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Post-bleaching mortality of a remote coral reef community in Seychelles, Western Indian Ocean

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Abstract
The 2015–2016 global coral reef bleaching event was the most persistent and widespread in history. In its aftermath, efforts are required to understand the extent of the post-bleaching coral mortality and the ability of reefs to recover. This study used benthic photographic data to assess the post bleaching mortality of a coral reef community at D'Arros Island and St Joseph Atoll in the Republic of Seychelles, Western Indian Ocean. Results showed that April 2016 exhibited anomalously high sea temperatures that were above the regional coral bleaching threshold. In response, hard coral cover declined significantly from pre-bleaching levels of 28.5% in 2015 to 14.7% in 2017. Post-bleaching coral cover was significantly affected by site, with shallow reefs dominated by acroporids and pocilloporids exhibiting greater declines in hard coral than deeper sites. There were no changes to the macroalgal community but significant post-bleaching increases in coralline algae, which could facilitate reef recovery. This may be influenced by the reef's associated herbivorous fish community and lack of concurrent anthropogenic stressors. Continued monitoring is required to assess long-term impacts of the bleaching event, however, initial evidence suggests D'Arros Island and St Joseph Atoll provide a suitable environment for post-bleaching coral recovery.

Keywords: Coral reefs, Coral bleaching, Post bleaching mortality, 3rd Coral Reef Bleaching Event, Western Indian Ocean Coral Reef

Introduction
Coral reefs are highly biodiverse ecosystems that provide important goods and services to an estimated 500 million people worldwide (Pratchett *et al.*, 2008; Burke *et al.*, 2011). Despite their economic and ecological value, coral reefs are threatened by a suite of human induced stressors (Wilkinson, 1999; Hughes and Connell, 1999; Hughes *et al.*, 2017a) of which sea temperature rise, resulting in coral bleaching, is arguably the most problematic (Baker *et al.*, 2008; Hoegh-Guldberg *et al.*, 2017; Hughes *et al.*, 2018). Mass regional coral bleaching and subsequent mortality was first noted in 1983 (Coffroth *et al.*, 1990; Glynn, 1993), with the first global bleaching event recognized in 1998 (Spalding and Brown, 2015). Further global bleaching events occurred in 2002, 2006, 2010 and 2015–2016, with the latter recorded as the longest and most widespread in history (Hoegh-Guldberg *et al.*, 2017; Hughes *et al.*, 2017b).

Research following past bleaching events suggests that reefs can recover from coral loss over decadal timescales if not affected again by mass bleaching or the presence of other anthropogenic stressors (Hoegh-Guldberg *et al.*, 2017). However, current trajectories of global warming make this scenario seem unlikely (Bellwood *et al.*, 2004; Zinke *et al.*, 2014; Perry and Morgan, 2017) and evidence from progressive bleaching events suggest that the recovery potential of reefs may be diminished with synergistic stress events

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(Hughes, 1994; Hughes *et al.*, 2017b). After the 1998 global bleaching event, coral cover in the Western Indian Ocean region declined substantially but reefs, particularly in Seychelles, showed signs of recovery following the event (Obura, 2005; Stobart *et al.*, 2005). However, after the 2015–2016 global bleaching event, an assessment of the risks to coral reefs suggested that coral reefs in Seychelles may be particularly susceptible to future decline (Beyer *et al.*, 2018). Thus, there remains a need to assess the post-bleaching status of coral reefs, particularly in Seychelles, and identify those that show signs of recovery in order to prioritize conservation efforts accordingly (Beyer *et al.*, 2018).

In this study, sea temperature data and benthic photographic data collected between 2011 and 2017 is assessed to determine the mortality of hard corals and the status of the post-bleaching benthic community at a remote coral reef in the Amirante Islands, Republic of Seychelles.

Material and methods

Study site

D'Arros Island and St Joseph Atoll are situated on the Amirantes Bank approximately 255 km southwest of Mahé in the Republic of Seychelles (Fig. 1) and together make up 3.03 km^2 of low lying land fringed by extensive reef flats and associated outer reef slopes (Stoddart *et al.*, 1979).

Sea temperature

Sea temperature was recorded at 10 minute intervals from 2012 to 2017 at 5m and 12m depth at D'Arros Island (Fig. 1) using HOBO ProV2 water temperature loggers.

Benthic surveys

Benthic surveys were conducted annually using a stratified random sampling protocol. Eleven representative sites were selected at D'Arros Island and St Joseph Atoll. Sites 1, 3, 5, 7 and 9 were located at a depth of 5m whilst sites 2, 4, 6, 8, 10 and 11 were located at a depth of 12m. Annually, 80 quadrats (1m^2) were positioned randomly within each selected site and photographs were taken of each quadrat by a diver positioned perpendicular to the substrate. Photographs were taken using a Nikon D7100 camera with a Nikon 10-22mm rectilinear lens and external strobes. Sampling was conducted in the months of November (2011, 2012, 2014, 2016), December (2015), January (2013), and July (2017).

Benthic classification

Benthic photographs were analysed using Coral Point Count with Excel extensions (CPCe) software v.4 (Kohler and Gill, 2006) whereby each photo quadrat was calibrated and 30 randomly generated points per sample were overlaid and categorised, generating 26,400 points a year. Each point was categorized as either: abiotic, algae, soft coral (including gorgonians),

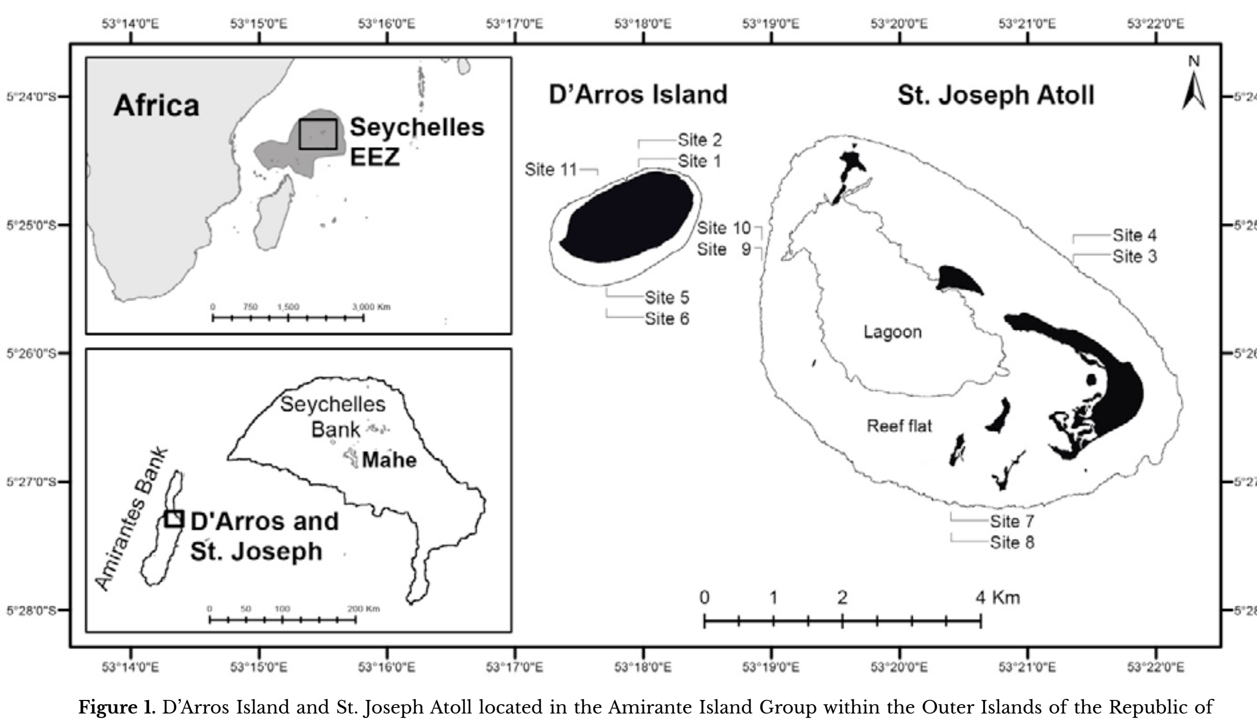

Figure 1. D'Arros Island and St. Joseph Atoll located in the Amirante Island Group within the Outer Islands of the Republic of Seychelles in the West Indian Ocean. Site numbers indicate survey locations (n=11).

hard coral or "other". Points that fell outside the quadrats were not included. Corals were classified as "healthy", "bleached", "fluorescing" and "recently dead". Additionally, abiotic classifications were categorized as bare rock, sand, or coral rubble (defined as "dead coral that had turned to rubble"), and algae was divided into either coralline algae or macroalgae. "Other" included mobile invertebrates, sessile invertebrates (sponges, giant clams) and fish.

Data analysis

All statistical analyses were performed in the R statistical platform (3.3.1; http://cran.r-project.org). CPCe produced annual per site averages of cover for hard coral, soft coral, bare ground (abiotic), macroalgae, coralline algae, and "other" which were used as response variables in analyses. Transformations were applied using square root to relevant variables (√hard coral and √macroalgae) to reduce skew and improve linearity. Response variables were tested for inter-correlation to identify serious collinearity ($r>0.7$ and $VIF>2$). One-way ANOVAs were used to compare benthic cover trends and annual per site averages from 2011 to 2017. Transformed data was normally distributed and met the assumptions for a one-way ANOVA. Any significant changes in benthic coverage across years were compared using a post hoc Tukey test to identify year to year differences for $p<0.05$.

The pre-bleaching hard coral cover in 2015 was also compared separately with the hard coral cover during the bleaching event in 2016 and after it in 2017. The data analysed consisted of 880 points per year, as opposed to annual averages used for previous analyses. These data were not normally distributed and could not be transformed, therefore nonparametric methods were used. A Kruskal-Wallis test compared hard coral cover across the three years and a post hoc Dunn's test determined specific year differences for $p<0.05$. Site differences were also tested for significant changes in coral cover from 2015 to 2017. Since the data were paired and not normally distributed, a nonparametric Wilcoxon signed-rank test was used. All summary data were calculated as means and standard deviation.

Results

Sea temperature

Between 2012 and 2015, mean monthly sea temperature at 5m at D'Arros Island typically peaked at 29.65 °C in April (Fig. 2). In April 2016, this figure rose to 30.25 °C, which was 0.50 °C warmer than the next warmest month on record (Fig. 2). Maximum annual sea temperatures recorded at 5m at D'Arros Island ranged between 30.42°C in 2013 and 31.31°C in 2016 over the six-year study period (Fig. 3). Similarly, maximum annual temperatures recorded at 12m ranged between 30.17°C in 2013 and 31.05°C in 2016. The coral bleaching temperature threshold, considered to be 30.5°C in Seychelles (NOAA), recorded at 5m depth was reached on 6 days in 2012, on 11 days in 2014, on 4 days in 2015, and on 38 days in 2016 (Fig. 3). Temperatures of 30.5 °C or more were also recorded at 12m depth for 20 days between March and May in 2016.

Hard coral cover

In 2011, mean hard coral cover was 18.8% (SD ± 15.9) across all sites and this increased steadily from 2013 until it reached 28.5% (SD ± 15.9) in 2015. Following bleaching in May 2016, hard coral cover decreased to 18.1% (SD ± 10.2), then went down further to 14.7%

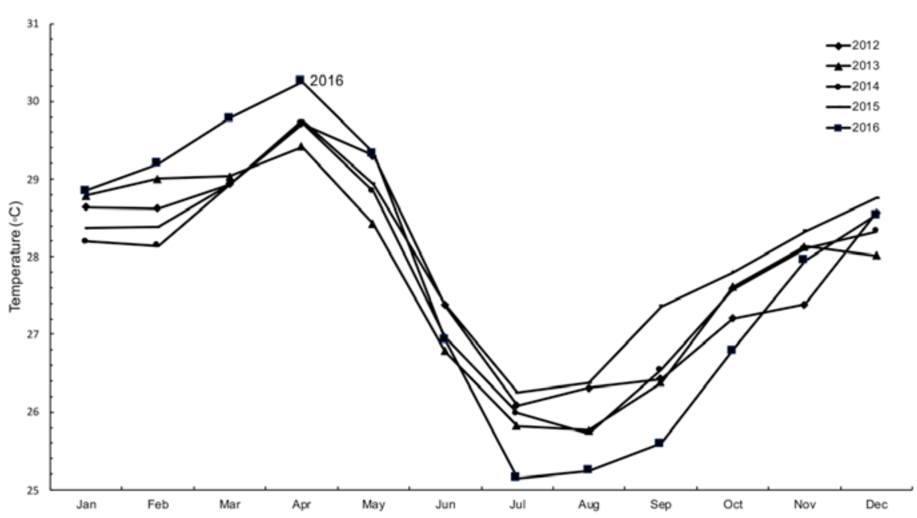

Figure 2. Monthly mean temperature recorded at 5m at D'Arros Island between 2012 and 2016.

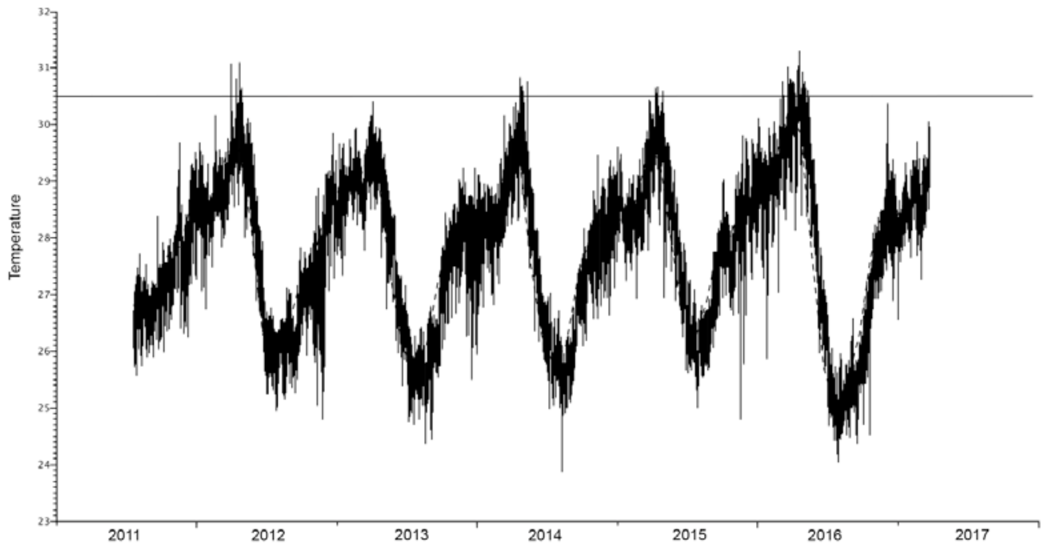

Figure 3. Daily sea temperature recorded at D'Arros Island at 5m between 2011 and 2017. Horizontal line represents the 30.5°C coral bleaching temperature threshold reported for the region.

(SD ± 7.9) in 2017 (Fig. 4). Between 2015 and 2017, the overall, mean hard coral cover reduced by almost half (48.3%), although the influence of year was not statistically significant when per site averages were compared (One-way ANOVA F(6, 70)=1.26, p=0.28). However, when change in average coral cover was compared between 2015 and 2017, a significant decline was apparent ($x^2(2)$=197.3, p=0.001, n=880) with 2015, 2016 and 2017 all exhibiting significant differences in post hoc testing (p<0.001).

Hard coral cover between survey sites

Fig. 5 illustrates pre-bleaching (2015), bleaching (2016), and post-bleaching (2017) hard coral cover at the 11 study sites. Sites 1, 4, 5 and 9 showed high average loss, equating to declines of 21% to 36%. Site 1 exhibited the greatest decrease in hard coral cover, declining from yearly averages of 50.8% to 14.08%. At sites 2, 3, 7, 8 and 10, declines of hard coral cover were small at only 1.8 to 5.1% between 2015 and 2017. Site 6 lost 14.6% of its coral cover, while Site 11 increased by 2.2% from 2015 to 2017. A Wilcoxon signed-rank test showed that the amount of hard coral cover before and after the 2016 bleaching was significantly affected by site (Z=-19.215, p=0.001 (two tailed)).

Benthic composition

Benthic composition differed across years, with a

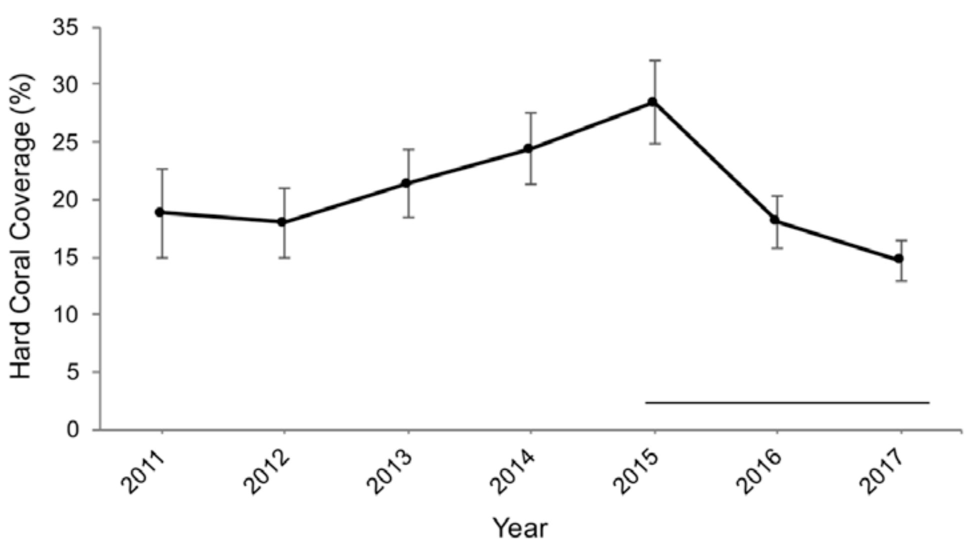

Figure 4. Mean hard coral cover across all sites surveyed between 2011 and 2017. Horizontal line represents significant difference between years. Error bars represent 95% confidence intervals.

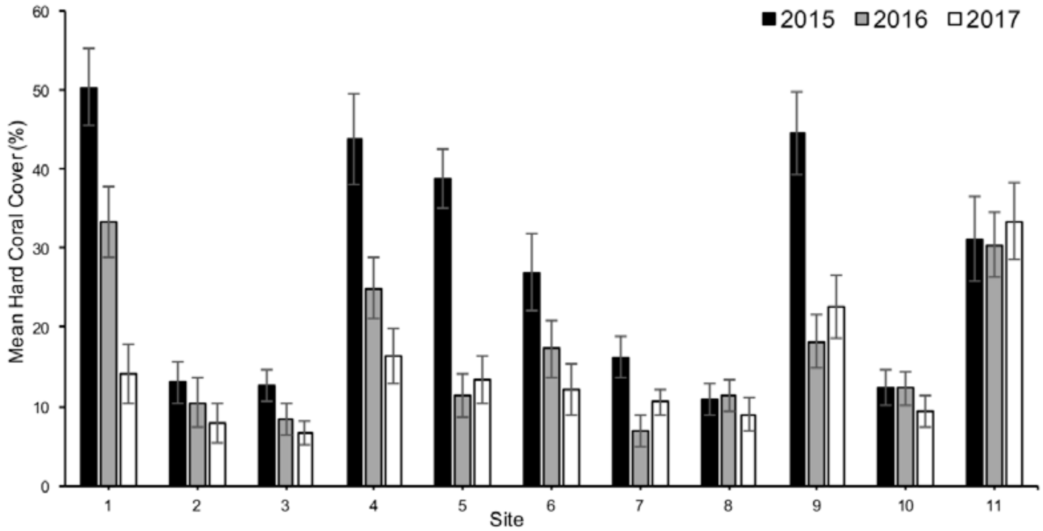

Figure 5. Mean hard coral cover for each survey site before the coral reef bleaching event in 2015, during it in 2016, and afterwards in 2017. Error bars represent 95% confidence intervals.

significant ($p<0.01$) increase in coralline algae cover for the two years following 2015 (Fig. 6). As hard coral cover decreased in 2016, coralline algae increased from 12.5% (SD ± 6.3) in 2015, to 22.7% (SD ± 10.9) in 2016. In 2017, coralline algae comprised 24.6% (SD ± 11.9) of the benthos which is close to the cover in 2011 of 25.3% (SD ± 15.7). Macroalgae remained between 2.35% and 2.37% from 2015 to 2017, comparable to coverage in 2011 of 2.4%. The amount of bare ground remained similar from 2011 to 2017, ranging from 51% to 55%. Soft corals and "other" did not exhibit significant differences across years.

Discussion

This study confirmed that D'Arros Island and St Joseph Atoll experienced anomalously high sea temperatures in April 2016, consistent with regional sea temperature anomalies associated with the global coral reef bleaching event of 2016 (Obura *et al.*, 2017). Persistently elevated sea temperatures above the regional coral bleaching threshold were presumed to be the primary driver of the mass coral bleaching in 2016 and associated post-bleaching mortality, although other factors such as solar radiation may have also contributed to the coral bleaching event (Berkelmans, 2002; Obura

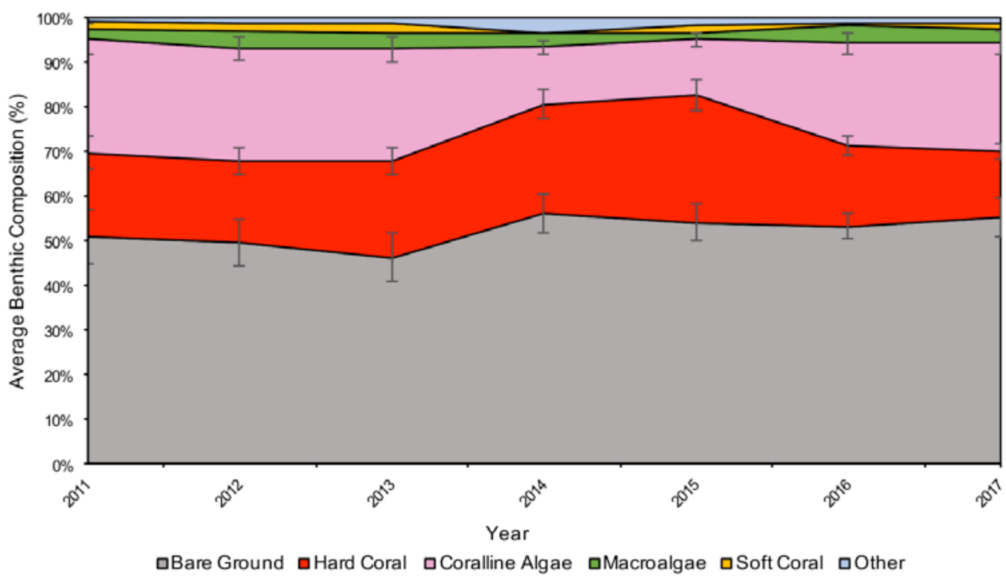

Figure 6. Benthic composition across all sites surveyed between 2011 and 2017. Error bars represent 95% confidence intervals.

et al., 2017). Due to the remote and relatively pristine environment at D'Arros Island and St Joseph Atoll, it is unlikely that local human disturbance influenced coral bleaching or post-bleaching coral mortality.

Evidence of increasing hard coral cover at D'Arros Island and St Joseph Atoll between 2011 and 2015 was similar to broader trends recorded in Seychelles as coral recovered after the 1998 and 2010 mass coral bleaching events (Obura *et al.*, 2017; Smith *et al.*, 2017). The observed loss of approximately half (48.3%) of the hard coral coverage in 2017 was less than the inner islands that exhibited on average 60% loss, but more than the average outer island loss of approximately 17% (Smith *et al.*, 2017; Gudka *et al.*, 2018). Additionally, the hard coral coverage decline described in this study was more than many other reports from the broader region (Tanzania, Kenya, Madagascar) but less than areas in Maldives (Gudka *et al.*, 2018; Perry and Morgan, 2017). However, caution should be taken when comparing hard coral coverage loss between regions due to the difference in methods employed to assess coverage (Gudka *et al.*, 2018). Nonetheless, the relative hard coral loss described in this study is consistent with regional studies that relied on the same methods (Gudka *et al.*, 2018)

While D'Arros Island and St Joseph Atoll exhibited a significant overall loss in hard coral cover after the 2016 bleaching event, there was some variability between sites. Typically, those that exhibited the greatest post-bleaching mortality were shallow (i.e. at 5m) with relatively high hard coral cover before 2016 (i.e. sites 1, 5 and 9). The low post-bleaching mortality at Site 7 was an exception perhaps because the site had a relatively high percentage of poritid colonies which are typically resistant to coral bleaching and associated mortality (Bridge *et al.*, 2014). Other sites with low post-bleaching mortality were 2, 8 and 10, all of which were at 12m and had relatively low coral cover before 2016. Additionally, deeper sites experienced fewer days at which the recorded temperature reached the regional coral reef bleaching threshold. As a whole, sites which exhibited the greatest decrease in hard coral cover (i.e. sites 1 and 9) were dominated by acroporids and pocilloporids which are thought to be particularly susceptible to bleaching (Marshall and Baird, 2000). In general, amongst the study sites, those where coral communities appeared most resistant to post-bleaching mortality had strong currents and were in proximity to deeper water. Previous research has shown that such conditions, alongside exposure to frequent upwelling events, may contribute to the resistance of bleaching induced coral mortality (West and Salm, 2003; Goreau *et al.*, 2000).

Benthic cover after the bleaching event in 2016 was largely unchanged for macroalgae, soft coral and bare ground. However, there was an increase in cover of coralline algae and a decrease in hard coral cover, similar to post-bleaching trends in Seychelles waters after the 1998 bleaching event (Stobart *et al.*, 2005). Such slightly increased coralline algal cover may help to facilitate coral reef recovery (McCook *et al.*, 2001; Friedlander *et al.*, 2014), especially if the macroalgal community remains stable (West and Salm, 2003). Indeed, the unchanged macroalgal community at D'Arros Island and St Joseph Atoll may be facilitated by the diverse and healthy herbivorous fish community as well as the relatively pristine environment with minimal anthropogenic influence (Hughes *et al.*, 2007; Daly *et al.*, 2018). Thus, ensuring the continued conservation of marine resources and limiting anthropogenic disturbance will likely promote conditions favourable to recovery of the local coral reef community at D'Arros Island and St Joseph Atoll (Fung *et al.*, 2011).

In summary, this study found that after the 2016 bleaching event, hard coral cover at D'Arros Island and St Joseph Atoll declined from 28.5% in 2015 to 14.7% in 2017. Although this represented a substantial decline in hard coral cover, the benthic community in general did not appear to shift to a rubble or algal dominated community over the timeframe of the study. However, further monitoring is required to assess the status of the coral reef community over broader timescales. Additionally, some monitored sites exhibited minimal post-bleaching coral mortality. Specifically, some deeper sites probably exhibited less hard coral cover decline as they experienced fewer days of sea temperatures above the regional coral reef bleaching threshold and were not dominated by corals susceptible to bleaching (acroporids and pocilloporids) compared to the shallower sites. A 2017 post-bleaching hard coral cover of 14.7% suggests that local coral recruitment will contribute to the slow recovery of coral reefs in the region (Graham *et al.*, 2015). Furthermore, the low level of anthropogenic impact at D'Arros Island and St Joseph Atoll in terms of minimal pollution, fishing pressure and coastal development provide a suitable environment for post-bleaching recovery (Wilkinson *et al.*, 1999; Fung *et al.*, 2011; Hughes *et al.*, 2017a).

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