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# Impact of two sequential super typhoons on coral reef communities in Palau

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**ABSTRACT:** Typhoons generally develop in the warm tropics, but rarely damage coral reefs between the latitudes 10° N and 10° S because they intensify at higher latitudes. However, climate change is forcing anomalous weather patterns, and is causing typhoons to take less predictable trajectories. For the first time in 70 yr, in December 2012, a super typhoon passed near the island of Palau, located at 7° N in the western tropical Pacific Ocean. A year later, another super typhoon passed over the northern reefs of Palau. This study characterized the impacts of both typhoons on coral and fish assemblages in 3 habitats (i.e. outer reefs, patch reefs, and inner reefs) and at 2 depths (i.e. 3 and 10 m). Loss of coral cover was highest on the shallow, eastern slopes (~60% coral cover). Juvenile coral densities decreased along the western reef slope and on the inner reefs, where overall coral cover scarcely decreased. These results suggested a potential stock-recruitment relationship with corals on the damaged eastern reefs. Early successional corals, particularly pocilloporids, recruited 6 mo after the second typhoon. Fish communities were generally unaltered by the first typhoon, except small parrotfishes, which doubled in density along the eastern reef-slope and increased on the inner reefs following the second typhoon. In combination, these findings demonstrate high spatial variability in coral loss, overall decreases in juvenile corals, and increases in herbivorous fishes on a tropical reef system that has rarely experienced large typhoon waves.

**KEY WORDS:** Typhoon · Corals · Fishes · Habitat · Climate · Recruitment · Resilience

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## INTRODUCTION

Climate change is forcing anomalous weather patterns and is changing the trajectories of tropical cyclones (hereinafter called typhoons, for geographic purposes) (IPCC 2013). In the Western Pacific region, coral reefs that have been regularly exposed to typhoons for millennia, including Guam (US territory) and Okinawa (Japan), support stout coral morphologies and highly cemented

reef crests (Chappell 1980, Scoffin 1993, Yamano et al. 2003). These stout coral morphologies and cemented reef crests are resistant to the large waves associated with seasonal typhoons. By contrast, reef systems in the tropics that rarely experience large wave impacts are more likely to undergo sudden changes when typhoons take low-latitude trajectories, especially those reefs dominated by branching and tabulate coral colonies (van Woesik et al. 1991, Harmelin-Vivien 1994,

Hughes & Connell 1999, Madin & Connolly 2006, Fabricius et al. 2008). The extent of coral loss also depends on the distance of a particular reef from the eye of a typhoon, and whether adjacent reefs act as barriers (Fabricius et al. 2008, De'ath et al. 2012, Beeden et al. 2015). Even at small spatial scales, of less than 1 km, coral damage caused by typhoons can vary considerably (Connell et al. 1997, Adjeroud et al. 2009, Guillemot et al. 2010, Adam et al. 2014).

Large typhoon waves can drastically alter 3-dimensional reef framework, removing the coral veneer (van Woelk et al. 1991, Harmelin-Vivien 1994). Such extensive changes to the reef can also affect the coral-associated fish assemblages (Wilson et al. 2006, Pratchett et al. 2008). Some studies have observed reduced fish densities (Lassig 1983, Bouchon et al. 1994), whereas others have observed minor effects of typhoons on fish assemblages (Lassig 1983, Walsh 1983, Fenner 1991, Cheal et al. 2002). Yet, fish with an obligate association with corals (such as butterflyfish) consistently decline following typhoons (Wantiez et al. 1997, Halford et al. 2004, Emslie et al. 2008), while the responses of herbivorous fish are not as predictable. Russ & McCook (1999) have shown a positive relationship between epilithic algae production and grazing-fish biomass on inshore reefs after the passing of a cyclone. Moreover, a recent study demonstrated that the loss of hard coral following typhoon or bleaching disturbances led to an increase in parrotfish density in the Philippines (Russ et al. 2015). Similarly, Sano et al. (1984, 1987) and Sano (2000) showed that herbivorous fishes increased after *Acanthaster planci* infestations damaged corals on reefs in southern Japan.

Algal communities can certainly undergo rapid transitions after physical and biological disturbances (Hughes 1994, Russ & McCook 1999, Adjeroud et al. 2009, Doropoulos et al. 2014, Roff et al. 2015a). For example, Roff et al. (2015a) recently showed that macroalgal blooms were evident on the outer reefs of Palau weeks after a typhoon. Macroalgae were, however, only prominent on wave-exposed sites in Palau, and not on leeward sites; although both habitats showed similarly extensive typhoon damage. Large stands of macroalgae can directly compete for space and prevent coral recruitment (Chong-Seng et al. 2014, Doropoulos et al. 2014), or can indirectly reduce the coral larval supply (Connell et al. 1997, Mumby 1999, Fabricius et al. 2008, Lukoschek et al. 2013). Yet, coral reef assemblages have been reported to

recover rapidly from disturbances in some localities in the Indo-Pacific region (e.g. Halford et al. 2004, Adjeroud et al. 2009, Gilmour et al. 2013, Doropoulos et al. 2015), including Palau (Golbuu et al. 2007). However, the predicted increase in the frequency and severity of human pressure, including global climate change (Bellwood et al. 2004, Hoegh-Guldberg et al. 2007, Hughes et al. 2010), may increase the extent of disturbance and slow the rates of recovery of reef assemblages in the near future.

The archipelago of Palau is located close to the equator (7° 21' N, 134° 28' E), bordering the main northwestern Pacific tropical typhoon zone. Palau's geographic location excludes it from most typhoon tracks in the region (Chu et al. 2012). Since 1945, which is the limit of the available typhoon records, only 1 typhoon passed near Palau, in 1990, but the impact on Palau's reefs was minimal and was restricted to the northern reefs (Maragos & Cook 1995). Therefore, prior to 2012, no major typhoons had caused significant damage to Palau's reefs for over 70 yr. In 2012, and again in 2013, Palau was impacted by 2 successive super typhoons (equivalent to category 5 on the Saffir-Simpson hurricane wind scale). Typhoon Bopha passed Palau on December 2, 2012, and Typhoon Haiyan passed Palau on November 6, 2013 (see Fig. 1). The eye of Bopha passed 40 km south of the southern island of Angaur (see Fig. 1). Typhoon Bopha had a central pressure of 920 to 930 mbar, maximum sustained northeast winds reached 135 knots, and breaking waves were recorded up to 8.7 m (Chu et al. 2012, Windguru 2015 daily archive data obtained from [www.windguru.cz](http://www.windguru.cz)). Eleven months later, the eye of Haiyan crossed directly over the northern atoll of Kayangel (see Fig. 1). Typhoon Haiyan had a central pressure of 906 mbar, maximum sustained northeast winds reached 155 knots, and breaking waves were recorded up to 8.6 m (Chu et al. 2012, Windguru daily archive data 2015).

This study examined the response of Palau's reefs to 2 successive super typhoons. We assessed the impacts of the typhoons on adult and juvenile coral colonies and on fish assemblages throughout Palau. The objectives of this study were to: (1) spatially quantify the loss of live corals, and the change in benthic community structure caused by the typhoons; (2) examine trends in juvenile coral (<5 cm) abundances pre- and post-disturbance; and (3) investigate the effects of coral loss on the composition and densities of fishes.

## MATERIALS AND METHODS

### Study sites and sampling

A total of 22 permanent study sites were surveyed in Palau, prior to the typhoons from October to December 2010, 1 mo after Typhoon Bopha from January to March 2013, and 6 mo after Typhoon Haiyan from June to July 2014. The 22 sites are part of the Palau International Coral Reef Center's long-term coral reef monitoring program. Sites include 3 different reef habitats: outer reefs ( $n = 12$ ), lagoonal patch reefs ( $n = 2$ ), and inner reefs ( $n = 8$ ). To determine whether differences in exposure influenced responses to typhoon damage, the outer reef sites were considered as either western reefs ( $n = 6$ ) or eastern reefs ( $n = 6$ ) (see Fig. 1).

At each site, five 50 m transects were haphazardly positioned at both 3 m and 10 m depths. Benthic cover, juvenile coral abundances, and coral colony sizes were measured at each replicated transect. Benthic cover was quantified by taking an image every meter along the transect tape with an underwater camera mounted on a  $0.5 \times 0.5$  m photoquadrat PVC frame. Fifty photos were taken per transect, characterizing  $12.5 \text{ m}^2$  of the benthos per transect. Images were analyzed using CPCe software (Kohler & Gill 2006), where 5 points were randomly allocated on every photograph, and the benthic substrate directly below each point was classified into benthic categories. Benthic categories included corals, fleshy macroalgae, and seagrasses (all to the resolution of genera), sponges, ascidians, crustose coralline algae, turf algae, and non-living hard substrata (e.g. sand and rubble). Table S1 in the Supplement at [www.int-res.com/articles/suppl/m540/p073\\_supp.pdf](http://www.int-res.com/articles/suppl/m540/p073_supp.pdf) provides the full list of the benthic categories that were used in the reef surveys. The percentage cover of each category was averaged among the 5 transects for each site, depth, and year. Juvenile corals were surveyed *in situ* by counting and identifying individual coral colonies smaller than 5 cm in diameter (Bak & Engel 1979, Roth & Knowlton 2009) within a 30 cm wide belt of the first 10 m of each 50 m transect. Care was taken not to include individuals produced by asexual fragmentation. Juvenile corals were identified to genus.

The abundance and size estimates (to the nearest cm) of 24 commercially important and protected species of fishes, in addition to all parrotfish (family Scaridae) species (see Table S2 in the Supplement), were recorded by an observer using SCUBA within 5 replicated 5 m wide by 50 m long belt transects. Fish

species that were surveyed included roving benthic herbivores (Acanthuridae, Scaridae, Siganidae), invertivores (Lethrinidae), and piscivores (Carangidae, Lutjanidae, Serranidae). Two experienced surveyors conducted the fish surveys. Both surveyors had received extensive size-calibration training using fish models (Bell et al. 1985).

### Interpolations of changes in coral cover

To visualize the spatial change in coral cover throughout Palau, interpolated maps were created using the software QGIS (QGIS Development Team 2015). The mean change in coral cover at each site, and at each depth, between the years (1) 2010 and 2013, and (2) 2013 and 2014, was used for subsequent interpolation. The maximum and minimum values of change in coral cover were manually set to the highest and lowest values for each year by depth, and 5 equal intervals of change were spatially interpolated for the study area using the Triangular Irregular Network (TIN) method (QGIS Development Team 2008). While all sites were used to visualize changes in coral cover over time, data from the patch reefs were excluded from all statistical analyses (described in the section below), because of the low spatial replication associated with patch reefs ( $n = 2$  sites located in the northwest). The interpolated raster layers were superimposed over the reef map of Palau.

### Data analyses

To investigate whether the typhoon explained spatial patterns of changes in total percentage coral cover, juvenile coral density, and fish densities, a series of linear mixed effects models were analyzed using the 'lme4' package in R (Bates et al. 2013, R Development Core Team 2015). Absolute changes in total percentage coral cover were examined for differences: (1) between years (i.e. between 2010 and 2013, and between 2013 and 2014); (2) between depths (i.e. 3 and 10 m); and (3) among habitats (i.e. inner reef, western outer reef slope, eastern outer reef slope), with sites treated as a random effect, nested within habitats. For total coral cover, no transformation was applied to the data, which conformed to normality and homogeneity of variances. Significant differences among habitats were further examined using the 'ghlt' function within the 'multcomp' package (Hothorn et al. 2008).

The average density of juvenile coral colonies (per m<sup>2</sup>) was compared among years (i.e. 3 levels) and among habitats (i.e. 3 levels), with sites treated as a random effect, nested within habitat. Pair-wise comparisons were explored for all significant effects using the same method as above, applying the 'mult-comp' package. The density of juvenile corals at 3 and 10 m depth were square-root transformed to conform to model assumptions of normality and homogeneity of variance.

Fish densities (per 100 m<sup>2</sup>) (from the subset of surveyed species, see Table S2 in the Supplement) were ln+1 transformed to conform to model assumptions. The data were again fit using the 'lme4' package in R. The size-frequency distributions of scarids were investigated visually and skewness values were pooled within each habitat (averaged at each site by depth) to examine whether there were changes over time (see Fig. S4 in the Supplement). Small-sized parrotfish appeared to increase post typhoon disturbance. To test this hypothesis, parrotfish were grouped into 2 different size classes that most likely represent juvenile and adult populations in Micronesia (Taylor & Choat 2014). The densities of scarids within 2 different size classes (smaller and larger than 15 cm total length [TL]) were ln+1 transformed and were compared among years and habitats using the same model structure as for total fish densities and juvenile coral densities.

Permutational multivariate analysis of variance (PERMANOVA) and principal coordinate analysis (PCO) (Anderson 2005) were conducted to compare benthic community cover (functional groups, including coral, algae, and rubble), coral-community cover (family), juvenile coral-community density (family), and fish communities (family) between depths (i.e. 3 and 10 m), among years (i.e. 2010, 2013, 2014), and among habitats (western outer reef, eastern outer reef, inner reef). Similarities were examined using the Bray-Curtis similarity index, and sites were included as a random effect, nested within habitat. A total of 999 permutations were run for each model, and significant differences were investigated using pair-wise comparisons. The data did not conform to assumptions of homogeneity prior to, or after, trans-

formations, tested using the homogeneity of dispersion test (PERMDISP); therefore, a highly conservative  $\alpha$  of 0.01 was used to infer statistical significance (Underwood 1996). Multivariate analyses were conducted using PRIMER-E v.6 with the PERMANOVA extension (Clarke & Gorley 2006, Anderson et al. 2008).

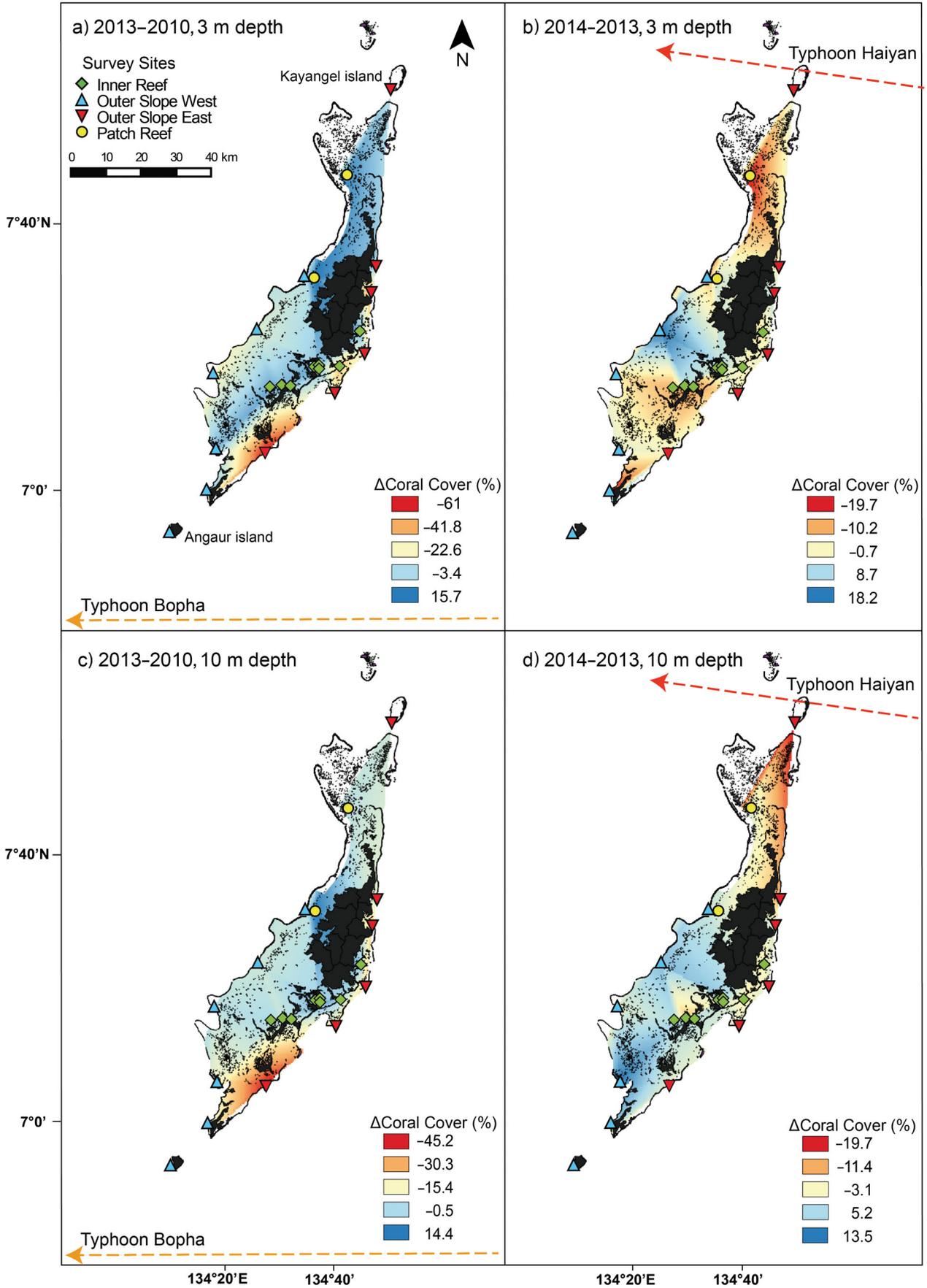
## RESULTS

### Benthic community structure

In 2010, prior to the typhoons, coral cover averaged 30% (3 m depth) and 32% (10 m depth) along the eastern outer reef slope, 34% (3 m) and 56% (10 m) along the western outer reef slope, and 51% (3 m) and 32% (10 m) on the inner reef (see Table S3 in the Supplement at [www.int-res.com/articles/suppl/m540p073\\_supp.pdf](http://www.int-res.com/articles/suppl/m540p073_supp.pdf)). Following the 2 typhoons, 3 major patterns were evident on the reefs (Fig. 1). Firstly, most of the eastern outer reefs were severely damaged following Typhoon Bopha (Fig. 1a,c), with up to 100% loss of coral cover on the southeastern slopes, which were closest to the typhoon's path (from 61% at 3 m and 45% at 10 m in 2010 to 0% at both depths in 2013) (see Table S3). Secondly, the most severe damage was recorded on the northeastern slopes following Typhoon Haiyan (Fig. 1b,d), with an average loss of 53% coral cover ( $n = 2$ , see Table S3). Thirdly, the overall extent of damage decreased with increasing depth (Fig. 1).

There were significant differences in coral cover between 2010 and 2013, both among habitats and between depths ( $p < 0.01$ ) (Fig. 1). There was a significant ( $p < 0.01$ ) decrease in coral cover along the eastern outer reef slope (−83% relative change at 3 m and −65% relative change at 10 m). By contrast, there was a moderate decrease in coral cover along the western outer reef slope (−20% relative change at 3 m and −10% relative change at 10 m), and a slight change in coral cover on the inner reefs (−3% relative change at 3 m and +3% relative change at 10 m). At both depths, the change in coral cover between the western outer reef slope and the inner

Fig. 1. Interpolation maps of change in coral cover between 2010 and 2013 at (a) 3 m and (c) 10 m, and between 2013 and 2014 at (b) 3 m and (d) 10 m.  $\Delta$ Coral Cover (%) indicates the change in live corals between years (2013 – 2010 and 2014 – 2013) at each depth. Survey sites (inner reef, outer slope west, outer slope east, and patch reef) are shown by the symbols defined in the key in (a). The tracks of Typhoon Bopha in December 2012 and Typhoon Haiyan in November 2013 are shown by the orange and red dashed arrows, respectively. See Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m540p073\\_supp.pdf](http://www.int-res.com/articles/suppl/m540p073_supp.pdf) for detailed typhoon tracks



reefs did not differ significantly ( $p > 0.3$ ). Between 2013 and 2014, there were no further significant changes in live coral cover among habitats at either depth.

In 2010, the eastern and western outer reef slopes shared similar communities, which were dominated by corals in the families Acroporidae, Pocilloporidae, and Faviidae (Fig. 2). However, between 2010 and 2013, there was a significant shift in coral community structure (families) toward non-coral substrates along the eastern outer reef slope (Fig. 2) (PERMANOVA,  $p < 0.01$ ). These non-coral substrates were identified as turf algae, rubble, and sand on the PCO (see Fig. S2 in the Supplement at [www.int-res.com/articles/suppl/m540p073\\_supp.pdf](http://www.int-res.com/articles/suppl/m540p073_supp.pdf)). A similar shift toward non-coral substrates occurred between 2010 and 2014 at both depths on the eastern outer reef slopes (PERMANOVA,  $p < 0.01$ ). By contrast, there were no changes to coral community structure (families) along the western outer reef slope over time (Fig. 2). Similarly, the inner reef coral community did not change over time, and was dominated by corals in the families Agariciidae, Mussidae, and Poritidae (Fig. 2).

### Juvenile corals

A decrease in the density of juvenile coral colonies occurred in all habitats and at both depths over time, and was most severe along the eastern outer reef slope (Fig. 3). At 3 m, juvenile coral densities decreased by 83%, from an average of 11 colonies per  $m^2$  in 2010, to 2 colonies per  $m^2$  in 2013 ( $p < 0.01$ ) (Fig. 3a). At 10 m, the density of juvenile corals along the eastern outer reef slope declined significantly from 10 individuals per  $m^2$  in 2010 to 2.5 individuals per  $m^2$  in 2013 ( $p < 0.01$ ) (Fig. 3b). There were no further changes following Typhoon Haiyan. There was a major decline in juvenile corals from the family Acroporidae over time, and an increase in juvenile coral colonies from the family Pocilloporidae at both depths over time (PERMANOVA,  $p < 0.05$ ) (Fig. 4, see Fig. S3 in the Supplement). Along the western outer reef slope, there was a significant decline in juvenile corals over time ( $p < 0.05$ ) (Fig. 3b), which was reversed a year later with an increase in juvenile coral colonies in 2014, but only at 3 m (Fig. 3a). The density of juvenile coral colonies within the inner reef was significantly lower in 2014 than in 2010 ( $p < 0.001$ ), and in 2013 at 3 m ( $p < 0.001$ ). The composition of the juvenile

coral assemblages did not change on the western slopes, nor did the assemblages change on the inner reefs throughout the study (PERMANOVA,  $p > 0.05$ ).

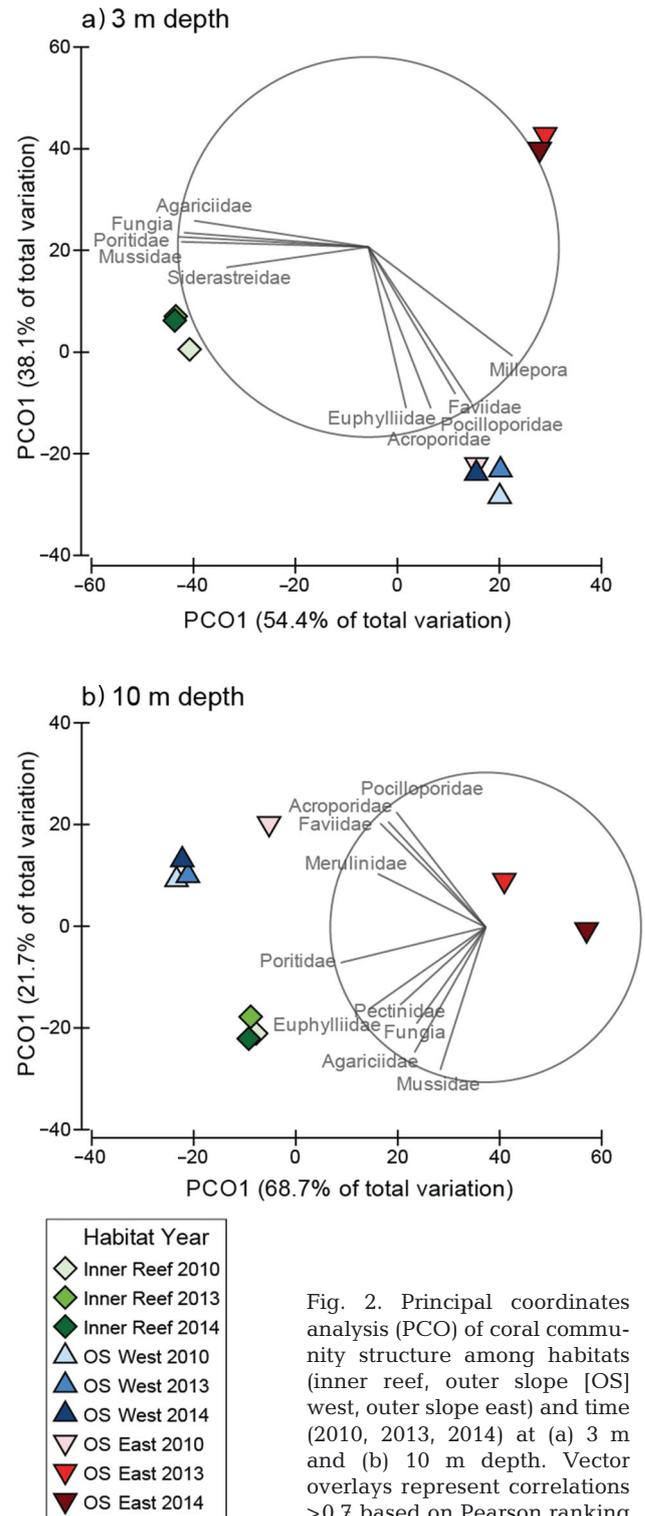


Fig. 2. Principal coordinates analysis (PCO) of coral community structure among habitats (inner reef, outer slope [OS] west, outer slope east) and time (2010, 2013, 2014) at (a) 3 m and (b) 10 m depth. Vector overlays represent correlations  $> 0.7$  based on Pearson ranking

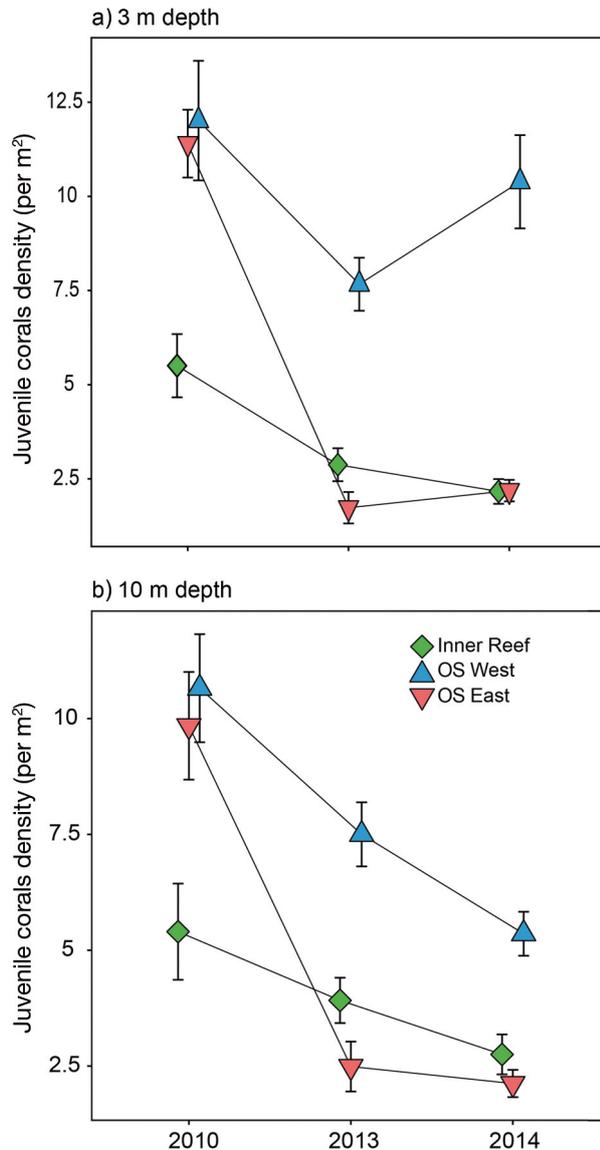


Fig. 3. Mean ( $\pm$ SEM) juvenile corals density per  $m^2$  among habitats (inner reef, outer slope [OS] west, outer slope east) and time (2010, 2013, 2014) at (a) 3 m and (b) 10 m depth

### Fishes

The abundance of fishes did not change at either depth along the eastern outer reef slope between 2010 and 2013 following Typhoon Bopha, but significantly increased ( $p < 0.05$ ) from approximately 5 individuals per  $100 m^2$  in 2010 to 10 individuals per  $100 m^2$  in 2014 following Typhoon Haiyan (Fig. 5a,b). There was also a significant increase ( $p < 0.05$ ) in fishes recorded at 3 m on the inner reefs (Fig. 5a), but there were no changes at 10 m on the inner reefs (Fig. 5b). The significant changes in the fish commu-

nities were a consequence of the doubling in the density of scarids, particularly on the eastern outer reef slope, and on the shallow inner reefs (Fig. 5c,d). The eastern outer reef slope had a higher density of small-bodied scarids (TL < 15 cm) in 2014 than in 2013 and in 2010, at both depths ( $p < 0.001$ ) (Fig. 6). This increasing trend also occurred on the inner reefs at 3 m depth ( $p < 0.01$ ) and on the western outer reef slope at 10 m depth ( $p < 0.001$ ) (Fig. 6). There was no change in the densities of scarids larger than 15 cm TL in all habitats at 3 m (Fig. 6). Large scarid densities significantly declined from 2010 to 2013 at 10 m ( $p < 0.001$ ) (Fig. 6).

### DISCUSSION

Our study in Palau highlights the high spatial variability in the loss of corals and fishes on a tropical reef system that has rarely experienced large typhoon waves. In 2010, before the typhoons, the reefs of Palau supported on average 30 to 50 % coral cover, depending on locality. The southeastern outer reef slopes were severely damaged by Typhoon Bopha, and the northeastern outer reef slopes were severely damaged by Typhoon Haiyan. There was, however, greater loss of coral cover on the shallow 3 m slopes than on the deep 10 m slopes. The spatial changes in coral cover in Palau were similar to changes reported for the Great Barrier Reef, and other Pacific localities, after the overpass of a major tropical cyclone (Fabricius et al. 2008, Adjeroud et al. 2009, Guillemot et al. 2010, De'ath et al. 2012, Beeden et al. 2015). In addition to the significant loss of live corals, juvenile coral density decreased drastically after the typhoons. Reductions in juvenile corals occurred in all habitats, including those habitats that were not directly impacted by storm waves. Although recent studies suggest macroalgae proliferation following major disturbances can reduce coral settlement resulting in bottlenecks to recovery (Chong-Seng et al. 2014, Doropoulos et al. 2014), there was no change in benthic cover in the 2 unimpacted habitats (western outer reef slope, inner reef) that showed reduced juvenile coral densities. While we cannot conclusively demonstrate the cause(s) of juvenile coral decline through correlative approaches, our results indicate the most likely causes are from (1) direct typhoon-related mortality occurring on exposed reefs; (2) indirect effects of the typhoons causing decreases in coral recruits, related to upstream losses in adult stock; or (3) some unmeasured variable was associated with the typhoon over-

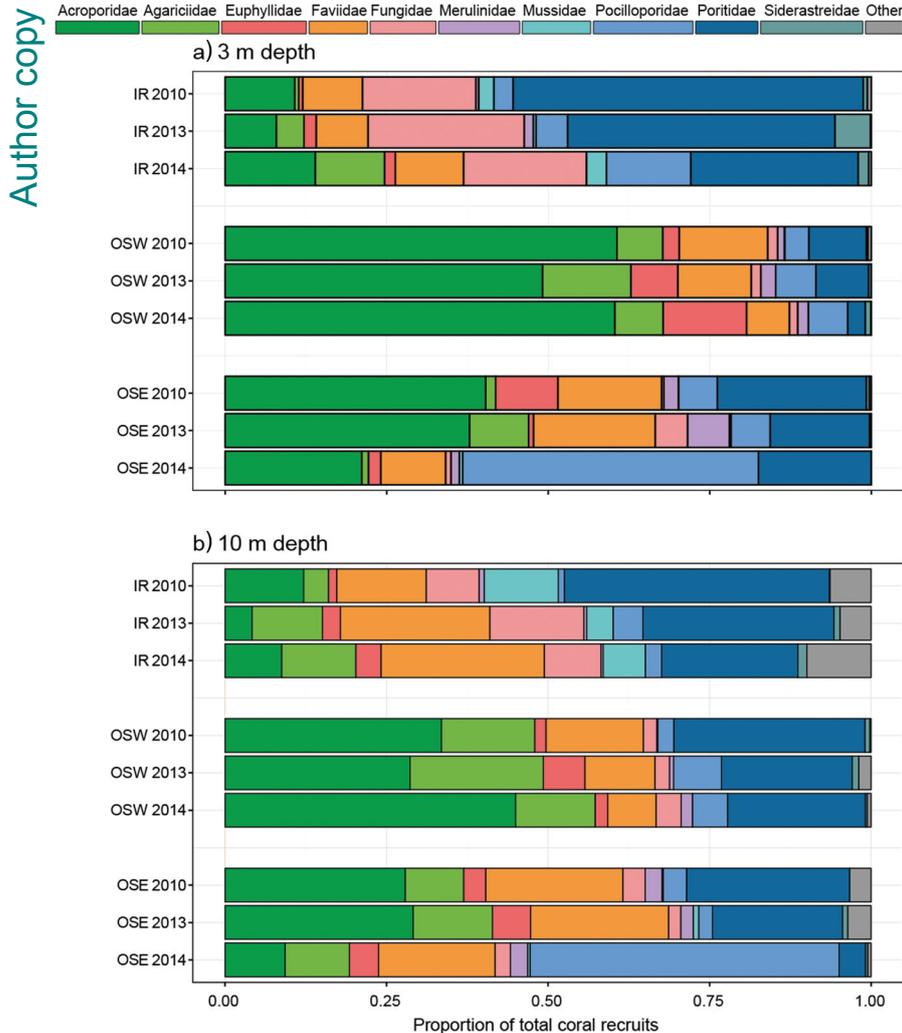


Fig. 4. Juvenile coral community composition showing the relative proportion of coral families within each habitat over time at (a) 3 m and (b) 10 m depth. IR = inner reef; OSW = outer slope west; OSE = outer slope east

pass, and caused differential mortality of juvenile colonies at all sites.

The eastern outer reef slope was the most typhoon-impacted habitat in Palau, where relative live coral cover declined by over 85% at both depths by 2014. The magnitude of the impact of Typhoon Bopha (December 2012) was immense, with 1 site in the southeast losing most of its live coral cover (–95% at 3 m and –99% at 10 m). Typhoon Haiyan (November 2013) had a similarly intensive impact on the reefs in the far northeast of Palau (M. Gouezo pers. obs.), even though there were no overall statistically significant changes in coral cover between the years 2013 and 2014. The lack of change most likely occurred because only a few sites were surveyed in the north-

east region ( $n = 2$ , see Table S3 in the Supplement at [www.int-res.com/articles/suppl/m540p073\\_supp.pdf](http://www.int-res.com/articles/suppl/m540p073_supp.pdf)), and because most eastern sites were previously impacted by Typhoon Bopha and supported low coral cover.

The loss of live coral cover led to the opening of space for turf algae (see Fig. S2 in the Supplement), which is a common phenomenon following major disturbances (Cheal et al. 2002, Fabricius et al. 2008, Adjeroud et al. 2009, Gilmour et al. 2013, Lukoschek et al. 2013). It appears that the abundance in algal turfs along the eastern reef slope provided food for small grazers, explaining the increased abundance of scarids and small acanthurids (particularly the species *Ctenochateus striatus*; M. Gouezo pers. obs.). The surveys were conducted at different times of the year, potentially capturing seasonal trends in fish abundance. However, small adult scarids (i.e. with adult body size of 30 to 35 cm) spawn consistently, and in some localities have been reported to spawn daily (Kuwamura et al. 2009). Therefore, the increase in scarids was not simply a consequence of seasonal fluctuations in densities. We suggest that the increase in the abundance of these fishes was a consequence of the increased availability of turf algae, which is a food resource for herbivorous fishes.

The increase in the density of parrotfish and other herbivorous fishes has not always been observed following typhoon disturbances (Lassig 1983, Bouchon et al. 1994, Cheal et al. 2002, Halford et al. 2004, Emslie et al. 2008); however, our results agree with similar observations following disturbances that cause coral mortality. Following coral bleaching on an isolated reef in Western Australia, the density of herbivorous fishes increased in response to the colonization of dead coral substrate by turf algae (Gilmour et al. 2013). Similarly, Sano et al. (1987) and Sano (2000) reported significant increases in turf algae and herbivorous fishes after a *Acanthaster planci* outbreak. Adam et al. (2011) also reported similar results, of a large increase in juvenile parrotfish abundances after an outbreak of *A. planci* in Moorea. In addition, a recent study on long-term observations of parrot-

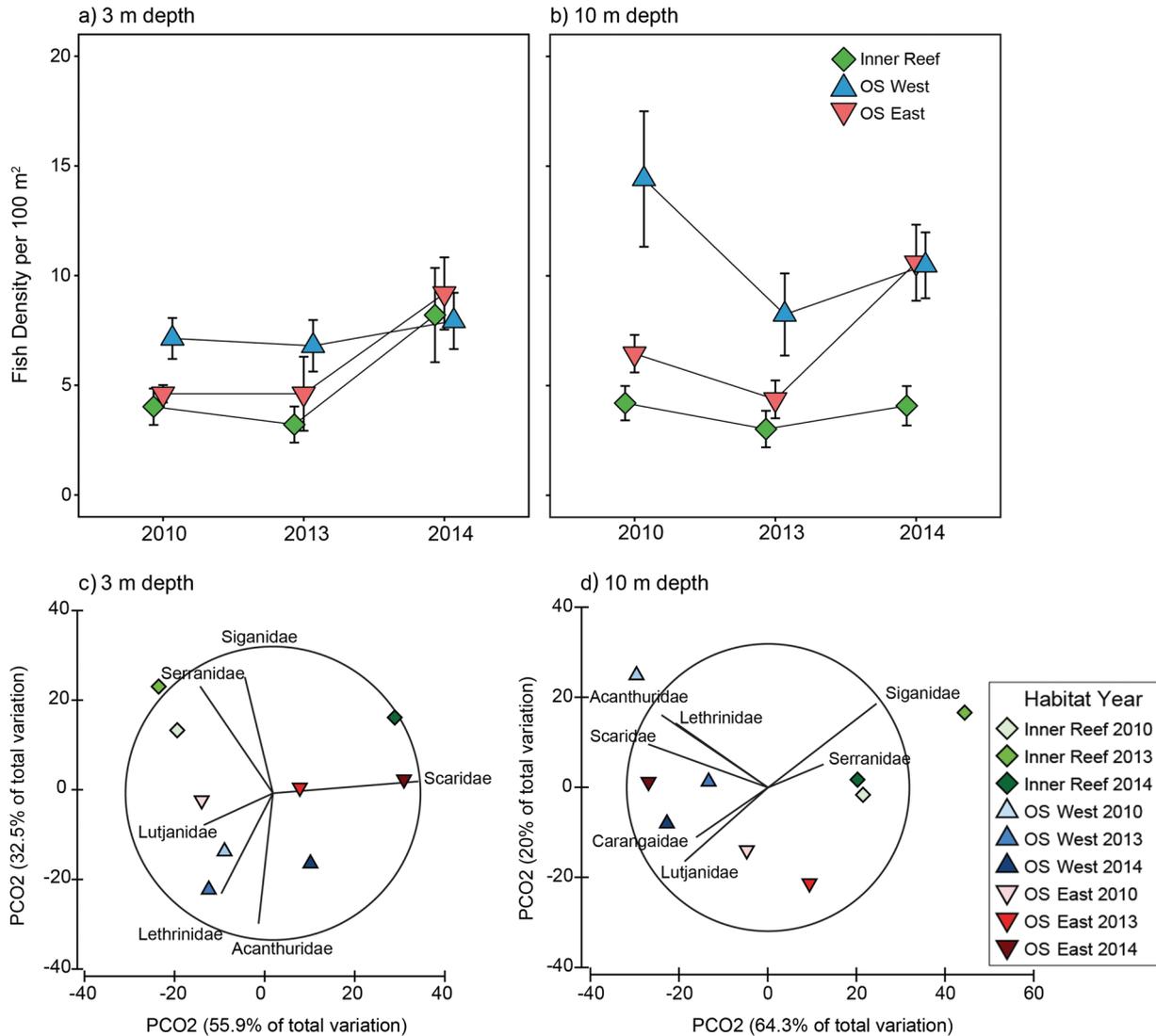


Fig. 5. Mean ( $\pm$ SEM) fish density per 100 m<sup>2</sup> (of commercially important species and all parrotfish species) among habitats (inner reef, outer slope [OS] west, outer slope east) and over time (2010, 2013, 2014) at (a) 3 m and (b) 10 m depth. Principal coordinate analysis (PCO) of fish community structure among habitats and time at (c) 3 m and (d) 10 m depth. Vector overlays represent correlations  $>0.2$  based on Pearson ranking

fish densities in the Philippines showed a strong positive relationship with the presence of dead substratum, following disturbances, and parrotfish densities (Russ et al. 2015). Together, these results imply that the increase in the density of scarids in our study may be related to an increase in food supply, enhancing the survival of parrotfishes and possibly other herbivorous fishes. The analysis of densities of scarids within 2 size classes showed a sharp increase in juvenile individuals ( $<15$  cm TL) after the typhoons, which were most likely new recruits. Indeed, growth curves of several Scaridae species show that individuals can grow to at least 10 cm within their first year (Taylor & Choat 2014). We suspect that the extensive

beds of turf algae were favorable grazing conditions for recruiting parrotfish. The abundance of juvenile scarids also increased in the inner reefs after the typhoons. Whether the scarids on the inner reefs recruited from the eastern reefs, or vice versa, is unknown.

The connectivity among the reefs was also reflected in the decrease in juvenile corals through time on the western reefs, where damage from typhoon waves was minimal. While juvenile corals on the eastern reefs were directly impacted by the typhoon, the reduction in juvenile corals on the western slopes was more likely a response to reductions in the eastern larval supply. The loss of mature

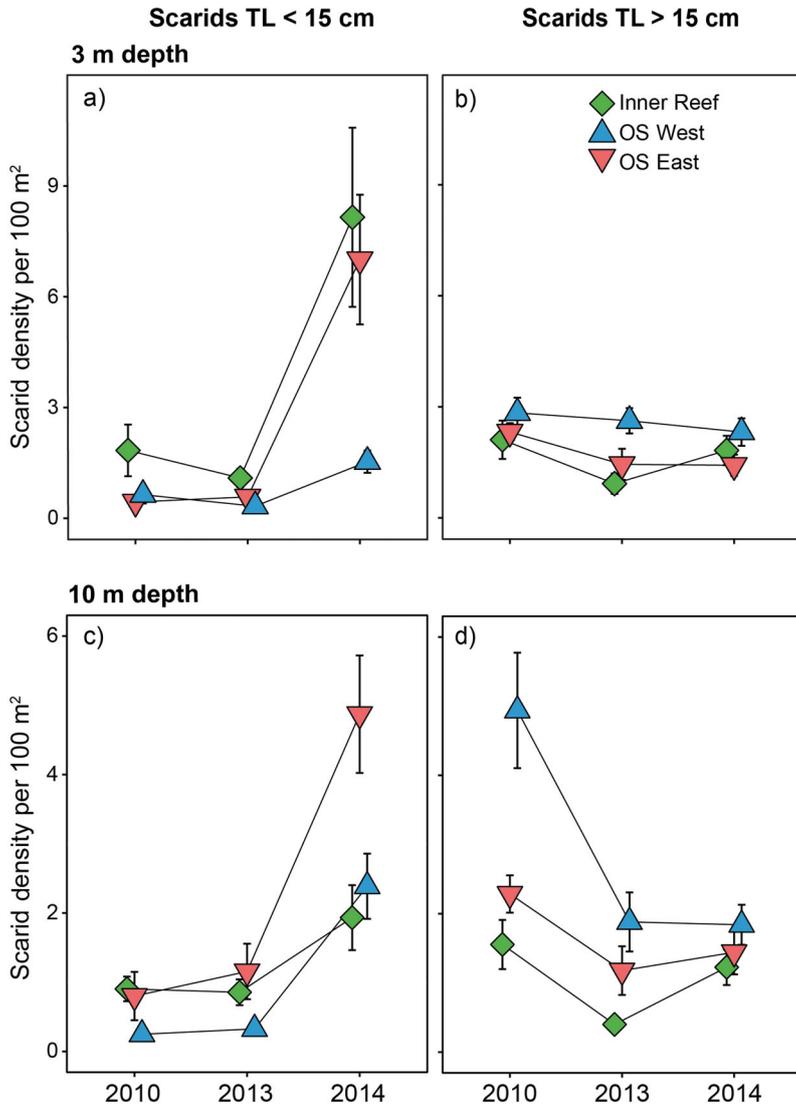


Fig. 6. Mean ( $\pm$ SEM) density of Scaridae per 100 m<sup>2</sup> among habitats (inner reef, outer slope [OS] east, outer slope west) and over time (2010, 2013, 2014) at (a,b) 3 m and (c,d) 10 m depth. (a,c) Individuals smaller than 15 cm total length (TL) and (b,d) larger than 15 cm TL.

colonies on the eastern slopes may have decreased coral recruitment around the archipelago. Despite the decrease in juvenile coral density, the community composition remained the same in all habitats and depths, except in 2014 on the eastern outer reef slope, which showed a shift from *Acropora* toward *Pocillopora*. By contrast to acroporids that broadcast unfertilized gametes, pocilloporids generally brood larvae that are mature upon release (Harrison & Wallace 1990). As such, pocilloporids can rapidly colonize locally disturbed habitats, as seen in our study and in others (Adjeroud et al. 2005, 2007, Magalon et al. 2005, Doropoulos et al. 2015). In the almost com-

plete absence of remnant coral colonies on the eastern outer reefs, coral recovery will be dependent on complex connectivity patterns and on the survival of coral recruits.

Still, the coral assemblages on Palau have been shown to be highly resilient to past disturbances (Golbuu et al. 2007, Victor 2008, van Woesik et al. 2012), and are strongly inter-connected through larval dispersal (Golbuu et al. 2012). Other than the 2010 thermal-stress event, which caused very low coral mortality (van Woesik et al. 2012), Palau has not experienced any major disturbances since the 1998 thermal-stress event caused considerable bleaching and coral mortality (Bruno et al. 2001). The reefs rapidly recovered from the 1998 thermal-stress event (Golbuu et al. 2007). Nevertheless, typhoon disturbances are rare in Palau, and rates of recovery are less predictable. Recently, 3 studies in Palau reported on both temporary and persistent shifts to macroalgae that were caused by Typhoon Bopha (Doropoulos et al. 2014, Roff et al. 2015a,b), which also reduced coral recruitment (Doropoulos et al. 2014). At the archipelago scale, our study highlights the fact that the impacts of acute typhoon disturbances are highly spatially variable. Palau's reefs display a mosaic of impacts, with the east slope being the most intensively damaged, and the inner reefs being the least intensively damaged. Such heterogeneity and connectivity is essential for recovery. The dispersion of coral larvae from surviving colonies in adjacent, highly connected habitats will greatly facilitate the recovery of damaged reef slopes (Hughes et al. 2000). Models

show that the northern reefs retain fewer larvae than the southern reefs (Golbuu et al. 2012). Therefore, we expect that the southeastern reefs of Palau will recover faster than the northeastern reefs, because of differential rates of larvae retention and recruitment. The high connectivity among reefs in Palau, along with multiple spawning events (Penland et al. 2004), high suitability of settlement substrate, and high densities of scarids and other herbivorous fishes (Mumby et al. 2013), are favorable conditions for successful coral recruitment and reef recovery.

The recovery process will be however dependent on the occurrence of future thermal stresses and

other disturbances. Although ocean warming and tropical-storm severity are predicted to increase in the northwestern Pacific region (Webster et al. 2005, Knutson et al. 2010, IPCC 2013), Palau, as a small island nation, has little influence on the challenge of greenhouse gas emissions. However, with regard to the management of local anthropogenic stressors, Palau has made great advances. Palau has an effective network of Marine Protected Areas (MPA), referred to as the Protected Areas Network (PAN), which was established in 2006. The PAN consists of terrestrial and marine protected areas covering all habitats, and is constantly evolving to 'better fit' larvae connectivity patterns around the archipelago. This network of MPAs will most likely facilitate reef recovery (McLeod et al. 2009). The increase in the abundance of scarids will also most likely benefit coral recovery, by freeing the substrate of fleshy macroalgae (Mumby 2006). In Palau, we expect that a combination of an effective MPA network and fishing regulations should improve the resilience of coral reefs, reducing their vulnerability to global climate change, and promote rapid recovery from the impact of the 2 sequential typhoons.

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