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Decadal variability in sponge abundance and biodiversity on an Indo-Pacific coral reef

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ABSTRACT: Natural communities can undergo large temporal changes in abundance and species composition that may be difficult to detect without long-term ecological monitoring. Characterizing temporal variability in coral reef fauna is critical for predicting how reef ecosystems will be impacted by environmental change. Sponges are an ecologically important component of coral reefs, yet descriptions of temporal dynamics of multi-species sponge assemblages are scarce. We studied temporal changes in abundance and biodiversity of an Indonesian coral reef sponge assemblage over 13 yr (2005–2017). Mean (±SE) sponge abundance (sponge patches m^{-2}) initially increased from 124.06 ± 8.46 to 183.73 ± 12.12 in 2005–2007 ($p < 0.001$), declined to 66.53 ± 10.62 in 2007–2014 ($p < 0.001$), and increased to 105.87 ± 15.42 in 2014–2017 ($p < 0.001$). These patterns in sponge abundance did not depend on water temperature. Overall, we recorded 141 sponge taxa. However, species composition showed strong temporal patterns driven by a few abundant taxa (e.g. *Protosuberites* sp., *Sycon* sp., and *Pericharax* sp., respectively accounting on average for ~25, 20, and 5% of total sponge abundance). Species richness increased with sponge abundance ($p < 0.001$), whereas evenness decreased due to dominance of some taxa in years of high sponge abundance ($p = 0.002$). Our study highlights that the abundance and biodiversity of Indo-Pacific sponge assemblages undergo dramatic temporal changes driven by species-specific population variability. This variability has important implications for designing monitoring programs, for interpreting experimental studies, and for understanding long-term responses of coral reefs to perturbations.

KEY WORDS: Sponge assemblage · Porifera · Indo-Pacific · Population variability · Long-term monitoring · Sponge diversity

1. INTRODUCTION

Demographic patterns and species composition of natural communities can display strong temporal variation. Interannual fluctuations of the abundance of natural populations have been well documented for many organisms; for example, plants (Gonzalez-Andujar et al. 2006), insects (Turchin et al. 1991), marine benthic infaunal communities (Frid et al. 2009), and coral reef organisms (Adjeroud et al. 2002, Shenkar et al. 2008). Within communities and multi-species assemblages, life-history traits of a species

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can influence its responses to environmental drivers, and this can result in species-specific population dynamics. As a consequence, the species composition and biological diversity of the assemblage can also be temporally variable (e.g. Mokany et al. 2015, Lamy et al. 2016).

Understanding the temporal dynamics of functional components of coral reef communities is challenging because of the complexity of interactions and the range of factors that drive them. Sponges are an important component of coral reefs, where they perform a variety of functional roles (Bell 2008). For example, sponges remove particles and organic matter from the water column through filtration (de Goeij et al. 2008) and make them available to higher trophic levels either as sponge detritus eaten by detritivores (Rix et al. 2018) or as sponge biomass eaten by sponge predators (McMurray et al. 2018, Pawlik et al. 2018). Sponges also influence the accretion–erosion balance of reefs, negatively by chemical-mediated bioerosion (Schönberg et al. 2017) and positively by rubble binding (Wulff 1984). Sponges also play an important role in silicon cycling (Maldonado et al. 2005) and provide biogenic habitat for associated microbial and macrofaunal communities (Wulff 2006a, Taylor et al. 2007). In the context of environmental change and reef degradation, sponges are receiving increasing attention due to their potential to become more abundant, and even dominant, on coral reefs with the decline of corals (Norström et al. 2009, Bell et al. 2013, Stubler et al. 2015, Bennett et al. 2017, 2018). An absolute increase in sponge abundance on coral reefs has already been observed in the Caribbean (Diaz & Rutzler 2001, McMurray et al. 2010) and at certain sites in the Indo-Pacific (Powell et al. 2010, 2014) and tropical Pacific (Schils 2012, Knapp et al. 2013, 2016). However, studies on temporal dynamics of tropical sponge assemblages are rare; most long-term surveys have been performed in the Caribbean (Butler et al. 1995, Wulff 2006b, 2013, 2017, Stevely et al. 2011), although recent reports have also emerged from the Central Pacific (Knapp et al. 2013, 2016) and Great Barrier Reef (Ramsby et al. 2017).

The Indo-Pacific is an important biodiversity hotspot for marine taxa, including fishes and corals (Roberts et al. 2002). Sponge assemblages in the Indo-Pacific are extremely complex and poorly understood (van Soest et al. 2012, Bell et al. 2015a), particularly with respect to variation in sponge abundance and diversity. Despite the paucity of information on sponge ecology in the Indo-Pacific, sponges from this region fill all the important ecological roles mentioned above: bioerosion (Marlow et al. 2018a), silicon cycling (Bertolino et al. 2017), competitors for space (de Voogd et al. 2004, Rossi et al. 2015), food sources for grazers (Powell et al. 2015), and hosts for bacterial communities (Cleary et al. 2018). Nevertheless, while studies have described the community composition of sponge assemblages at some locations in Indonesia (Cleary & de Voogd 2007, de Voogd & Cleary 2008, de Voogd et al. 2009, Calcinai et al. 2017) and short-term temporal changes in monospecific sponge populations (Biggerstaff et al. 2017), no information exists on temporal dynamics of entire sponge assemblages. These knowledge gaps severely restrict our understanding of benthic dynamics on potentially threatened reefs. Understanding patterns in abundance, demography, and the taxonomic composition of sponge assemblages is important for distinguishing between changes that are a result of natural population variability and those that may be a result of anthropogenic disturbance.

Of the many environmental drivers that can influence the temporal dynamics of a community, changes in seawater temperature have variable effects on sponge populations. Widespread sponge mortality has been documented after exposure to increased water temperature in temperate and tropical systems (reviewed in Bell et al. 2017). However, some sponge assemblages are resistant to acute warming associated with El Niño Southern Oscillations (Kelmo et al. 2013), and sponges have been proposed as potential winners on warmer coral reefs under near-future climate scenarios (reviewed in Bell et al. 2018). Warming trends over the past few decades have been reported for the Indo-Pacific (Heron et al. 2016), and bleaching events in this region have been documented for corals (Bruno and Selig 2007, Wilson et al. 2012) and the bioeroding sponge *Cliona* aff. *viridis* (Marlow et al. 2018b). However, the effects of temporal changes in seawater temperature on sponge assemblages in this region remain unexplored.

Long-term monitoring is important to understand the effects of perturbations on communities. This study quantified long-term temporal variation of sponge abundance (measured as the number of sponge patches), diversity, and assemblage composition on an Indonesian coral reef between 2005 and 2017 in order to (1) characterize the temporal dynamics of the sponge assemblage; (2) investigate the effect of seawater temperature on sponge assemblage demographics; (3) investigate whether fluctuations in sponge abundance correspond to changes in the biodiversity of the assemblage; and (4) perform an analysis of the assemblage composition to identify which taxa contribute most to the observed demographic fluctuations.

2. MATERIALS AND METHODS

2.1. Site description and sampling protocol

The study location (known locally as Buoy 3; 05° 28.34' S, 123° 45.43' E) is a vertical reef wall off the south-west coast of Hoga Island in the Wakatobi Marine Park (SE Sulawesi, Indonesia; Fig. 1). At this location, 3 replicate sites (A, B, and C, herein referred to as 'sites') approximately 100 m apart from one another were established in 2005 at a depth of 10–12 m. Shallow-water marine sponges generally have limited dispersal capabilities (Maldonado 2006), with dispersal distances on the order of <25 m for small encrusting species that produce philopatric larvae (Blanquer et al. 2009) and 60–140 m for larger species like *Xestospongia* spp. in the Indo-Pacific (Bell et al. 2014). Therefore, the distance between replicate sites was considered sufficient to minimize between-site recruitment for most of the surveyed sponge taxa. Due to the configuration of the reef, Sites A and B were established on a 90° wall, whereas Site C was inclined at approx. 80°. At each site, 5 permanent 1 m^2 fixed replicate quadrats were established on the vertical reef wall along an approximately 1 m long reef tract. Permanent quadrats were chosen as the most appropriate method to monitor temporal dynamics of the same sponge assemblage in the same reef area while ensuring consistency between reef surfaces that were being sampled through time (e.g. to standardize for shading, orientation, surface angle, and fractal surfaces). The quadrats were positioned haphazardly at each site because if permanent plots are placed by judgement this may give a biased picture of the population (Hill et al. 2006). After establishing the quadrats, initial surveys were conducted to identify the dominant sponge species inhabiting the area. Tissue samples were collected from approximately 50 sponges in the first year to identify the dominant sponge taxa at the highest resolution possible. Taxon identification, where possible, of these sponges was based on external and internal (spicule and structure) morphological features and carried out with the aid of published resources (e.g. van Soest 1989, Hooper & van Soest 2002). Reference information for *in situ* identification of the sponges in subsequent years was maintained, with additional sampling performed any time a new taxon was recorded in the quadrats (although material was only able to be exported in the first year for full taxonomic work). While the majority of taxa were not formally identified, we were able to consistently classify the same taxa through time since the same observer collected all data, allowing us to examine overall assemblage dynamics.

While there are several ways that sponge abundance can be characterized (Bell et al. 2017), here we selected total sponge abundance based on number of patches, where one sponge patch corresponds to a delimited growth form of a single sponge taxon. Patches were selected as a measure of sponge abundance for several logistical and practical reasons. The sponge assemblage at this reef primarily consists of small encrusting species (ranging from a few mm^2 to ~0.25 m^2 for the largest sponge; see Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m620p063_supp.pdf for scales), found in small patches at high densities (often >200 sponges m^{-2}). An accurate estimation of the individual volume or biomass of these sponges

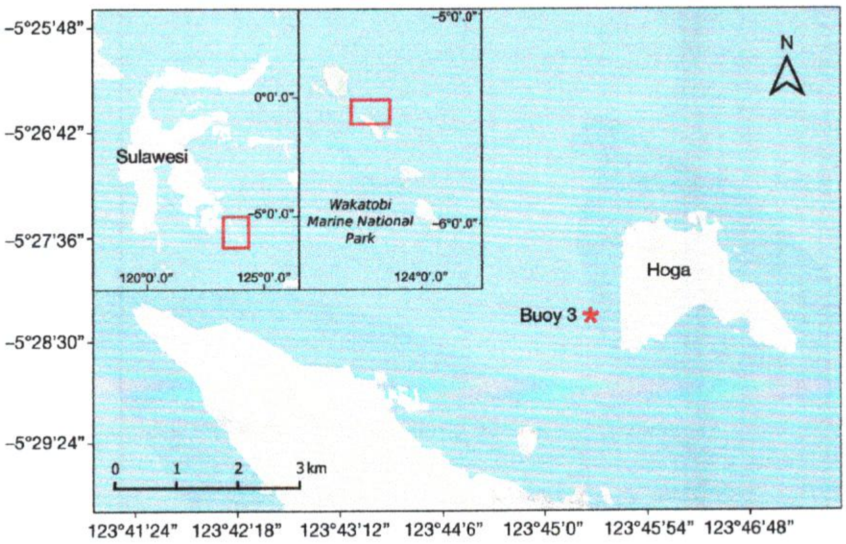

Fig. 1. Hoga Island, the Wakatobi National Marine Park, and Sulawesi. Star: location of study site. Map data: © OpenStreetMap contributors (https://www.openstreetmap.org). Map created in QGIS (QGIS Development Team 2018)

was therefore impractical due to their morphology (>90% of sponges patches were encrusting) and dimensions. Furthermore, while photographic methods were trialed to estimate percentage cover, the high diversity and coverage of non-sponge benthic organisms meant a large number of sponges could not be seen in the photographs. For these reasons, the number of sponge patches was considered the most appropriate measure to capture sponge abundance and diversity in this study. Sponges were counted *in situ* by the same observer, using SCUBA, between June and July every year from 2005–2017, except for in 2010 and 2012. We identified a total of 141 sponge taxa on the reef over the study period. A complete list of the taxonomically identified sponges and pictures of the most common taxa can be found in Supplement 1 (Table S1, Fig. S1).

2.2. Temporal changes in sponge abundance

Given total sponge abundance, N, in each quadrat, for each pair of consecutive years, y and $y + 1$, the annual percentage population growth rate, g, for sponges in each quadrat was calculated as $g = [(N_{y+1} - N_y)/N_y] \times 100$. Temporal and spatial differences in N were explored by fitting linear mixed effect models (LMMs; R package 'nlme', Pinheiro et al. 2018) with normally distributed errors and random intercepts. Despite the limited dispersal range of sponges (Blanquer et al. 2009), between-quadrat recruitment was possible within the same site. Therefore, to account for the quadrat-associated variation in the data, quadrat was used as random factor in all models (Davies & Gray 2015). Models were built with years from the start of the survey and site as fixed effects and with quadrat as a random effect to account for between-quadrat variability. To account for repeated measures, a continuous autocorrelation structure of order 1 was fitted to the models. The autocorrelation structure built into the model accounts for dependence of the response variable N at time y on its own value at time $y - 1$ (i.e. the previous year), with strength of the correlation declining for measures that are further than 1 time step away. The most appropriate combination of fixed effects was selected with the likelihood ratio test (LRT). A variance–covariance matrix accounting for between-quadrat heteroscedasticity was then fitted to the model selected with LRT. Equal variance and normality of the errors were checked for all models with analysis of the normalized residuals. Reef-level differences in N between specific time points (e.g. start and end of the survey, and times of maximum and minimum N) were then detected with Wilcoxon signed rank tests for paired samples with Bonferroni correction. Differences in N between sites were detected with Mann-Whitney tests with Bonferroni correction. For all tests a significance level of 5% was used.

2.3. Effects of SST on N and g

Sea surface temperature (SST) and SST anomaly (SSTANOM) data for the studied period were obtained from the National Oceanic and Atmospheric Administration's (NOAA) Coral Reef Watch programme (resolution 50 km; https://www.ospo.noaa.gov/data/cb/TS_vs/vs_ts_Wakatobi_Indonesia.txt, Coral Reef Watch 2000, Figs. S2 & S3 in Supplement 1). Data from the Wakatobi Virtual Station (5° S, 124° E; ~59 km from Buoy 3) was used as it is nearest to the study site. SST and SSTANOM were averaged for the 6 mo (December to May) preceding each sponge survey event. A 6 mo period was chosen to capture the warmest months preceding each sponge census (Fig. S2). LMMs were used to investigate the effect of mean SST and SSTANOM over the 6 mo prior to each sponge sampling event on (1) N and (2) g. Models were built with SST and SSTANOM as fixed effects, quadrat as a random effect, and model structure as described in Section 2.2. Time series of SST and SSTANOM were decomposed with moving averages to identify trends.

2.4. Species richness, diversity, and evenness

For each quadrat, we calculated species richness, diversity, and evenness of the assemblage. Species richness (S) was defined as the number of taxa represented by at least one sponge patch, species diversity was expressed with Shannon's H', and evenness with Simpson's evenness index, $E_{1/D}$ (Williams 1964). $E_{1/D}$ satisfies the requirement of independence from S and is a commonly used evenness index when the importance of rare species is considered limited (Smith & Wilson 1996). Given the extreme rarity of some of the taxa recorded, this index was deemed the most robust and was selected to complement H', which gives the same weight to dominant and rare species. Species richness has been shown to have a positive relationship with abundance (Bock et al. 2007). To understand whether temporal changes in N would correspond to changes in biodiversity, relationships between S and N, between H' and N, and between $E_{1/D}$ and N were explored with LMMs. Models were built with N as a fixed effect, quadrat as a random effect, and a model structure as described in Section 2.2.

2.5. Spatio-temporal changes in species composition

Temporal and spatial variation in sponge assemblage composition were investigated using a combination of unconstrained and constrained ordination methods (Anderson & Willis 2003). First, the abundances of the 141 sponge taxa per quadrat over the 11 yr sampled were log transformed [log(x + 1)], and a Bray-Curtis dissimilarity matrix was calculated for the assemblage. Non-metric multidimensional scaling (nMDS) was performed on the matrix, using sites and years as factors in order to evaluate patterns in the assemblage composition in space and time. The number of k-dimensions for the nMDS ordination was set to $k = 4$. This was derived by iterating the ordination with a growing number of k-dimensions, starting from $k = 2$, and by determining at which point the stress function fell below 0.2. Permutational MANOVA (Anderson 2001) was performed to test for a significant effect of space and time on assemblage composition. Sites, years, and the interaction between the 2 were used as factors for the analysis, using 9999 permutations. Finally, a canonical analysis of principal coordinates (CAP) was performed to disentangle the contribution of the most abundant taxa to the assemblage variation in space and time and to understand how samples from different sites and years were related in terms of species composition. The log transformation of sponge abundance was chosen to reduce the effect of dominant and rare species. The analysis of the Bray-Curtis matrix was repeated using a square-root transformation, and consistency of results was checked to avoid possible biases due to the data transformation. Multivariate analysis was performed with the R package 'vegan' (Oksanen et al. 2016). All analyses and plotting were performed in R v.3.4.3 (R Core Team 2019) and the package 'ggplot2' (Wickham 2009).

3. RESULTS

3.1. Sponge assemblage dynamics

Results from LMMs showed that N changed over time and between sites ($p = 0.015$; Table 1). Mean (±SE) N (sponge patches m^{-2}) at this reef initially increased from 124.06 ± 8.46 to 183.73 ± 12.12 (+47 %, $p < 0.001$), then declined to 66.53 ± 10.62 between 2007 and 2014 (−63 %, $p < 0.001$), and then increased again to 105.87 ± 15.42 between 2014 and 2017 (+59 %, $p < 0.001$). No significant change in total N was detected between the start and the end of the survey period ($p = 0.073$). This pattern was consistent within and across the 3 sites. N at Site B was generally lower than at Sites A and C (both $p < 0.001$), and it was similar between Sites A and C ($p = 0.25$; Fig. 2). The full data set of sponge abundance per taxa is available in Table S2 in Supplement 2 at www.int-res.com/articles/suppl/m620p063_supp.xlsx.

Table 1. Coefficients of linear mixed effects models. The fixed model term, coefficient estimate, SE, df, t- and p-value are reported for all dependent variables (N: sponge abundance; S: species richness; H': Shannon's diversity; $E_{1/D}$: Simpson's evenness). Significant results ($p < 0.05$) highlighted in **bold**

Dep. var.	Coefficient	Estimate	SE	df	t	p
N	Intercept	169.282	17.894	149	9.460	**<0.001**
	Years from 2005	−4.779	1.040	149	−4.595	**<0.001**
	Site B	−63.264	21.526	12	−2.939	0.012
	Site C	−13.688	22.747	12	−0.602	0.558
S	Intercept	11.467	1.370	147	8.373	**<0.001**
	N	0.029	0.007	147	4.005	**0.001**
	Site B	−1.752	1.931	12	−0.908	0.382
	Site C	2.029	2.101	12	0.966	0.353
	[N]:[Site B]	0.059	0.015	147	3.941	**0.001**
	[N]:[Site C]	0.020	0.012	147	1.587	0.115
H'	Intercept	1.983	0.123	147	16.064	**<0.001**
	N	−0.0004	0.0006	147	−0.777	0.439
	Site B	0.150	0.171	12	0.876	0.398
	Site C	0.291	0.171	12	1.701	0.115
	[N]:[Site B]	0.003	0.001	147	2.484	**0.014**
	[N]:[Site C]	0.001	0.001	147	1.099	0.274
$E_{1/D}$	Intercept	0.429	0.038	147	11.155	**<0.001**
	N	−0.001	0.0002	147	−4.580	**<0.001**
	Site B	0.304	0.056	12	5.417	**0.002**
	Site C	0.114	0.060	12	1.910	0.080
	[N]:[Site B]	−0.002	0.0004	147	−5.062	**<0.001**
	[N]:[Site C]	−0.0004	0.0003	147	−1.382	0.169

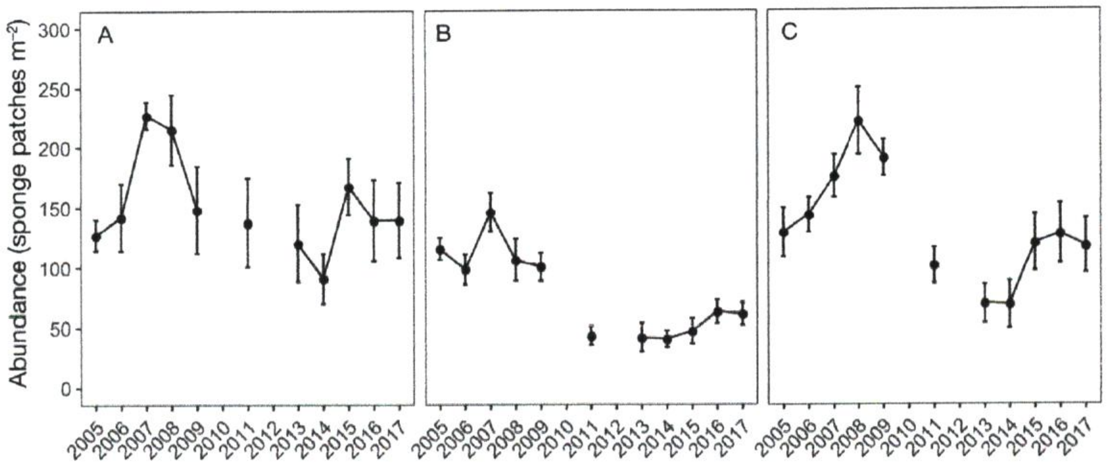

Fig. 2. Mean ± SE total sponge abundance from 2005–2017 at the 3 replicate sites (A–C) at Buoy 3 (Hoga Island, Wakatobi National Marine Park, Indonesia)

3.2. Effects of water temperature on N and g

We found no significant effect of SST or SSTANOM on N or g. SST anomalies were always positive in 2016, indicating a particularly warm year (Fig. S3). However, decomposition of the time series with moving averages of both SST and SSTANOM showed no clear temporal trend (Figs. S4 & S5 in Supplement 1), indicating that SST and SSTANOM have not increased at this site over the study period. Due to lack of evidence for effects of temperature on temporal changes of this sponge assemblage and lack of clear temporal trends in sea water temperature at this station over the study period, we excluded SST and SSTANOM from further steps in this investigation.

3.3. S, H', and $E_{1/D}$

Fluctuations in S followed similar patterns as in N. Maximum mean (±SE) S at this reef was recorded in 2007 at the time of highest N (22.60 ± 0.88 species quadrat^{-1}), whereas the minimum was recorded in 2013 (12.8 ± 0.89). Assemblage evenness followed the opposite pattern, being lowest in 2007 (0.29 ± 0.02) and highest in 2013 (0.49 ± 0.05). The overall minimum number of species quadrat^{-1} recorded was 6 in 2013 (Site A, quadrat 4), whereas the highest was 34 in 2009 (Site C, quadrat 1). On average, S was highest at Site C in 2007 and 2009 (mean ± SE: 25.8 ± 0.97 and 25.8 ± 2.35 species quadrat^{-1} respectively) and lowest at Site B in 2013 (10.8 ± 0.73 species quadrat^{-1}). Mean H' was highest at Site B in 2009 (2.73 ± 0.32) and lowest at Site A in 2015 (1.66 ± 0.18). However, H' did not show temporal patterns consistent across quadrats and sites as found for N and S.

N had a site-specific positive effect on S ($p < 0.001$) and a site-specific negative effect on $E_{1/D}$ ($p = 0.002$). N and site had an interactive effect on H' ($p = 0.05$), but this effect was generally weak and was statistically different from 0 only at Site B. Best LMM fits are shown in Fig. 3. Full LMM results and coefficients are reported in Table 1.

3.4. Spatio-temporal changes in species composition

nMDS showed that the sponge assemblage composition varied in both space and time (stress = 0.16; Fig. 4A). Quadrats from Site B were partially separated from quadrats at Sites A and C, which were more similar to each other. *Sycon* sp., *Pseudoceratina* sp. 1, and *Protosuberites* sp. were dominant at Sites A and C and were less strongly associated with Site B, whereas some less abundant taxa (e.g. *Cliona* sp. and *Clathrina* sp. 2) were mostly found at Site B (Fig. 4B & Fig. S6; also see Fig. S7 [both figures in Supplement 1] for year-by-year nMDS plots). Samples from the same year tended to cluster together both within and across sites, and samples from adjacent years were also relatively close to each other. Permutational MANOVA showed that time (years) explained 21% of the variation (F = 4.83, $p < 0.001$), site explained 12% (F = 13.38, p <

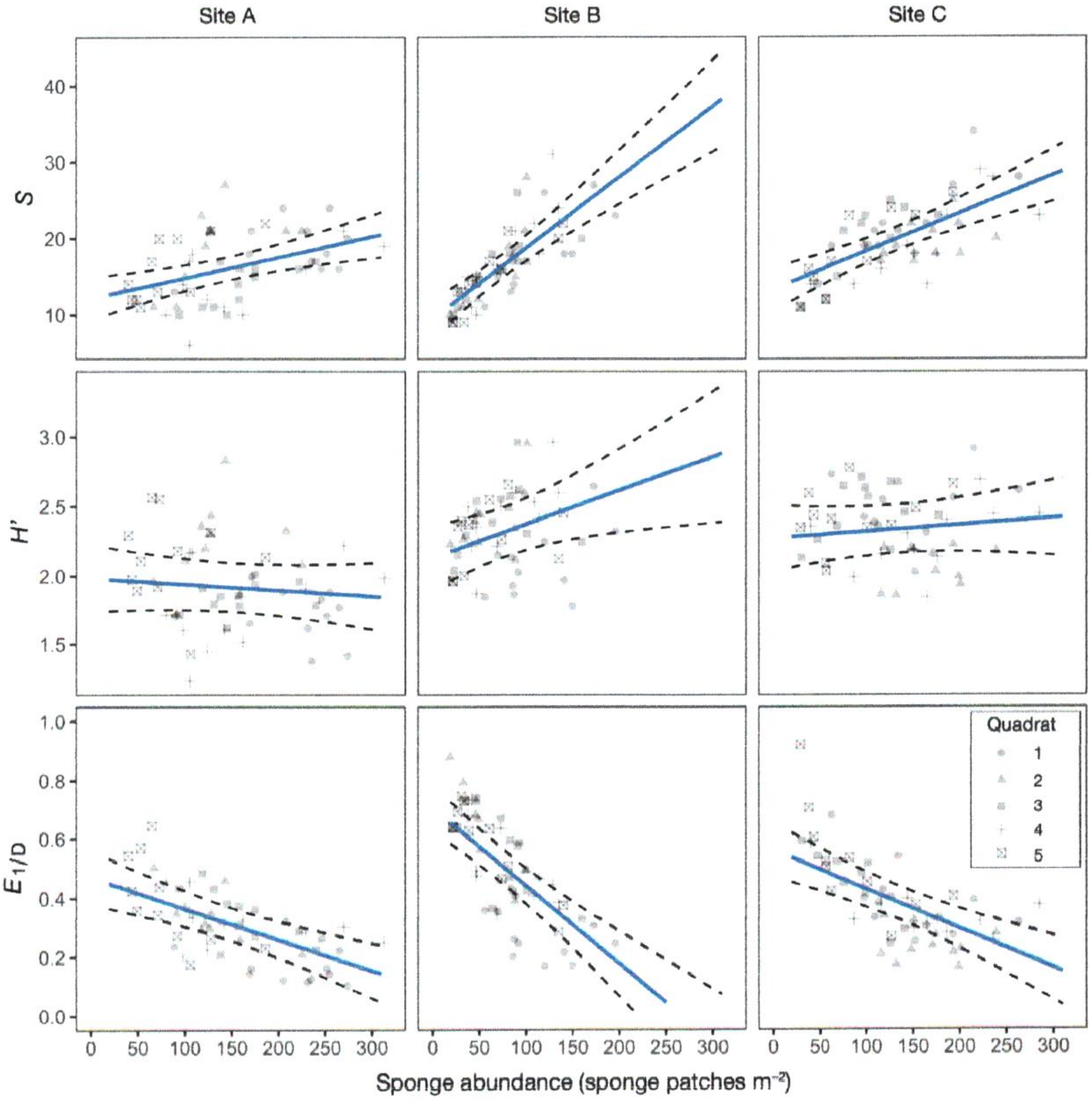

Fig. 3. Effect plots showing the best linear mixed model (LMM) fits for the biodiversity metrics (species richness S, Shannon's diversity H', and Simpson's evenness $E_{1/D}$) modelled as function of sponge counts and site. Blue lines: best LMM fit; black dashed lines: 95% confidence intervals of the model parameters; grey dots: observed data. Different shapes of the dots represent different quadrats within each site

0.001), and the interaction between these 2 factors explained a further 10% (F = 1.17, p = 0.031). Finally, the CAP plot highlighted a difference in the composition of the assemblage between years of high and low N (Fig. 4B). Specifically, years with high N were characterized by high numbers of *Protosuberites* sp., *Sycon* sp., and *Pericharax* sp. All 3 are heterotrophic sponges but are taxonomically distant (*Protosuberites* sp. is a demosponge; *Pericharax* sp. and *Sycon* sp. are calcareous sponges). Proportions of these taxa in the assemblage varied between sites and over time, but on average they accounted for ~25, 20, and 5% of total sponge abundance, respectively. Population dynamics of the most abundant sponge taxa (Table 2) during the study period is shown in Fig. S6.

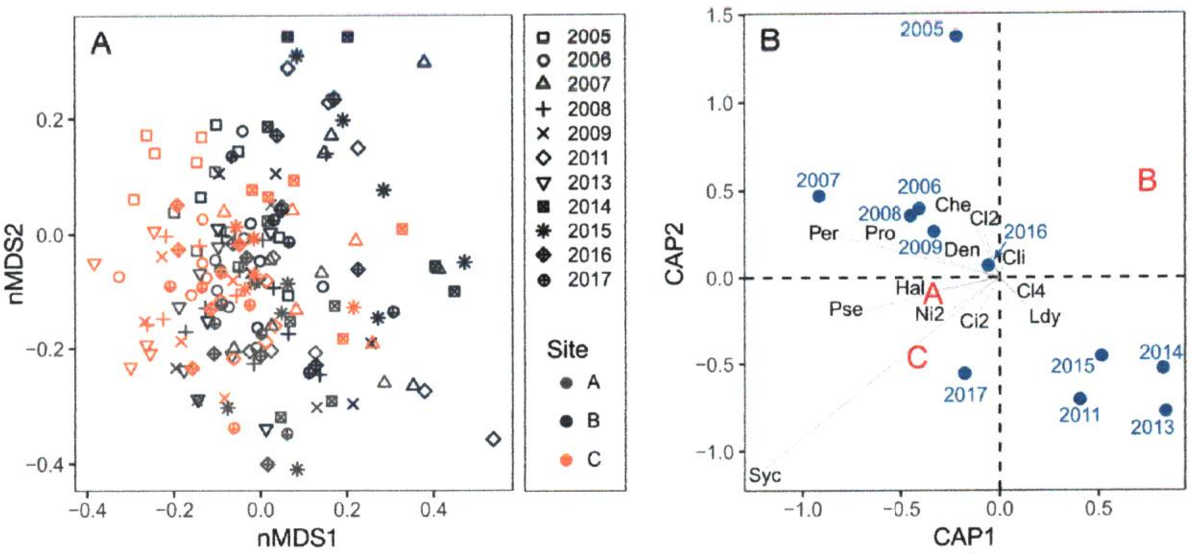

Fig. 4. Spatial and temporal variation of sponge assemblage composition. (A) Non-metric multi-dimensional scaling (nMDS) plot for the sponge assemblages at the 3 sites between 2005 and 2017. Each sample corresponds to a quadrat. (B) Canonical analysis of principal coordinates (CAP) plot. Years and sites represent the centroid for each set of samples. For visualization purposes, only the taxonomically identified taxa that varied the most between sites and years are plotted (but all taxa were included in the analysis). See Table 2 for species abbreviations

4. DISCUSSION

4.1. Temporal changes in sponge abundance

Considerable temporal variation was evident in the abundance and species composition of the sponge assemblage on this Indonesian coral reef over a 13 yr period. We found that a subset of species had large population variability and determined the magnitude of the fluctuations in total sponge abundance. Biodiversity also changed considerably over the studied period, with species richness generally increasing with sponge abundance. However, due to a few dominant species, assemblage evenness was lowest when total sponge abundance was highest.

In the Caribbean, rapid declines in sponge abundance due to widespread mortality events have been reported and these may or may not be followed by recovery. For example, Butler et al. (1995) found that 80% of sponges were decimated in Florida Bay after being exposed to a cyanobacterial bloom in 1991, and the remaining sponges died in a second bloom in 1992. Subsequently, Stevely et al. (2011) showed that the same sponge assemblages displayed signs of overall long-term recovery, while Wulff (2006b) reported a 42.6% decline in sponge volume on a Panamanian reef over 14 yr, but that decline was not followed by recovery. In the present study, the Indo-Pacific sponge assemblage showed a continual decline over about 7 yr, in contrast to the abrupt drops caused by acute disturbance observed in some earlier studies (e.g. Stevely et al. 2011). This suggests that the changes in sponge abundance reported in this study were unlikely to be driven by an acute disturbance. However, total sponge abundance followed the same pattern of fluctuation both within and across the 3 replicate sites, suggesting that independent stochastic variation was also unlikely to have driven the observed demographic trends.

A direct and important consequence of the observed variability is that shorter-term sampling within the studied period could have yielded different information on sponge abundance on this coral reef. For example, if sampling had occurred solely in 2007 (year of maximum mean *N*), it would have shown almost 3 times as many sponge patches as if it had occurred only in 2014 (year of minimum mean *N*). The rarity of long-term studies of sponge dynamics and ecology highlights the need to complement studies considering spatial variability across environmental gradients at single time points with continuous and regular monitoring of assemblages.

4.2. Temporal changes in taxonomic composition and biodiversity

The sponge assemblage in the Wakatobi Marine Park was highly diverse, with a total of 141 sponge taxa recorded over 13 yr in an area of only 15 m^2 (see Bell 2007, Bell & Smith 2004 for a list of sponge families at Hoga Island and Table S1 for the complete list

Table 2. Most common taxonomically identified sponge taxa (with mean ±SE abundance) from Hoga Island, Wakatobi, Indonesia. Of the sponge taxa that, summed, comprised >90% of the total sponge abundance in each photoquadrat (30 of the total 141 taxa), the following 25 could be identified to genus level or lower. Abbreviations used in the CAP plot (Fig. 4B) are reported in the taxon column. Mean abundances for this reef during the study period are reported

Taxon (CAP abbreviation)	Family	Class	Mean ±SE sponge abundance (sponge patches m^{-2})
Aaptos sp.	Suberitidae	Demospongiae	1.02 ± 0.10
Axinyssa sp.	Halichondriidae	Demospongiae	0.27 ± 0.06
Chalinula milnei	Chalinidae	Demospongiae	1.81 ± 0.24
Chalinula sp.	Chalinidae	Demospongiae	0.47 ± 0.13
Chelonaplysilla sp. 1 (Che)	Darwinellidae	Demospongiae	3.18 ± 0.22
Cinachyrella sp. 2 (Ci2)	Tetillidae	Demospongiae	0.33 ± 0.05
Cinachyrella sp. 3	Tetillidae	Demospongiae	0.32 ± 0.05
Clathria (*Microciona*) *mima*	Microcionidae	Demospongiae	0.35 ± 0.08
Clathrina sp. 1	Clathrinidae	Calcarea	0.17 ± 0.08
Clathrina sp. 2 (Cl2)	Clathrinidae	Calcarea	2.22 ± 0.41
Clathrina sp. 4 (Cl4)	Clathrinidae	Calcarea	0.44 ± 0.08
Clathrina sp. 5	Clathrinidae	Calcarea	0.43 ± 0.07
Clathrina sp. 6	Clathrinidae	Calcarea	0.09 ± 0.03
Cliona sp. (Cli)	Clionaidae	Demospongiae	0.15 ± 0.08
Dendrilla sp. (Den)	Darwinellidae	Demospongiae	1.45 ± 0.19
Haliclona sp. (Hal)	Chalinidae	Demospongiae	4.55 ± 0.42
Lamellodysidea herbacea (Ldy)	Dysideidae	Demospongiae	3.89 ± 0.44
Niphates sp. 1	Niphatidae	Demospongiae	0.21 ± 0.05
Niphates sp. 2 (Ni2)	Niphatidae	Demospongiae	0.88 ± 0.1
Niphates sp. 3	Niphatidae	Demospongiae	0.05 ± 0.04
Pericharax sp. (Per)	Leucettidae	Calcarea	7.33 ± 0.60
Placospongia melobesioides	Placospongiidae	Demospongiae	0.74 ± 0.11
Protosuberites sp. (Pro)	Suberitidae	Demospongiae	32.27 ± 2.73
Pseudoceratina sp. 1 (Pse)	Pseudoceratinidae	Demospongiae	5.50 ± 0.58
Sycon sp. (Syc)	Sycettidae	Calcarea	20.30 ± 1.79

of taxonomically identified taxa). Such sponge diversity is comparable to previous reports from other parts of Indonesia or higher when considering that it was recorded at a single reef. Cleary & de Voogd (2007) reported 151 taxa from 9 reefs in the Spermonde Archipelago; de Voogd & Cleary (2008) counted 118 sponge species at 30 reefs in Thousand Islands; de Voogd et al. (2009) reported 168 sponge taxa from 18 sites in NE Kalimantan; and Calcinai et al. (2017) reported 94 sponge species from 26 sites in North Sulawesi. However, most of these previous studies did not survey small encrusting sponges. When sponges were most abundant, a few taxa were dominant (e.g. *Protosuberites* sp., *Sycon* sp., and *Pericharax* sp.). The decline of these taxa determined the observed lower overall *N*, and their population variability caused the composition of the overall assemblage to change over time.

Studies that describe and account for temporal variation of assemblage structure are rare, although tropical sponge assemblages have been reported to undergo rapid fluctuations and species-specific dynamics. Wulff (2006b) documented a 51% decline in sponge species richness at a reef in Panama over a 14 yr period, with massive growth forms suffering disproportionate losses. Similarly, Wulff (2013) showed that sponges in an assemblage on the Belize Barrier Reef that had been monitored from 2006–2012 had species-specific responses and recovery patterns to cyanobacteria-induced mortality. These studies show examples of taxa-specific response to the same disturbance. However, different sponge species have also been found to have similar temporal dynamics in response to a perturbation. For example, in a long-term transplantation experiment, Wulff (2017) observed that all 12 ecologically and phylogenetically different sponge species responded by growing faster under higher picoplankton concentrations. Similarly, the very diverse assemblage from Hoga Island showed some taxonomically unrelated species having similar temporal dynamics, although the magnitude of the fluctuations was different for different species (Fig. S6). Similar temporal dynamics of different taxa suggest that the observed dynamics are not stochastic fluctuations and may be caused by a common driver (see discussion below).

Whereas species richness often increases with abundance (Bock et al. 2007), richness and evenness of biodiverse communities are often negatively correlated (Stirling & Wilsey 2001, Zhang et al. 2012). In this assemblage, the negative linear relationship between $E_{1/D}$ and N was due to the dominance of some abundant taxa (e.g. *Protosuberites* sp., *Sycon* sp., *Pericharax* sp.). Whilst their abundance fluctuated, these dominant taxa were present in the community even at times of low N. This means that, although these species had the highest absolute population variability, other less common sponge taxa appeared in years of high N, thus contributing to S.

Spatially, the assemblage also showed differences in abundance, composition, and biodiversity metrics between sites. Site B generally had lower N than Sites A and C and also had a different assemblage composition. This difference is likely attributed to different local-scale environmental conditions at the reef wall at Site B, compared to Sites A and C. The importance of local-scale factors in affecting sponge abundance and zonation patterns has been documented previously. For example different exposure to light, reef aspect, and sedimentation can have an important impact on sponges and other benthic organisms (Cheshire & Wilkinson 1991, Bell & Barnes 2000, Carballo 2006, Bell et al. 2015b, McGrath et al. 2017).

4.3. Potential causes of temporal variability

Temporal dynamics of sponge assemblages can be controlled by large-scale climatic factors and by local environmental drivers (Carballo et al. 2008). Although the consistency of sponge demographics within and across all sites suggested that stochastic fluctuations were not the only driver of this sponge assemblage, we could not detect any effect of seawater temperature on N and g. There is almost no information on how Indo-Pacific sponge assemblages respond to changes in water temperature. Powell et al. (2014) reported that temperature accounted for only 4 % variation of sponge assemblage composition across sites. A temperature-induced bleaching event was documented for the bioeroding sponge *Cliona* aff. *viridis* on Hoga Island following a period of above-average water temperature in May 2016 (Marlow et al. 2018b). However, we suggest that if water temperature had an effect on sponge demographics at this site during our survey, the effect was only weak and could not be detected due to interannual population variability. McCain et al. (2016) showed that resurvey and time-series studies struggle to detect chronic effects of climate change stressors on natural population dynamics due to stochastic population variability, unless the population is highly stable or the stressor has a very strong impact. Whilst these authors simulated the effects of climate change on natural populations on a longer time scale than our study (3–5 decades), McCain et al. (2016) also showed that survey length is less relevant than interannual population variability in the accurate detection of climate-driven changes on population abundance. Moreover, investigating the relationships between larger-scale environmental data (e.g. daily satellite measurements of SST) and local biological data is particularly challenging. Averaging the fine-scale variable (e.g. SST) to match the resolution of the less frequently sampled parameter (e.g. N) causes a loss of information on its temporal variability (Ferguson et al. 2017). That is, the mismatch in the resolution of 2 time-series data can hinder the ability to detect relationships between them. If changes in N of this assemblage were caused by short-term thermal anomalies like the one reported by Marlow et al. (2018b), averaging temperature data may have made such anomalies undetectable by our analysis.

We did not investigate the role of local environmental covariates or biotic interactions in regulating sponge abundance and biodiversity in this study, because such covariates have not been regularly sampled at this site. Previous research in the Wakatobi showed that sedimentation and light availability are the main environmental factors influencing spatial patterns of sponge biodiversity (Bell & Smith 2004) and functional diversity (Bell 2007). Sedimentation in the Wakatobi was found to reduce sponge diversity (Powell et al. 2014, Biggerstaff et al. 2017), limit bioerosion rates of boring sponges (Marlow et al. 2018a), and cause an energetic cost associated with mucus production (McGrath et al. 2017). Settled sediment data was available for Buoy 3 for years 2014 and 2015 (from Marlow et al. 2018a), but sedimentation data from adjacent years would be unlikely to show changes in sedimentation rates that are strong enough to drive changes in sponge demographics, mostly due to the relatively low levels of settled sediments on this vertical reef compared to more degraded sites (Marlow et al. 2018a).

The effect of spongivory on sponge assemblages has been primarily studied in the Caribbean (reviewed in Pawlik et al. 2018). There is debate over whether bottom-up food limitation (Lesser & Slattery 2013, Slattery & Lesser 2015) or top-down biotic interactions are the most important drivers for sponges (Wulff 2006a, 2017, Loh & Pawlik 2012, Pawlik et al. 2013, 2015). While recent evidence points towards a synergistic action of top-down and bottom-up controls (Wulff 2017), such interactions may be restricted to lagoonal habitats, with sponge assemblages on fore-reefs likely to be structured by predation (Pawlik et al. 2018). The role of top-down control on sponge assemblages in the Indo-Pacific remains largely unexplored. Previous research from the Wakatobi reports a weak effect of spongivorous fish abundance on the composition of sponge assemblages (6% of variation; Powell et al. 2014). Powell et al. (2015) found that nudibranchs and at least 16 fish species engage in trophic interactions with sponges in the Wakatobi region; however, excluding predators from sponges with cages showed no effects on the abundance of non-cryptic sponges. Further research is needed to elucidate the role of spongivory in this region, but from these studies it seems unlikely that predation alone could drive the broad temporal changes in sponge abundance of this assemblage.

4.4. Implications of assemblage variability for coral reef monitoring

Temporal fluctuations in the abundance and diversity of sponges can have major implications for the ecological functioning of coral reefs. Functions carried out by sponges, such as water filtering (de Goeij et al. 2008) and interactions with other benthic organisms and predators (Wulff 2006a), will change with variation in sponge abundance. This has important implications for resource management and conservation, especially if sponges become more abundant or dominant on future coral reefs (Bell et al. 2013). Sponges are abundant at this reef, with sponge cover estimated at 29.5 ± 7% shortly before the start of the study period (Bell & Smith 2004). A sponge reef that fluctuates between states of high and low sponge abundance is also likely to be characterized by a different associated food web, with potential implications for fisheries and other ecosystem services. Although trophic interactions of sponges in the Indo-Pacific remain largely unknown, evidence of spongivory from several fish species and from nudibranchs (Powell et al. 2015) suggests that strong temporal changes in abundance and taxonomic composition of sponge assemblages may result in a modified diet for opportunistic feeders (Wulff 2006a), and as a consequence, potential alteration of food web dynamics (Bell et al. 2013). Sponges in the Indo-Pacific have also been found to overgrow live corals (de Voogd et al. 2004), occupy dead coral substrate (Rossi et al. 2015), and bioerode the reef framework (Marlow et al. 2018a). Therefore, an increase in the abundance of some species may have negative impacts on live reef-building corals, the availability of free space, and reef structure. Fluctuations in sponge abundance may also have effects on benthic composition due to symbiotic relationships between some sponge species and other sessile reef organisms in the Indo-Pacific, like coralline algae (Calcinai et al. 2006) and soft corals (Calcinai et al. 2013).

Understanding the causes of temporal variability in sponge assemblages will play an important role in projecting how they may respond to environmental change. The high temporal variability and species-specific dynamics of this sponge assemblage could hamper the detection of environmental impacts on sponges as a single group over sub-decadal scales. However, disentangling the relative contributions of single species to changes in abundance and taxonomic composition of the assemblage over time allowed for an estimation of species-specific population variability. Features like long survey time, consistent sampling protocol, and characterization of specific population variability are needed to clarify our understanding of the effects of perturbations on natural populations (McCain et al. 2016).

Our annual sampling design did not allow us to capture intra-annual variations in sponge abundance or assemblage composition. Although there is limited information on the life history of sponge species from this region, calcareous sponges are known to have short life spans (weeks to months; Padua et al. 2016) and seasonal changes in metabolic rates (Burlando et al. 1992). Since the calcareous sponges *Sycon* sp. and *Pericharax* sp. were abundant at this reef, it is possible that the abundance and diversity of this assemblage experienced seasonal changes that our sampling design could not detect.

Monitoring coral reefs in remote locations is often expensive and logistically challenging, and the optimal duration and design of a sponge monitoring program for a sponge assemblage depends on the questions and resources at hand (Bell et al. 2017). We showed that a monitoring protocol that (1) uses permanent monitoring units, (2) is repeated over multiple years, ideally 5 to 10 yr, and (3) is carried out with consistent techniques, allowed us to study temporal changes in abundance and biodiversity of this Indo-Pacific sponge assemblage. To avoid a mismatch in the spatial or temporal scale of environmental and biological data, we suggest that environmental covariates (like water temperature, sedimentation, and other drivers that may impact the studied sponge fauna) be measured *in situ* and accompany sponge surveys where possible. Limitations of using abundance as a metric for sponge monitoring have been discussed in Bell et al. (2017) and include the possible confusion between fragmentation of a sponge patch and recruitment, and between fusion of sponge patches and mortality. Moreover, temporal dynamics of abundance and biomass or percent cover may be different in some cases. For example, if one larger sponge patch grows in size while no increase in total sponge abundance occurs, sponge percent cover in the quadrat may increase while total sponge abundance stays the same. While we contend that repeated counts of sponge patches is a time-efficient, non-invasive method of quantifying temporal variation of a sponge assemblage, other measures of abundance to complement sponge counts are desirable, as long as they can be obtained with non-destructive sampling (e.g. cover or volume estimates) and are logistically practical.

Our study highlights the value of long-term monitoring of sponge assemblages and natural systems in general. The importance of accounting for short-term seasonal variation in the monitoring of sponge assemblages has been highlighted by Berman & Bell (2016). Here, we showed that longer-term dynamics (encompassed by annual sampling) can also be highly variable. Mean total sponge abundance on this reef went through phases of increase as well as decline, decreasing by as much as 63 % over a 7 yr period, with the species composition of the assemblage also varying substantially. Thus, when drawing conclusions from short-term ecological studies, it is imperative to put results into a temporal context, because data from a single time point can lead to misleading assessments of assemblage abundance and biodiversity.

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