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The implications of recurrent disturbances within the world's hottest coral reef

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ABSTRACT

Determining how coral ecosystems are structured within extreme environments may provide insights into how coral reefs are impacted by future climate change. Benthic community structure was examined within the Persian Gulf, and adjacent Musandam and northern Oman regions across a 3-year period (2008–2011) in which all regions were exposed to major disturbances. Although there was evidence of temporal switching in coral composition within regions, communities predominantly reflected local environmental conditions and the disturbance history of each region. Gulf reefs showed little change in coral composition, being dominated by stress-tolerant Faviidae and Poritidae across the 3 years. In comparison, Musandam and Oman coral communities were comprised of stress-sensitive Acroporidae and Pocilloporidae; Oman communities showed substantial declines in such taxa and increased cover of stress-tolerant communities. Our results suggest that coral communities may persist within an increasingly disturbed future environment, albeit in a much more structurally simple configuration.

1. Introduction

Coral reefs are one of the worlds' most biodiverse ecosystems, and provide coastal populations with economically valuable goods and services (Moberg and Folke, 1999; Sheppard et al., 2009). However, coral reefs are in global decline. The combined effects of eutrophication, sedimentation, overfishing, outbreaks of disease and predation, and recurrent bleaching events associated with elevated sea temperatures are having a marked effect on the structure and functioning of reef systems (Hoegh-Guldberg, 1999; Hughes et al., 2003; Riegl et al., 2009). The capacity for reefs to resist change and/or recover from these escalating threats (i.e., resilience, sensu Walker et al., 2004) will be, in part, determined by the localised environmental context in which communities occur (Coles and Riegl, 2013; Hoegh-Guldberg, 1999). Abiotic factors, in particular temperature, salinity, and light, can strongly influence the growth, mortality, fecundity, and settlement of corals (Baird and Marshall, 2002; Hoegh-Guldberg, 1999; Riegl and Purkis, 2012b), and hence their capacity to re-assemble following disturbance (Glynn, 1996; Hoegh-Guldberg et al., 2007). Corals and associated organisms that occur in highly variable physical environments are physiologically acclimated and/or genetically adapted to the extreme conditions to which they are exposed, allowing them to persist in environments that are often outside the physiological thresholds for most communities (Hoegh-Guldberg, 1999; Rowan, 2004; Sheppard, 2003). Understanding how benthic communities in extreme environments respond to disturbances may therefore provide important insights into how reefs in other regions may respond to future disturbance under increasing climate change and anthropogenic pressure (Brown, 1997; Burt et al., 2011a).

The Persian Gulf is among the most physically hostile environment in which coral reefs currently exist (Coles and Riegl, 2013; Sheppard et al., 1992). The Persian Gulf is a small, shallow sea (mean depth <30 m) that has relatively restricted water exchange with the wider Indian Ocean (Riegl and Purkis, 2012a). As a result, the physical environment is characterised by thermal extremes, with sea surface temperatures (SSTs) ranging over 22 °C every 6 months; from <13 °C in winter to >35 °C in summer (Coles, 2003). This is the largest thermal range and highest maximum temperature experienced by extant coral reef communities (Coles, 2003; Sheppard et al., 1992; Sheppard and Loughland, 2002). In addition, limited freshwater input and the arid nature of the surrounding landscape causes high evaporation, and as a result salinity regularly exceeds 42 psu on reefs in the region (Coles, 2003; Riegl and Purkis, 2012b). Despite these extreme conditions, there are extensive reef systems in shallow coastal areas throughout the Persian Gulf, and these offer a 'natural laboratory' in which to study the impact

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of extreme and variable environmental conditions on the structure and function of coral reef fauna (Foster et al., 2012; Sheppard et al., 2012).

The Gulf of Oman is biogeographically connected to and at the same latitude as the Persian Gulf. The Gulf of Oman is deep (mean depth > 1000 m) and well mixed with the wider Indian Ocean, resulting in relatively benign environmental conditions (SST: 22–32 °C, salinity: 35–37 psu; Böhm et al., 1999; Coles, 1997, 2003), making these regions ideal for comparative studies of the role of environmental extremes in structuring reef communities (Burt et al., 2011b; Feary et al., 2010).

Coral communities around the Arabian Peninsula, like reefs in other regions, have been subject to an increasing frequency and/or intensity of disturbances in recent years (Burt et al., 2011a; Riegl and Purkis, 2012a; Sheppard et al., 2012). In 2007, category 5 cyclone Gonu, the strongest cyclone ever recorded for the Arabian Peninsula, caused extensive damage to reefs in the Gulf of Oman (Coles et al., 2015; Foster et al., 2011; Fritz et al., 2010). This was followed by a widespread harmful algal bloom (HAB) in 2008/2009 that resulted in mass coral mortality in both the Persian Gulf and Gulf of Oman (Bauman et al., 2010; Riegl et al., 2012c), and recurrent large-scale bleaching events in 2010 and 2011 (Riegl and Purkis, 2012b). The objective of this study was to examine temporal changes in benthic reef communities in three locations around the Arabian Peninsula: the Persian Gulf (Abu Dhabi), the Gulf of Oman (Fujairah), and the Straits of Hormuz (Musandam Peninsula, which connects the two Gulfs). By comparing benthic assemblages over a period that included several large-scale disturbances this study may provide insights into how reefs may respond to disturbance under environmental extremes associated with future climate change.

2. Methods

Benthic coral reef communities were surveyed at six sites around the Arabian Peninsula, with two sites surveyed at each of three locations; the Gulf of Oman (Al Aqa, Dibba), Persian Gulf (Saadiyat, Ras Ghanada) and Musandam Peninsula in the Straits of Hormuz (Al Harf, Coral Garden) (Fig. 1). Sites within each location were separated by 13–33 km. All sites were initially surveyed in September/November 2008, at the start of a widespread harmful algal bloom (HAB) event, and resurveyed 3 years later (2011). The HAB started at Dibba in the Gulf of Oman in August 2008 and lasted until May 2009, initially expanding north to the Straits of Hormuz, before spreading westward and southward through coastal areas of Iran, Qatar, and the United Arab Emirates (Richlen et al., 2010). A total of 1200 km of coastline was affected by the HAB, with extensive fish kills and/or coral damage recorded in Oman, Fujairah, Iran, Dubai, Abu Dhabi, and Ajman (Bauman et al., 2010; Coles et al., 2015; Richlen et al., 2010). In 2010, a major bleaching event was also observed in the Persian Gulf, where corals were exposed to the highest temperatures recorded in the region (>35 °C) for a period of 3 weeks (Riegl et al., 2011, 2012a). A second major bleaching event was recorded in coastal UAE reefs in 2011 (Riegl et al., 2012c).

At each site the benthic community was quantified along six randomly placed 30-m transects at depths of 2–8 m. The depth of the surveys was determined by the reef topography and available hard substrata at each site, and depths surveyed were consistent between years. Transects were placed parallel to each other with a minimum of 3 m between adjacent transects. Along each transect eleven 0.5×0.5 m (i.e. 0.25 m^2) quadrats were placed at 3 m intervals and photographed ($n = 66$ quadrats per site per year). The substratum-type and coral composition within each quadrat was quantified under 50 random points using Coral Point Count with Excel Extensions (CPCe) software (Kohler and Gill, 2006). Substratum type was categorised into seven broad groups: (i) live scleractinian coral, (ii) fleshy and turf algae, (iii) crustose coralline algae (CCA), (iv) other live organisms (which encompassed all live benthic organisms that do not belong to the former groups; primarily barnacles, bivalves, sponges, and urchins), (v) dead coral framework, (vi) terrestrial derived rock, and (vii) unconsolidated substrata (i.e., sand and rubble). To quantify the composition of coral assemblages all live corals recorded were identified to genus (Riegl et al., 2012b; Veron, 2000). Percent cover of all benthic categories were then pooled to the transect level, and the relative abundance for each transect within each site calculated.

Two non-metric multi-dimensional scaling (nMDS) analyses and Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson et al., 2008) were used to investigate variation in (i) benthic community composition and (ii) scleractinian coral composition among regions (Persian Gulf, Musandam, Gulf of Oman) and years

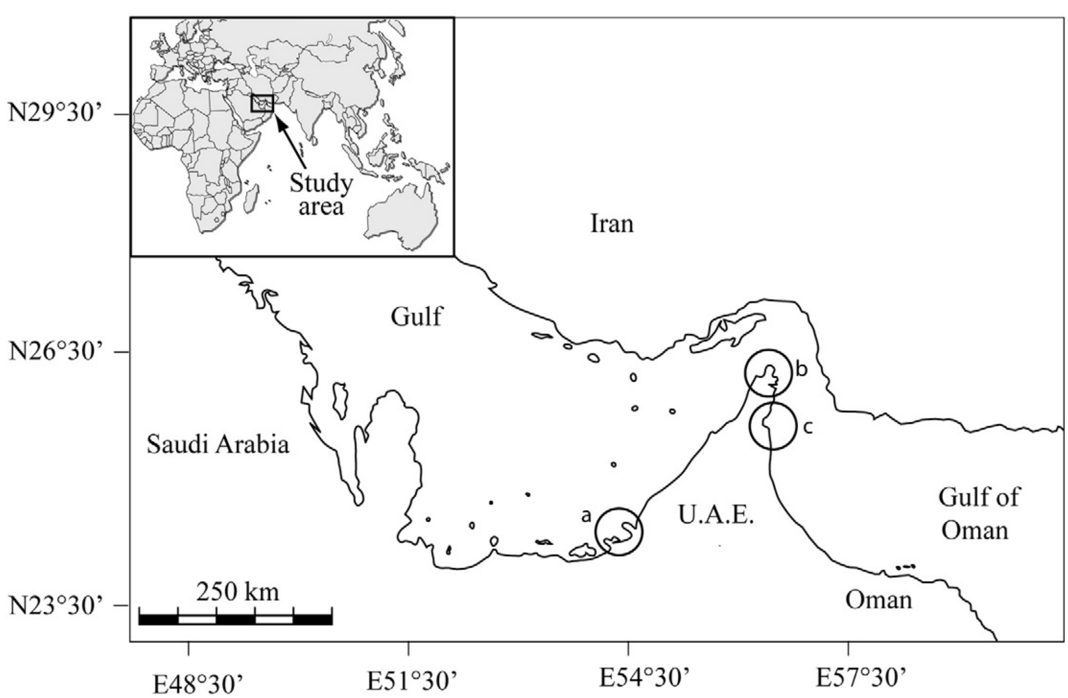

Fig. 1. Map of the Arabian Peninsula showing the geographic position of the three locations where the benthic communities were surveyed. a) Persian Gulf (Saadiyat and Ras Ghanada), b) Musandam (Al Harf and Coral Garden), and c) Gulf of Oman (Dibba and Al Aqa).

(2008 vs. 2011). The analyses were based on the mean proportion of each substratum category and coral family, respectively at each site within each year. The analyses were based on Bray–Curtis similarities of arcsin-square root transformed data.

A series of 3-factor ANOVA's were used to determine the effect of region, year, and site (nested within region) on the relative abundance of each of the benthic substratum categories, and coral families. Assumptions of the ANOVA were examined by residual analysis. Prior to analyses the proportional cover of each of the benthic categories and coral families was arcsine–square root transformed, and coral genus richness $\log_{10}$ transformed, to improve normality and homoscedasticity. Fishers LSD tests were used to identify which means contributed to any significant differences detected.

3. Results

3.1. Changes in benthic composition

The nMDS of benthic community composition showed some separation between regions and years (Fig. 2A), and these differences were supported by the PERMANOVA (region: pseudo-F = 18.63, p = 0.001, year: pseudo-F = 8.87, p = 0.001). Overall, the Musandam and Persian Gulf sites were separated from the Gulf of Oman sites along the first dimension of the nMDS. The Musandam and Persian Gulf sites were characterised by a relatively high cover of live coral, dead coral and sand and rubble, while the Gulf of Oman sites were characterised by a high cover of rock, 'other' live organisms, and algae (Fig. 2B). In addition to spatial variation, there was also a separation of benthic communities between years at the Musandam and Persian Gulf sites, with the cover of live coral being generally greater in 2011 than 2008. In contrast, the Gulf of Oman sites had lower cover of live coral and higher cover of rock in 2011 than in 2008 (Fig. 2).

The distribution of all benthic categories, except dead coral, was influenced by an interaction between region and year, indicating that temporal changes in the cover of each category was not consistent among regions (live coral: ANOVA $F_{2,60} = 7.81$, p = 0.001, algae: $F_{2,60} = 3.43$, p = 0.039, CCA: $F_{2,60} = 16.76$, p < 0.001, 'other' live organisms: $F_{2,60} = 46.94$, p < 0.001, rock: $F_{2,60} = 12.69$, p < 0.001, sand and rubble: $F_{2,60} = 17.77$, p < 0.001; Table S1). Live coral cover increased significantly in the Persian Gulf (2008: 31.7%, 2011: 56.1%, Fishers LSD: p < 0.001, Fig. 3A) and Musandam regions (2008: 46.9%, 2011: 58.5%, Fishers LSD: p = 0.037, Fig. 3B), while there was a small but non-significant decline in live coral cover within the Gulf of Oman (Fishers LSD: p = 0.17, Fig. 3C). The increase in coral cover within the Persian Gulf was accompanied by relatively small increases in the cover of algae and 'other' live organisms, and decreases in CCA, dead coral and sand/rubble (Fig. 3A). In contrast, the increase of live coral in the Musandam region was accompanied by an increase in sand/rubble, and decreases in the cover of CCA, 'other' live and rock (Fig. 3B).

3.2. Changes in coral composition

A total of 29 coral genera from 11 families were recorded across all surveys, with 4 families (Acroporidae, Faviidae, Pocilloporidae, and Poritidae) accounting for 97% of all corals surveyed. The composition of coral assemblages varied markedly between regions (PERMANOVA: pseudo-F = 15.23, p = 0.001), but displayed less variation between years (PERMANOVA: pseudo-F = 2.81, p = 0.042; Fig. 4). The

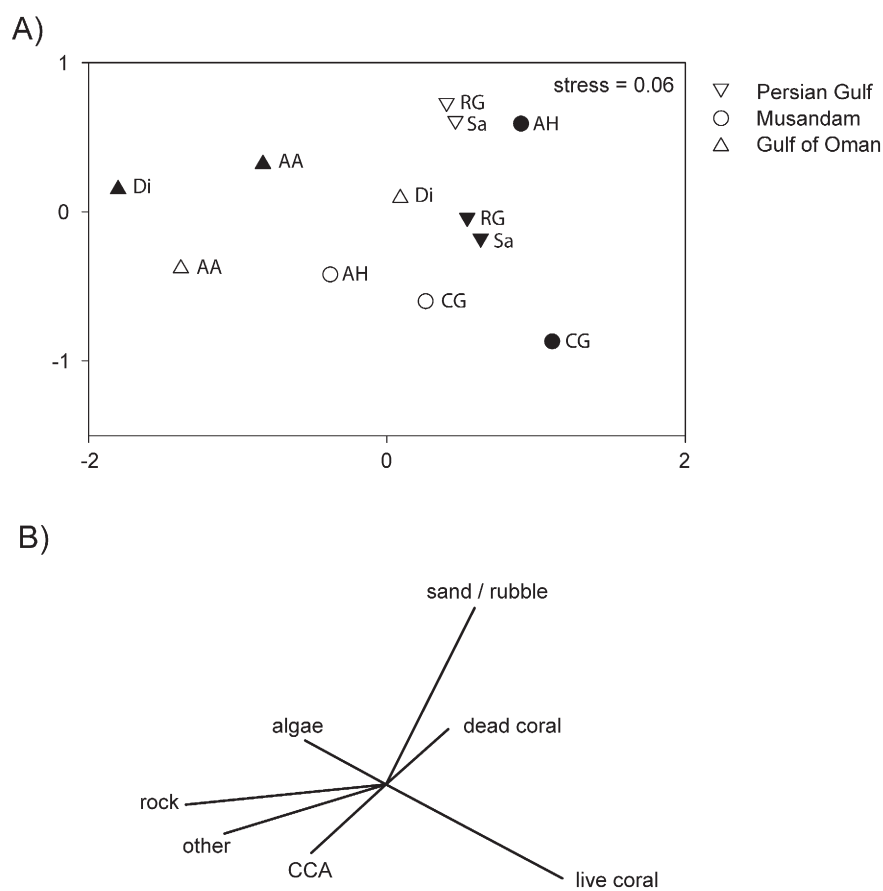

Fig. 2. Spatial and temporal variation in benthic communities around the Arabian Peninsula. A) Non-metric multi-dimensional scaling (nMDS) of benthic assemblages at two sites within each of the Persian Gulf (inverted triangle), Musandam (circle) and Gulf of Oman (triangle) in 2008 (open symbols) and 2011 (filled symbols). Letters indicate the individual sites (Di: Dibba, AA: Al Aqa, AH: Al Harf, CG: Coral Garden, Sa: Saadiyat, RG: Ras Ghanada). B) Vectors represent the partial regression coefficients of the original variables (benthic categories) with the two dimensions. Lengths of the vectors are proportional to the squared multiple correlation coefficient.

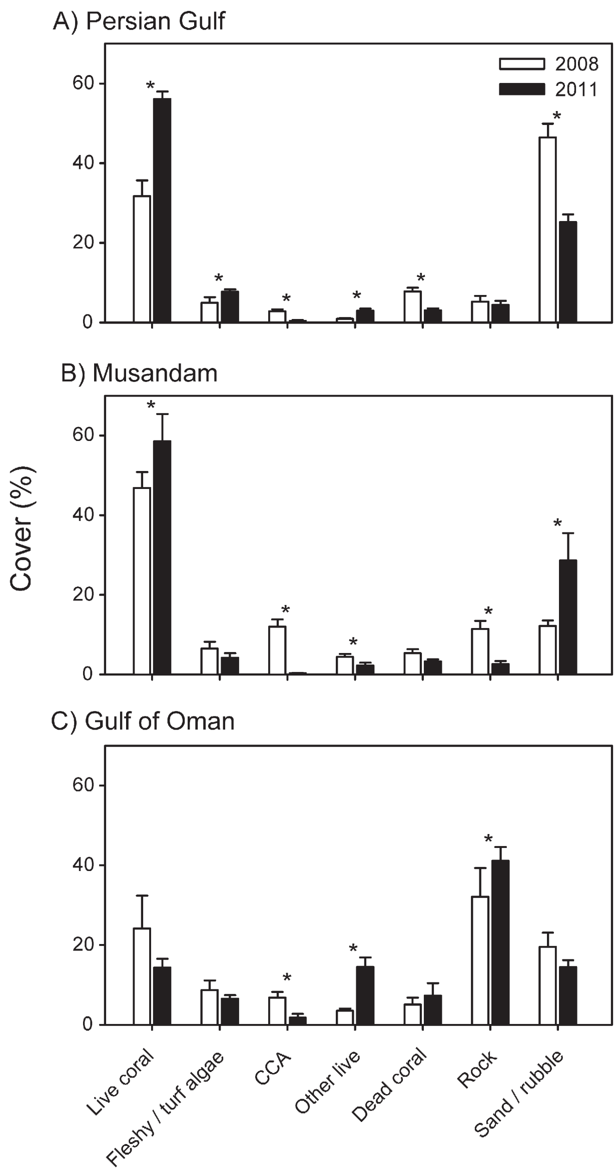

Fig. 3. Temporal variation in benthic components within (A) the Persian Gulf, (B) Musandam, and (C) Gulf of Oman before the beginning of a harmful algal bloom (2008), and 3 years after (2011). Bars represent mean percentage cover (± standard error). * indicates significant ($p < 0.05$) difference identified by Fishers LSD test.

composition of coral assemblages was relatively consistent among sites and years within Musandam and the Persian Gulf, with both being characterised by a relatively high cover of Poritidae and Faviidae (Fig. 4). The Musandam sites were also characterised by high cover of Acroporidae (Fig. 4). Coral assemblages were more spatially variable within the Gulf of Oman with one site (i.e., Dibba) being characterised by a high cover of Pocilloporidae, and the other site (i.e., Al Aqa) by a relatively high cover of Pectinidae and Mussidae (Fig. 4).

Comparisons of the cover of the four most abundant coral families revealed that the distribution of three of these families were influenced by an interaction between region and year (Faviidae: ANOVA $F_{2,60} = 11.96$, $p < 0.001$; Pocilloporidae: $F_{2,60} = 4.47$, $p = 0.01$; Acroporidae: $F_{2,60} = 5.28$, $p = 0.01$; Table S2). The cover of poritid and faviid corals increased significantly at the two Persian Gulf sites from 2008 to 2011 (Fig. 5A), yet displayed no change or small decreases in cover at the Musandam and Gulf of Oman sites (Fig. 5B, C). The cover of Pocilloporidae decreased significantly over the same time at the Gulf of Oman sites and did not change at the Musandam sites; this family was absent from the Persian Gulf sites in both years (Fig. 5). The cover of Acroporidae increased significantly at the Musandam sites from 2008 (4.9%) to 2011 (16.4%), but was rare in the Gulf of Oman and Persian Gulf (Fig. 5). See Tables S3 and S4 for complete details of benthic categories and coral composition among regions, sites, and years.

4. Discussion

Coral reefs are being increasingly impacted by a suite of anthropogenic and natural stressors, with these effects being greatly compounded by climate change (Bellwood et al., 2004; Gardner et al., 2003). Future predictions of increased frequency and/or intensity of disturbances paint a bleak picture of accelerated declines and coral loss (Carpenter et al., 2008; De'ath et al., 2012; Hoegh-Guldberg, 1999; Hughes et al., 2003; Pandolfi et al., 2003; Riegl, 2003). Despite the extreme environmental conditions (e.g., high and variable SST and salinity) and numerous acute and chronic stressors (e.g., coral bleaching, HAB, intensive coastal development) impacting reefs around the north-eastern Arabian Peninsula during the course of this study, there were no significant declines in coral cover over the 3-year period (2008–2011) with coral cover actually increasing at two of the three locations (Persian Gulf and Musandam). There were, however, temporal changes in the composition of coral communities, and consistent differences in the composition of the overall benthic communities and scleractinian coral communities between the three locations. This spatial variation likely reflects the local environmental conditions (e.g., Bauman et al., 2013; Fishelson, 1973; Maina et al., 2011); and disturbance history of each location (e.g., Berumen and Pratchett, 2006; Hughes, 1989).

Coral communities within the Persian Gulf were dominated by massive and submassive Poritidae and Faviidae, which collectively accounted for over 95% of all corals recorded on these reefs. Poritid and faviid corals are generally viewed as being relatively tolerant to a range of stressors, including thermally-induced bleaching, predation by Crown-of-Thorns starfish, and storms (Baird and Marshall, 2002; Baird et al., 2013; Guest et al., 2012; Loya et al., 2001; Madin and Connolly, 2006; McClanahan et al., 2007). Consequently, coral assemblages dominated by these stress tolerant taxa are often indicative of a disturbed system. Indeed historical accounts of coral communities within the Persian Gulf describe these reefs as being dominated by *Acropora*, such as the tabular *Acropora clathrata* and *Acropora downingi*, up until the mid-1990s (George and John, 1999; Shinn, 1976). However, recurring bleaching events and coral mortality in 1996, 1998, 2002, 2010, and 2011 (Burt et al., 2008; George and John, 1999; Riegl, 1999, 2003; Sheppard and Loughland, 2002; Riegl and Purkis, 2012a), coral disease (Riegl et al., 2012c), and extensive coastal development and modification (Burt, 2014; Sale et al., 2011), over the past two decades have shifted these reefs from an *Acropora*-dominated configuration to a poritid- and faviid-dominated community (Bauman et al., 2013; Burt et al., 2011a; Riegl and Purkis, 2012b; Sheppard et al., 2012). Similar shifts in coral species composition have been recorded in response to disturbances in other regions (e.g., Indian Ocean: Ateweberhan et al., 2011; French Polynesia: Berumen and Pratchett, 2006; Pratchett et al., 2011; Kenya: McClanahan and Graham, 2005; Western Australia: Speed et al., 2013; Taiwan: Kuo et al., 2012) and has led to suggestions that in the face of continuing or increasing disturbances reefs will persist in these altered, or novel, states (Darling et al., 2013; Graham et al., 2014).

Although there has been a marked shift in coral assemblages in the Persian Gulf over the past two decades, the current poritid and faviid-dominated assemblages appear to be relatively insensitive to stressors. Multiple disturbances within the Persian Gulf during 2008–2011 had minimal impacts on coral assemblages at our study sites, with the cover of poritid and faviid corals not only being maintained but exhibiting a >60% increase. The apparent resilience of these assemblages is remarkable given the 2010 thermal anomaly was the highest on record for the region (>35 °C for 3 weeks; Riegl et al., 2011,

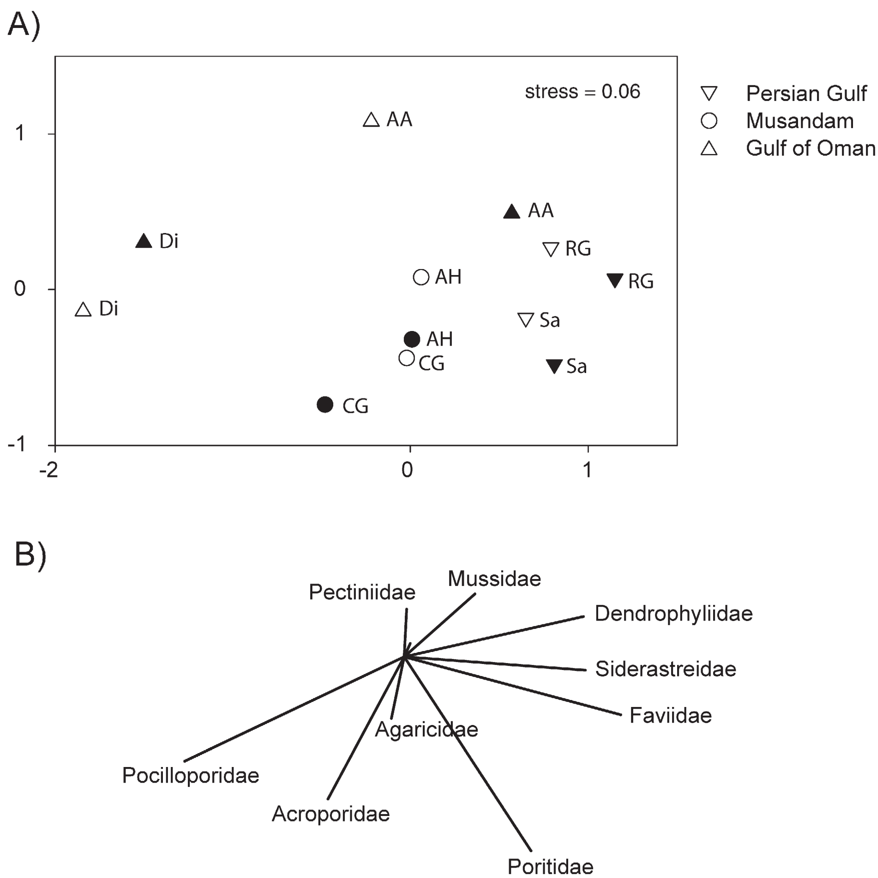

Fig. 4. Spatial and temporal variation in coral family composition around the Arabian Peninsula. A) Non-metric multi-dimensional scaling (nMDS) of coral families composition at two sites within each of the Persian Gulf (inverted triangle), Musandam (circle) and Gulf of Oman (triangle) in 2008 (open symbols) and 2011 (filled symbols).). Letters indicate the individual sites (Di: Dibba, AA: Al Aqa, AH: Al Harf, CG: Coral Garden, Sa: Saadiyat, RG: Ras Ghanada). B) Vectors represent the partial regression coefficients of the original variables (coral families) with the two dimensions. Lengths of the vectors are proportional to the squared multiple correlation coefficient.

2012a), and several degrees higher than has been shown to cause extensive bleaching elsewhere (Coles, 2003; Riegl et al., 2012a). The cover of *Acropora* remains low on reefs in this region (<1% cover, Burt et al., 2008; Foster et al., 2012; present study) and given the limited input from larval sources (Bauman et al., 2014) recovery seems unlikely. Recent observations using artificial substrata (i.e., settlement tiles) demonstrated that newly-settled corals in the Persian Gulf were dominated by poritids and 'other' corals, with few *Acropora* and no *Pocillopora* recorded (Bauman et al., 2014). This is in marked contrast to similar studies elsewhere in which *Acropora* dominate assemblages of coral recruits (e.g. Hughes et al., 1999; Penin et al., 2010; Gilmour et al., 2013). Further, field-based fecundity estimates and demographic modelling predicts that acroporids will remain functionally extinct in the southern Persian Gulf under the current disturbance regime (Riegl and Purkis, 2009; Howells et al., 2016). The current poritid and faviid-dominated assemblages, although less diverse and structurally complex than the previous *Acropora*-dominated assemblages (Burt et al., 2011a; Burt et al., 2008), appear to be resilient to the extreme environmental conditions and frequent disturbances of this region.

In contrast to the Persian Gulf, reefs within the Musandam Peninsula and Gulf of Oman typically experience less extreme and less variable environmental conditions (Bauman et al., 2013) and have been subjected to fewer major disturbances in recent years (Riegl et al., 2012a,c). It is perhaps not surprising that reefs in these regions support a higher diversity of coral families, including the stress-sensitive Acroporidae and Pocilloporidae. Reefs in the Musandam Peninsula displayed a ca. 20% increase in overall coral cover from 2008 to 2011, which was primarily driven by increases in pocilloporid and acroporid corals. Increased coverage of these fast growing but stress-sensitive corals reflect the lack of major disturbances in the region.

Reefs in the Gulf of Oman, although having the least variable environmental conditions of the three regions examined (Bauman et al., 2013), experienced a ca. 75% decline in cover of pocilloporid corals over the study period. This decline in cover was largely offset by small, but non-significant increases in portiid and faviid corals, resulting in limited change in overall live coral cover from 2008 to 2011. Historically, the Gulf of Oman has had little documented exposure to substantial disturbances (Coles et al., 2015; Richlen et al., 2010), however a region-wide harmful algal bloom (HAB) that initiated in the Gulf of Oman and extended into the Persian Gulf in 2008–9, had its most severe impacts on reefs in the northern Gulf of Oman (Richlen et al., 2010; Riegl et al., 2012c). The HAB caused >80% mortality of corals (including acroporids, pocilloprids, faviids, and poritids) on reefs in the northern Gulf of Oman, including those in the present study (Bauman et al., 2010; Foster et al., 2011, 2012). It is likely that the decline in Pocilloporidae in the present study was directly related to the impact of the HAB. The similarity in the magnitude of coral mortality immediately following the HAB (Bauman et al., 2010) and the reduction in the cover in the present study suggest there has been little, if any, recovery of the previously dominant pocilloporid populations 3 years after the HAB. Interestingly, poritids and faviids also experienced mortality from the HAB (Riegl et al., 2012c) but appear to have recovered, and even increased in cover in the subsequent 3 years. The shift in coral composition, therefore, may be related to the differential recovery of coral populations, rather than differential mortality. It remains to be seen if this represents a long-term shift in community structure or a transitional configuration. Several studies have reported variable

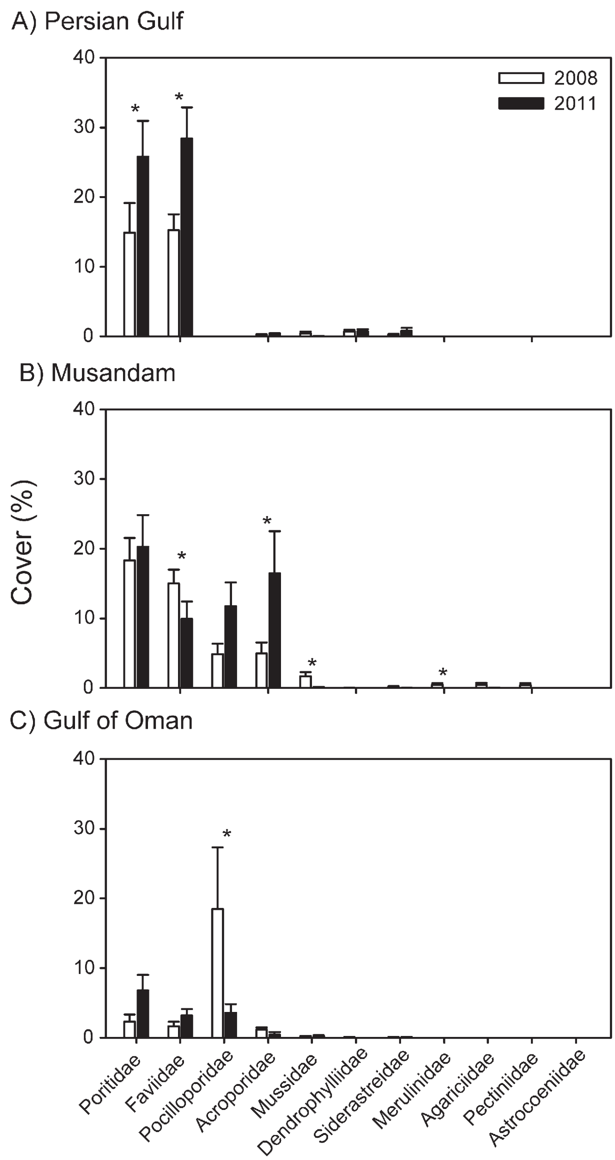

Fig. 5. Temporal variation in the cover of the eleven most abundant coral families within (A) the Persian Gulf, (B) Musandam and (C) the Gulf of Oman. Bars represent mean percentage cover (± standard error). * indicates significant ($p < 0.05$) difference identified by Fishers LSD test.

timeframes for recovery of coral populations following disturbances, with the rate of recovery being dependent on a range of factors including the supply of larvae, connectivity, and competition with other benthic organisms (e.g., Ceccarelli et al., 2011; Gilmour et al., 2013). Pocilloporids are often abundant on marginal or subtropical coral reefs (e.g., Hoey et al., 2011), however being brooding spawners larval supply for this coral species is tightly linked to local adult abundance, and is likely to lead to protracted population recovery within the Gulf of Oman.

Understanding how coral reefs in extreme environments respond to disturbance may provide insights into how reefs in other regions may respond to disturbance under ongoing climate change (Sheppard et al., 2012). Although there have been some suggestions that accelerating climate change and anthropogenic stressors will cause coral reefs to decline to such an extent that they will be largely unrecognizable by the middle of this century (Caldeira and Wickett, 2003; Donner, 2009; Donner et al., 2005; Hoegh-Guldberg, 1999, 2005; Hoegh-Guldberg et al., 2007; Orr et al., 2005; Veron et al., 2009), it appears more likely that reefs will persist, albeit in a different configuration (Graham et al., 2014). Set against a backdrop of extreme environmental conditions and frequent disturbances, the stability of faviid and poritid-dominated reef in the Persian Gulf is remarkable and may provide a window into the future configuration of reefs under climate change. Although this may be a cause for some optimism, these novel configurations are structurally simple and will invariably lead to reductions in the diversity and abundance of reef associated fishes (Pratchett et al., 2014) and the goods and services they provide.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.marpolbul.2015.10.006.

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