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ACROPORA SIZE-FREQUENCY DISTRIBUTIONS REFLECT SPATIALLY VARIABLE CONDITIONS ON CORAL REEFS OF PALAU

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ABSTRACT

The extreme thermal stress event of 1998 caused extensive coral mortality on Palau's reefs. While impact varied in accordance with coral species (Scleractinia) and habitat, the acroporid corals were the most vulnerable, and there was much concern about how long it would take the reefs to recover. Seven years after the thermal stress, long-term monitoring has shown rapid recovery of coral coverage, which was highest on the western reefs of Palau, although higher *Acropora* recruitment favored the east coast. Differential recovery may have resulted from higher remnant regrowth, higher post-settlement survival, or more rapid growth of recruits on the western reefs. Here we test the latter two hypotheses to examine which processes were favored on the western outer reefs. If corymbose *Acropora* colony densities on western reefs are the same or higher than eastern reefs, we can infer favorable post-settlement survival on western slopes, because *Acropora* recruitment was higher on eastern reefs. In contrast, differential growth capacity would show larger colonies on the western reefs with similar colony densities. We undertook an extensive, depth-stratified spatial survey of corymbose *Acropora* size-frequency distributions. The western reefs had significantly larger *Acropora digitifera* (Dana, 1846) at 3 m, and larger *Acropora nasuta* (Dana, 1846), *Acropora cerealis* (Dana, 1846), and *Acropora selago* (Studer, 1878) at 10 m, while colony densities did not differ spatially. We conclude that for the dominant *Acropora* colonies post-recruitment survival is higher and coral-colony growth is more favorable on the western reef slopes of Palau.

Coral reefs are culturally and economically important to island nations such as Palau (Hawkins and Roberts, 1994; Yukihira et al., 2007). Yet, coral reefs are subjected to both local threats, which include overfishing and land-use change, and warming oceans, linked to a changing climate. To reduce local threats, Marine Protected Areas (MPAs) have become a popular management tool in Palau and throughout the Micronesian region. While a network of marine protected areas may lead to conservation benefits for Palau, global seawater temperature stress events are unmanageable at the local scale. Nonetheless, the network may add regional resilience by protecting some habitats that are more tolerant to seawater temperature stress.

Indeed, global-climate change has been most obvious on coral reefs in the form of thermal stress and coral bleaching (Baird and Marshall, 1998; Loya et al., 2001; Aronson et al., 2002). While a variety of physical and chemical factors cause bleaching (Downs et al., 2002; Edmunds, 2005; Fabricius, 2006), bleaching in 1998 was a consequence of anomalous thermal stress that resulted globally in extensive reef-coral mortality. *Acropora* species were particularly hard-hit (Loya et al., 2001; McClanahan et al., 2001) because they are sensitive to high irradiance and temperature. Of the 315 sites examined on Palau in 2001, > 80% of the sites had 0%–5% *Acropora* cover (Golbuu et al., 2007). There was much concern regarding the time frame of recovery at Palau (Bruno et al., 2001).

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Palau coral reefs did eventually recover. In 2004, Golbuu et al. (2007) noticed that western reefs had recovered faster at 10 m than eastern reefs at the same depth. They suggested that remnant regrowth was largely responsible in the early stages of recovery, particularly at 10 m, but after 2004, the shallow reefs (3 m) recovered more rapidly because of high recruitment pulses. Their data also indicated that while more recruits on average were found on western reefs, the eastern reefs supported more *Acropora* recruits (in 2001 and 2002) (Golbuu et al., 2007). While the Golbuu et al. (2007) study identified important changes to the reef "state," the underlying processes that caused the spatial differences in recovery remained unknown.

If a disturbance is intense and reefs become depauperate of live corals, then size-frequency distributions provide a useful proxy of integrative processes responsible for larval recruitment, their survival, and differential colony growth (Bak and Meesters, 1998; van Woesik, 2000; Dikou and van Woesik, 2006; Zvuloni et al., 2008). But size-frequency distributions alone cannot distinguish differential recruitment from post-settlement mortality and subsequent growth. Therefore, we chose to examine both the size-frequency distribution of corymbose *Acropora* species and their densities to test whether differential post-recruitment survival or differential growth was causing the major differences in coral-cover recovery between the western and eastern outer reefs of Palau.

We selected corymbose *Acropora* for three main reasons: (1) it is an important Indo-Pacific reef builder (Wallace, 1978; van Woesik and Done, 1997), (2) the shallow reef slopes of Palau appear to have been dominated by mixed assemblages of *Acropora* corals for long-time periods (Kawaguti, 1944; Kayanne et al., 2002), and (3) corymbose *Acropora* colonies, when compared with poritids and faviids, do not heal well from remnant survival. Therefore, the remnants of damaged corymbose *Acropora* colonies are not easily confused with colonies that have recruited and subsequently grown from sexual recruits.

Even though past studies found higher *Acropora* recruitment on the east coast, we suspect that the western outer reefs are most favorable for both survival and growth, given that the western reefs recovered more rapidly than the eastern reefs (Golbuu et al., 2007). We test the hypotheses that (1) post-recruitment survival is higher on the western reefs, and (2) that coral-colony growth is more favorable on the western reefs. These hypotheses were tested by comparing spatial differences in both colony density and size-frequency distributions, respectively. *Acropora* recruitment was higher on eastern reefs, near the time of survey, therefore (1) if densities of post-juveniles are similar on eastern and western reefs or (2) if we find higher densities on western reefs, we can infer favorable post-settlement survival on western slopes. If we find larger corymbose *Acropora* colonies on western reefs we can infer favorable growth conditions on western reefs 7 yrs after the thermal disturbance.

Materials and Methods

Field Sampling.—The islands of Palau are located in Western Micronesia (Fig. 1). In 2001, the Palau International Coral Reef Center (PICRC) launched a long-term monitoring program. For the present study, we include only nine outer reef sites, five on the western reefs, and four on the eastern reefs. Sampling was undertaken at 3 m and 10 m using replicate belt transects. At each depth, five replicated 20 m transects were placed along the substrate and each *Acropora* colony within 30 cm of either side of the transect, was measured for maximum

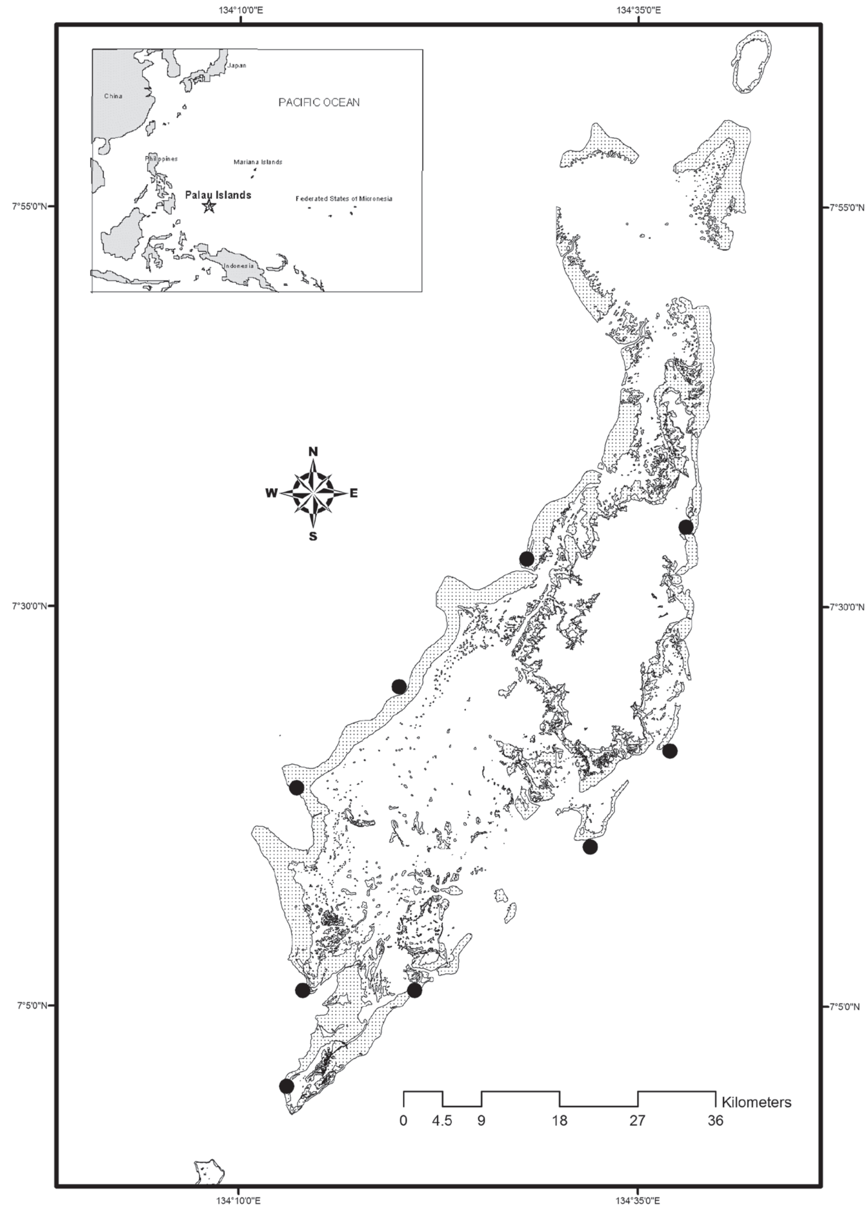

Figure 1. Map of Palau showing location of the nine study sites (marked by dots), inset (showing general location of Palau).

diameter (mm) (i.e., belt transects were 0.6 m × 20 m), and only colonies with their center within the belt were measured, minimizing biases (Zvuloni et al., 2008).

Data Analysis.—All data analyses were conducted in Statistica®. Because some species were uncommon, insufficient numbers prevented statistical comparisons among sites (Table 1). We focused on the following species: the *Acropora humilis* group (*Acropora digitifera*, *A. humilis*, and *Acropora gemmifera*), the *Acropora nasuta* group (*A. nasuta, Acropora cerealis*, and *Acropora secale*), the *Acropora selago* group (*A. selago, Acropora tenuis*, and *Acropora striata*), and *Acropora hyacinthus*. We used the Mann-Whitney U test to compare coral-colony densities between the western and eastern reefs, and the Kolmogorov-Smirnov test (K-S test) to test for differences in size-frequency distributions.

Table 1. Site occupancy and density of *Acropora* species found at two depths (3 m and 10 m) on the exposed reefs of Palau in 2005. Although 49 species were recorded in the field surveys, only 37 are presented here because 12 species were very rare and only recorded in one transect.

Species	% site occupancy (9 sites)	Colony density per 0.6 m × 20 m transect (± SE) 3 m	10 m
Acropora digitifera (Dana, 1864)	100	3.32 (0.71)	0.22 (0.09)
Acropora gemmifera (Brook, 1892)	78	0.62 (0.24)	0.14 (0.07)
Acropora millepora (Ehrenberg, 1834)	78	0.28 (0.07)	0.14 (0.09)
Acropora cerealis (Dana, 1846)	78	0.28 (0.10)	0.56 (0.25)
Acropora humilis (Dana, 1846)	100	0.26 (0.08)	0.06 (0.02)
Acropora secale (Studer, 1878)	67	0.19 (0.08)	0.03 (0.02)
Acropora subulata (Dana, 1846)	33	0.12 (0.08)	0.12 (0.06)
Acropora hyacinthus (Dana, 1846)	78	0.11 (0.05)	0.24 (0.16)
Acropora austera (Dana, 1846)	11	0.12 (0.12)	< 0.01
Acropora microclados (Ehrenberg, 1834)	33	0.07 (0.05)	< 0.01
Acropora listeri (Brook, 1893)	22	0.06 (0.03)	< 0.01
Aacropora nasuta (Dana, 1846)	56	0.05 (0.03)	0.13 (0.08)
Acropora loripes (Brook, 1892)	44	0.05 (0.04)	0.16 (0.10)
Acropra selago (Studer,1878)	44	0.05 (0.04)	0.37 (0.33)
Acropora macrostoma (Brook, 1891)	33	0.05 (0.03)	0.02 (0.02)
Acropora monticulosa (Bruggemann, 1879)	56	0.04 (0.02)	0.04 (0.01)
Acropora horrida (Dana, 1846)	44	0.03 (0.03)	0.05 (0.03)
Acropora anthoceris (Brook, 1893)	33	0.03 (0.02)	0.02 (0.01)
Acropora abrotanoides (Lamarck, 1816)	11	0.03 (0.02)	0.05 (0.03)
Acropora cytherea (Dana, 1846)	33	0.02 (0.02)	0.06 (0.06)
Acropora tenuis (Dana, 1846)	22	0.02 (0.02)	0.05 (0.02)
Acropora abrolhosensis Veron, 1985	22	0.01 (0.01)	0.02 (0.02)
Acropora formosa (Dana, 1846)	11	0.01 (0.01)	0.04 (0.02)
Acropora globiceps (Dana, 1846)	11	0.01 (0.01)	< 0.01
Acropora lutkeni Crossland, 1952	11	0.01 (0.01)	< 0.01
Acropora nobilis (Dana, 1846)	11	0.01 (0.01)	< 0.01
Acropora divaricata (Dana, 1846)	56	< 0.01	0.19 (0.14)
Acropora bruggemanni (Brook, 1893)	44	< 0.01	0.17 (0.16)
Acropora clathrata (Brook, 1891)	22	< 0.01	0.07 (0.04)
Acropora granulosa (Milne-Edwards and Haime, 1860)	22	< 0.01	0.02 (0.01)
Acropora wardii (Verril, 1902)	22	< 0.01	0.10 (0.08)
Acropora donei Veron and Wallace, 1984	11	< 0.01	0.01 (0.01)
Acropora florida (Dana, 1846)	11	< 0.01	0.02 (0.01)
Acropora kimbeensis Wallace, 1999	11	< 0.01	0.06 (0.06)
Acropora microphthalma (Verril, 1859)	11	< 0.01	0.03 (0.02)
Acropora stodartii Pillai and Scheer, 1976	11	< 0.01	0.01 (.01)
Acropora striata (Verril, 1866)	11	< 0.01	0.02 (0.02)

RESULTS

We recorded 49 species of *Acropora* at nine sites, which is well over 50% of the known *Acropora* species for Palau (Randall, 1995; Table 1). *Acropora digitifera* was the most ubiquitous regionally, and the most abundant species locally, particularly

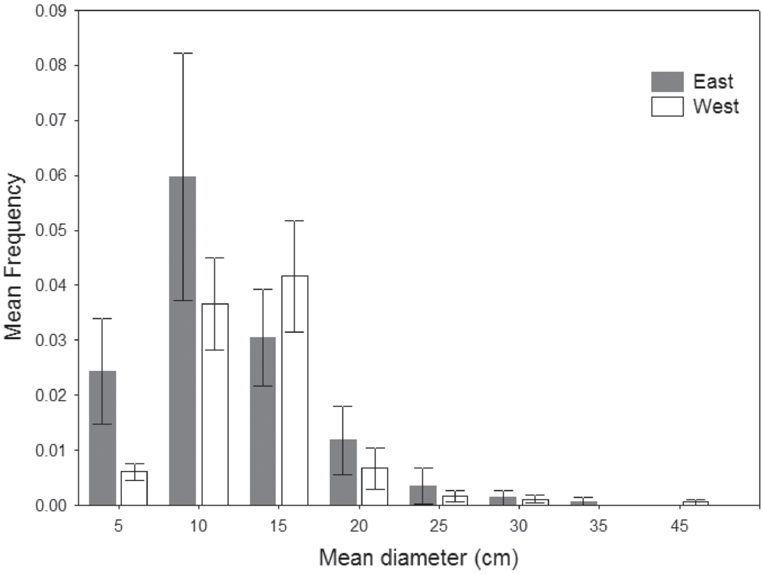

Figure 2. Mean (± SE) size-frequency distribution of *Acropora digitifera* on the east and west exposed reefs of Palau in 2005.

at 3 m. At any given shallow wave-exposed site, *A. digitifera* constituted 75% of the colonies recorded in 2005. *Acropora gemmifera, Acropora millepora, A. cerealis* and *A. humilis* were also common, with the latter occupying every site (Table 1). *Acropora digitifera* did not dominate 10 m slopes, comprising < 1% of the *Acropora* community, where *A. brueggemanni, A. cerealis, A. selago*, and *A. hyacinthus* were most common (Table 1).

At 3 m, *A. digitifera* colonies ranged in size from 5–15 cm maximum diameter. There was no significant difference in densities of *A. digitifera* between localities, but size-frequency distributions on shallow, western reefs differed significantly from those on shallow eastern reefs (K-S test: $P < 0.001$; Fig. 2); the shallow western slopes had more 15 cm size class colonies, and fewer 5 cm colonies than the eastern reefs. *Acropora humilis* and *A. gemmifera* did not occur in different densities or have different size-frequency distributions between localities (Table 2). At 10 m, *A cerealis, A. nasuta,* and *A. selago* colonies showed no significant differences in density, but had significantly different size-frequency distributions between the locations (K-S test: $P < 0.001$; Table 2). The eastern reefs supported more *A. cerealis* colonies < 10 cm in diameter, whereas there were more colonies > 15 cm in diameter on western reefs (Fig. 3). Similar results were evident for both *A. nasuta* and *A. selago.*

Discussion

Acropora size-frequency data provided a glimpse into the dynamics of spatial recovery of corals at Palau. Western Palauan reefs supported larger *A. digitifera* colonies at 3 m, and larger *A. cerealis, A. nasuta*, and *A. selago* colonies at 10 m, than eastern reefs. There were, however, no overall significant differences in *Acropora* colony densities between localities, yet the shallow eastern reefs supported more,

Table 2. Summary table of mean maximum colony diameter (± SE), and [number of colonies] of common *Acropora* species relative to location and depth on the exposed reefs of Palau in 2005. The K-S test examined differences in size-frequency distribution and the Mann-Whitney U-test examined differences in colony densities for each species. ns is not significant.

	Mean size (± SE) [density]				
Species	West	East	Depth (m)	K-S test P-value	Mann-Whitney U-test P-value
Acropora digitifera	11.1 (0.32) [169]	9.8 (0.37) [190]	3	0.001	ns
Acropora humilis	15.8 (1.64) [16]	13.2 (2.62) [12]	3	ns	ns
Acropora gemmifera	12.2 (5.34) [52]	12.7 (6.07) [31]	3	ns	ns
Acropora hyacinthus	21.8 (2.49) [22]	12.6 (3.54) [4]	10	ns	ns
Acropora cerealis	19.1 (1.85) [30]	7.1 (0.45) [31]	10	0.001	ns
Acropora nasuta	18.0 (3.70) [5]	6.6 (0.408) [9]	10	0.025	ns
Acropora selago	29.9 (1.47) [43]	16.5 (4.87) [4]	10	0.05	ns

small *A. digitifera* colonies than the western slopes, reflecting the higher recruitment pulses reported by Golbuu et al. (2007).

Indeed, on the western slopes, Golbuu et al. (2007) measured significantly higher recruitment for all taxa combined (in 2001 and 2002), but found significantly more *Acropora* recruits on the eastern reefs in both years. Yet, Golbuu et al. (2007) showed no relationships between recruitment densities and coral-cover recovery, and argued that recovery was most likely a consequence of high-remnant survival and regrowth at 10 m, particularly in the first few years of monitoring, followed by contributions from (sexual) recruits and their growth in subsequent years.

Although larval supply is indeed essential for the recovery of highly damaged reefs, subsequent survival of those recruits and their growth is also critical (Hughes et al., 1999; van Woesik et al., 1999; van Woesik, 2000). There are several possibilities that may have lead to the differences in size-frequency distribution of the dominant corymbose *Acropora*, favoring larger colonies on the western reefs. We note that the Kruskal-Wallis tests merely examine cumulative differences in size-frequency distributions, and do not differentiate between either large or small colony differences. But examination of Figures 2 and 3 shows more small colonies on the eastern reefs, and more large colonies on western reefs. These results suggest favorable recruitment yet suppressed growth on the eastern reefs. These findings are similar to results from Sesoko Island, Japan, whereby the median of the size-frequency distribution of *Porites* species increased over 5 yrs after a disturbance, while the size-frequency distribution of *Acropora* species remained suppressed by the environmental conditions (van Woesik, 2000). We also report here no differences in colony densities among localities, although *Acropora* recruitment was higher on eastern reefs at the time of survey. Therefore, we can infer favorable post-settlement survival and, most likely, favorable conditions for growth on western slopes, 7 yrs after the thermal disturbance, particularly for the dominant *A. digitifera* at 3 m, and *A. nasuta, A. cerealis,* and *A. selago* at 10 m.

We add a caveat that our study does not necessarily infer favorable colony growth on western slopes in the form of calcification *per se.* These slopes also may have had lower rates of colony dislodgment than the eastern reefs. Both processes (i.e., favorable calcification and lower-dislodgement rates) would show similar size-frequency differences. Indeed, the eastern reefs experience greater wind exposure, for longer

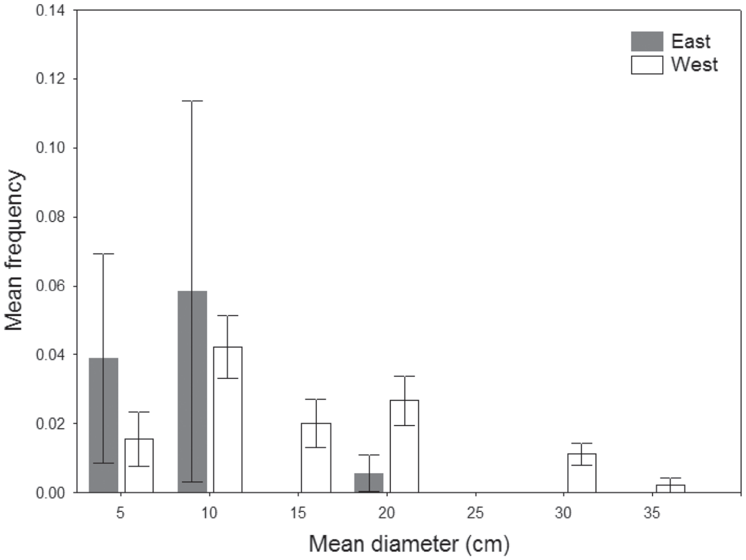

Figure 3. Mean (± SE) size-frequency distribution of *Acropora cerealis* on the east and west exposed reefs of Palau in 2005.

periods, than the western reefs. Exposure to high-wave energy increases the likelihood of colony overtoppling and dislodgement. Therefore, further field studies that track specific colonies through time, on both eastern and western slopes, will clarify the discrepancies between these two potentially important processes. We further note that many of the *Acropora* species showed no size-frequency differences between localities: for example, *A. hyacinthus* at 10 m, and *A. humilis* and *A. gemmifera* at 3 m. Although our results suggest favorable post-recruitment effects on western reefs because recruitment was higher on the eastern reefs. However, to unequivocally substantiate these claims, species-specific post-settlement processes should be tracked through time.

While the *Acropora* coral populations have rapidly recovered on Palauan reefs, the "massive" slow-growing coral colonies such as the faviids, which suffered considerable partial or absolute mortality, are still small and are recovering more slowly (Golbuu et al., 2007). In contrast, *A. digitifera* is a weedy species with 100% site occupancy. At a regional scale, high-site occupancy may have compensated for local vulnerability. But the origin of the *Acropora* recruits following the thermal stress event remains unknown. Reefs to the northeast of Palau, including Yap were not affected by the 1998 thermal stress event. Coral recruits may have come from Yap, although it is more likely that coral recruits came from a local source, which "escaped" high mortality during the thermal stress event in 1998. For example, coral on the deep eastern patch reefs and the reefs around the inner bays, where light levels are generally lower than outer reefs (Golbuu et al., 2007), experience less photoinhibition and less bleaching under high thermal stress (Takahashi et al., 2004). In this context, a widespread distribution, or high-site occupancy, enhances survival by increasing the likelihood that some sites will provide refuge for thermal stress events, thereby increasing the capacity to recovery.

High *Acropora* fecundity and rapid-growth rates potentially allow regional resilience as long as some refuge sites preserve *Acropora* populations through stress events. Locating these refuges has become a regional and indeed a global priority (Glynn, 1996; Riegl and Piller, 2003). Recovery of highly impacted, thermally stressed sites may be facilitated through recruitment from upstream refuge sites. Therefore, protecting a variety of habitats may provide regional resilience for coral reefs at scales much greater than the scales at which they are presently managed. However, in Palau, the near-shore reefs, which faired well through the 1998 thermal stress event, are currently being affected by land-use runoff (Victor et al., 2004), thus these reefs may be in most need of protection in a time of global climate change. In conclusion, reducing local anthropogenic impacts and building regional conservation resilience strategies, through hedging protection across a variety of habitats, is critical, especially on small vulnerable islands that are not immune to global scale disturbances.

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