by the movement of animals and plant propagules (PISCO 2007). Well-designed MPA networks provide important links to maintain ecosystem processes and connectivity, in turn increasing resilience and reducing vulnerability to disease or disaster as a result of improved connectivity; often ensuring long-term sustainability of populations much more effectively than single sites can (NRC, 1999).

Connectivity is highlighted by Obura and Grimsditch (2009) as a strong driver of coral reef resilience offering re-seeding of impacted reefs through coral larvae dispersal in currents, ecological interactions between adjacent reefs through agile predators and herbivores and factors such as available substrate for successful larval settlement. Modelling studies have identified how larval dispersal and the spatial configurations of MPAs interact to promote population persistence (Crowder et al. 2000; Botsford et al 2003).

Well connected reef systems are also expected to contain the pockets of refugia required for landscape-scale recovery (Folke et al. 2001). As demonstrated by the recovery of well-connected reef systems in mainland Kenya and Tanzania post 1998 El Nino, compared to the recovery of the isolated reefs of the inner Seychelles.

Brock et al. (2012) identified 4 scientific guidelines for designing resilient MPA networks in the face of a changing climate. Guideline 1 is to protect species habitats with crucial ecosystem roles, or those of special conservation concern. Guideline 2 identifies the importance of protecting carbon sinks, and 3 suggests protecting ecological linkages and connectivity pathways for a wide range of species. Finally, guideline 4 highlights the necessity of protecting the full range of biodiversity present in the target biogeographic area.

There is, however, a need for new NTAs, incorporated into existing networks that protect source reefs resilient to large-scale disturbance, and areas likely to retain their physical structure. This will help sustain the upstream spawning stocks of corals and specialised fish species required for landscape-scale recovery. Such management is likely to be unsuccessful in isolation, and improved management of entire reef systems, reducing the stresses and pressures to areas outside NTAs will be necessary to maximise the capacity for systems to recover from large scale and ongoing disturbance (Graham et al. 2008).

5. Conclusion

This study concludes that there are strong ecological benefits of MPAs for a coral reef ecosystem, and that, although unable to completely mitigate the effects of rising SST and subsequent coral bleaching, recovery trends of both coral species and coral-dependent species are stronger within the MPA. The significant difference in changes in population bleaching inside and outside the MPA, with mean bleaching levels within the MPA staying consistent from 2013 - 2016 and mean levels of bleaching outside the MPA increasing, would also suggest that coral within the MPA has a greater thermal resilience.

Recovery after bleaching is hindered by local-scale ecological forces that may inhibit coral recruitment and delay reef recovery, such as coral predators or competition with fleshy algae (Knowlton 1988; Hughes and Tanner 2000). This study shows that a well-managed MPA can decrease such factors hindering recovery; by reducing depletion of key herbivorous fish groups, control of macro-algal colonisation can be regained, enabling further post-bleaching recovery, larval settlement and growth. Concluding that well managed, and inter-connected MPAs are an effective tool in promoting coral resilience and recovery post-disturbance through local management.

Although there are greater signs of post bleaching recovery within the MPA ecosystem, of both corals and indicator fish species, the declines seen by most species during El Nino 2015, inside and outside the MPA, are severe. As climate change and bleaching events increase in severity, it is likely that we will see greater species decline and possible extirpation during severe bleaching episodes. The implementation of well managed MPAs has the potential to improve coral thermal resilience and improve recovery rates post bleaching, however, this is not a long-term solution to combatting rising SST. As bleaching events increase in frequency and severity with climate change, alongside increasing ocean acidity and pollution, marine ecosystems will become increasingly weakened and unable to withstand such pressures. Reducing immediate anthropogenic impacts such as overfishing, through MPAs, may buy us time in the fight to save our coral reefs but long-term solutions require global efforts to reduce carbon emissions and greenhouse gases. MPAs play a key role in combatting not only thermal stress, but anthropogenic disturbance and over exploitation of coral reefs. However, in order to create sustainable management techniques and achieve conservation goals, MPA networks must be partnered with global legislation change in regard to carbon emissions, fishing practices, land use and waste disposal; offering insurance for the future of the world's coral reefs.

Appendix A.

Invertebrate target species used within CCC's methodology.

Banded Coral Shrimp (*Stenopus hispidus*)
Brittle Star (*Ophiuroidea*)
Cushion Star (*Choriasta granulatus*)
Christmas Tree Worm (*Spirobranchus giganteus*)
Collector Urchin (*Tripneustes gratilla*)
Conch (*strombidae*)
Cone Shell (*conidae*)
Cowrie (*cypraeidae*)
Culcita novaguinae
Cuttlefish (*Sepiida*)
Crown of Thorns Starfish (*Acanthaster planci*)
Drupella (*Drupella cornus*)
Feather Duster Worm (*Sabellidae*)
Feather Star (*Crinoidea*)
Flatworm (*Platyhelminthes*)
Gastropod (Other) (*Gastropoda*)
Giant Clam (*Tridacna gigas*)
Greenfish Sea Cucumber (*Stichopus chloronotus*)
Linkia laevingata
Lobster (*Nephropidae*)
Longspine Sea Urchin (*Diadema antillarum*)
Nudibranch (*Nudibranchia*)
Octopus (*Octopoda*)
Pencil Urchin (*Heterocentrotus mammillatus*)
Pinkfish Sea Cucumber (*Holothuria edulis*)
Prickly Redfish Sea Cucumber (*Thelenota ananas*)
Squid (*Teuthida*)
Tritons Trumpet (*Charonia*)
Top Shell (*trochidae*)

All recorded coral reef impacts used in CCC's methodology.

Black Band Disease

Bleaching (colony)

Bleaching (population)

Coral Damage (fishing)

Coral Damage (Boat / Anchor)

Coral Damage (Dynamite)

Coral Damage (other)

Trash (fishing)

Trash (general)

White Band Disease

Appendix B.

All recorded fish target species used within CCC's methodology.

Anemonefish (amphiprioninae)

Angelfish (*pomacanthidae*)

Barracuda (*sphyraenidae*)

Butterflyfish (*chaetodonidae*)

- Eastern Triangle Butterflyfish (*Chaetodon baronessa*)
- Kleins Butterflyfish (*Chaetodon kleinii*)
- Redfin Butterflyfish (*Chaetodon trifasciatus*)
- Humphead Bannerfish (*Heniochus varius*)
- Longnose Butterflyfish (*Forcipiger flavissimus*)
- Raccoon Butterflyfish (*Chaetodon lunulatus*)
- Vagabond Butterflyfish (*Chaetodon vagabundus*)

Cardinalfish (*apogonidae*)

Emperor (*lethrinidae*)

Fusillier (*caesionidae*)

Goatfish (*mullidae*)

Grouper (*serranidae*)

- Humpback Grouper (*Cromileptes altivelis*)

Jack (*carangidae*)

Lionfish (Pterois)

Lizardfish (synodontidae)

Moorish Idol (*zanclidae*)

Moray Eel (*muraenidae*)

Parrotfish (*scaridae*)

- Bumphead Parrotfish (*Bolbometopon muricatum*)

Pufferfish (*tetraodontidae*)

Rabbitfish (*iganidae*)

- Virgate (*Siganus virgatus*)

Ray (Batoidea)

Sandperch (*pinguipedidae*)

Sargeant Damselfish (*Abudefduf vaigiensis*)

Shark (*carcharhinidae*)

Snapper (*lutjanidae*)

Spadefish (*ephippidae*)

Spinecheek (*nemipteridae*)

- Twoline (*Scolopsis bilineatus*)

Squirrel / Soldierfish (*holocentridae*)

Surgeonfish (*acanthuridae*)

Sweetlips (*haemulidae*)

Toby (*tetraodontidae*)

Triggerfish (*balistidae*)

Unicornfish (*Naso*)

Wrasse (*labridae*)

- Crescent Wrasse (*Thalassoma lutescens*)
- Humphead Wrasse (*Cheilinus undulatus*)
- Red-Breasted Wrasse (*Cheilinus fasciatus*)

Appendix C.

Substrate categories and retrospective codes used within CCC's methodology.

RK (Rock)

RB (Rubble)

SD (Sand)

SI (Silt)

RKC (Recently Killed Coral)

NIA (Nutrient Indicator Algae)

CM (Non-*Acropora* hard coral. Lifeform: Massive)

CS (Non-*Acropora* hard coral. Lifeform: Submassive)

CB (Non-*Acropora* hard coral. Lifeform: Branching)

CE (Non-*Acropora* hard coral. Lifeform: Encrusting)

CF (Non-*Acropora* hard coral. Lifeform: Foliose)

CMR (Non-*Acropora* hard coral. Lifeform: Mushroom)

ACB (*Acropora* spp. hard coral. Lifeform: Branching)

ACT (*Acropora* spp. hard coral. Lifeform: Tabulate)

CME (Fire Coral (*Millepora*))

OP (Organ Pipe Coral (*Tubipora*))

SC (Soft Coral)

SP (Sponge)

OT -

- CRM (Corallimorph)
- ZO (Zooanthid)
- ANEM (Anemone)

Appendix D.

Species	Mean Abundance Inside MPA	Standard Error	Mean Abundance Outside MPA	Standard Error	U	N1	N2	P
Angelfish (<i>Pomacanthidae</i>) (H)	8.2	0.4	6.7	0.6	3607	96	96	0.009
Surgeonfish (<i>Acanthuridae</i>) (H)	4.1	0.4	0.7	0.2	1905	96	96	0.0001
Unicornfish (<i>Naso</i>) (H)	0.7	0.3	0.2	0.9	4274	96	96	0.123
Moorish Idol (<i>Zanclus cornutus</i>) (FC)	0.9	0.1	0.4	0.1	3449	96	96	0.0001
Other Rabbitfish (<i>Siganidae</i>) (H)	1.6	0.2	0.3	0.1	2426	96	96	0.0001
Virgate Rabbitfish (<i>Siganus virgatus</i>) (H)	0.2	0.1	0.5	0.4	4180	96	96	0.011
Anemonefish (<i>Amphiprionidae</i>) (H)	8.2	1.4	5.1	0.5	3924	96	96	0.074
Sergeant Damselfish (<i>Acanthuridae</i>) (H)	0.2	0.01	0.2	0.1	4509	96	96	0.394
Other Spinecheek (<i>Nemipteridae</i>) (H)	0.7	0.1	1.1	0.2	4022	96	96	0.073
Twoline Spinecheek (<i>Scolopsis bilineata</i>) (H)	1.4	0.2	0.8	0.1	3678	96	96	0.008
Humphead Wrasse (<i>Chelinus undulatus</i>)	0.06	0.06	0	0	4560	96	96	0.317
Crescent Wrasse (<i>Thalassoma lunare</i>)	2.5	0.3	2.6	0.3	4148	96	96	0.225
Redbreasted Wrasse (<i>Chelinus fasciatus</i>)	0.8	0.1	0.5	0.1	4284	96	96	0.334
Emperor (<i>Lethrinidae</i>)	0	0	0	0	4419	96	96	0.102
Sweetlips (<i>Plectorhynchus</i>)	0.1	0.1	0.1	0.2	4563	96	96	0.722
Triggerfish (<i>Balistidae</i>) (FC)	3.4	0.2	1.2	0.2	1960	96	96	0.0001
Goatfish (<i>Mullidae</i>)	0.6	0.1	0.9	0.2	4554	96	96	0.864
Fusilier (<i>Cesionidae</i>)	34.4	9.2	33	7.9	4357	96	96	0.491
Cardinalfish (<i>Apogonidae</i>)	12.1	2.4	17.4	2.5	3777	96	96	0.028
Jack / Traveller (<i>Carangidae</i>)	0.5	0.1	0.1	0.1	3612	96	96	0.0001
Pufferfish (<i>Tetraodontidae</i>) (FC)	0.8	0.1	0.4	0.1	3834	96	96	0.018
Toby (<i>Canthigaster</i>)	0.6	0.1	0.9	0.3	4426	96	96	0.572
Sandperch (<i>Pinguicidae</i>)	0.5	0.1	2	0.2	2582	96	96	0.0001
Lizardfish (<i>Synodontidae</i>)	1.5	0.2	1.2	0.2	4513	96	96	0.793
Lionfish (<i>Pterois</i>)	0.1	0.1	0.2	0.1	4122	96	96	0.039
Barracuda (<i>Sphyraena</i>)	2.1	0.8	1.7	0.1	4532	96	96	0.694
Squirrel / Soldierfish (<i>Holocentridae</i>)	0.9	0.2	0.1	0.1	3811	96	96	0.001
Spade / Batfish (<i>Chaetodontus faber</i>) (H)	0.1	0	0	0	4512	96	96	0.156
Moral Eel (<i>Muraenidae</i>)	0.1	0	0.1	0	4466	96	96	0.395
Total Parrotfish (<i>Scaridae</i>) (H)	9	0.7	7.1	0.8	4546	96	96	0.006
Total Grouper (<i>Epinephelinae</i>)	3.4	0.3	1.2	0.1	1890	96	96	0.0001
Snapper (<i>Lutjanidae</i>)	1.8	0.3	1.1	0.2	3631	96	96	0.007
Vagabond Butterflyfish (<i>Chaetodon vagabundus</i>) (FC)	0.3	0.1	0.1	0	4312	96	96	0.146
Kleins Butterflyfish (<i>Chaetodon kleinii</i>) (FC)	1.1	0.2	0.3	0.1	3288	96	96	0.0001
Eastern Triangle Butterflyfish (<i>Chaetodon baronessa</i>) (OC)	5.9	0.3	5.7	0.4	4398	96	96	0.584
Redfin Butterflyfish (<i>Chaetodon lunulatus</i>) (OC)	1.6	0.2	0.2	0.1	2369	96	96	0.0001
Longnose Butterflyfish (<i>Forcipiger flavissimus</i>) (FC)	0.3	0.1	0	0	4032	96	96	0.0001
Raccoon Butterflyfish (<i>Chaetodon lunula</i>) (FC)	0.4	0.1	0.2	0.1	4328	96	96	0.213
Other Butterflyfish (<i>Chaetodontidae</i>)	0.5	0.2	0.2	0.1	4605	96	96	0.99
Humphead Bannerfish (<i>Henniichus varius</i>) (FC)	0.9	0.2	0.6	0.2	3767	96	96	0.005

Table 2 – Mann-Whitney U results for all target fish species compared inside and outside the MPA. Species with abundance significantly higher within the MPA are highlighted in green and species abundance significantly higher outside the MPA highlighted in orange.

ii: Facultative Corallivores (FC), Obligate Corallivores (OC) and Herbivores (H) of interest are identified.

Species	Mean Abundance Inside MPA	Standard Error	Mean Abundance Outside MPA	Standard Error	U	N1	N2	P
Feather Duster Worm (<i>Sabellidae</i>)	10.3	1	10.3	1	4414	96	96	0.614
Christmas Tree Worm (<i>Spirobranchus giganteus</i>)	1.3	0.2	3.7	1	3020	96	96	0.0001
Flatworm (<i>Platyhelminthes</i>)	0.7	0.1	1.2	0.3	4392	96	96	0.526
Banded Coral Shrimp (<i>Stenopus hispidus</i>)	0.1	0	0.1	0	4560	96	96	0.701
Lobster (<i>Nephropidae</i>)	0.3	0.1	0	0	4560	96	96	0.317
Conch (<i>Strombidae</i>)	0.1	0	0.1	0	4514	96	96	0.657
Cowrie (<i>Cypridae</i>)	0.1	0	0.1	0	4513	96	96	0.677
Cone Shell (<i>Conidae</i>)	0.6	0.1	1.1	0.2	3935	96	96	0.054
<i>Drupella cornus</i>	6.4	0.8	6	0.9	4060	96	96	0.151
Topshell (<i>Tegulidae</i>)	0.5	0.1	0.5	0.1	4566	96	96	0.893
Nudibranch (<i>Nudibranchia</i>)	2.2	0.2	2	0.2	4508	96	96	0.791
Other Gastropod (<i>Gastropoda</i>)	9.3	0.9	7.9	0.8	4365	96	96	0.527
COTS (<i>Acanthaster planci</i>)	0.1	0	0.1	0	4465	96	96	0.451
<i>Linkia laevigata</i>	2.5	0.2	1.9	0.2	3459	96	96	0.002
<i>Choriata granulatus</i>	0.1	0	0.3	0.1	3979	96	96	0.009
<i>Culcita novaguinea</i>	0.1	0.1	0.2	0.1	4020	96	96	0.013
Feather Star (<i>Crinoidea</i>)	25.4	2	26.1	1.7	4066	96	96	0.159
Brittle Star (<i>Ophiuroidea</i>)	46	3	40.1	2.6	4166	96	96	0.25
Longspine Sea Urchin (<i>Diadema antillarum</i>)	8.2	0.9	7.1	0.9	4322	96	96	0.455
Pencil Urchin (<i>Heterocentrotus mammillatus</i>)	0	0	0.7	0	4272	96	96	0.007
Collector Urchin (<i>Tripteneustes gratilla</i>)	0	0	0.1	0	4320	96	96	0.013
Othee Sea Cucumber (<i>Holothuroidea</i>)	0.8	0.1	0.4	0.1	3626	96	96	0.003
Giant Clam < 10cm (<i>Tridacna maxima</i>)	0.1	0	0.2	0.1	4220	96	96	0.035
Giant Clam 11cm - 20cm (<i>Tridacna maxima</i>)	0.1	0	0.2	0	4130	96	96	0.03
Giant Clam 21cm - 30cm (<i>Tridacna maxima</i>)	0.1	0	0.1	0	4545	96	96	0.762
Giant Clam 31cm - 40cm (<i>Tridacna maxima</i>)	0.1	0	0.2	0	4224	96	96	0.017
Giant Clam 41cm - 50cm (<i>Tridacna maxima</i>)	0	0	0	0	4512	96	96	0.156
Giant Clam > 50cm (<i>Tridacna maxima</i>)	0	0	0	0	4560	96	96	0.651
Total Giant Clams (<i>Tridacna maxima</i>)	0.4	0.1	0.6	0.1	4320	96	96	0.363
Coral Damage (Boat / Anchor)	0.1	0	0	0	4513	96	96	0.413
Coral Damage (Other)	1.5	0.2	1.3	0.1	4228	96	96	0.303
Fishing Trash	0.5	0.1	0.5	0.1	4308	96	96	0.349
General Trash	0.5	0.1	0.8	0.1	3750	96	96	0.013
Population Bleaching (%)	1	0.2	2.7	0.9	4198	96	96	0.249
Colony Bleaching (%)	20	2.8	19	2.6	4384	96	96	0.54
White Band Disease (%)	1	0.6	0.5	0.4	4368	96	96	0.122

Table 3 – Mann-Whitney U results for Invertebrate abundance inside and outside Napantao MPA. Species with significantly higher abundance within the MPA highlighted in green; species with significantly higher abundance outside the MPA highlighted in orange.

Substrate	Mean Abundance Inside MPA	Standard Error	Mean Abundance Outside MPA	Standard Error2	U	N1	N2	P
Coral (Massive) (<i>Scleractinia</i>)	2.7	0.3	1.5	0.2	3690			0.015
Coral (Encrusting) (<i>Scleractinia</i>)	1.7	0.2	1.4	0.2	4535			0.842
Coral (Submassive) (<i>Scleractinia</i>)	3	0.3	2.4	0.3	4023			0.123
Coral (Foliose) (<i>Scleractinia</i>)	2.1	0.3	0.9	0.1	3412			0.001
Organ Pipe Coral (<i>Tubipora</i>)	0.1	0	0.2	0.5	4432			0.387
Fire Coral (<i>Millepora</i>)	0.8	0.1	0.9	0.1	4480			0.705
Coral (Mushroom) (<i>Scleractinia</i>)	0.5	0.1	1.4	0.2	336			0.0001
Blue Coral (<i>Heliopora</i>)	0.1	0	0.2	0.1	4555			0.73
Coral (Branching) (<i>Scleractinia</i>)	1.7	0.2	1.5	0.2	4433			0.638
Rock	8.5	0.4	6.8	0.4	3416			0.002
Rubble	4.4	0.3	4.9	0.4	4386			0.561
Sand	3.2	0.3	9.3	1	3026			0.0001
Recently Killed Coral	0.5	0.2	0.6	0.2	4529			0.779
Nutrient Indicator Algae	0.4	0.1	0.6	0.1	4223			0.184
Sponge (<i>Porifera</i>)	1.6	0.2	1.9	0.2	4207			0.285
<i>Acropora</i> (Branching)	4.1	0.4	1.3	0.2	2582			0.0001
<i>Acropora</i> (Tabulate)	0.7	0.1	0.4	0.1	4172			0.149
Soft Coral (<i>Alcyonacea</i>)	0.5	0.1	0.5	0.1	4363			0.419
Other	2.6	0.3	3.2	0.3	4424			0.63

Table 4 – Mann-Whitney U results for Substrate abundance inside and outside the MPA. Significantly higher substrate abundance within the MPA highlighted in green and significantly higher substrate abundance outside the MPA highlighted in orange.

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