Changes in the structure of coral populations and communities in the central Maldives archipelago since the last major mass-bleaching

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Increasing frequency and severity of disturbances is resulting in degradation of coral reef ecosystems. However, specific changes in the structure of coral populations and communities have been poorly documented at most locations. This study examined temporal changes in live coral cover and coral composition in the central Maldives from 1997 to 2016, encompassing two bleaching events, a tsunami, and an outbreak of *Acanthaster planci*. We also examined the contemporary size structure for five dominant coral taxa (tabular *Acropora, Acropora muricata, Acropora humilis , Pocillopora spp,* and massive *Porites*) and tested whether depth and reef typology had an effect. Total coral cover has generally increased throughout the study period, with marked increases following the 1998 mass-bleaching. The relative abundance of key genera has also changed through time, where *Acropora* and *Pocillopora* (which are highly susceptible to bleaching) were under-represented following the 1998 bleaching but increased until outbreaks of *A. planci* in 2015. The contemporary size-structure for all coral taxa was dominated by larger size classes with over-centralized, peaked distributions. This suggests that recent disturbances had a disproportionate impact on smaller colonies, or that recruitment is currently limited. This may suggest that the resilience of coral populations has been compromised by recent disturbances, and further bleaching (expected to occur in 2016) could lead to highly protracted recovery times. This study showed that Maldivian coral reef did recover in the aftermath of the 1998 mass-bleaching event, but it took up to a decade, and ongoing disturbances may be eroding reef resilience.

Introduction

Disturbances play an important role in the development, structure and function of natural communities and are a necessary part of ecosystem dynamics (Lugo and Scatena 1996; Connell 1997). Intermediate levels of disturbance make an important contribution to increasing biodiversity (Connell 1978). However, increasing anthropogenic stresses (e.g., agricultural land use, overfishing, and pollution) are compounding upon natural disturbances, and inevitably leading to degradation of both terrestrial and aquatic ecosystems (Chazdon 2003; Connell 1997). Natural communities constantly experience some level of disturbance, and are always recovering from past disturbances (Lugo and Scatena 1996). Some species recover rapidly in the aftermath of disturbances and make substantial contributions to overall habitat structure, such ground cover or benthic cover (e.g., Halford et al. 2004) while other longer-lived and slow growing species, may take centuries to regain pre-disturbance levels of abundance (Guariguata and Ostertag 2001).

The recovery and resilience of natural communities to major acute disturbances (e.g. fire, cyclones, droughts, bleaching or predation) depends upon the spatial and temporal scales of the disturbance, the disturbance history, contemporary community structure, as well as background rates of mortality (Beadle and Costin, 1952; Highsmith et al 1980; Pickett and White 1985; Hughes 1994; Dayton et al 1992; Hughes et al. 2003; Graham et al. 2011;

Pisapia et al. 2016). Importantly, rates of recovery are typically measured based on the time it takes for either overall abundance of key groups of organisms (e.g., total coral cover) or the specific abundance of individual taxa to reach levels apparent immediately prior to the disturbance (e.g., Turner et al 1998; Halford et al. 2004), which can be very fast or slow depending upon relative abundance of fast- and slow-growing species (e.g., Linares et al. 2011, Pratchett et al. 2013). Fast-growing tabular and branching corals, for example, are the primary habitat-forming species (e.g. Coker et al. 2014) and are usually very common because they are able to rapidly re-colonise reef habitats following a disturbance (Highsmith 1982, Tunnicliffe 1983, Hughes et al. 1992, Hall & Hughes 1996, Linares et al. 2011, Pratchett et al. 2013). However, these corals are also the most susceptible to acute disturbances such as coral bleaching (Marshall & Baird 2000), outbreaks of *A. planci* (Pratchett 2010), and cyclones (Woodley et al 1981; Madin and Connolly 2006). Other growth forms such as massive and columnar, even though they have slower growth and lower rates of population turnover, they tend to be more resistant to acute disturbances (Connell 1973).

It is also important to realize that recovery from periodic and unpredictable acute disturbances operates against a background of chronic and more persistent disturbances, which can exert significant influence on demographics and biological interactions (Connell et al. 1997; Death et al. 2009), thereby affecting susceptibility to, and recovery from, acute disturbances (Andres and Witman 1995). There are no periods free of disturbances on coral reefs, as is the case for most ecosystems (Lugo and Scatena 1996; Lewis et al. 2004; Wakeford et al. 2008; van Mantgem et al. 2009; Pisapia et al. 2016). It is becoming increasingly clear that corals are routinely subject to significant rates of injuries and indeed, whole colony mortality (Pisapia and Pratchett 2014; Madin et al. 2014; Pisapia et al. 2016), and these can negatively affect the recovery capacity of populations between major acute disturbances (Wakeford et al 2008).

Good appreciation of the cumulative impacts of multiple and often diverse disturbances on coral reef organisms (Trapon et al 2011), as well as the capacity to effectively project consequences of future disturbances (e.g., Riegl and Purkis 2009) is fundamentally dependent upon access to long-term data. While there are some locations that benefit from established long-term monitoring programs (e.g., Australia's Great Barrier Reef: Death et al 2012), information on long-term changes in the abundance and structure of coral assemblages is increasingly being generated from analyses of meta-data (Gardner et al 2004; Trapon et al 2011). While there is often strong recovery in the aftermath of major disturbances (Zahir et al 2009; Trapon et al 2011; Gilmour et al 2013; Morri et al 2015) most long-term studies reveal sustained declines in live coral cover (e.g., Gardner et al 2004; Death et al 2012). Moreover, there have been pronounced shifts in the structure of coral assemblages (e.g., Aronson and Precht 2001*;* Berumen and Pratchett 2007; Pratchett 2010; Trapon et al 2011).

In the aftermath of major disturbances, total coral cover can increase very rapidly, but this is often conditional upon rapid growth of remnant tabular and/ or branching corals (Halford et al. 2004, Golbuu et al. 2007, Adjeroud et al. 2009). Recovery of population structure (e.g. the size structure distribution of coral populations) and community structure (e.g., the proportional representation of slow growing corals) will inevitably, take much longer. Since demographic processes such as survival, growth and fecundity are strongly size-dependent in corals (Hughes and Jackson 1980, 1985), the size structure of coral populations is an important driver of their dynamics (Bak and Meesters 1998, Meesters et al. 2001). Given inherent population dynamics, coral populations typically comprise many small individuals and relatively few large colonies (Bythell et al. 1993, Bak and Meesters 1998). In highly

perturbed environments (e.g., due to high levels of chronic disturbances or in the immediate aftermath of major acute disturbances) the size-structure of coral population is likely to be even more truncated than usual (e.g., Bak and Meesters 1999; Meesters et al. 2001; Linares et al 2011), with obvious consequences for reproduction, recruitment and population growth.

The purpose of this study was to explore trajectories in coral cover and composition within the central Maldives archipelago, especially since the 1998 mass-bleaching event. Maldivian coral reefs are among the most biodiverse reefs in the western Indian Ocean (Rosen 1971; Sheppard 2000), but are also highly vulnerable to climate change and have been increasingly exposed to anthropogenic disturbances over the last two decades (Jaleel 2013). We examined temporal changes in live coral cover and coral composition (from 1997 to 2016) and investigated the contemporary size structure of six dominant groups of corals. Importantly, we tested whether spatial variation in the contemporary structure of coral assemblages was related to differences in abiotic factors such as depth and reef typology (e.g., oceanic versus lagoonal reefs) to test whether such factors confer increased resilience on coral reef habitats (*sensu* Graham et al. 2015). Given widespread degradation of coral reef ecosystems there is increasing impetus for identifying specific reef types or environmental settings that confer increased resilience (Mumby et al 2014; Graham et al 2015), prioritizing conservation of such locations to mediate longer-term effects of changing disturbances regimes (McClanahan et al 2008) and importantly assessing the fate of coral assemblages given the predicted mass bleaching event in 2016.

Results

Long-term changes in coral cover
Mean coral cover declined from 40.08% (±12 95% CL) in 1997 to 1.69% (±3.59 95% CL) in 1998, due to the mass-bleaching. Since that time, coral cover increased fairly consistently until 2012 despite the occurrence of a tsunami in 2004, and a mild bleaching event in 2010 (Fig 1). The average annual rate of change, across all sites was 93.5% ± 3.08, and did not vary significantly between lagoon versus oceanic island, nor with depth. Since 2012, there have been some marked declines in coral cover at some islands (Bandos, Emboodhoo and Velidhu), but not others (Fesdu, Rasfari and Kuda Kandu, Udafushi) due the ongoing outbreak of *Acanthaster planci* (Table S1). Overall coral cover has not exhibited a systematic decline through time (Fig 1, Table S1), rather live coral increased in few sites (Table S1), however it showed a downward trend in 2016 in the face of the predicted mass bleaching event (Fig 1).

Aside from causing marked changes in total live cover, acute disturbances occurring in Maldives from 1997 to 2016 changed the relative abundance of key genera through time (Fig 2). In 1998, live cover of *Acropora* and *Pocillopora* was nearly 0%, while *Porites* was <2%. In 2009 live coral cover of branching and tabular *Acropora* increased to 12.6%±3.53 and was significantly higher than *Pocillopora* and *Porites* (1.51% ± 0.75 and 1.8% ±0.51 respectively) (Fig 2). *Acropora* showed an upward trend until 2016 however during the outbreak of *A. planci* live cover was lower that the other taxa and started to decline at 10 m (Fig 2).

Coral size-frequency distributions
A total of 1966 colonies were surveyed in 2016, across 42 transects at 7 sites. muricata. The structure of coral populations varied significantly among taxa (ANOVA, $F_{7,1922} = 44.56$, p = <0.001). Based on Tukey's post hoc test, *A. muricata* surface area was significantly larger than all other species reaching 3846.45 cm (± 17.66 SE), while *Porites* spp had the smallest

colony size 0.04 cm (± 4.93 SE). Within taxa, size-frequency distributions did not vary between depths or between inner versus outer islands (KS test, P > 0.01). When using the untransformed data, there was a prevalence of smaller colonies (Fig 3) in all coral taxa except for *A. muricata*, resulting in positively skewed size-frequency distributions (Fig 3). *A. muricata* had a larger percentage (62%) of colonies in the largest class size (>10.000 cm^2) compared to the other species (Fig. 3). By log-transforming the data, the size-frequency distributions became more normally distributed compared to the untransformed data (Fig. 3). Transformed size-frequency distributions for all coral taxa were negatively skewed, with a preponderance of colonies in the largest size-classes (Fig 3, Table 1). Size-frequency distributions were also leptokurtic, peaked and highly centralized around the mean, indicative of slower population growth (Fig 3, Table 1).

Tabular *Acropora* had the greatest mean colony size (4.57 cm^2), followed by *A. muricata* (4.07 cm^2), while *Porites* spp (3.35 cm^2) had similar to that of *Pocillopora* (3.34 cm^2) (Table 1). The CV ranged from 19.9 for *Porites* spp, to 27.1 for *Pocillopora* (Table 1). The total range of skewness (g_1) was −0.01 (for *A. humilis*) to -0.49 (for *Pocillopora*). Kurtosis (g_2) was highly positive for all the species ranging from 2.34 in to 3.15 in *A. muricata*.

In *Porites* spp, tabular *Acropora* and *A. muricata* percentage of partial mortality increased as the colonies became larger (Fig 3), while in *Pocillopora* spp and *A. humilis* percentage of partial mortality increase with increasing size but then decrease in the largest size classes (Fig 3). Mean percentage of dead tissue was highest in *A. muricata* and *Porites* (27.1% ±2.3 and 11.3% ±0.6 respectively) while it was lowest in tabular *Acropora* (3.1% ±1.3) (Fig 3).

Except for *A. muricata*, mean colony surface area varied significantly among the study sites in all coral taxa (Table 3) with all the sites differing one from another (Tukey test >0.005). There was not a clear distinction, but rather a great variability among sites (Table 2). Mean colony surface area did not vary with depth in any coral taxa while varied with reef typology in *Porites* and *Pocillopora* with slightly larger colonies in the oceanic reefs (Tukey test <0.05).

Discussion

This study shows that coral assemblages in the Maldives slowly recovered in the immediate aftermath of the 1998 mass coral bleaching event, whereby coral cover increased from 1.69% to 37.4% within a decade (average annual rate of change in coral cover was 93.5% ± 3.08). In 1997, coral communities were mostly dominated by *Acropora* (Bianchi et al. 1997) while after the 1998 mass bleaching event only bleaching-tolerant massive and sub-massive genera such as *Porites* and *Pavona* survived, even though in very low abundance (Edwards et al 2001; Zahir 2002). The1998-bleaching event extirpated the temperature sensitive competitive dominant genera, such as *Acropora*, *Pocillopora* and *Montipora* (Edwards et al 2001; Bianchi et al. 2003; McClanahan et al. 2007). Abundance of these sensitive taxa was lower compared to the rest of the Western Indian Ocean region (Tamelander 2002; Bianchi et al. 2003; McClanahan et al. 2014) but then increased up until 2016. In Kenyan reefs *Pocillopora* and *Acropora* started to recruit in 2001 (Tamelander 2002), while in Maldives recruits of *Acropora* and *Pocillopora* only increased in 2009–2014 (Morri et al. 2015), in 2001 *Pavona* was the most dominant recruit (Zahir et al 2002). Recovery of degraded reefs depends on the relative contribution of growth of remnant corals versus recruitment and subsequent growth of new colonies (Halford et al. 2004). The low percentage of surviving *Acropora* and *Pocillopora* colonies after the 1998 bleaching event suggests that regeneration at the study

sites has been through sexual recruitment.

Research on coral reef disturbances, and corresponding changes in the structure of coral populations and communities, almost invariably focuses on large-scale, unpredictable and acute disturbances (e.g., De'ath at al. 2012), essentially overlooking more chronic disturbances that can have important impacts on population and community dynamics (Lugo and Scatena 1996; Wakeford et al 2008; Madin et al 2014; Pisapia et al 2016). Similarly, there is very limited effort to quantify chronic disturbances in Maldives (e.g., fishing pressure, sedimentation, and/or eutrophication), let alone assessing potential impacts (e.g., rates of background injury and mortality, or the extent to which coral growth is suppressed) on corals. It also appears that loss of corals is largely explained by the occurrence of acute disturbances, including bleaching, tsunami, and outbreaks of *A. planci*, all of which have contributed to significant coral depletion in other locations in the Indian Ocean and Pacific (Wilson et al 2006; Death et al 2012). Importantly, Maldives are experiencing a growing human pressure due to coastal development and tourism growth (Jaleel 2013). However, water chemistry seems to be similar regardless human pressure, indicating that pollution may play a minor role in structuring Maldivian reefs (Spezzaferri et al under review).

Coral cover in the Maldives has recovered since the 1998 mass bleaching, but still very little is known about the longer term (multi-decadal) trend and this largely limits current predictions on recovery rates following the major mass bleaching event expected to occur in 2016. If coral cover only returned to pre-bleaching coral cover after more than a decade, recovery following the ongoing outbreak of *A. planci* and the predicted bleaching in 2016 might be seriously protracted. From 1997 to 2016, there was a major mass bleaching event in 1998, one tsunami, a mild bleaching event in 2010 and one outbreak of *A. planci* on Maldivian reefs (Zahir et al. 2010; Morri et al 2015), while no large storms impacted the study sites (Zahir et al., 2010; Tkachenko 2012). Outbreaks of *A. planci* are one of the principal causes of coral loss in the Indo-Pacific (Bruno and Selig 2007; Death et al 2012), often killing up to 90% of scleractinian corals (Done 1985). *A. planci* outbreaks were previously reported in the Maldives in the 90's (Ciarapica and Passeri 1993), however in 2014-2015 density of starfish was reported to be higher (Saponari et al 2014). Recovery of coral cover following outbreaks is typically very slow (Randal 1973) and it may take between 10 and 40 years (Randal 1973; Colgan 1981; Done 1988; but see Trapon et al 2011).

Coral reefs in the Maldives are highly vulnerable to climate change [the threshold for coral bleaching is just below 31°C (NOAA Coral Reef Watch 2015)] and are exposed to high levels of human stress (Jaleel 2013). The recovery rate after the 1998 mass bleaching event has been variable both in terms of coral cover and return to the original coral community composition (Zahir et al 2010; Morri et al 2015). This and few other studies (e.g., Zahir et al 2002; Edwards et al 2001; Morri et al 2015) suggested that coral cover was around 40.08% ± 12.07 in 1997 (Zahir et al 2002) and only returned to pre-bleaching values in 2012 (42.1% ± 1.26) before it started to decline again due to the 2015 *A. planci* outbreak. This showed a slow recovery compared to Chagos archipelago (Sheppard et al., 2008) and other remote Indian Ocean locations (Gilmour et al., 2013) with similar oceanographic conditions. Importantly, in Maldives many coral taxa have not come back yet after the 1998 mass bleaching event (Morri et al. 2015).

Aside from temporal changes in coral cover, the present study also explored the size-frequency distribution of five major dominant coral taxa, providing significant insights into potential effects of recent disturbances and the likely future for these dominant and

ecologically important coral populations. Some populations comprised many smaller colonies, however once log-transformed, the size-frequency distributions of all coral species were dominated by larger size classes with over-centralized, peaked distributions (negatively skewed with positive kurtosis). Tabular *Acropora*, *A. muricata*, *A. humilis* and *Pocillopora* spp were expected to show a flat size-frequency distribution which is characteristic of species with fast growth and high population turnover (Guzner et al. 2007). Conversely, kurtosis was positive (e.g., peaked distribution) likely due to increased incidence of disturbances suggesting that recent disturbances rather than fast growth rates are structuring size-frequency distribution of these coral taxa at the study sites. Positive kurtosis observed here results from high mortality of small and large colonies and this may likely be due to the ongoing *A. planci* outbreaks in Maldives. Importantly, *A. planci* has been shown to increase rates of partial mortality and total mortality in all size classes (Done 1988).

In this study, however, the negative skewness observed in the transformed size-frequency distributions indicated that the smaller size classes were generally under-represented. There are two possible explanations for this pattern; i) recent disturbances (especially outbreaks of crown-of-thorns starfish) may be having a disproportionate impact on small corals, or ii) this may suggest that populations are recruitment limited and receiving less replenishment than expected. Since recruitment rates of *Acropora* and *Pocillopora* were high in 2014 (Morri et al. 2015), it is likely that the ongoing outbreak of *A. planci* is killing the small corals leaving behind larger colonies. Also disturbance history can greatly affect the population response to new disturbances (Fong and Glynn 2000). Since fecundity is strongly and positively correlated to colony size (e.g., Hughes & Jackson, 1985; Babcock, 1991), the larger colonies observed here may contribute disproportionally to the reproductive output of their population and may provide sufficient larval supply to replenish coral losses (Riegl 2002; Baker et al. 2008).

In this study, partial mortality increased with colony size in *Porites* spp, tabular *Acropora* and *A. muricata.* Similarly to fragmentation, partial mortality is critical in determining the size of coral colonies, as the loss of living tissue can cause colonies to regress in size (Hughes 1984; Wallace 1985). The vulnerability of an individual to agents of partial mortality increase with colony size, while the probability of whole-colony mortality decreases because in large colonies some parts are likely to survive lesions (Jackson 1979; Hughes and Jackson 1985; Babckcok 1991). Different incidence of partial mortality among size classes observed here, suggests size-specific susceptibility to agents of coral mortality such as sedimentation, predation, fragmentation and competitive interactions (Bak and Meesters 1998). Higher rates of tissue loss with increasing size may also be due to accumulation of old injuries. Regeneration of injuries is often incomplete and larger and therefore older colonies may have more time to accumulate multiple old lesions (Meesters et al. 1996). The energetic costs of regeneration likely vary with different size classes. An injury on a small individual affects a greater area than on larger colonies and is likely to have a higher energetic cost in terms of regeneration due to limited resources available within a colony (Henry and Hart 2005).

While there was significant spatial variation in mean colony size of all coral taxa (except *A. muricata*), this study did not detect any clear and consistent difference between depths and between exposed and less exposed locations. Only *Porites* and *Pocillopora* showed slightly larger colonies in the oceanic reefs compared to the lagoonal ones. These findings may suggest that other factors including disturbance regime and life history processes further modify the structure of coral populations. Differences in recruitment, growth, partial and total mortality rates may also cause spatial variation in the size structure as they can vary with

small spatial scale (Baird & Hughes 1997).

This study documented long-term changes in coral communities and showed how disturbance regime structured size frequency distribution in the focal species. We showed that Maldivian systems are slowly capable of recovery following multiple recurrent disturbances, however this will likely change in a scenario of more frequent and severe disturbances. From 2012 to 2016 coral cover showed a downward trend due to the ongoing outbreak of *A. planci*, in addition a major mass bleaching event is expected to occur in 2016, which will likely lead to highly protracted recovery times. With increasing frequency of acute disturbances and escalating effects of climate change and human pressure, it is important to increase understanding on ecosystem recovery capacity, and changes in communities (Darling et al., 2013). Degradation and loss of coral reef ecosystems has serious ramifications for structure and dynamics of reef communities, such that knowledge of long term changes in coral composition and life-history dynamics is fundamental to effective ecosystem management. Changes in habitat quality and quantity need to be evaluated and long-term monitoring is the key to understand the future evolution of coral reef ecosystems.

Material and Methods

Study site

The Maldives comprise 16 complex atolls with ca.1120 islands arranged along the Chagos-Maldives-Laccadive ridge in the central Indian Ocean from about 7°07′ N to 0°40′ S. This study surveyed 7 islands in three atolls in the central Maldives archipelago. A total of three islands with exposed ocean-facing reefs on the atoll rim and four islands inside the sheltered atoll lagoon were considered to test for differences in contemporary habitat structure based on reef typology. In February-March 2016, the cover and composition of corals, as well as size structure for six distinct coral taxa (*Acropora hyacinthus, Acropora cytherea, Acropora muricata, Acropora humilis , Pocillopora spp,* and massive *Porites*) were measured at two depths (5m and 10m), at both inner and outer reef locations at each of 7 islands (Table 3). The focal species were selected based on their reported abundance across all study sites (Morri et al 2010) but also because of their contrasting morphologies and life-history strategies (Darling et al. 2013).

To measure size structure of coral species, three replicate 10 x 2m belt transects were laid parallel to the reef edge, on both the reef crest (5 meters) and slope (10 meters). For every colony sampled, the maximum diameter was recorded. Partial mortality (percentage of tissue loss) was also visually estimated *in situ* to the nearest 5% for each surveyed colony and causes of injuries were also recorded, where possible following Pisapia and Pratchett 2014. Estimates of total coral cover and composition (relative abundance of all genera) were derived using line transect methods, following Loya 1978, along the fiberglass tape used to delineate each belt transect.

Long-term changes in coral cover

Recent changes in coral cover and composition were explored by compiling data from 13 distinct studies (Zahir 2000, 2002, Zahir et al 2002; Zahir et al 2005, 2010; Edwards et al 2001; Lasagna et al 2008, 2010; Muthiga 2008; Morri et al 2010, 2015; McClanahan and Muthiga 2014; Rilwan et al 2016), which provide historical estimates of total coral cover, largely based on single surveys at individual locations between 1993 and 2014 (e.g., Zahir 2000, 2002; Zahir et al 2002a, Zahir et al 2009, 2011). There has however, been routine monitoring at five of the sites considered in this study, using mostly consistent methods since

1998 (Zahir 2000, 2002; Zahir et al 2002, 2010; Rilwan et al 2016), prompted by the desire to document recovery of coral assemblages following the 1998 mass-bleaching (Zahir et al 2010). Initial surveys were conducted in 15 sites across 6 atolls at 5 m almost every year until 2005 using three replicate 50-m line intercept transects. Since 2009 data were collected in the same sites at both 5m and 10m depths, but using four replicate 20-m point intercept transects (Rilwan et al 2016).

Data analyses

The temporal occurrence and severity of major disturbances such as coral bleaching, tsunami, management regime and outbreaks of crown-of-thorns *Acanthaster planci* (COTS) was assessed with published literature. To quantify total coral cover trends, annual geometric rate of change in coral cover for each year was calculated following Côté et al. 2005. Geometric rates of change in live coral cover were calculated based on the relative change in coral cover between respective samples, and it was taken into account that the temporal changes in coral cover were nonlinear following Côté et al. 2005 (e.g., considering change from year to year in exponentially declining or increasing coral cover).

Differences in coral cover trend from 1997 to 2016 between outer and inner islands and between 5 m and 10 m were analyzed using a Generalized Least Squares model. Coral cover was the dependent variable while island position, water depth and time were the predictors. Models were compared by maximum likelihood and the model with the lowest Akaike information criterion (AIC) was chosen as the best representation of the variation in the data.

To better understand consequences of recent disturbances on the population's structure of dominant coral taxa, we examined size-frequency distributions the maximum diameter (cm) was used to approximate the 2-dimensional projected surface area of each coral colony, following Linares et al. (2011). Colony surface area (cm^2) was converted to living area by subtracting the percentage of mortality for each colony. Colony surface-area data were log_{10} transformed to normalize size- frequency distributions and increase resolution among smaller size classes, following Bak & Meesters (1998).

Variation in the population structure of dominant coral taxa between depths (5 m versus 10 m) and between reefs (outer islands vs inner islands) was investigated using 2- sample Kolmogorov–Smirnov (KS) tests. Variation in colony sizes, coefficient of variation, (CV), skewness (g_1) and kurtosis (g_2) were calculated. The geometric mean provides relative measures of colony size providing information relevant to other key demographic process, such as reproductive output (Hall and Hughes 1996). The CV is the standard deviation as percentage of the mean and describes the variation in the data set and allows for comparisons irrespective of the mean. Skewness describes the relative abundance of colonies that are smaller or larger than the geometric mean. If the skewness is negative, the population is skewed to the left, with a relatively larger proportion of colonies in the larger size classes than in the smaller size classes (Bak and Meesters 1998). If the skewness is positive the population is skewed to the right, containing a larger number of individuals in the smaller size classes. Kurtosis describes the concentration of data around the central mode of a distribution among populations indicating whether the data is peaked or flat relative to the normal distribution. If kurtosis is negative, the distribution is platikurtic with a wide peak around the mean. Conversely, a positive kurtosis indicates the distribution is leptokurtic, which is peaked and highly centralized around the mean (Adjeroud et al. 2007).

Differences in surface area of living tissue (SA) among sites were simultaneously tested for

each coral taxa using a Three-ways ANOVA with surface area as dependent variable and sites, reef typology (lagoon vs oceanic) and depth (5m and 10m) as independent. In all the analyses *A. hyacinthus* and *A. cytherea* were pooled because sample sizes were small (less than 100 individuals for each species) and demographics expected to be very similar for these two "tabular" corals. Difference in surface area of living tissue (SA) among species were tested using a One-way ANOVA and a Tukey's post hoc test was then utilized to determine specific differences among species.

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Acknowledgment

Figure Legend

Fig 1. Variation in mean (±95% CL) coral cover at 5 meters in all study sites. The occurrence of the 1998 and 2010 coral bleaching events, the tsunami in 2004 and outbreaks of *A. planci* in 2015 is shown with arrows. Data for 2016 were collected during the present study, while historical data on study sites from 1997 to 2013 were extrapolated from Zahir 2000, 2002, 2005, 2009, 2011; Lasagna et al 2008, 2010; Edwards et al 2001; Muthiga 2008; Morri et al

2010, 2015; McClanahan and Muthiga 2014 and Rilwan et al 2016.

Fig 2. Temporal variation in mean percentage live coral cover (±95%CL) of major coral genera *Acropora, Pocillopora* and *Porites* at the study sites at 5m and 10m depth in 1998, 2009 and 2016.

Fig 3. Log-transformed and untransformed size-frequency distributions of *Acropora muricata*, tabular *Acropora*, *Acropora humilis*, *Pocillopora* spp and *Porites* spp. The black line indicates average partial mortality (%) for each size class.