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NOTE

Demographic recovery of corals at a wave-exposed reef following catastrophic disturbance

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Abstract Rapid recovery of coral cover following acute disturbance has been documented on many reefs. Yet measuring coverage alone can mask shifts in community and demographic structure. Here, we quantify long-term changes in population size structure for three common genera (*Acropora*, *Pocillopora*, and *Stylophora*) at an eastern outer reef in Palau, Micronesia, following catastrophic loss of corals due to typhoon Bopha in 2012, based on size measurements from 3648 coral colonies. Mean colony size returned to pre-disturbance levels within 4 and 6 years for *Stylophora* and *Pocillopora*, respectively. By 2020, *Pocillopora* colony density far exceeded pre-disturbance levels, with rapid successful recruitment following typhoon Bopha. Despite recovery of *Acropora* colony density by 2020, populations remained dominated by smaller colonies. We demonstrate that full demographic recovery can occur more rapidly for pocilloporids (within 6 years) compared to *Acropora* which had not fully recovered by 8 years post-disturbance, possibly due to fewer annual recruitment events and larger maximum colony sizes. Our results highlight the value of demographic metrics as early indicators of recovery.

Keywords Hard corals · Size frequency distributions · Population dynamics · Palau

Liam Lachs and Piera Biondi shared co-first authorship.

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Introduction

Coral reefs are increasingly vulnerable to climate disturbances such as destructive storms (Cheal et al. 2017) and marine heatwaves (Oliver et al. 2018), which are both predicted to worsen under climate change. To persist, coral populations need sufficient time for recovery following disturbances (Gilmour et al. 2013), yet recovery intervals are becoming shorter (Cheal et al. 2017; Oliver et al. 2018) due to a greater frequency of disturbance events. Recovery rates following disturbance vary greatly among reefs, but can be extremely rapid (e.g., 5–10 years) (Doropoulos et al. 2015). Most studies documenting recovery focus on total coral cover or taxonomic community structure (Adjeroud et al. 2018; Gouezo et al. 2019). However, it is also critical to quantify demographic structure (Edmunds and Riegl 2020), because certain coral colonies and taxa, particularly those that reach large sizes, can have a disproportionate influence on aspects of coral reef function (Ortiz et al. 2021). Demographic recovery to pre-disturbance levels or beyond can be measured using various metrics, including population size (or proxies like coral density) and the mean, skewness, or kurtosis of coral size-frequency distributions.

Assessing the demographic structure of populations, or the distribution of individuals of different sizes (Capdevila et al. 2020), can provide insights into coral population dynamics (Bak and Meesters 1998), including recruitment events (Doropoulos et al. 2015) and size-dependent growth

and mortality rates (Madin et al. 2014, 2020). Understanding long-term changes in population size structure can aid in monitoring population recovery, as they provide insights into new arrival rates, cohort growth, and mortality rates (Gilmour 2004; Lachs et al. 2021), which are much harder to detect in coral coverage data. For instance, high skewness of the size distribution and high density of small colonies can indicate recruitment, provided that small colonies have not come about through fragmentation. Although many long-term datasets on benthic coverage are collected for coral reefs, most assessments of population size-frequency distributions focus on single surveys (e.g. Anderson and Pratchett 2014; Victor et al. 2009), with few published long-term studies (e.g., Babcock 1991; Gilmour 2004; Zhao et al. 2014; Lachs et al. 2021), despite the potential insights that can be obtained from time series of population-level data (Gonzalez et al. 2016).

The eastern barrier reef of Palau suffered unprecedented damage in December 2012 as super typhoon Bopha moved westward toward the Philippines (Gouezo et al. 2015, 2019; Roff et al. 2015), with a second super typhoon, Haiyan, causing further damage in November 2013 (Gouezo et al. 2015). Almost the entire shallow coral community was lost, including *Acropora*, *Montipora*, *Porites*, Merulinidae, *Pocillopora*, and Agaraciidae (Gouezo et al. 2019). These reefs had approximately 30% coral coverage before Bopha and near 0–1% coverage afterwards. This catastrophic mortality event provided a unique opportunity to quantify the duration required for demographic recovery in a coral population (Tomascik et al. 1996).

Here, we apply a recently-developed demographic image analysis workflow to a long-term benthic monitoring dataset to assess the demographic recovery of the most-dominant branching corals in the aftermath of typhoons Bopha and Hayian. We focus on branching corals given their key role in the establishment of structural complexity in coral reef habitats. Specifically, we test whether population mean colony size recovers to pre-disturbance levels or beyond, with additional consideration of other demographic metrics including colony density, and population size structure skewness and kurtosis. By comparing benthic coverage against colony density we aim to test whether demographic metrics can be used as early signs of recovery.

Materials and methods

Field surveys

In this note, we document the demographic recovery of the three most common branching coral genera at Ngetngod reef, surveyed every two years from 2012 to 2020, and in 2013 after super typhoon Bopha. On each occasion, five 50 m transects were laid consecutively at 10 m depth, and downward-facing 0.5 m × 0.5 m quadrat photos were taken every metre using a Canon G16 camera mounted to a PVC quadrat frame. All colonies of the most dominant branching taxa (*Acropora*, *Pocillopora*, and *Stylophora*) were outlined following the SizeExtractR workflow determining colony size as the geometric mean diameter (GMD) (Lachs et al. 2022). Dead portions of colonies were excluded, while partial mortality and paling or bleaching were recorded as binary variables. Only colonies which were > 90% inside each quadrat were included. Notably, we included a number of large colonies that were only partially in the quadrat and thus have a downward biased size estimation, however, these were extremely rare (16 colonies, < 1% of total). The detected occurrence of colonies less than 2 cm GMD (approaching the detection size limit for image-based methods) was very low (4% of colonies).

Statistical analysis

Size frequency distributions were visualised using density kernels. Shifts in GMD among years (categorical fixed effect) and genera (fixed effect) were tested using a generalised linear mixed effect model (GLMM) (glmmTMB package, Brooks et al. 2017) with a gamma error distribution under log link. Quadrat, and transect within year were included as nested random effects to account for non-independence of observations. As large coral colonies contribute disproportionately to populations, we reran this GLMM based on only the colonies greater than the 90th percentile colony size (determined by genus and year).

Coral density was calculated for each quadrat (colonies/m^2), and differences in density among years and genera were tested with a GLMM, using transect within year as a nested random effect, applying negative binomial error distribution under log link, and testing for overdispersion and ability to predict zeros (Zuur et al. 2013). To test size-specific trends, an additional colony density GLMM was fitted using size class as a fixed effect (small: < 5 cm, medium: 5–15 cm, large: > 15 cm).

Results and discussion

We analysed a total of 1466 photo quadrats, and measured the size of 3648 coral colonies (781 *Acropora* of 1–65 cm GMD, 2367 *Pocillopora* of 1–32 cm GMD, 500 *Stylophora* of 1–41 cm GMD). Partial mortality and bleaching were very rare across all colonies (4% and 3%, respectively). Catastrophic loss of corals occurred on Ngetngod reef between 2012 and 2013 due to typhoon Bopha (Fig. 1b, 2012 vs. 2013). However, after a pulse of small coral colonies visible on photos in 2014 (1–4 cm GMD), the subsequent years

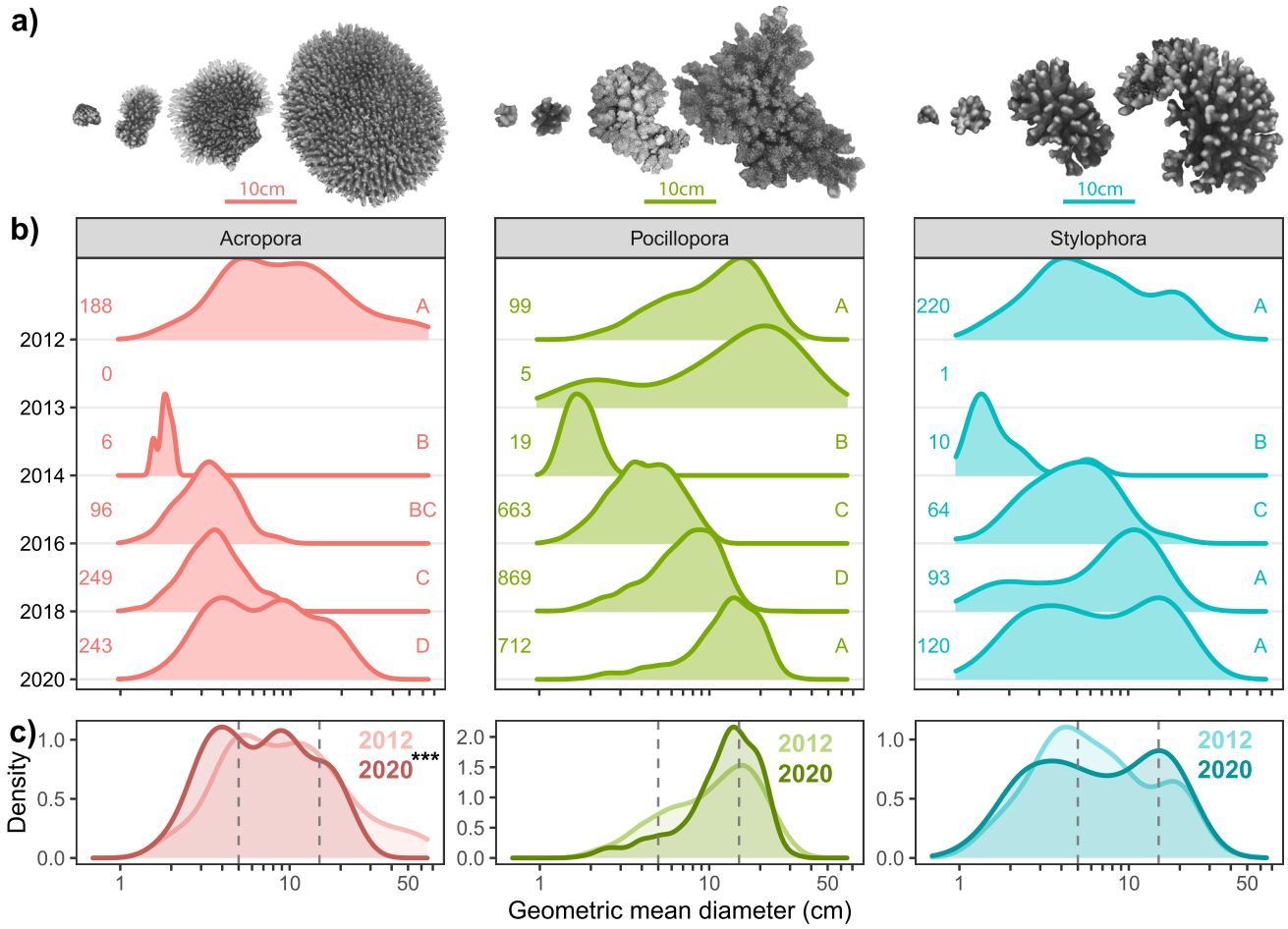

Fig. 1 Coral population size structure trends. **a** Scaled coral colonies of *Acropora* (red), *Pocillopora* (green), and *Stylphora* (blue). **b** Shifts in size structure (density kernels) from 2012 to 2020 with severe coral loss in November 2012 due to typhoon Bopha, showing the total number of colonies corrected to 62.5m^2 reef area (numbers, left) and years without significant differences in colony size (letters, right) based on a GLMM Tukey test (see Fig. 2a). **c** Comparison of size distributions before (2012, pale) and after (2020, dark) Bopha and Haiyan, with size cutoffs at 5 and 15 cm (grey dashed lines), showing differences in mean colony size from the same Tukey test and associated *P* values, with $P<0.001$ (***) and $P>0.05$ without any asterisk

showed successive increases in colony size (Figs. 1b, 2a), indicating that successful recruitment, cohort growth, and low mortality have occurred across all genera.

Mean colony size for *Stylophora* and *Pocillopora* recovered to pre-Bopha levels by 2018 and 2020, respectively (Fig. 1b, Tukey test with $P>0.05$). In comparison, the size of *Acropora* colonies remained smaller than that of the pre-disturbance population throughout the study (Fig. 1b, c, $P<0.001$). The same genera-specific trends were also found for the largest corals (those greater than the 90th percentile), highlighting that recovery of size structure can occur faster for pocilloporid populations (see Gouezo et al. 2020a) than for *Acropora*, which have fewer annual recruitment events and include species that can reach larger colony sizes several metres in diameter.

Colony density also increased steadily in the years after typhoon Bopha and Haiyan (Fig. 2b), recovering to pre-disturbance levels by 2016 and 2020 for *Acropora* and *Stylophora*, respectively. Notably, *Pocillopora* colony density rebounded remarkably quickly, with 9–13 individuals/m^2 recorded only 3 years after the two typhoons (in 2016), and the maximum density in a single quadrat of 48 individuals/m^2. This also represents a shift toward *Pocillopora* dominance during the study.

Distinct size-dependent patterns in coral density emerged among genera (Fig. 2c). A large pulse in the density of small *Pocillopora* colonies visible on photos in 2016 was followed by a shift to larger size classes over the coming years, suggesting a short-lived post-disturbance recruitment pulse with high survival and cohort growth. A similar but lagged recovery trajectory was present for *Acropora*, with small colony dominance in 2018 (Fig. 2c) shifting toward large colony dominance by 2020, again indicating cohort growth. Comparatively, *Stylophora* showed a slower

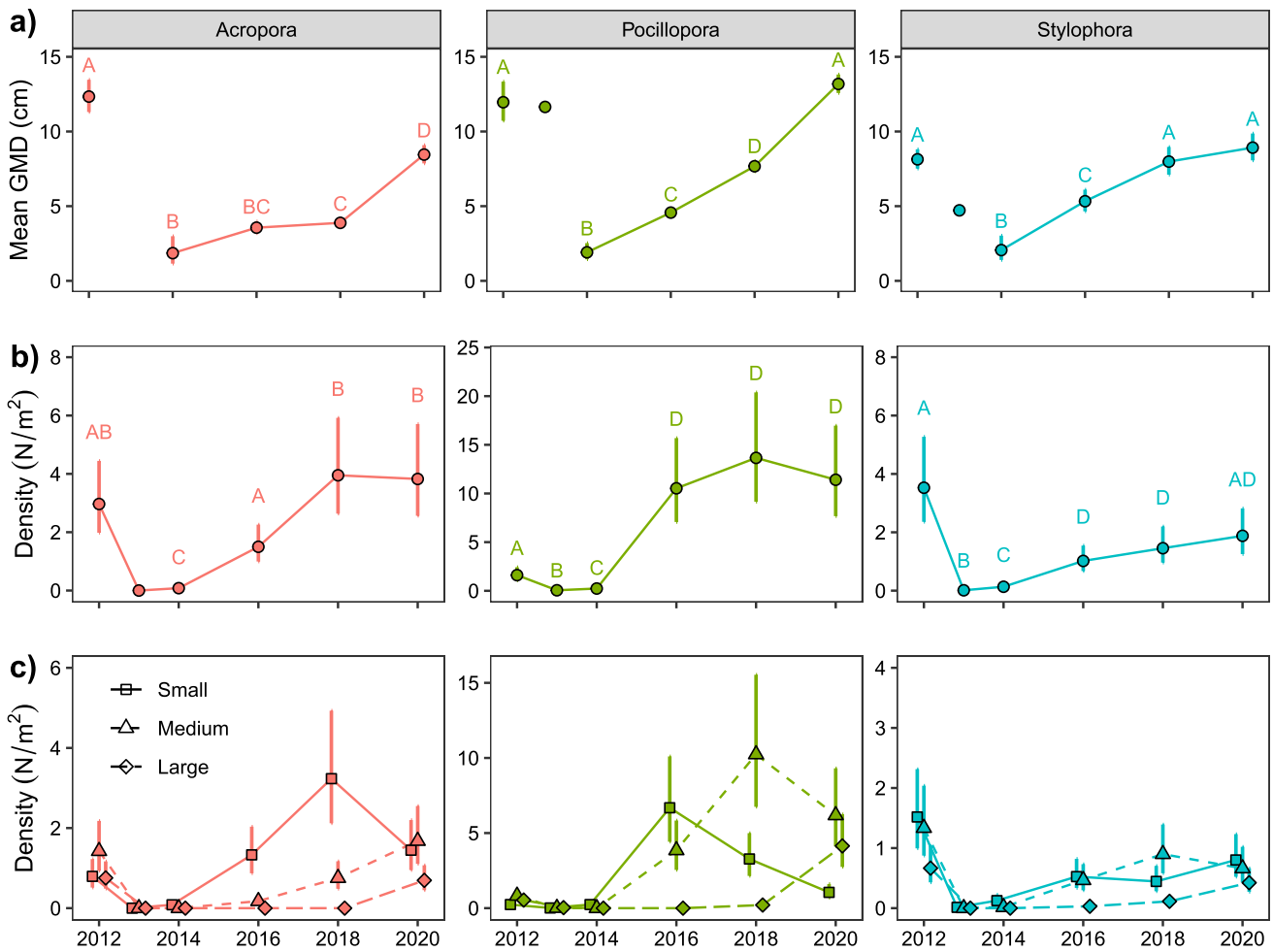

Fig. 2 Demographic time series for *Acropora* (red), *Pocillopora* (green), and *Stylphora* (blue) populations. Shifts in **a** colony size (GMD), **b** overall coral density, and **c** density of different size classes (small: < 5 cm GMD, medium: 5-15 cm GMD, and large: > 15 cm GMD) are as mean ± 95% confidence intervals. Shared capital letters denote years with no statistically significant differences in response (tested with GLMMs and post-hoc Tukey tests by genus)

recovery of colony density, with successful recruitment pulses in 2016 and 2020 indicated by high densities of small colonies in those years (Fig. 2c). Notably, the recovery of pocilloporids was characterised by rapid shift to positive skewness in the first years post-disturbance (2014) followed by a shift to negative skewness (Fig. S1a). This represents successful cohort growth and lower concurrent recruitment, with more abundant larger-than-average-sized corals. Comparatively, skewness for *Acropora* remained closer to zero throughout, suggesting that size classes were more evenly distributed throughout recovery (Fig. S1a, Fig. 2c). Leptokurtic peaked size distributions across taxa and years (Fig. S1b) show that average-sized coral colonies were more dominant than larger or smaller colonies, characteristic of slow recovery of large coral sizes.

Reef monitoring typically focuses on measuring benthic coverage and taxonomic community structure, not demographic coral metrics. However, it is not known whether demographic recovery trajectories correspond to changes in coral coverage. By comparing benthic coverage of each studied genus against their colony density, a clear 'r-shaped' response pattern emerges over the duration of the recovery period (Fig. 3, 2013 onward). Rapid increases in colony density in the years after typhoon disturbance (i.e., by 2016) predate subsequent increases in coral coverage, suggesting that such demographic approaches can provide early indications of population recovery. By the end of this study in 2020, the benthic coverage of *Acropora* had still not returned to pre-disturbance levels. However, by qualitatively extrapolating the *Acropora* trend for an additional 2–4 years (Fig. 3) we could expect the small *Acropora* colonies present in 2020 to grow and lead to subsequent increases in *Acropora* coverage toward pre-disturbance levels or beyond, provided mortality remains low. Comparably, the coverage of *Pocillopora* by 2020 far exceeded pre-disturbance levels. Notably, the genera studied here accounted for a small proportion (8–10%)

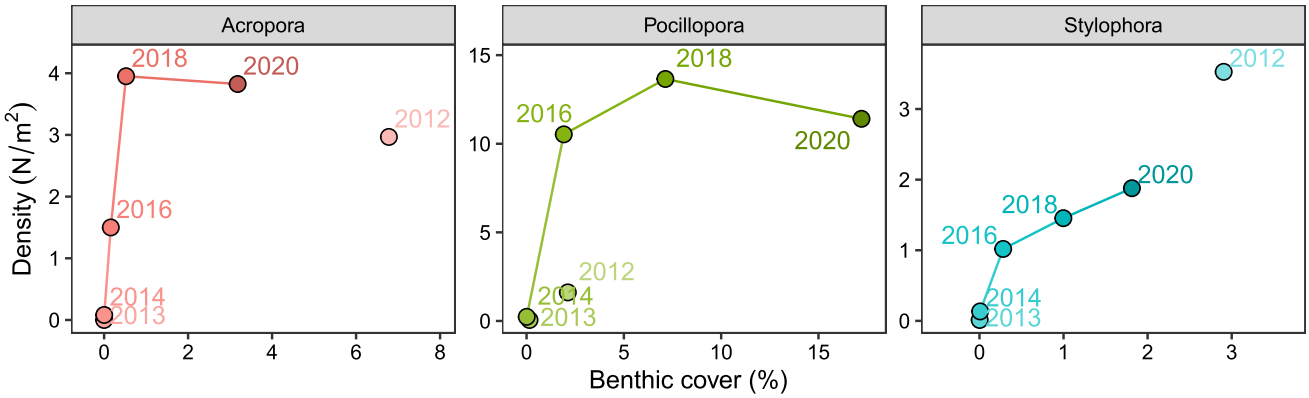

Fig. 3 Benthic coverage versus mean coral density through time. Coverage is calculated as total colony area for each genus divided by total sampled area. Temporal trajectories from 2012 (pale) to 2020 (dark) highlight an r-shaped recovery trajectory from 2013 onwards, with recovery detectable in coral density earlier than coral coverage

of pre-disturbance total coral coverage, but by 2020 have become the most dominant coral genera (> 80% of total coral cover) (personal observation).

Here, we document the decadal recovery trajectories of three common coral genera on a reef that suffered catastrophic coral loss from super typhoon Bopha in 2012. For pocilloporids, average colony size and colony density had both recovered to or exceeded pre-disturbance levels within 7 years. However, *Acropora* showed a slower recovery response; although colony densities recovered within 5 years, colonies remained smaller than the pre-disturbance population throughout the duration of this study. Given that the 2020 *Acropora* size structure still contained a large proportion of small- to medium-sized colonies, it is possible that large *Acropora* colonies will start emerging over the coming years.

Differences in reproductive biology among genera may have influenced recovery rates (see Doropoulos et al. 2015, and Edmunds et al. 2010). *Acropora* colonies are broadcast spawners, releasing egg sperm bundles during mass spawning events that occur predominantly in March/April in Palau (Gouezo et al. 2020b). Non-favourable oceanographic and weather conditions during this window could lead to low larval supply, for instance, if wind, waves or currents transport coral larvae to the western reefs and open ocean, a common phenomenon for the eastern outer reefs of Palau (Gouezo et al. 2020c). In contrast, the family Pocilloporidae comprises a mix of spawning and brooding species (Edmunds et al. 2010), and their spat are typically found settling year-round (Edmunds et al. 2010; Gouezo et al. 2020a), increasing their opportunity for successful recruitment. All genera seemed to be growing at much the same rates, but densities of *Pocillopora* increased earlier than *Acropora* or *Stylophora*, indicating that recruitment was driving the differences in demographic recovery. Why post-disturbance recruitment would be fastest for *Pocillopora* (compared to other taxa) remains unresolved given our dataset, but factors related to reproductive biology and larval ecology for these taxa could have played a role (Baird, et al. 2009; Connolly and Baird 2010). In addition, recovery can take longer for taxa that reach very large colony sizes, such as tabular *Acropora*, which have a critical ecological importance yet are more vulnerable to disturbances (Ortiz et al. 2021). It is likely that healthy populations of stress-tolerant coral genera, such as massive *Porites*, may take several decades for recovery of population size structure in the case of catastrophic disturbances (Zhao et al. 2014), unless remnant tissue can rapidly regenerate and reskin dead skeletons of large colonies (Roff et al. 2014). As such, further demographic analysis of slower-growing massive coral taxa could prove insightful into how recovery potential in Palau varies across life history strategies.

Our study highlights the greater mechanistic insights that can be gained using demographic techniques on historic long-term monitoring data. While coral coverage can suggest that recovery is slow or non-existent, demographic features like size frequency distributions or coral colony density can provide early signs of population recovery. Under climate change, disturbance events are increasing in magnitude, and recovery intervals are becoming progressively shorter. Here we documented complete loss of corals at an east Palauan outer reef, and subsequent population recovery within 5–7 years for more rapidly recruiting pocilloporids, and over 8 years for broadcast-spawning *Acropora* that have fewer annual recruitment events. As other reef habitats within the reef system of Palau escaped the impacts of typhoon Bopha and Haiyan (Gouezo et al. 2019), larval supply from these reefs to typhoon damaged reefs likely promoted their recovery. Yet recovery may be much slower for reef systems with impaired recruitment, for example, following widespread mass mortality events. Understanding how contemporary coral communities may change in the future

will require further research on the recovery potential of different coral taxa and on disentangling the combined effects of environmental impacts and ecological interactions on population dynamics.

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Author contributions LL and PB contributed equally to this work and can therefore each list this publication as first author in their curriculum vitae. LL, PB, JG, and YG conceived the study, MG, VN, and DO conducted field surveys, LL and PB wrote the first draft, and all authors contributed to writing of the final draft.

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Data availability All original data and R code is available on figshare at https://doi.org/https://doi.org/10.25405/data.ncl.22153790.

Declarations

Conflict of interest The authors have no conflict of interest.

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