

15 years of coral reef monitoring demonstrates the resilience of Palau's coral reefs



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Summary

Worldwide, coral reefs are affected by both acute and chronic disturbances. Acute disturbances have a short-term but intense impact that often spreads over large spatial scales. Ecological monitoring is then very useful to follow changes after acute disturbances and understand how coral reefs recover. Yet, in Palau, before 2001, no coral reef monitoring data at the scale of the island were available to quantify disturbance impacts, coral mortality, and recovery time. PICRC's long term monitoring program was set up in 2001 to document these changes through time and to inform stakeholders about coral reef status and trends. The aim of this report is to document coral reef trends through time in different habitats and depths, and to highlight spatial and temporal differences in recovery time following the 1998-related bleaching event and more recently typhoon disturbances. Our findings showed that coral reefs took a minimum of 10 to 12 years to fully recover from the 1998-El Nino related mass bleaching event. In the absence of further large-scale disturbance, coral communities within the inner reefs and western outer reefs appeared to have reached a coral-dominated stable phase. PICRC's long term monitoring data on fish and macro-invertebrates provided useful insights into differences among habitats and general trends through time. However, we highlighted some gaps in data collection and survey design which are now considered; an adapted monitoring protocol has been implemented at PICRC to better inform management in the future regarding commercially-targeted fish stocks.

Introduction

Coral reefs around the world provide valuable goods and services, especially to the populations of small island nations (Moberg and Folke 1999; Costanza et al. 2014). Both natural and anthropogenic disturbances alter coral reef states, thereby decreasing the direct and indirect benefits that the reefs provide (Hoegh-Guldberg et al. 2007; Cinner et al. 2009; Ainsworth et al. 2016; Cheal et al. 2017). Coral reef communities are susceptible to physical and biological forces which operate at different spatial scales, frequencies, and intensities; these are often classified as either chronic or acute disturbances (Connell 1997; Paine et al. 1998). While acute disturbances have a short term but catastrophic impact on communities (e.g. mass bleaching event, typhoons, Crown-of-thorns starfish (COTS), disease outbreak), chronic disturbances have a slower effect spreading over long periods of time (e.g. overfishing, pollution, climate change) (Connell 1997; Jackson et al. 2001; Fabricius 2005; Hoegh-Guldberg et al. 2007; Death et al. 2012).

The coral reef communities in Palau have been highly resilient to past disturbances (Golbuu et al. 2007; Victor 2008; van Woerik et al. 2012). Although chronic disturbances are occurring at varying degrees of intensity, mainly due to over-harvesting and sediment pollution (Golbuu et al. 2011; Bejarano et al. 2013; Prince et al. 2015), the major disturbances that impacted coral reefs over large spatial scales were 1998-related bleaching events (Bruno et al. 2001a) and the subsequent occurrence of two super typhoons on the eastern barrier reefs (Gouezo et al. 2015). During the 1998-related bleaching event, Bruno et al. (2001b) documented that nearly half of the corals surveyed were completely bleached. In the absence of quantitative surveys at the archipelago scale prior to the occurrence of this disturbance, it was difficult to estimate the extent of coral mortality induced by bleaching events in Palau's different habitats (outer reefs, inner bay reefs, and patch reefs). One qualitative reef assessment was conducted in 1991 across different habitats and reported an overall high coral coverage except for the North-eastern exposed outer reefs (Maragos and Cook 1995). In 2012 and 2013, two super typhoons hit the entire stretch of the eastern outer reefs of Palau, with an average of 60% absolute coral reef loss within this habitat (Gouezo et al. 2015).

Government led ecological monitoring programs are often established globally to document ecosystem changes, especially after large-scale disturbances, with the aim to inform conservation managers, adapt policies, and improve conservation management of natural resources. The Palau International Coral Reef Center implemented a long-term monitoring program in late 2001 to follow the status and trends of coral reef communities through time and quantify the impacts of large-scale disturbances in the archipelago.

This study aims to describe 15 years of change among coral reef communities within three reef habitats and between two depths in Palau. This report seeks to inform a broad audience about the status and trends of coral reefs communities, and to highlight spatial and temporal

differences in recovery time following large scale disturbances such as mass bleaching events and typhoon disturbances.

Methods

Study sites

Since the launch of the Palau International Coral Reef Center's long-term monitoring program in 2001, coral reef monitoring was conducted at several sites throughout the archipelago within three habitats: outer reefs, inner bay reefs, and patch reefs. Reefs were surveyed approximately every two years unless a large-scale disturbance happened. The first year of surveys in 2001/2002 had nine site replicates in the outer reef (four on the East and five on the West), two site replicates in the inner reef and patch reef habitats, respectively. Overtime, site replicates increased within each habitat until reaching a total of 6 site replicates each in the eastern and western outer reefs respectively; six site replicates in the inner reefs; and three site replicates in the patch reefs (Figure 1). Because two category 5 typhoons in 2012 and 2013 severely impacted the eastern outer reefs (Gouezo et al. 2015), the outer reef habitat was separated into two different habitats: western and eastern outer reefs.

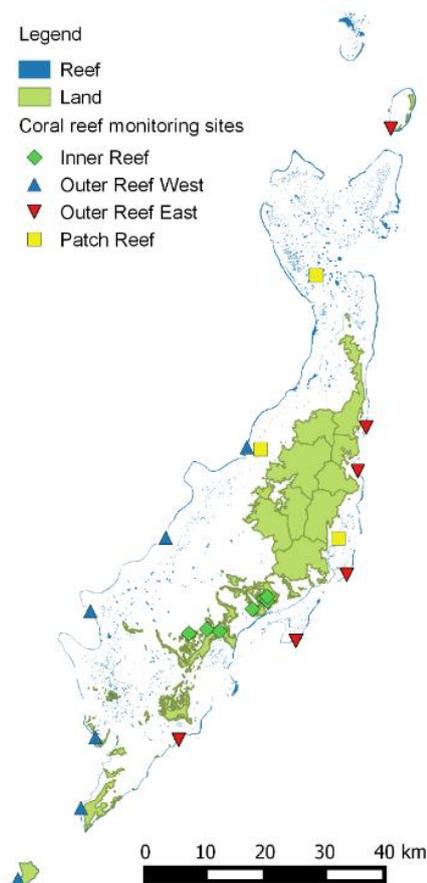


Figure 1. Map of long term coral reef monitoring sites in Palau

Reef assessment methodology and data extraction

The coral reef monitoring protocol was conducted as previously described in several published studies (Golbuu et al. 2007, 2016; Barkley et al. 2015; Gouezo et al. 2015). Briefly, at each site and depth (3m and 10m), five 50 m transects were haphazardly placed following the depth contour of the reef, leaving a few meters in between transects. Along each transect, data on benthic coverage, fish abundance and size, and juvenile coral density and size were recorded. For benthic coverage, between 2001 and 2009, an underwater digital video camera recorded onto DV mini-cassettes a ~0.5 x 0.5m video sequence along the transect by keeping a distance of ~0.7m above the reef (Golbuu et al. 2007). Since 2010, benthic coverage was quantified by taking photographs of a 0.5 x 0.5m quadrat every meter along each transect using an underwater camera mounted on a PVC frame. Over time, 40 to 50 benthic images per transect were analysed using 5 random points by (1) projecting images on a screen with 5 randomly placed crosses (2002 to 2009) and (2) randomly allocating 5 points per images using CPCe software (2010 to 2016) (Kohler and Gill 2006). For both data extraction methods, the same benthic categories were used: live corals and macroalgae (to the genus resolution), sponges, ascidians, crustose coralline algae, turf algae, and non-living substrate (sand, rubble).

The density of juvenile corals, those with a size ≤ 5 cm in diameter, was recorded along the first 0.3m x 10m of each transect. Juvenile corals were identified to genus level, but if not possible to the family resolution. Juvenile coral density was standardized per m^2 .

The abundance of commercially-targeted fish (~35 species) was recorded within a 5m wide belt along each transect. A total of six observers participated in these surveys which added variability to this dataset. Only after 2007 were surveys conducted so that that fish size was estimated to the nearest centimetre by only three observers who received extensive size-calibration training using fish models (Bell et al. 1985). Thus, biomass data will only be presented for years later than 2007. Biomass values were calculated using the total length-based equation: $W = (aTL)^b$, where W is the weight of the fish in grams, TL the total length of the fish in centimetres (cm), and a and b are constant values from published biomass-length relationships (Kulbicki et al. 2005) and from Fishbase (Froese and Pauly 2001). Fish abundance data was standardized per 100 m^2 and fish biomass was converted into grams per m^2 for ease of comparison with other studies.

The abundance and size of commercially-targeted invertebrates was recorded within five transect belts of 50m by 2m, making a total area of 100 m^2 per transect.

All data were entered into Microsoft Excel and organized into a database using Microsoft Access.

Data analyses

To quantify differences among habitats and depths of each of the ecological indicators, a generalized linear model was used on several ecological variables (juvenile coral density, fish abundance and biomass, macro-invertebrates' abundance) using habitat and depth as fixed factors and sites nested within habitat as random terms to account for variability associated with repeated measurements over time.

When possible, we described trends of each ecological indicator through time using general additive mixed model (GAMM) analysis. This analysis examined the effect of time (continuous), habitat, and depth on the coverage of major benthic groups using spline smoothing function for time, and depth and habitats and their interactions as fixed factors. Similarly, sites were nested within habitats and were included as a random term into the model to account for repeated measurements through time.

To visualize changes within the coral community over time among habitats and depths, non-metric multidimensional scaling was conducted on a log+1 transformed Bray-Curtis dissimilarity matrix. We used nMDS ordination and stress values to interpret how well the ordination summarizes the observed distances among year samples, within each habitat and depth (Oksanen 2015). To quantify differences of coral community matrix through time, adonis tests followed by pair-wise comparison was run among years within each habitat and depth combination.

All analyses were conducted using R statistical software (R Development Core Team 2016) using lme4, gamm4, and vegan packages (Oksanen et al. 2007; Wood and Scheipl 2013; Bates et al. 2014).

Results

1. Benthic communities

Among each benthic group, our analysis revealed a significant interaction between habitat and depth through time ($P < 0.001$) (Figure 2). In 2002, the live coral cover among habitats and depths was different. The inner reefs had the highest coral coverage, averaging around 45% at 3m and 34% at 10m. On the outer reefs, live coral cover was ~11.5% at 3m and ~20% at 10m. Lastly, patch reefs had a live coral cover of 7.5% at 3m and 2.6% at 10m. In 2002, macroalgae cover was low (<10%) in all habitats, except in the patch reefs at 10m (~15%). Live coral cover gradually increased in all habitats through time but at different paces, apart from the eastern outer reefs where coral cover dropped from ~35% to ~6% at both depths in 2013 because of two typhoon disturbances. On the inner and western outer reefs, live coral cover

started to asymptote after 2008-2010 at ~60% and 30% cover at 3m and ~40% and ~50% at 10m respectively. In the patch reefs, the habitat that was the most affected by the 1998-bleaching event, coral cover reached 31% at 3m and 24% at 10m in 2016.

Throughout time, macroalgae cover was quite low (<12%) except on the patch reefs (maximum cover: 18.3% in 2007). There was a significant increase in macroalgae cover through time in the inner reefs (P <0.01) but remained low (<10%). The coverage of turf and CCA is tightly correlated with coral cover and time. Available substrate for settlement (i.e. CCA, turf, carbonate) decreases as coral cover increases within each habitat and depth combination. The coverage of rubble and sand was stable in the inner and western outer reefs. It increased on the eastern outer reefs following typhoon disturbances. The highest coverage of rubble and sand was found in the patch reefs (>50%).

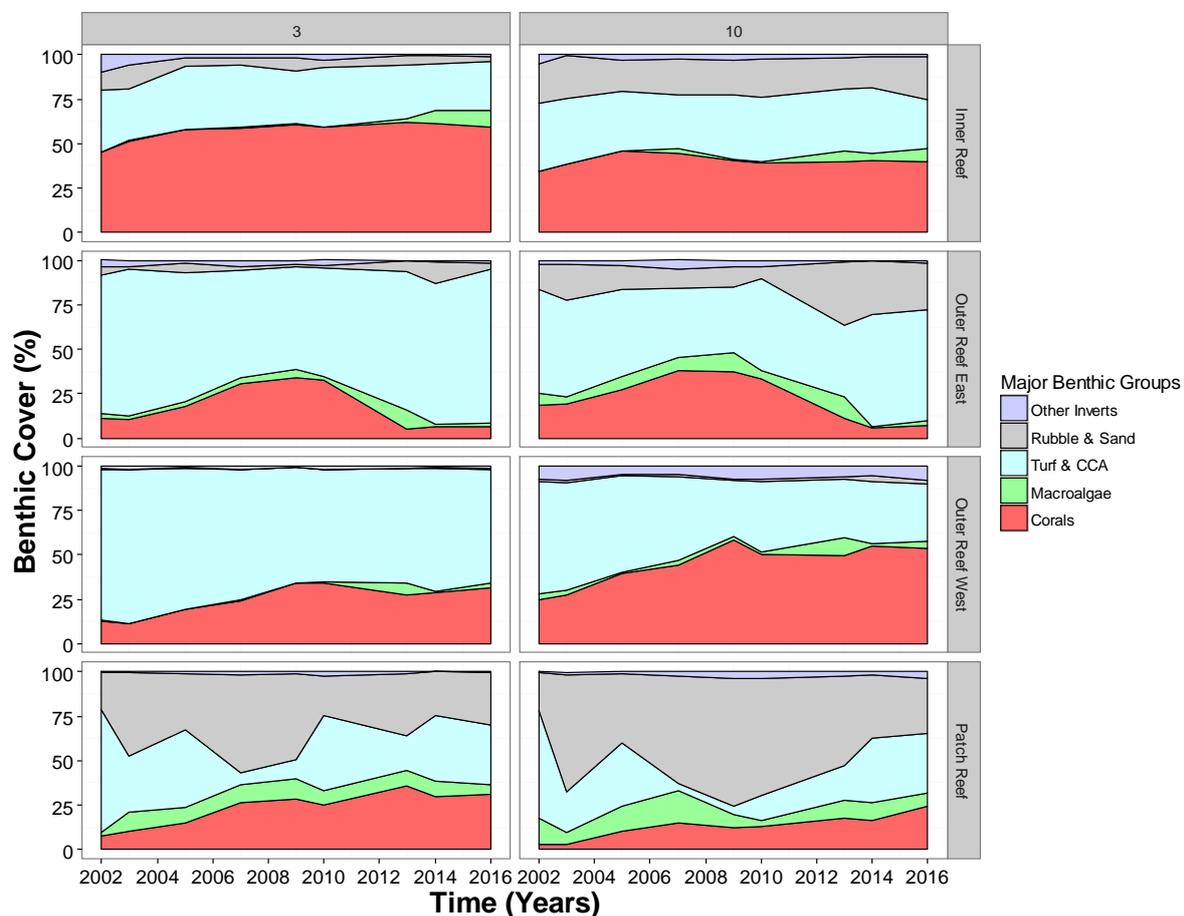


Figure 2. Mean cover of the major benthic categories trends over time in different habitats and depths

Over time, the habitat that had the highest generic diversity was the western outer reef (with a maximum of 22 recorded coral genera) and the lowest generic diversity was found in the patch reefs (16 recorded coral genera). Despite relatively high generic diversity, coral communities are largely dominated (>75% or more) by *Porites* (mostly massive and *Porites*

rus), Merulinidae and Agaraciidae spp. in the inner reefs; *Acropora*, *Montipora*, *Porites* and Merulinidae spp. on the outer reefs; and *Acropora*, *Montipora*, and *Porites* spp. in the patch reefs. The diversity of coral genera increased significantly through time in all habitats and depths ($p < 0.001$), except in the inner reefs where it was quite stable, and on the eastern outer reefs where coral coverage dropped after the occurrence of typhoons (Figure 3). In all habitats except the patch reefs, the diversity of coral genera was higher at 10m compared to 3m ($p < 0.001$).

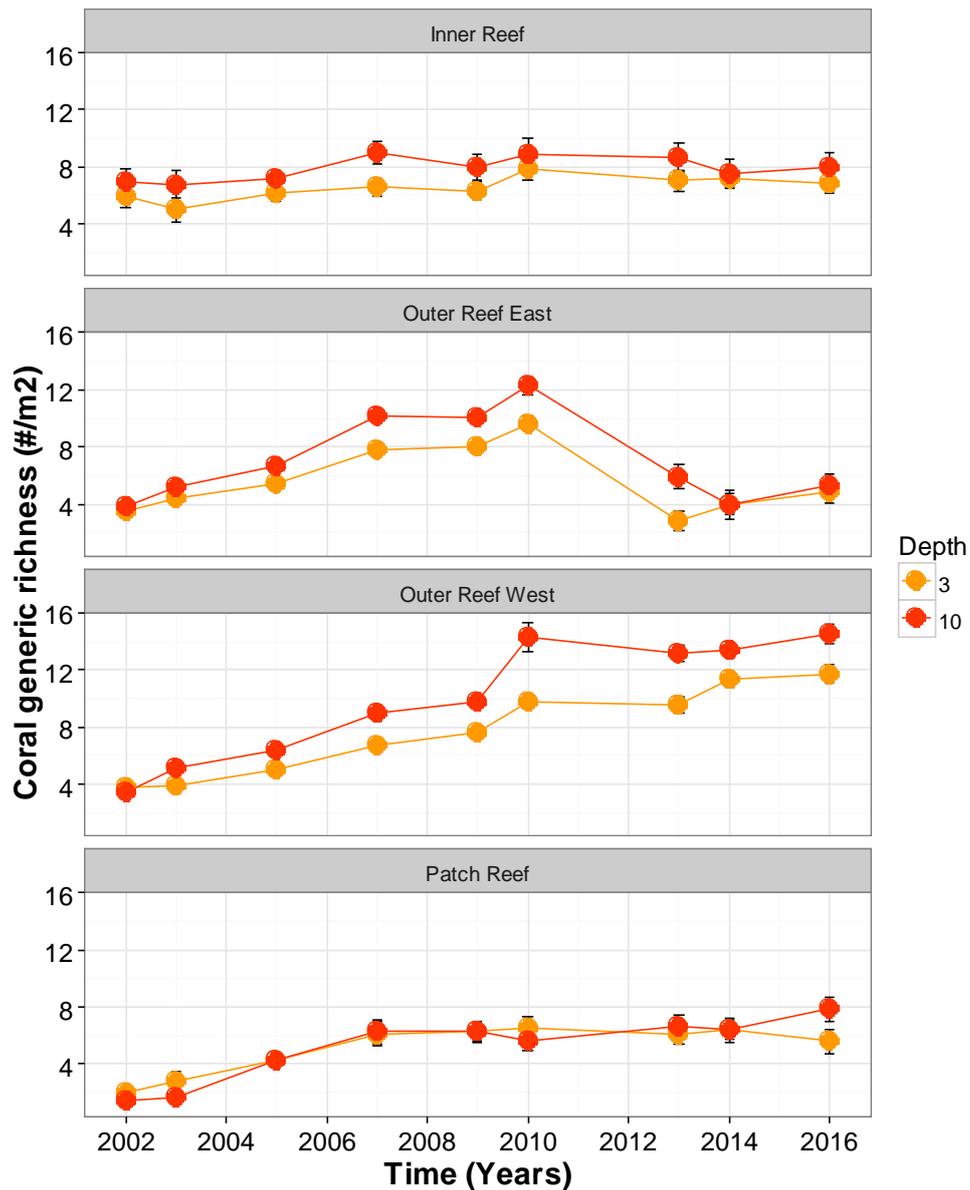


Figure 3. Mean coral genera diversity (\pm SE) over time in different habitats and depths

Non-metric multidimensional scaling plots showed differences in coral community trajectories within each habitat and depth through time (Figure 4). Within each habitat, despite the differences in community structure, communities followed a similar re-assembly trajectory (same directions) (Figure 3). Within the inner reefs, coral communities stabilized

around 2007, with no differences in community structure from 2007-2016 ($P > 0.05$ from pairwise comparisons following adonis test), excepting 2010 where communities slightly diverged. For eastern outer reefs, coral communities transitioned consistently following the 1998 bleaching until prior to the 2012 typhoon disturbance ($P < 0.05$, adonis test). Within the western outer reefs, communities were clustering around 2010, although 2013 communities diverged slightly. Lastly, within the patch reefs, the distance between coral communities through time decreased from 2010, but there is no clear cluster.

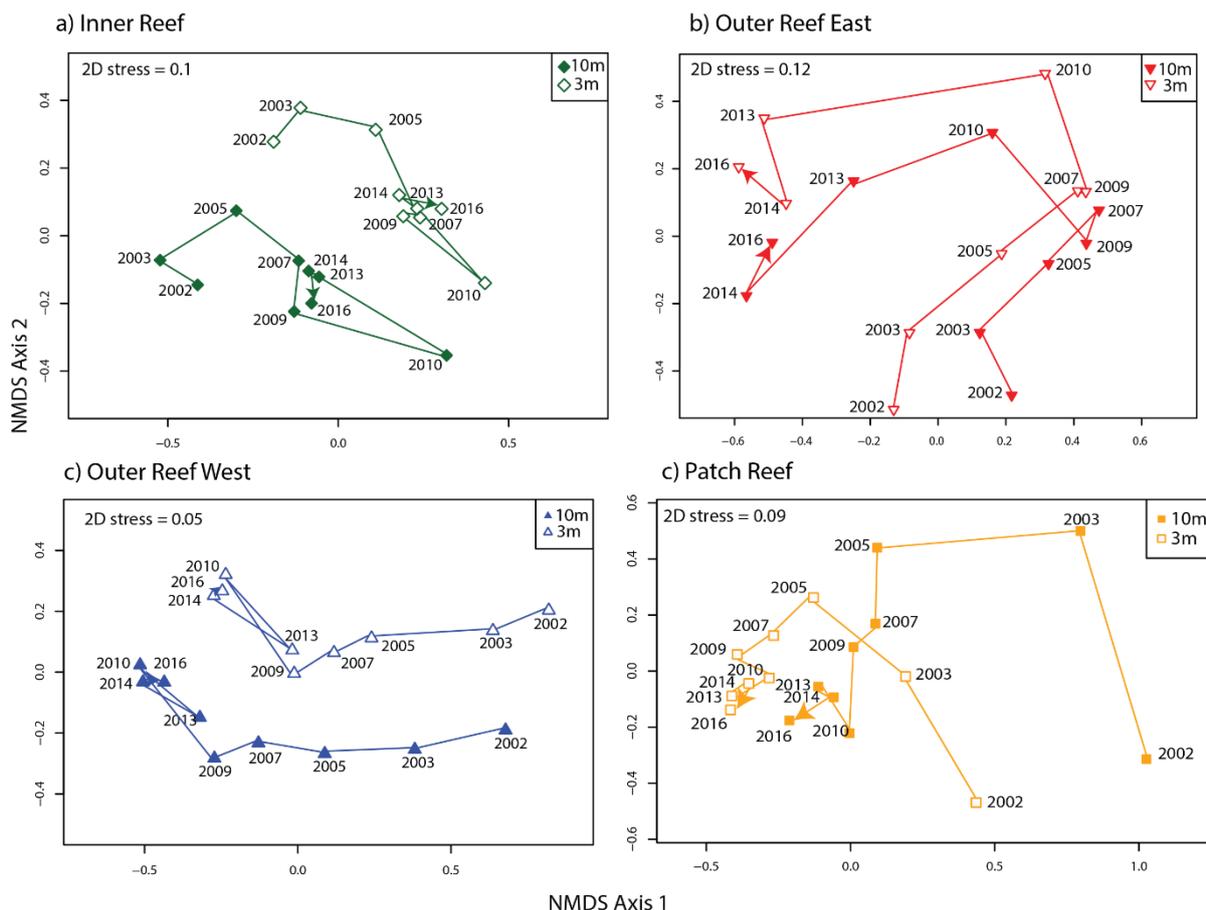


Figure 4. Non-metric multidimensional scaling plots (nMDS) of log+1 transformed Bray-Curtis coral community matrix within each habitat and depth with lines connecting sample years showing community trajectories.

2. Juvenile coral density

In every year of surveys, the abundance of juvenile corals was significantly higher in the western outer reefs than in the inner reefs and patch reefs ($P < 0.001$) (Figure 5). There was no significant difference between depths in all habitats. Throughout time, trends are non-linear and are likely driven by recruitment pulses.

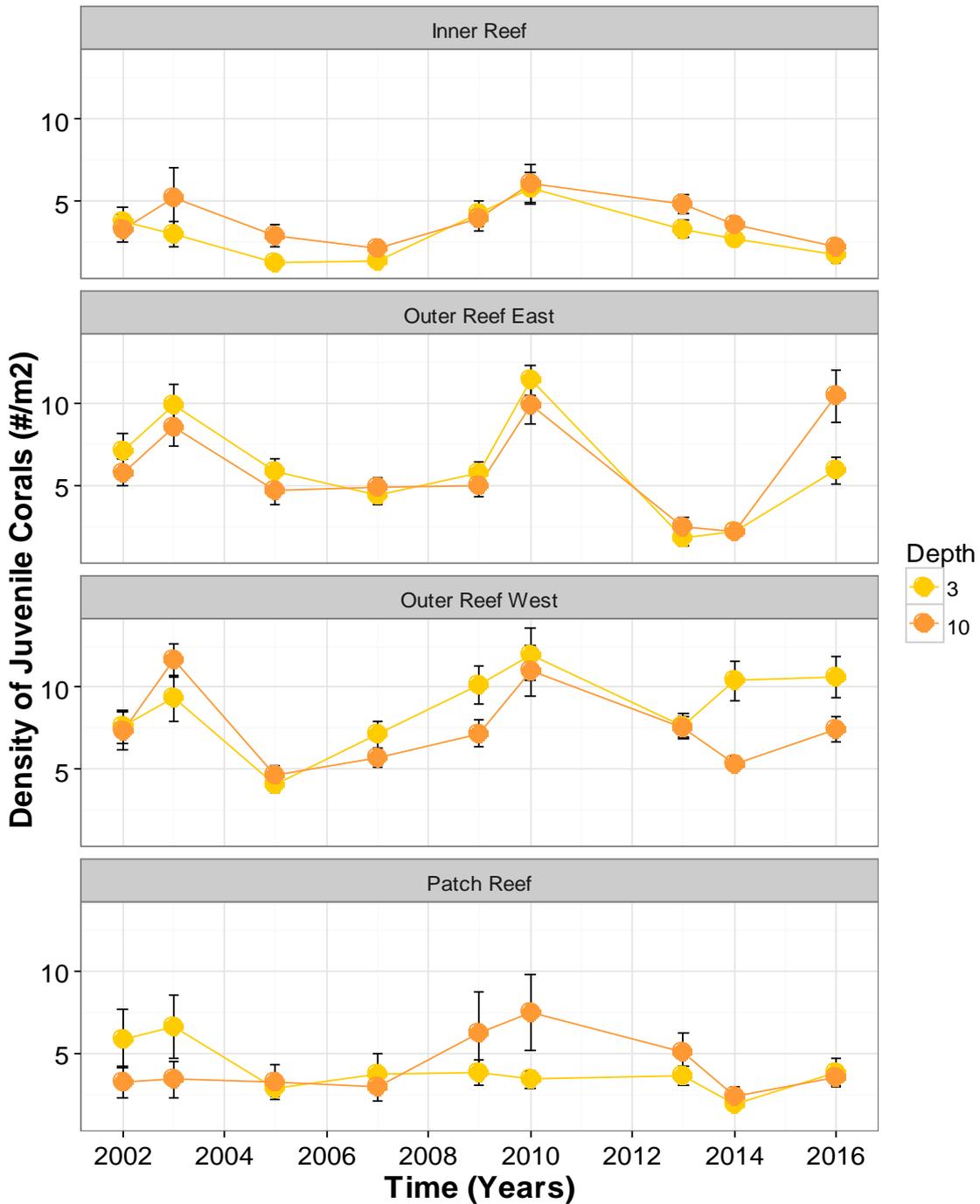


Figure 5. Mean density of juvenile corals per m² (± SE) within habitats and depths

3. *Commercially-targeted fish species abundance and biomass*

The trends in fish abundance and biomass through time were found to be significantly different through time, among habitats and between depths ($P < 0.01$) (Figure 6). Throughout the past 15 years, the fish abundance and biomass was significantly higher in the outer reefs than in the inner reefs ($P < 0.001$), except for the eastern outer reefs at 3m. In addition, the abundance of fish was found to be higher in the patch reefs at 3m compared to inner reefs at

both depths ($P < 0.01$). Within the outer reefs, the abundance and biomass was significantly higher at 10m than 3m ($P < 0.01$), while in other habitats they did not differ between depths.

Throughout time and within each habitat, the high variability within samples and among years makes it very difficult to analyse trends statistically and draw conclusion about the direction of the trends. For the purpose of this report, we will describe trends visually (Figure 6). The most obvious direction of both abundance and biomass of fish trends was observed on the outer reefs habitats where it appears to be decreasing through time. The biomass and abundance of fish within the inner reefs is low but seems stable overtime. In the patch reefs, the abundance of fish appears stable, but the biomass appears to be decreasing through time.

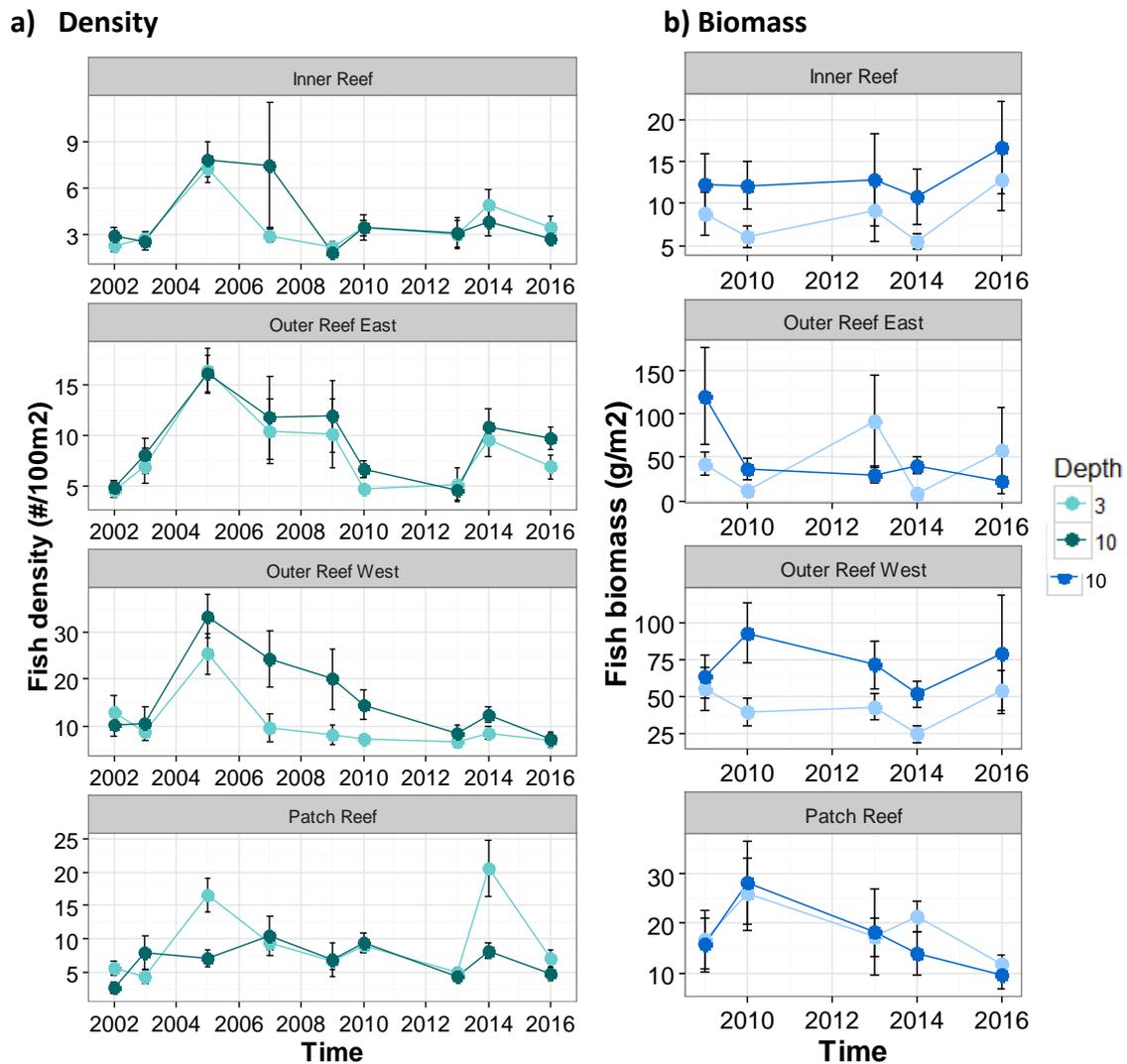


Figure 6. Mean fish abundance per 100 m²(a) and biomass in g per m² (b) (\pm SE) through time within each habitat and depth. *Note: for fish biomass, samples in 2009 were excluded because of large observer errors and/or no accurate size estimations were conducted.*

4. The abundance of macro-invertebrates

The abundance of macro-invertebrates was closely driven by clam species (*Tridacna crocea*, *T. maxima*, *T. squamosa*, *T. derasa* and *T. gigas*) (Figure 7). The trends of clam density through time were found to be significantly different among habitats and between depths ($P < 0.001$). Within the outer reefs, especially at 3m depth, the density of clams significantly increased from 2014 to 2016. On the inner reefs, while there is a very low abundance of clams at 10m depth, the density of clams decreased sharply through time at 3m depth ($P < 0.05$). The abundance of clams was low in the patch reefs. The abundance of sea cucumber spp. and *Trochus* spp. in all habitats was low (< 2 individuals per 100 m^2) throughout the years.

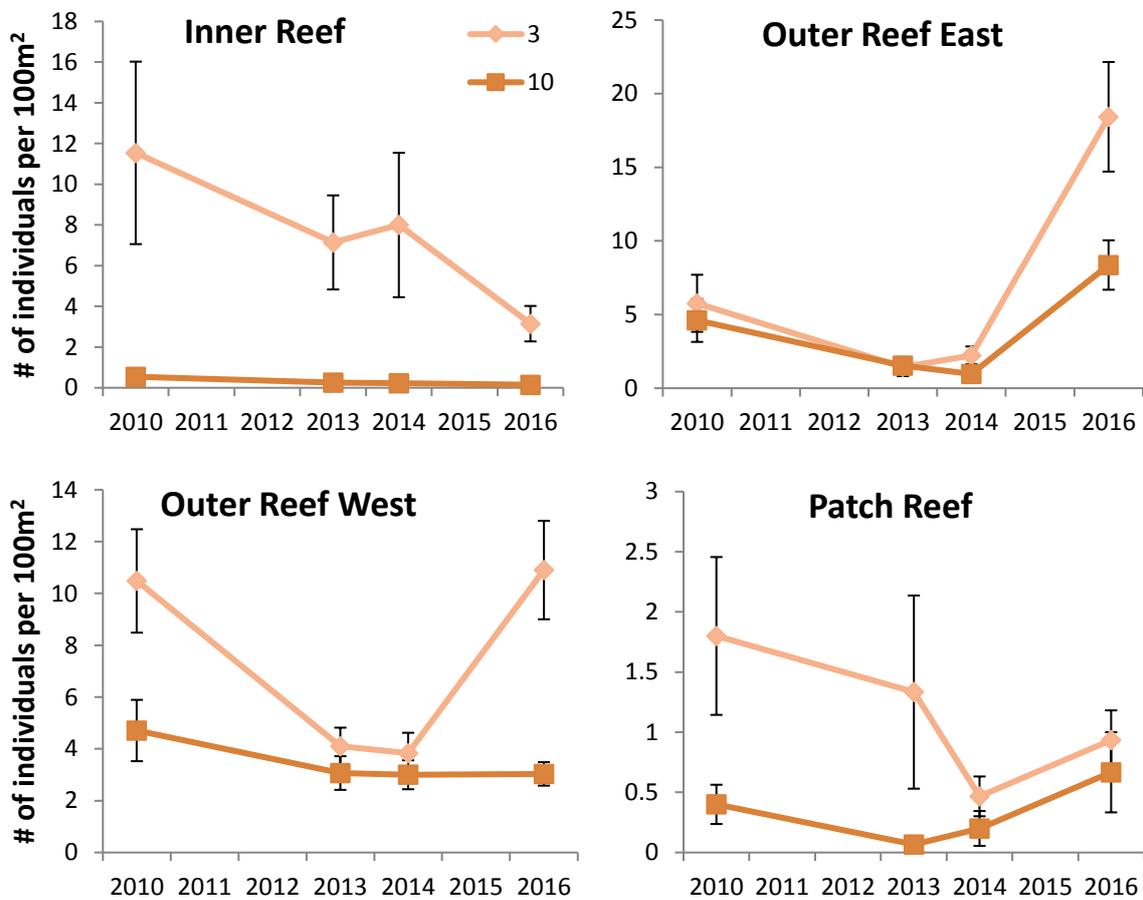


Figure 7. Mean clam abundance per $100\text{ m}^2 (\pm \text{SE})$ through time within each habitat and depth

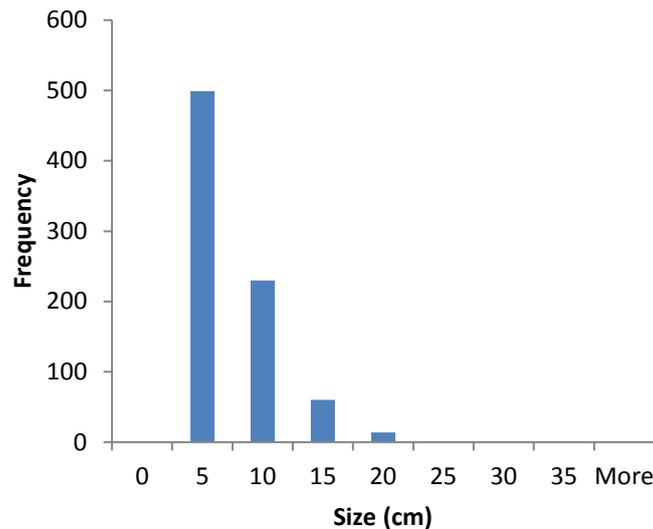


Figure 8. Histogram of size distribution of *T. crocea* and *T. maxima* on the eastern outer reefs in 2016

Discussion

The availability of PICRC's long term monitoring data allowed to explore the trends and status of coral reef communities over the past 15 years. This study highlighted spatial heterogeneity of large-scale disturbance impacts (1998-related bleaching event) and recovery time of coral reefs at the scale of the archipelago. Although this long-term monitoring program was not designed to follow up on the status of food fish and macro-invertebrates, our results provided some insights into general trends of targeted fish and macro-invertebrates over time and habitat preferences.

Disturbance impacts and recovery of benthic communities

The live coral coverage in 2002 was different among habitats (>30% in the inner reefs, <20% on the outer reefs, and <10% in the patch reefs), showing the heterogeneity of mortality induced by mass coral bleaching in 1999. The intensity of bleaching impacts is tightly correlated with sea surface temperature, irradiance level, coral taxon, morphology and size of corals, and algal symbiont (Baker et al. 2008), potentially explaining the differences among habitats. The inner bay reefs were the least impacted. The taxonomic structure and adaptation of coral reefs within the inner reefs in Palau was shown to be very resilient to thermal stress (van Woesik et al. 2012) and ocean acidification (Shamberger et al. 2014; Golbuu et al. 2016). On the other hand, coral reefs within the patch reefs were the most impacted with very low coverage in 2002. In all habitats, from 2002, live coral cover gradually increased and coral communities reassembled following distinct trajectories until 2016, with the exception of the eastern outer reefs which were intensely damaged by two typhoons in 2012 and 2013 (Gouezo et al. 2015). Within the inner reefs and western outer reefs, coral

communities appeared to have recovered and regained their structure, shown by (1) the presence of an asymptote toward a maximum coral coverage and (2) clusters of coral communities in years following 2010 on nMDS plots. In the absence of major acute disturbance within these habitats since 1999, it appears that about 10 to 12 years following bleaching disturbance, these communities have reached stability. The stability of coral reefs is often controversial because of the frequent occurrence of large scale disturbance making coral reefs extremely dynamic systems (Tanner et al. 1994; Connell et al. 1997). Instead, more attention has been centred on the resilience aspect of these systems (Holling 1973; Hughes et al. 2005; Scheffer et al. 2012; Mumby and Anthony 2015) which focuses on how fast a system returns to equilibrium. However, in the right environmental settings, as shown by our findings, achieving stability within defined bounds (free of disturbances) is likely for these two habitats, especially within the very sheltered inner bay reefs of Palau. On the other hand, the communities on the eastern outer reefs were far from a coral-dominated stable phase when the typhoons damaged the reefs. Lastly, within the patch reefs, coral communities are still slowly recovering, demonstrating no clear asymptote or clusters in our analysis.

Throughout time, the coverage of macroalgae was low, particularly on the outer reefs, but was found to be increasing slightly in the inner reefs. Macroalgae cover affects coral negatively by inhibiting coral settlement, and overgrowth (Birrell et al. 2008). Macroalgal biomass on reefs is controlled by bottom up (nutrients), top down (herbivory rate), and other physical processes (dispersal, flow)(Diaz-Pulido et al. 2007; Roff and Mumby 2012). The constant low coverage of macroalgae on the outer reefs highlights that herbivory rate and physical processes are sufficient to reduce macroalgae settlement and overgrowth, as this habitat is oligotrophic (poor in nutrients). On the other hand, the inner reefs displayed a small but significant increase in macroalgal coverage through time, which could be caused by either of the three processes (low herbivory, high nutrient environment, high recruitment) or combinations of these. Although it is a small increase, with the ongoing coastal development in Palau, nutrients/sediment concentration and macroalgae bloom should be closely monitored and documented.

The density of juvenile corals was higher on the outer reefs habitats, oscillating between 5 and 12 individuals per m², than on the inner and patch reefs where it fluctuated between 3 and 7 individuals per m² over the years. The fluctuations of juvenile corals through time is likely driven by several processes including adult coral stocks and their fecundity (Baird et al. 2009), connectivity patterns (Jones et al. 2009; Golbuu et al. 2012), settlement success (Harrington et al. 2004; Price 2010), and post-settlement survival (Doropoulos et al. 2016, 2017). Each of these processes interplay and shape the demography of juvenile coral populations. In Palau, connectivity and recruitment patterns were studied at the scale of the archipelago by Golbuu et al. (2012). This study highlighted self-seeding areas which correlated to some extent with areas with a high density of juveniles *Acropora* colonies. These areas are located around the middle and southern part of the island, while the northern part has lower larval retention mainly because of constant exposure to the dominant eastern current.

Golbuu et al. (2012) also showed that on rare occasion (once every 10 years or so), Palau may receive coral larvae from Yap (located north-east of Palau). While this study provided very useful insights into stock-recruitment relationship of *Acropora* corals, little is known about processes interacting for other coral groups and following larval settlement. Doropoulos et al. (2016, 2017), using both experimental and field studies, showed that microhabitats (crevices), predation by herbivores and corallivores, CCA coverage, and exposure had some major effects on the survival of coral recruits in Palau.

Trends and status of commercially-targeted fish and macro-invertebrates' species

The highest abundance and biomass of commercially-targeted fish species was found on the outer reef habitats over the last 15 years. This finding is not surprising as this habitat is known to be more productive because of higher water flow as well as being located further away from land, therefore diminishes access, particularly in bad weather conditions. The temporal replication of our fish surveys attempted to document the direction of the trend over time. The presence of high variability within the samples and among years make it difficult to analyse these trends through time accurately. There are several reasons for the high variability within our data sets including (1) lack of spatial replication to truly represent a habitat, (2) observer errors (size overestimations, count outside of the belt area, swimming speed), and (3) replication through time (seasonal, year-year variation). Despite this variability, it appears on the graphs that the abundance and biomass of targeted fish species has been decreasing on the outer reefs. This is not a surprising finding, as Palauan fishermen have been saying that over the years as their fishing effort increase but fish numbers and sizes are decreasing, and catch assemblages are changing compared to 20 or more years ago. Nevertheless, targeted fish species biomass in Palau remains quite high in comparison to other Micronesian islands (Harborne 2016) and to other coral reef countries (MacNeil et al. 2015). McNeil et al. (2015) compared biomass values of the entire fish assemblages in different locations and implied that collapsed fish assemblages have a biomass value of approximately 100 kg per ha (10g per m²) and recovered fish assembles have biomass values averaging around 900 kg per ha (90g per m²). PICRC monitoring protocol not only focuses on commercially-targeted but also large fish species. In 2016, on the outer reefs, targeted fish biomass values (which do not represent the entire fish assemblage) averaged around 50 to 75g per m² on the undisturbed western outer reefs, which approaches recovered assemblage values from McNeil et al. (2015) study. On the other hand, within the disturbed eastern outer reefs, biomass values were much lower (20 to 50g per m²). Fish biomass values from McNeil studies cannot be compared to reef habitats other than the outer reefs, as this habitat naturally hosts higher fish abundance and biomass. Our findings also document a low but stable biomass trend within the inner reefs. Our monitoring sites within this habitat are known for not hosting high fish biomass and mostly juvenile fishes (Geory Mereb, personal communication). Lastly, within the patch reefs, the abundance of fish appears quite stable through time, however the biomass is decreasing. This means that the size of targeted fish species is likely decreasing. Patch reefs are easily accessible by fishermen as they are

protected from wave disturbance and are often good places for bottom fishing, which could potentially explain the observed trend within this habitat. Our findings provided useful information on the status of food fish over time, however, conclusions must be carefully made as this monitoring protocol was not designed for this purpose. PICRC has now implemented a monitoring program to accurately document food fish status and trends over time using stereo-video to eliminate observer bias, get accurate size distribution, and decrease variability within habitats by increasing spatial replication.

The abundance of macro-invertebrates was dominated by clam species. Our findings showed that *T. crocea* and *T. maxima* individuals (<5cm) were found in greater abundance in 2016 than in other years, especially on the eastern outer reefs, which could be caused by a recruitment pulse following typhoons disturbance. In fact, growth studies and models of *T. crocea* and *T. maxima* showed that it takes about 2 years for individuals to reach a size greater than 5 cm (Hart et al. 1998; Hean and Cacho 2003). Therefore, it is likely that clams recruited following substrate disturbance caused by typhoon waves in 2012 and 2013, and were then visible to observers in 2016 surveys. Sea cucumbers were found at very low abundance within all reef habitats since 2010 which could either be a sign of long time overharvesting, or habitat preference, or both. Lastly, *Trochus spp.* were only found on the outer reef habitat at low abundance. It is important to note that this survey was not designed to address overharvesting issues; these surveys need more spatial replication to estimate stock size (like for food fish). A recent report by PICRC and BMR was done to assess *Trochus* population in 2016 and density was reported too low (<3.5 individuals per 100 m²) to re-open harvesting (Gouezo et al. 2016).

PICRC's long term monitoring data provided very useful information on status and trends of coral reef communities at the scale of archipelago. Our study highlighted that coral reefs recovered quickly from the 1998-El Nino related mass bleaching event. In addition, in the absence of large disturbance, coral communities within the inner reefs and western outer reefs appeared to have reached a coral-dominated stable phase. While PICRC's long term monitoring data on fish and macro-invertebrates provided some useful insights into differences among habitats and general trends through time, we highlighted some gaps in data collection and survey design which are now considered, and an adapted monitoring protocol is being implemented at PICRC to better inform management in the future about sea food stocks.

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