The impact of the 2016 coral bleaching event on the reef life of Christmas Island

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Executive summary

Christmas Island experienced a severe coral bleaching event in April 2016 that was part of a global bleaching event - the largest on record. The bleaching event was associated with a strong El Niño that caused sea surface temperatures to rise above the thermal tolerances of corals. The purpose of this study was to determine the impact of the bleaching event on coral reefs at Christmas Island. The level of bleaching differed considerably between taxa and the most vulnerable corals were *Hydnophora*, *Isopora*, *Gardineroseris*, *Cyphastrea* and *Acropora* (>60% of colonies bleached). More detailed surveys of eight common taxa revealed similar levels of bleaching across all seven survey sites; however, bleaching was consistently higher (55% of colonies affected) at 5 m depth compared to 20 m depth (36%). After the bleaching event, follow-up surveys revealed that live hard coral cover had decreased from 58% to 41% (averaged across all surveyed sites and depths). Coral mortality was greatest at 5 m depth on north coast reefs where hard coral cover halved, decreasing from 70% to 34%. Of the eight common coral taxa, the highest mortality was recorded for *Acropora* plate (71% decrease in cover), branching (59% decrease), and bushy corals (50% decrease). Tagging experiments in 2 – 12 m depth at Flyingfish Cove revealed 99% of *Acropora* plate corals (n = 75) and 100% of *Acropora* bushy corals (n = 28) had died. As per theoretical predictions, the loss of coral had noticeable flow-on effects to the species that most rely on corals for food or habitat. There was a 34% decline in abundance of obligate coral-feeding butterflyfishes, whereas there was no noticeable change in the abundance of other butterflyfishes that do not rely on coral. The overall abundance of commensal fauna (crabs, shrimps, gobies) living within *Acropora* bushy corals declined with the lost of their host corals, but changes in density were mixed. Anemones also bleached during the event with 7% dying, and anemonefish abundance decline by 18%.

Overall, the loss of coral at Christmas Island during the 2016 global bleaching event was not as great as many other locations around the world and the remaining coral cover (41%) is higher than most other locations. Around Christmas Island, areas of high coral cover will aid recovery by reseeding areas that experienced high coral mortality. Based on other studies, it would take approximately six years to recover the coral cover lost in the bleaching event, assuming no other impacts. However, as sea temperatures continue to rise, coral bleaching events are predicted to increase in frequency and severity, particularly in the region that includes Christmas Island. This will test the resilience of Christmas Island's coral reefs. If coral cover becomes low at Christmas Island, the ability to recover from increasing bleaching events may be restricted because the isolation of the island limits the influx of coral larvae from elsewhere. Thus to minimise coral mortality and increase the resilience of Christmas Island's coral reefs there is a need for management to mitigate other disturbances and limit local impacts (e.g. pollution, introduced species).

Introduction

Corals are very sensitive to elevated sea temperatures, and will bleach and die if temperatures exceed their thermal tolerances. Coral bleaching is a stress response whereby the coral becomes transparent (due to expulsion of symbiotic algae – zooxanthellae) and appears white due to visibility of the underlying white skeleton (Brown, 1997). Corals can regain their colour (by reabsorbing zooxanthellae) and will recover if sea temperatures decrease. If temperatures do not decrease, the entire bleached coral will die (total mortality). In some borderline cases, only part of the coral dies (partial mortality) before the temperature decreases. The continued rise in sea temperatures associated with climate change is expected to increase the frequency and severity of coral bleaching events (Hoegh-Guldberg 1999) unless corals (and their symbiotic zooxanthellae) can acclimate or adapt in time. To better manage corals reef in a changing climate requires an understanding of the type of reefs and coral species that are most vulnerable, and those that are most resilient, to rising temperatures.

The severity of coral bleaching has been found to vary across different spatial scales (see reviews by Glynn, 1996; West and Salm, 2003). Bleaching can differ between: depths (Hoegh-Guldberg and Salvat, 1985; Marshall and Baird, 2000; Mumby et al., 2001; Sebastian et al., 2009), reef zones (Cook et al., 1990; Hoeksema, 1991), sites (Hoegh-Guldberg and Salvat, 1985; Marshall and Baird, 2000) and regions (Goreau et al., 2000). This spatial variability is probably influenced by: assemblage composition (McClanahan et al., 2007); intrinsic (Loya et al., 2001; Sampayo et al., 2008) and extrinsic factors (see Glynn, 1996; Ateweberhan et al., 2011 and references therein); and interactions between these factors (Yee et al., 2008,). This spatial variability is important to coral reef resilience because areas that provide a refuge from bleaching may be crucial to the regeneration of areas that have suffered extensive mortality.

Understanding taxonomic differences in bleaching susceptibility will also be important to predicting the future composition of coral reef communities. Several studies have described a taxonomic hierarchy of vulnerability that has acroporids and pocilloporids among the most likely to bleach (Salvat 1991; Gleason and Wellington, 1993; Hoegh-Guldberg and Salvat, 1985; Marshall and Baird, 2000; Loya et al. 2001; McClanahan et al., 2004). Corals that tend to be most resistant to bleaching include *Leptastrea*, *Galaxea*, *Porites*, *Pavona*, *Cyphastrea*, *Goniopora* (McClanahan et al., 2004). Taxonomic patterns in bleaching do not always reflect patterns of mortality (McClanahan, 2004). Thus it is necessary to monitor bleached corals to determine their fate. Determining taxonomic differences in bleaching and mortality will help predict how coral communities will change with rising sea temperatures and will also aid in developing management strategies that minimise other stressors on the most vulnerable taxa.

Coral bleaching, and subsequent mortality, has flow on effects to the thousands of other species that inhabit coral reefs. These effects are most pronounced in species that directly rely on live corals for food or shelter (Pratchett et al., 2008;

Wilson et al., 2008; Stella et al., 2011). Those species that have obligate relationships with vulnerable coral taxa are likely to be affected the most by coral bleaching. For example, the chevron butterflyfish feed predominately on live *Acropora* plate corals that are highly vulnerable to bleaching. The loss of live *Acropora* plate corals causes a significant decline in the abundance of the chevron butterflyfish (Pratchett et al., 2006). The flow on effects from declining quantity and quality of corals will depend on a species' reliance on corals and their ability to changed diet or habitat use.

The year 2016 was the hottest on record and caused coral bleaching on reefs across the globe (Hughes et al., 2017). NOAA's Coral Reef Watch program uses satellite data on sea surface temperature to predict (months in advance) the timing and severity of bleaching anywhere in the world. Following NOAA's predictions, in March 2016 elevated sea temperatures off the east coast of Australia caused the most severe coral bleaching event in recorded history on the Great Barrier Reef (Hughes et al., 2017). NOAA also predicted severe bleaching was likely on reefs off the West Australian coast (Eastern Indian Ocean) in April 2016. This area included Christmas Island.

To document the impacts from this coral bleaching event a monitoring study was established at Christmas Island with the following aims:

1. To determine whether the level of bleaching and mortality of corals varied between sites and depths.
2. To determine which coral taxa were the most and least vulnerable to bleaching and dying.
3. To determine which butterflyfishes were the most affected by the loss of coral following the bleaching event.
4. To determine how commensal species (crabs, shrimps, gobies) are affected by the loss of coral following the bleaching event.
5. To determine how the bleaching event affected anemones and anemonefishes.

Coral reef surveys were conducted during (April 2016) and after the bleaching event (June 2017) to determine the level of bleaching and mortality, respectively.

Methods

To determine variability in spatial and taxonomic bleaching patterns, underwater visual surveys were conducted at eight sites around Christmas Island (Figure 1). These sites are locally referred to as Thomas Point, Jackson's Point, Thundercliff Cave, Million Dollar Bommie, Eisvold, Flying Fish Cove, Ryan's Ravine and Ethel Beach. At each site, a bleaching assessment was made for the 30 most common coral genera. This was done at 5 and 20 m depth and involved classifying the bleaching status of colonies (following Hughes et al., 2017) as: 1 = No bleaching, 2 = 1-10% bleaching, 3= 11-30%, 4 = 31-60%, 5 = 61-90%, 6 = >90%. In addition, a more detailed survey was conducted for eight common taxa and involved recording the number and bleaching status of coral colonies in 3 replicated 20 x 2 m transects per depth (5 and 20 m). The eight taxa were: *Acropora* plates, *Acropora* bushy (corymbose), *Acropora* branching, *Montipora* encrusting, *Porites* massive, *Galaxea*, *Pocillopora eydouxi* and *P. verrucosa*. At the same survey sites, changes in coral cover were quantified by recording the benthos every 1 m along a 50 m point intercept transect. Three replicate transects were done per depth (5 and 20 m). All surveys were completed between 16th of April and 3rd of May 2016, which represented the height of the bleaching event.

At the same time as the coral bleaching surveys, corals and anemones were tagged at one site (Flyingfish Cove) to determine their fate (Appendix 1). Ninety *Acropora* plate corals (*Acropora clathrata*, *A. cytherea* and *A. hyacinthus*), 50 *Acropora* bushy corals (*Acropora monticulosa*) and 85 anemones (*Heteractis magnifica*, *Cryptodendrum adhaesivum*, *Stichodactyla mertensii*) were tagged. These corals and anemones were chosen because they are normally among the most vulnerable to bleaching and because many other species (e.g. butterflyfishes, anemonefishes, and coral shrimps, crabs and gobies) directly rely on these corals/anemones for food and/or shelter.

To determine patterns of bleaching-induced coral mortality, each site and depth (5 and 20 m) was resurveyed in June 2017 using the same transect methodology as the bleaching surveys. There were no other mortality events (e.g. cyclones, crown-of-thorns starfish outbreaks) that occurred between the bleaching event and resurveying. Thus all the coral mortality detected in the June 2017 surveys was due to the bleaching event in April 2016. Resurveying corals involved repeating the 20 x 2 m transects and the 50 m point intercept transects at both depths at each survey sites, and resurveying the tagged corals and anemones in Flyingfish Cove. One of the survey sites, Ryan's Ravine, could not be resurveyed due to adverse weather conditions.

To determine flow-on effects of the bleaching event on non-coral species, changes in the fish community were quantified using 50 x 5 m transects. Three replicate transects were done at each depth (5 and 20 m) at seven survey sites. To detect changes in abundance, surveys were done in April 2016 (during the bleaching event) and 14 months later (June, 2017). The main groups that were monitored included butterflyfishes and anemonefishes. The butterflyfish family contains species that differ in their reliance on live coral for food and therefore

should be affected differently by the loss of coral. Species that have a total reliance on corals (obligate corallivores) should be affected the most, whereas species that are partly reliant (facultative corallivores), or have no reliance on coral (e.g. benthic invertebrate feeders) should be least affected. We classified each butterflyfish as an obligate corallivore, facultative corallivore or benthic invertebrate feeder following Cole and Pratchett (2014). Anemonefishes were also monitored in the same surveys because they completely rely on anemones for habitat, and anemones can also bleach and die during periods of elevated water temperatures (Hobbs et al., 2013). Anemonefishes cannot exist without anemones and thus will be directly affected if anemones die (e.g. Hattori, 2002).

In addition to these fish surveys, the coral infauna of *Acropora monticulosa* corals was monitored (Appendix 1). These bushy corals support specialist species of shrimp, crabs and coral gobies (Stella et al., 2011). These inhabitants only exist within the branches of live corals, and once a coral dies the species are no longer present. The numbers of shrimp, crabs and coral gobies that live within each coral were recorded, along with the size of each coral (average diameter). This provided an estimate of the density of inhabitants per unit area of live coral tissue. Surveys were conducted during (April, 2016) and after (June, 2017) the bleaching event to determine how the loss of bushy *Acropora* corals impacts inhabiting species.

Data were analysed using ANOVA's and *t*-tests with suitable transformations beforehand if required. For the analysis of the coral infauna, it was necessary to standardise data to density per unit area of live coral. Corals tend to be circular in shape, and the area of live coral was estimated using πr^2. The radius (r) was calculated from field measurements of average diameter. All results are presented as mean and standard error (± SE), unless stated otherwise.

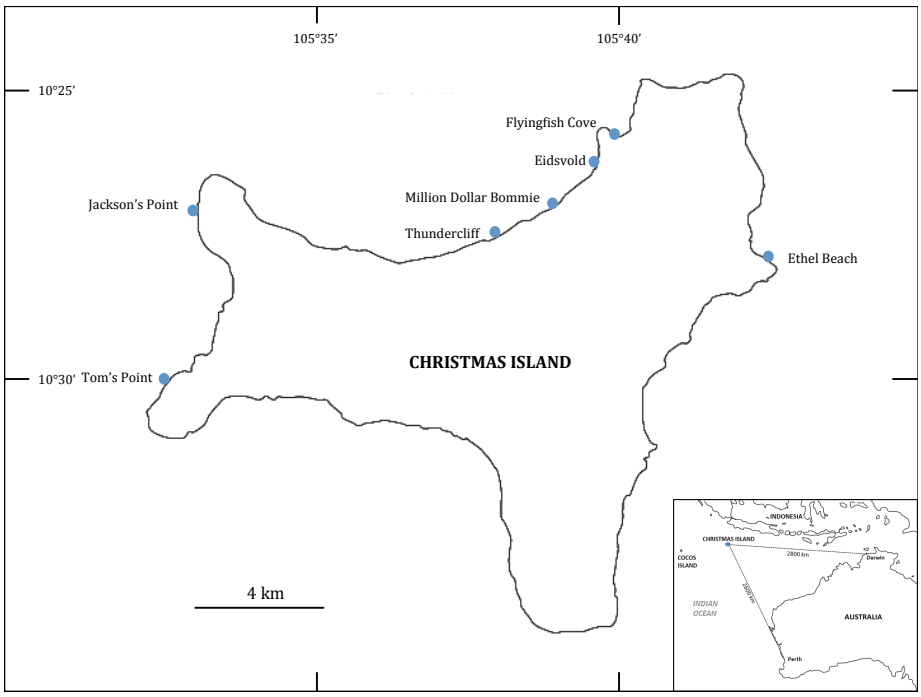

Figure 1. Map of the seven sites that were surveyed during the coral bleaching study at Christmas Island.

Results

Surveys conducted at 5 and 20 m across seven sites for the 30 most common coral genera at Christmas Island revealed that 29 genera experienced some level of bleaching during the bleaching event (April, 2016). The genera that had the highest levels of bleaching were: *Hydnophora*, *Isopora*, *Gardineroseris*, *Cyphastrea*, *Acropora*, *Echinopora* (Table 1). The genera with the lowest levels of bleaching were: *Galaxea*, *Montipora*, *Montastrea* and *Porites* (Table 1). Bleaching was not observed in *Goniopora* corals.

More detailed surveys were done on 3294 colonies of eight abundant taxa and revealed that the proportion of bleached colonies varied more than 10-fold between taxa (Figure 2). Across seven sites and both depths (5 and 20 m), the most vulnerable of the eight taxa were *Acropora* plates (90% of colonies bleached, n = 303), *Acropora* corymbose (89%, n = 404) and *Acropora* branching (86%, n = 284). The least susceptible was *Galaxea* (6%, n = 284). Interestingly, *Pocillopora eydouxi* (83%, n = 208) was much more vulnerable to bleaching than its congeneric *P. verrucosa* (22%, n = 459).

Bleaching was greater at 5 m depth (55% of colonies) then at 20 m depth (36%) (Figure 3, 2-way ANOVA - depth: $F = 1.6$, $p < 0.001$, d.f. = 1). The proportion of colonies that bleached was similar (38-50%, combined depths) across all seven sites (2-way ANOVA - site: $F = 1.6$, $p = 0.2$, d.f. = 6; interaction: $F = 2.2$, $p = 0.07$, d.f. = 6).

After the 2016 bleaching event, mean hard coral cover across all surveyed sites and depths decreased from 58% (± 3.5 SE) to 41% (± 2.7) ($t = 3.8$, $p < 0.001$, d.f. = 82). Although the level of bleaching was similar across survey sites (see above), the level of coral mortality differed between sites (ANOVA year×site interaction, $F = 7.4$, $p < 0.001$, d.f. = 6). North coast sites (Flyingfish Cove, Thundercliff, Eisvold, Million $ Bommie) had higher coral mortality compared to west coast sites (Jacksons Point and Thomas Point) (Figure 4). The east coast site (Ethel Beach) already had low coral cover (9%) before the bleaching event due to the damage caused by a cyclone in 2014 (Appendix 1).

In accordance with depth-related patterns of bleaching severity (see above), coral mortality was much greater at 5 than 20 m depth, with mean hard coral cover decreasing from 61% (± 5.7) to 36.5% (± 4.1). At 20 m depth, mortality was less severe and mean coral cover decreased from 54% (± 4.1) to 45% (± 3.6). The initial low coral cover at Ethel Beach proved problematic during the analysis, and once this outlying site was removed from the analysis the year by depth interaction was significant ($F = 14.4$, $p < 0.001$, d.f. = 1) because mortality at 5 m (coral cover declined from 80% to 43%) was much greater than at 20 m depth (66% down to 53%).

The level of mortality varied significantly between coral morphologies. *Acropora* plate, branching and bushy corals suffered the greatest mortality with more than 50% reduction in cover (averaged across all sites and depths, Figure 5). Massive, foliose and encrusting corals had less mortality with 6 to 28% reduction in cover

(Figure 5). Mortality rates were highest in the shallows (5 m) at north coast sites (Figure 5). Across all sites and depths, plate corals were the worst affected group and their cover decreased by 71%. After the bleaching no plate corals were recorded on line-intercept transects at any of the four north coast sites (both depths). However, plate corals were still present on the west coast, with mean cover decreasing from 19% to 8% at 20 m depth at Jackson Point. Across all sites and depths the mean cover of turf algae increased from 14% to 23% after the bleaching event (Figure 5).

To better understand the fate of individual corals of the most susceptible morphologies, a tagging experiment was established for *Acropora* plate and bushy corals between two and 12 m depth at Flyingfish Cove. After the bleaching, 75 tagged plate corals were located and 74 had experienced total mortality and one experienced partial mortality. Twenty-eight tagged bushy corals were also located and all had experienced total mortality.

Butterflyfishes feed on corals to varying degrees and monitoring surveys revealed that after the bleaching event the greatest declines in abundance were seen in those species that rely the most on live corals for food. Thirteen obligate corallivorous species were surveyed and their collective abundance decreased 34% from a mean of 6.1 (± 0.5) to 4.0 (± 0.5) individuals per 250 m^2 (t = 2.7, p = 0.008, d.f. = 82)(Figure 6). Of these corallivores, the chevron butterflyfish (*Chaetodon trifascialis*) is the most specialised and it was the most affected by coral loss with its mean density declining 82% from 1.2 (± 0.4) to 0.2 (± 0.1) individuals per 250 m^2 (t = 3.2, p = 0.002, d.f. = 82). There was no significant difference in the abundance of facultative corallivores (9 species, t = 1.1, p = 0.29, d.f. = 82) or benthic invertebrate feeders (4 species, t = 1.4, p = 0.17, d.f. = 82) following the bleaching event (Figure 6).

To determine how bleaching impacts commensal species living in bushy corals (*Acropora monticulosa*), the number of crabs, shrimps and gobies was monitored in Flyingfish Cove. The majority of bushy corals in the monitoring area died (see above) during the bleaching event and these dead corals were devoid of species that are commensal with live coral. However, the remaining live bushy corals did contain commensal crabs, shrimps and gobies. On these remaining live corals, the density of commensal crabs and shrimps had increased 30% and 12%, respectively (Figure 7). In contrast, the density of commensal gobies decreased by 52% (Figure 7).

To determine how decreases in the quantity or quality of anemones affect anemonefish, the abundances of three species of anemones and anemonefishes were monitored. Across both depths (5 and 20 m) and seven survey sites, a total of 12 anemones were present in surveys during the bleaching event and four (33%) were bleached. The 12 anemones were inhabited by a total of 36 anemonefish. After the bleaching event the same depths and sites were resurveyed and only eight anemones were recorded, representing a 33% decline. The total number of anemonefish had also decreased 50% to 18 individuals.

To gain a more detailed understanding of bleaching impacts on anemones and anemonefish, a tagging program was conducted at Flyingfish Cove. The pink anemonefish (*Amphiprion perideraion*) inhabits the anemone *Heteractis magnifica* and 64 anemones were monitored. After the bleaching event four anemones were gone (presumed dead), representing a 6% decline. Over the same period, the number of pink anemonefish decreased 11% from 133 to 119 (Figure 8).

At Christmas Island, Clark's anemonefish (*Amphiprion clarkii*) predominately inhabits the pizza anemone (*Cryptodendrum adhaesivum*) and rarely *Stichodactyla mertensii*. Sixteen pizza anemones were monitored and the majority (75%) bleached and 1 died. Following the bleaching event the number of Clark's anemonefish decreased 31% from 51 to 35 (Figure 8).

The third anemonefish (skunk anemonefish – *Amphiprion sandaracinos*) inhabits *Stichodactyla mertensii* and five anemones were monitored. One anemone bleached and died. Following the bleaching event, the number of skunk anemonefish decreased 40% from 10 to six individuals (Figure 8).

Table 1. Bleaching vulnerability of 30 common coral genera at Christmas Island. Values are based on categories of percent bleaching in each colony with 1 representing no bleaching, 2 = 1-10% bleaching, 3 = 11-30%, 4= 31-60%, 5 = 60-90%, 6 = >90%. Values presented for each genus are calculated from all surveys across seven sites and both depths (5 and 20 m). Genera are ordered from most vulnerable to bleaching to least vulnerable.

Coral genus	Bleaching vulnerability (1 = low, 6 = high)
Hydnophora	5.875
Isopora	5.333333333
Gardineroseris	5.285714286
Acropora	5.1875
Cyphastrea	5.1875
Echinopora	5.166666667
Fungia	5
Halomitra	5
Platygyra	5
Astreopora	4.8125
Pavona	4.8125
Merulina	4.8
Psammocora	4.777777778
Lobophyllia	4.769230769
Echinophyllia	4.75
Leptoria	4.727272727
Goniastrea	4.5
Leptastrea	4.357142857
Favia	4.25
Ctenactis	4.2
Favites	4.2
Diploastrea	4.125
Stylocoeniella	4
Symphyllia	3.7
Pocillopora	3.5625
Porites	3.375
Montastrea	3
Montipora	2.125
Galaxea	1.5
Goniopora	1

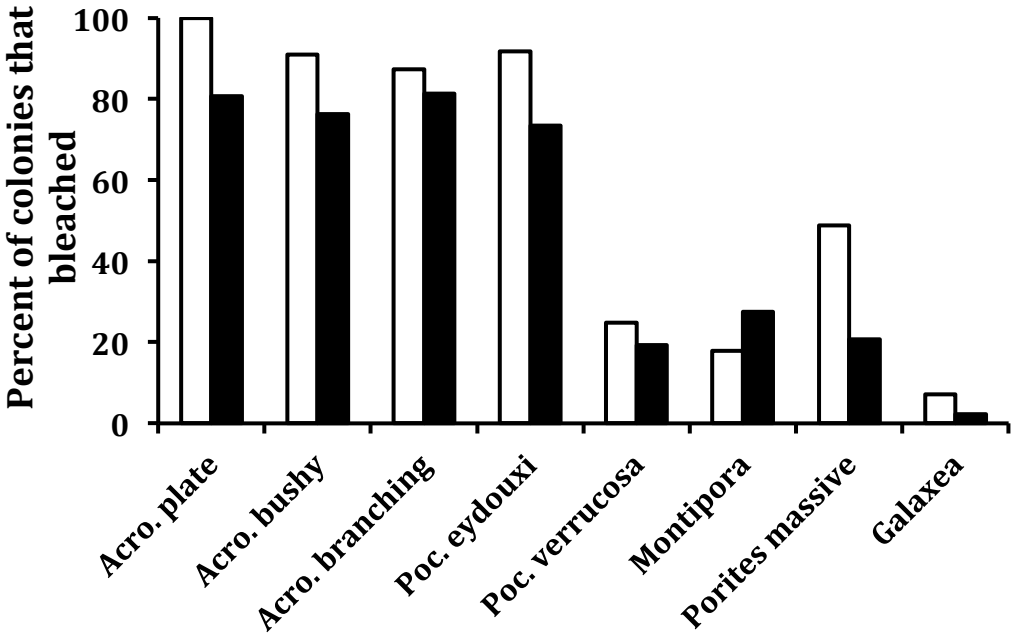

Figure 2. The percent of colonies in each coral taxa that experienced bleaching at 5 and 20 m depth during the 2016 bleaching event. Values are based on totals across all seven surveys at Christmas Island for eight common coral taxa. Acro. = *Acropora*, Poc. = *Pocillopora*.

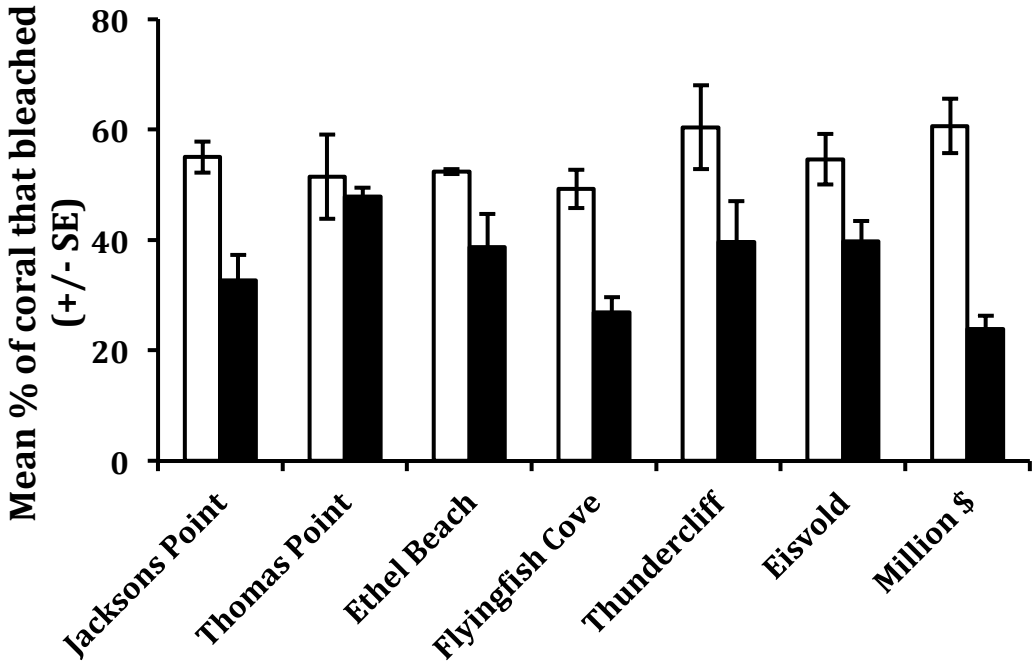

Figure 3. Mean percent (+/- SE) of corals that were bleached at seven survey sites around Christmas Island during the 2016 bleaching event. Values are based on eight common coral taxa. White bars represent surveys done at 5 m depth and black bars are surveys done at 20 m depth.

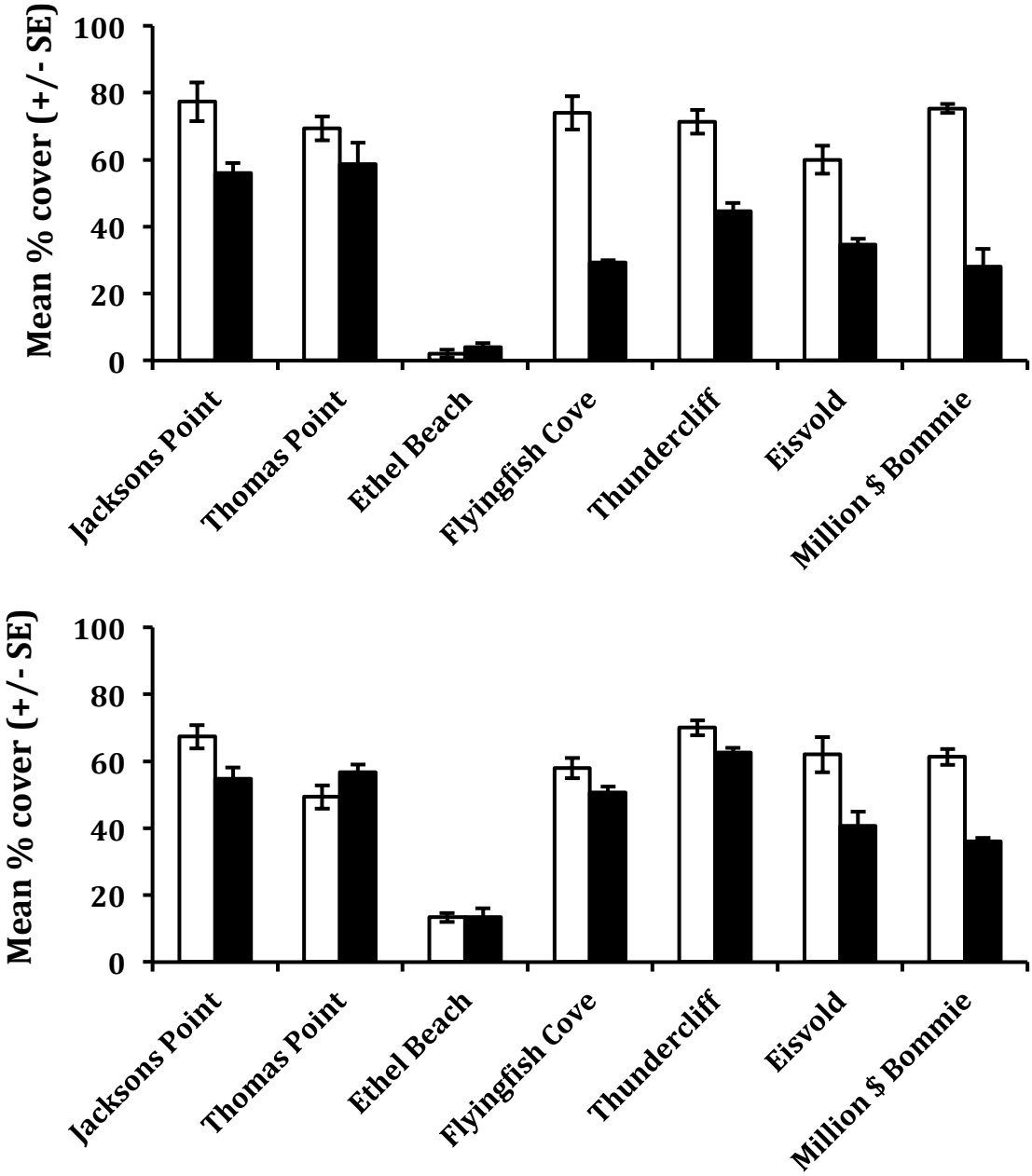

Figure 4. Mean % cover (+/- SE) of live hard coral during (white bars) and after (black bars) the 2016 coral bleaching event at (a) 5 m depth and (b) 20 m depth.

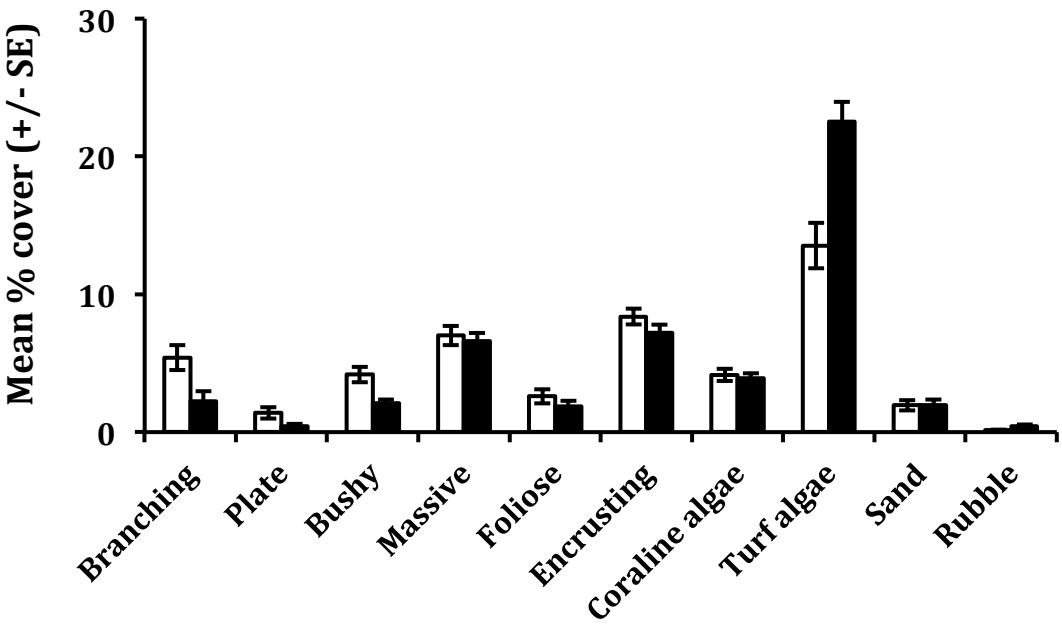

Figure 5. Mean % cover (+/- SE) of coral and non-coral substrates during (white bars) and after (black bars) the 2016 coral bleaching event. Values have been average across all seven sites and both depths (5 and 20 m).

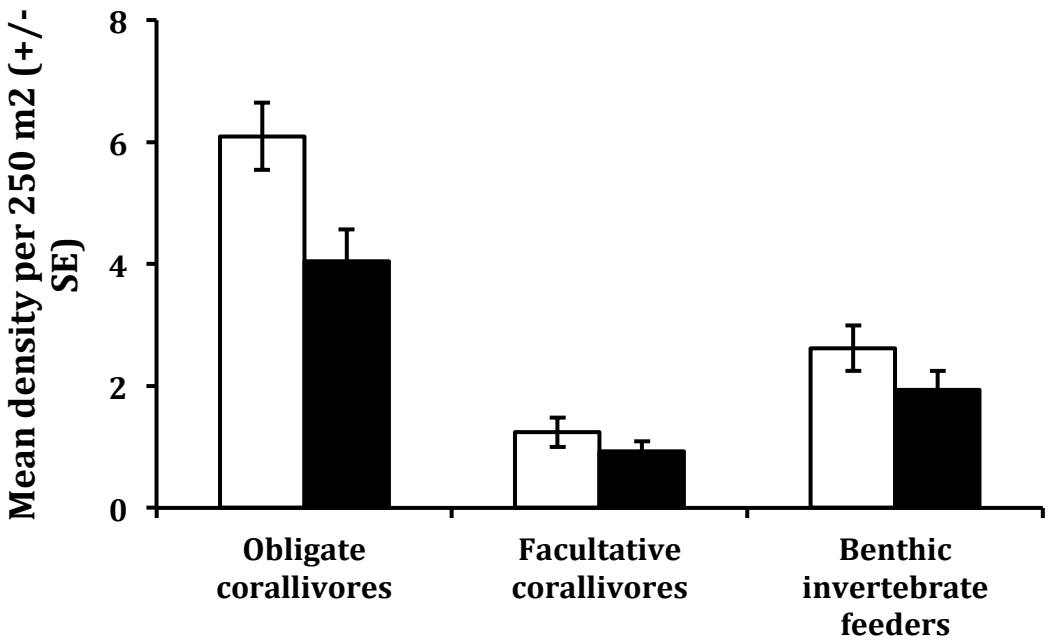

Figure 6. Mean density per 250m2 (+/-SE) of butterflyfishes during (white bars) and after (black bars) the 2016 bleaching event. Butterflyfish species are grouped according to their reliance on live coral for food following Cole and Practhett (2014). Obligate corallivores n = 13 species, facultative corallivores n = 9 species, Benthic invertebrate feeders n = 4 species.

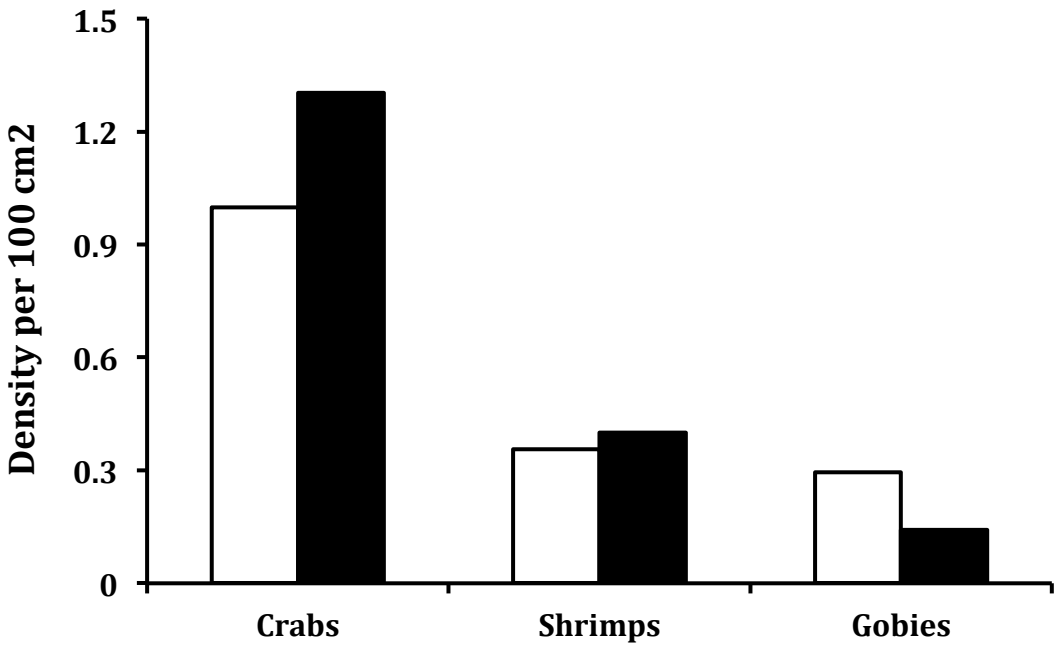

Figure 7. The density (per 100 cm2) of crabs, shrimps and gobies that are commensal with live *Acropora monticulosa* corals during (white bars) and after (black bars) the 2016 bleaching event. The density estimates were obtained by calculating the total number of crabs, shrimps and gobies observed in surveys and dividing by the total estimated surface area of the surveyed corals.

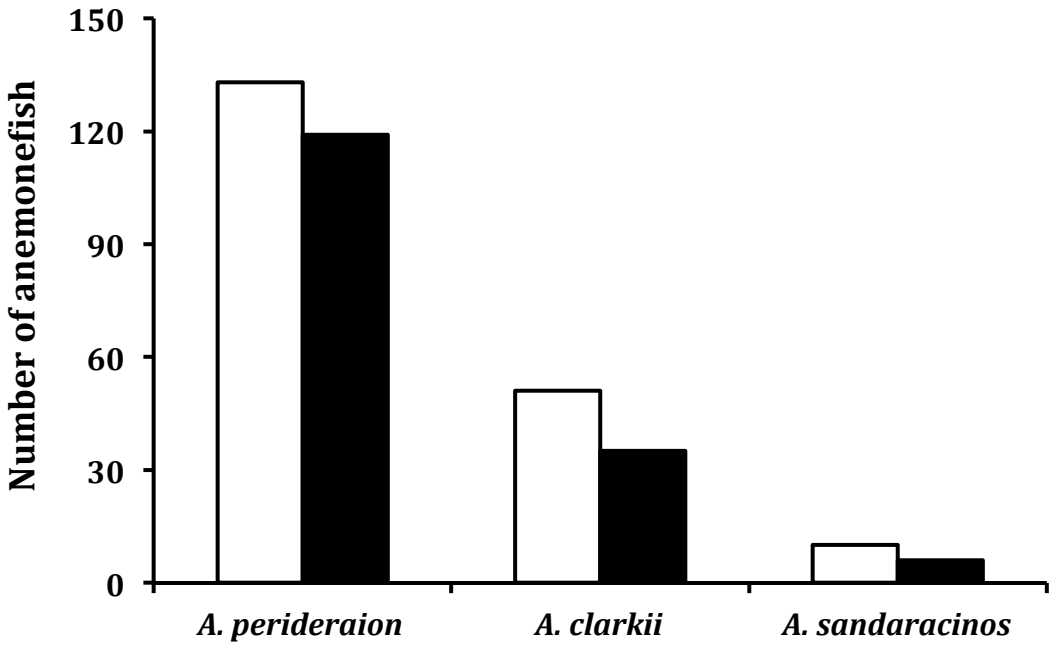

Figure 8. The number of anemonefish (genus *Amphiprion*) during (white bars) and after (black bars) the 2016 bleaching event. Values are totals summed across all tagged anemones within Flyingfish Cove.

Discussion

Following the 2016 coral bleaching event, live coral cover on reefs around Christmas Island decreased from 58% to 41%. This equates to 30% mortality of coral tissue, that is, approximately one third of the total surface area of corals has died. Once the coral died, turf algae colonised the surface and consequently turf algae have increased substantially on reefs around the island. Coral mortality was not uniform around the island, but rather was most severe in shallow waters, particularly on the north coast. In addition, mortality rates varied between coral taxa, with *Acropora* plates, bushy and branching corals the most susceptible. The loss of live coral had flow on effects to the species that most rely on live coral tissue for food or shelter. In addition, anemones also bleached and died, leading to a decline in the abundance of anemonefish.

The 2016 bleaching event has been the largest cause of coral mortality at Christmas Island for at least the last 19 years. Prior to this event, there was considerable bleaching at Christmas Island during 1983 and 1998 (Berry, 2000; Goreau et al., 2000,). Although these earlier events caused extensive coral mortality (Berry, 2000, T. Hamanaka pers. comm.) there were no estimates of mortality rates, which make it impossible to determine which bleaching event has caused the most damage to Christmas Island reefs. The three severe bleaching events (1983, 1998, 2016) at Christmas Island coincided with the three major global bleaching events and the strongest El Niño periods on record. Thus patterns of coral bleaching at Christmas Island are not unique but reflect global patterns. Severe bleaching events at Christmas Island are predictable and occur at times when climatic conditions associated with strong El Niño cause sea temperatures to rise across the globe. Indeed, the timing and severity of the 2016 bleaching event at Christmas Island was predicted months in advance by NOAA based on forecasts of climate and sea surface temperatures (NOAA Coral Reef Watch Program).

In addition to these three severe bleaching events, there was a moderate bleaching event in 2010 that caused bleaching in approximately 25% of corals and 5% mortality (Hobbs unpubl. data). In 2005, there was also a minor bleaching event, with bleaching affecting about 5% of corals. The 2005 bleaching event was short-lived (two weeks), restricted to small areas of shallow reef, only affected the most susceptible taxa (anemones and *Acropora* plate, bushy and branching) and no coral mortality was observed (Hobbs pers. obs). That three bleaching events have been recorded in the last 12 years and only two in the preceding 22 years indicates that either bleaching events were under reported in the 1980's and 1990's or that bleaching events are increasing in frequency. On the Great Barrier Reef, a longterm monitoring program confirms that the frequency of bleaching events is increasing (Hughes et al., 2017). Furthermore, increases in the frequency and severity of bleaching events are expected to continue with rising sea temperatures associated with climate change (Hoegh-Guldberg, 1999), particularly in the region including Christmas Island (Sheppard, 2003).

The coral bleaching and mortality experienced at Christmas Island in 2016 was part of a global bleaching event – the worst on record. Many places in the Indian Ocean experienced bleaching including Indonesia, which represents the nearest reefs to Christmas Island (approximately 400 km north). However, elevated water temperatures missed the Cocos (Keeling) Islands (1000 km west of Christmas Island) and no bleaching occurred. Bleaching was widespread in the Pacific and Atlantic Oceans with the worst bleaching on record for the Great Barrier Reef (Hughes et al., 2017). Prior to the 2016 global bleaching event, average hard coral cover was approximately 22% throughout Indonesia and the Pacific Ocean (Bruno and Selig, 2007), 14% across the Great Barrier Reef (De'ath et al., 2012), 10% on Caribbean reefs (Gardner et al., 2003; Côté et al., 2005), and below 40% for most reefs in Western Australia (Speed et al., 2013). In comparison, the hard coral cover at Christmas Island (averaged across all survey sites) was 58% before the bleaching, and 41% afterwards. Thus, despite considerable coral mortality from the 2016 bleaching event, the coral cover at Christmas Island is still higher than most other places in the world.

Around Christmas Island, the amount of coral lost from the bleaching event varied between depths and sites. Shallow reefs (5 m) experienced greater bleaching and mortality than reefs in deeper water (20 m). This pattern has been observed previously at other locations and may be related to higher temperatures and solar irradiance, and/or differences in symbiont communities (Rowan and Knowlton, 1995; Rowan et al., 1997; Glynn 1996; Mumby et al 2001; Ruiz Sebastián et al 2009). North coast sites experienced the greatest decrease in coral cover, and west coast sites experienced the least. Elsewhere, differences in bleaching and mortality rates between sites have been attributed to differences in hydrographic features, bleaching history and coral communities and their symbionts (Glynn et al., 1996; Marshall and Baird, 2000; McClanahan et al., 2004). There is evidence that some of these factors differ between the north and west coasts at Christmas Island. Compared to the north coast sites, the west coast receives more swell and the survey sites are on points that are likely to receive more water movement (from currents and swell) (Richards et al., 2016). The composition of the coral community on the west coast is also considerably different to the north coast (Richards et al., 2016). Differences in coral composition will translate into differences in the decline of coral cover due to taxonomic differences in vulnerability to bleaching. Sites that are less affected by bleaching (e.g. Thomas and Jackson's Points) are particularly important to the resilience of Christmas Island's reefs because they may act as refuges and provide larvae to colonise areas that have experienced high mortality.

There were obvious taxonomic differences in vulnerability to bleaching and mortality. *Acropora* corals (plates, bushy, branching) were highly vulnerable to bleaching, while *Porites*, *Goniopora*, *Galaxea* had very low rates. This pattern of bleaching vulnerability has been reported elsewhere (Glynn, 1996; Marshall and Baird, 2000; McClanahan et al., 2004) and may be due differences in a range of factors including symbiont communities, morphology, respiration rates, heterotrophy and life history (Glynn et al., 1996; Rowan et al., 1997; Grotolli et al., 2006). For example, species that grow fast and have branching, bushy or plating morphologies (e.g. *Acropora*) tend to be more vulnerable to a range of

impacts, compared to slowly-growing mound-shaped species (e.g. *Porites*)(Glynn, 1996; Marshall and Baird, 2000). Surprisingly, *Pocillopora eydouxi* was four times more likely to bleach than *P. verrucosa*, indicating that large differences in bleaching susceptibility can exist on the same reef between congeneric corals with similar morphology.

Differences in the thermal tolerances of corals create winners and losers in bleaching events. However, the losers tend to be fast growing "weedy" species and reductions in these species may increase coral diversity because their death opens up space for recruitment and growth of slow growing species (which tend to be winners during bleaching events). Consequently, the composition and diversity of future coral reefs will depend on the frequency and severity of bleaching events and the recruitment and growth rates of different species following such events. If bleaching events (or other impacts) are too frequent then the fast growing losers will not recovery in time before the next event. However, if bleaching events become too severe, then winners also suffer high mortality rates. At Christmas Island a taxonomic hierarchy of winners and losers was evident because the bleaching was not too severe; however, at many locations on the Great Barrier Reef the bleaching event was so severe that all species bleached (Hughes et al., 2017).

The differential loss of coral species has flow on effects to other organisms and the severity of the impact depends on their level of reliance and which corals are relied upon. At Christmas Island, the group of butterflyfishes that declined the most in abundance were those that rely entirely on corals for food (obligate corallivores). Furthermore, of this group, the species that declined the most was the chevron butterflyfish because it feeds predominately on *Acropora* plates and these corals had the highest mortality rates. In the 2016 bleaching event, there was little change in the abundance of species that were less reliant on corals. These results fit with previous studies and theoretical predictions that the most specialised species are the most vulnerable to losses of coral (Pratchett et al., 2006; 2008; Wilson et al., 2008).

Species that rely on corals may be able to persist if they can alter their diet/habitat use; however, this is probably most difficult for extreme specialists. In this study the coral infauna are extreme specialists and no changes were observed in their habitat use. The shrimps, crabs and gobies living in the bushy *Acropora monticulosa* corals did not move to other coral species when theirs died. Furthermore, there was little evidence that remaining live corals could support higher densities. Thus, declines in the population of these specialist species will match declines in their host coral until the coral becomes so rare that it can no longer support viable populations of specialist species. In previous a bleaching event at Christmas Island, the longnose filefish went extinct because the coral it feeds exclusively on (*Acropora* branching corals) experienced mass mortality (Hobbs et al., 2010) and the filefish did not change its diet. Specialisation increases the risk of extinction (McKinney, 1997); and this generates clear predictions as to which species are likely to suffer the most from increasing bleaching events (Munday, 2004; Pratchett et al., 2008; Wilson et al., 2008).

Another group of coral reef fishes that specialise on vulnerable habitats is the anemonefish. In this study, several anemones bleached and died and this lead to a decline in the number of anemonefishes. Similar declines were observed on the Great Barrier Reef following the 2016 bleaching event (Scott and Hoey, 2017). Local extinctions of anemonefishes have occurred following severe declines in abundance of anemones (Hattori, 2002; Thomas et al., 2014). Although all host anemones can bleach (Hobbs et al., 2013), taxonomic differences in bleaching vulnerability will lead to varying impacts on different anemonefish species (Hattori, 2002; Scott and Hoey, 2017). The greatest impact will be on those anemonefish species that inhabit the most vulnerable host anemones and cannot alter their host use or move to another anemone (e.g. competitively inferior species).

Recovery

Long term field studies in Western Australia and on the Great Barrier Reef estimate that coral cover increases at a growth rate of about 2.9% per year (De'ath et al., 2012; Gilmour et al., 2013). If the growth rate of corals was similar at Christmas Island, then it would take approximately six years to recover the 17% of coral cover lost during the 2016 bleaching event. This recovery assumes that there are no other disturbances, which is unlikely. Bleaching events are predicted to become more frequent especially in the region that includes Christmas Island (Sheppard, 2003). Also coral mortality has occurred previously at Christmas Island due to other impacts such as coral disease, pollution and cyclones (Hobbs, 2014; pers. obs.). In 2008, white syndrome coral disease caused 36% mortality of *Acropora* plate corals (Hobbs et al., 2015), while a cyclone in 2014 destroyed the reef at Ethel Beach reducing coral cover to 9%. Although local management agencies have limited capacity to mitigate global impacts, they can minimise local impacts (e.g. pollution, introduced species), which will aid the recovery of Christmas Island's reefs.

Christmas Island is an isolated oceanic island and these attributes are also likely to influence the recovery of its coral reefs. On isolated oceanic reefs the majority of coral larvae are likely to be locally produced, rather than arriving from distant locations (Ayre and Hughes, 2004). Consequently, when a severe bleaching event causes extensive coral mortality (>90%) recover is slow (Graham et al., 2006) because of the extremely small number of remaining corals, the reduced reproductive output of remaining corals (Szmant and Gassman, 1990; Baird and Marshall, 2002), and the lack of larvae arriving from other locations as the distance exceeds the dispersal capabilities of coral larvae. If bleaching is less severe and sufficient corals remain, then recovery can occur rapidly through asexual and sexual reproduction of remaining corals. However, when coral cover reaches low levels (>10%), recruitment can be low in the following years and recovery will be slow, particular if coral mortality is still occurring due to other impacts or chronic stressors (Gilmour et al., 2013).

The causes and consequences of the 2016 bleaching event at Christmas Island matched predictions. The bleaching occurred during the global bleaching event,

and the severity and timing (within days) was predicted months in advance based on models of sea surface temperatures (NOAA Coral Reef Watch). The patterns of bleaching, greatest in the shallows and in certain taxonomic groups, fit with other studies. The consequences of bleaching were greatest for the specialist species that rely the most on living corals (or anemones), as per other empirical studies and theoretical predictions (Munday, 2004; Pratchett et al., 2006; 2008; Wilson et al., 2008). Given that causes and consequences of bleaching match expectations, the impacts of future bleaching events at Christmas Island are predictable and likely to reflect other locations. Consequently, results from studies done elsewhere could be applied to Christmas Island given the lack of research and resources available for doing such studies at Christmas Island. However, it is important to consider that unlike many other locations, the isolation of Christmas Island means that factors (such as a lack of larval supply from other locations and effects from local impacts) are likely to have a greater effect on the recovery of Christmas Island's reefs.

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Appendix 1

Underwater photos taken at Christmas Island before and after the 2016 coral bleaching event. The majority of photos were taken at the seven survey sites and highlight the major findings of the study and the study species.

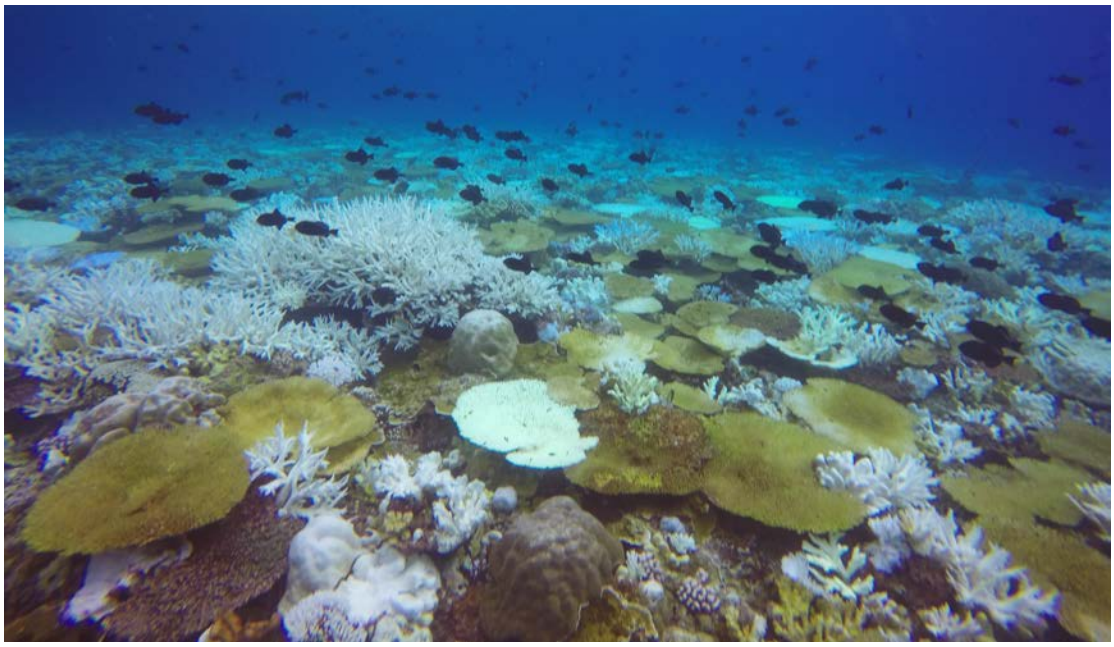

Photo 1. Extensive coral bleaching at 6 m depth at Rhoda Beach Wall (North Coast) in April 2016. The most susceptible taxa were *Acropora* plate and branching corals, which appear as bleached (white) or recently dead (covered with brown/green turf algae).

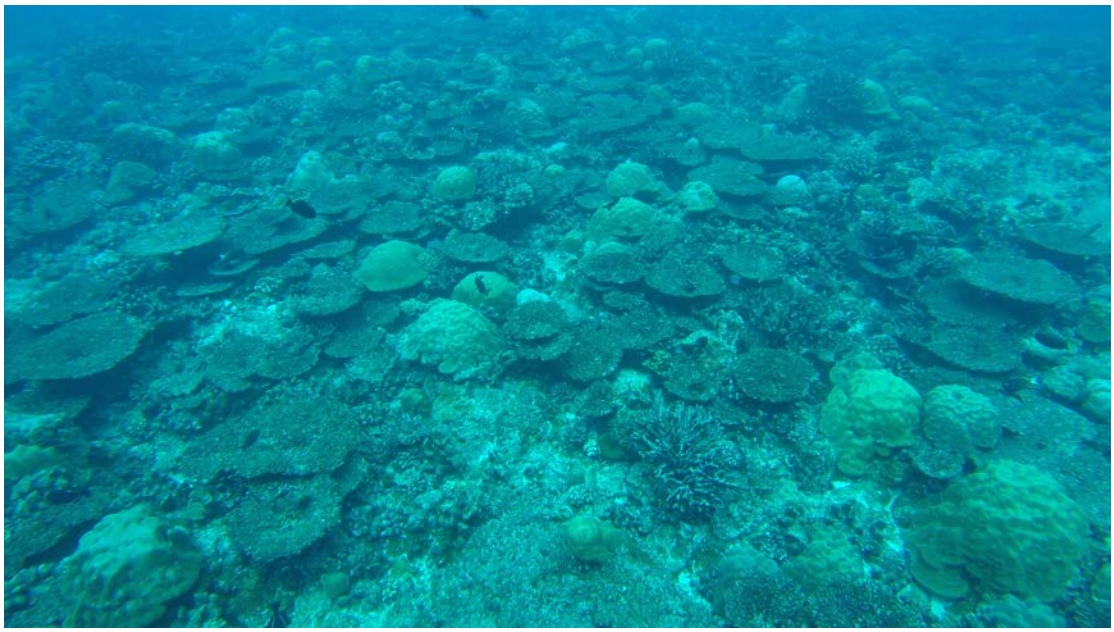

Photo 2. Dead corals, particularly *Acropora* plate and branching corals, at 6 m depth at Rhoda Beach Wall (North Coast) after the bleaching event (June, 2017).

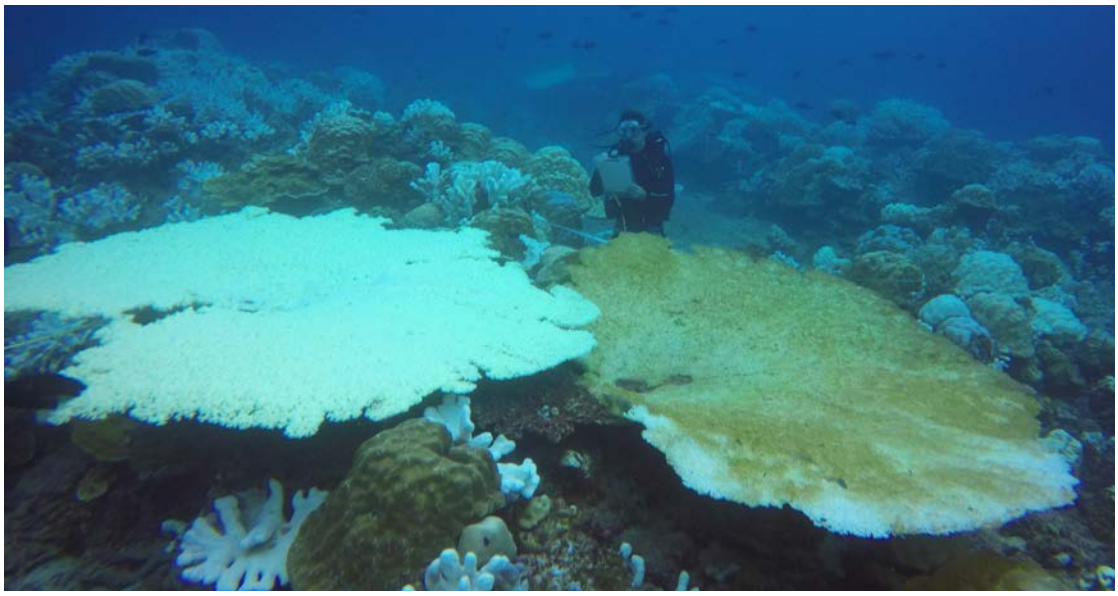

Photo 3. A bleached (left) *Acropora* plate coral and another colony (right) that has recently died and is being colonised by turf algae. Photo taken at 8 m depth in Flyingfish Cove.

Photo 4. Although *Acropora* plate corals were highly vulnerable to bleaching and suffered high mortality rates, there were some places where many *Acropora* plate corals survived. These places are important refuges that will help reseed areas that suffered high mortality. This photo was taken after the bleaching event (June, 2017) at 20 m depth at Jackson's Point.

Photo 5. Although *Acropora* branching corals were highly vulnerable to bleaching and suffered high mortality rates, there were some places where many *Acropora* branching corals survived. These places are important refuges that will help reseed areas that suffered high mortality. This photo shows a large area of live branching *Acropora* (*A. abrotanoides*) and was taken after the bleaching event (June, 2017) at 10 m depth at Jackson's Point.

Photo 6. Reefscape photo of Ethel Beach (5 m depth) showing dead coral rubble and no live coral. The majority of coral was lost at this site during the devastation caused by a cyclone in 2014, rather than the 2016 bleaching event.

Photo 7. Differences in vulnerability to bleaching between coral taxa. In this photo bleached corals include *Acropora* bushy, *Acropora* branching, *Pocillopora eydouxi* and *Isopora*. Non bleached corals include *Pocillopora verrucosa*. On the right side of the photo, one *Acropora* bushy colony and an *Isopora* colony have died and are covered in turf algae. Photo taken at Million $ Bommie at 8 m depth.

Photo 8. *Galaxea* was one of the corals that was highly resistant to bleaching, even in shallow waters and when exposed at low tide. Photo taken on the reef flat at Flyingfish Cove.

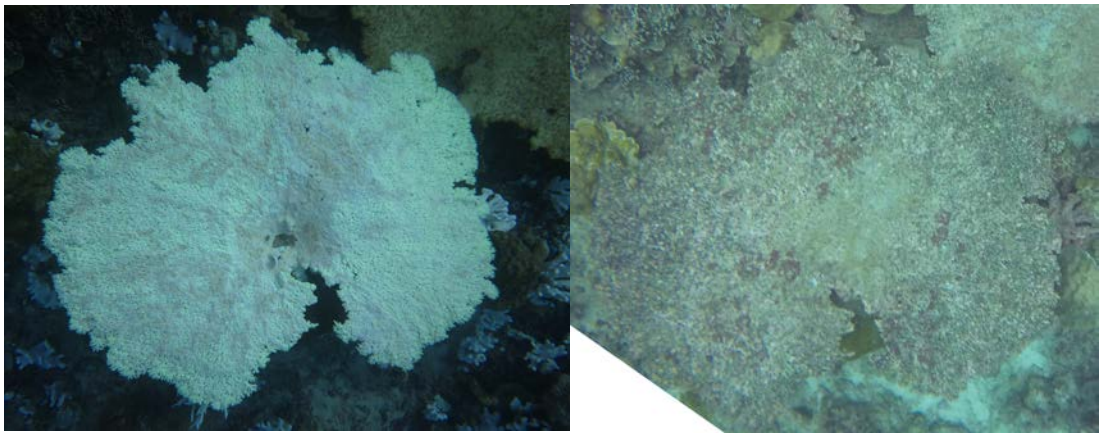

Photo 9. A tagged *Acropora* plate coral (#173) that was bleached (left) during the bleaching event and dead (right) after bleaching event (June, 2017). The diameter of the plate coral is approximately 2.5 metres.

Photo 10. A chevron butterflyfish (*Chaetodon trifascialis*) feeding on a bleached *Acropora* plate coral. The chevron butterflyfish is an obligate corallivore that specialises its feeding on plate corals. Photo taken at 10 m depth in Flyingfish Cove.

Photo 11. Tagging a bleached *Acropora* bushy coral (*Acropora monticulosa*) at 3 m depth in Flyingfish Cove. These corals are inhabited by small commensal shrimps, crabs and gobies that spend their entire lives within the bushy coral.

Photo 12. A coral goby (*Gobiodon*) inhabiting a bleached *Acropora* bushy coral (*Acropora monticulosa*). These fish spend their entire lives residing in between the branches of the bushy coral. Photo taken at 3 m depth in Flyingfish Cove.

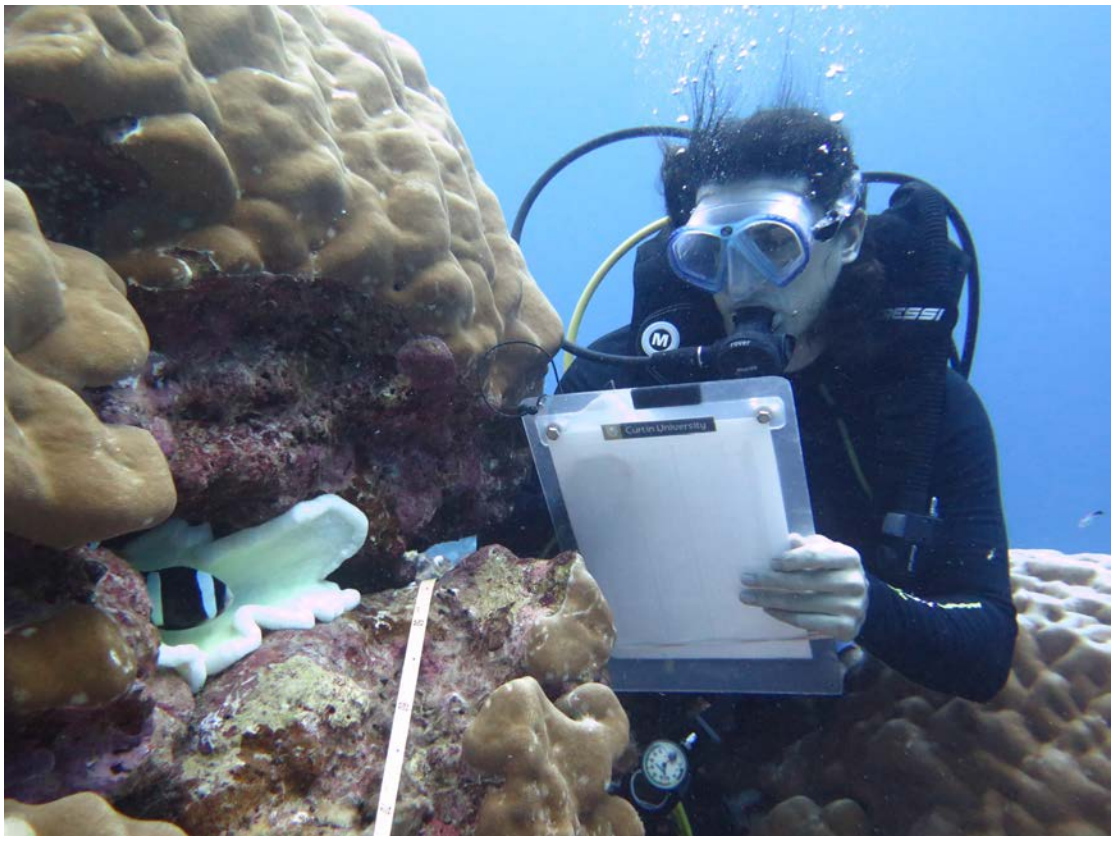

Photo 13. Surveying anemonefish (*Amphiprion clarkii*) in a bleached anemone (*Cryptodendrum adhaesivum*) during the tagging study at 12 m depth in Flyingfish Cove.