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Dynamics of large benthic foraminiferal assemblages: A tool to foreshadow reef degradation?

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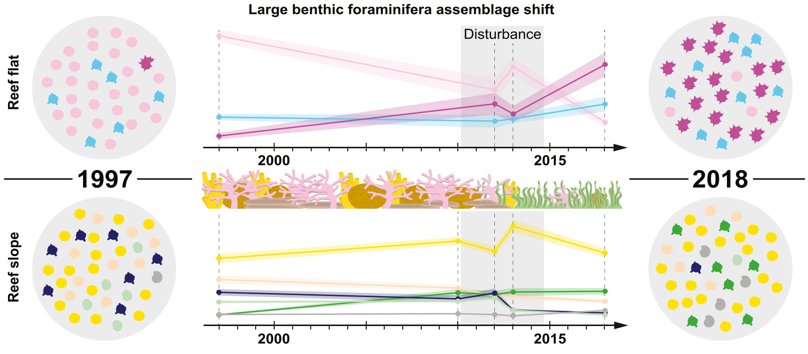
HIGHLIGHTS

- Changes between coral reef states are difficult to predict due to system complexity.
- First analysis of a 20-year time series of living large benthic foraminiferal (LBF) assemblages in the Indo-West Pacific.
- Foraminiferal assemblages shifted towards more algal associated species dominance.
- LBF can be used to detect reef degradation at an early stage.

GRAPHICAL ABSTRACT



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ABSTRACT

Ecological regime shifts in the marine realm have been recorded from a variety of systems and locations around the world. Coral reefs have been especially affected, with their benthic habitat changing from a dominance of stony corals to a dominance of other organisms such as fleshy algae. To detect changes in the benthic habitat of coral reefs, simple tools applicable on a global scale are necessary for future monitoring programs. Hence, the aim of this research is to explore the hypothesis that shifts in assemblages of large benthic foraminifera (LBF) can detect early signs of degradation in the reef benthic habitat. To do so, data on living assemblages of LBF collected between 1997 and 2018 at 12 islands in the Spermonde Archipelago (South Sulawesi, Indonesia) were analyzed. Foraminiferal specimens were morphologically identified to the species level and statistical analyses performed to assess changes in their assemblage composition. A clear temporal shift was observed. Typical foraminiferal assemblages in a coral-dominated (e.g., *Amphistegina lobifera, Calcarina spengleri, Heterostegina depressa*) and fleshy algae-dominated (e.g., *Neorotalia gaimardi*, *C. mayori*) reef habitats were identified and significantly linked to the substrate type. Other species (e.g., *Elphidium* spp., *Peneroplis planatus* and *Sphaerogypsina globulus*) seem to reflect a spatial and temporal gradient of anthropogenic pollution from local inhabited islands and ongoing urban development on the mainland. Hence communities of LBF consistently follow gradual shifts in environmental conditions. Additionally to foraminiferal assemblages being an indicator for actual reef condition, closely monitoring LBF may provide early information on reef degradation, in time to take action against identified stressors (e.g., eutrophication or intensive fishing) at local and regional scales. The circumtropical distribution of LBF is such that they can be included worldwide in reef monitoring programs, conditional to calibration to the regional species pool.

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1. Introduction

Ecological regime shifts in both the marine and terrestrial realms have been recorded worldwide (Biggs et al., 2018; deYoung et al., 2008; Hoegh-Guldberg and Bruno, 2010; Parmesan, 2006; Scheffer and Carpenter, 2003). Such events are characterized by "abrupt changes on several trophic levels leading to rapid ecosystem reconfiguration between alternative states" (Andersen et al., 2009, p. 49). Regime shifts lead to modifications in the trophic structure and associated ecological functions of the reconfigurated environment (Hempson et al., 2018). Coral reef ecosystems have been particularly affected by such regime shifts, also referred to as "phase shifts" (Done, 1992). After stress-induced disturbances, fleshy algae (or other non-coral groups) settle on the reef substratum, leading to a change in the benthic community composition and an alternative state often referred to as "degraded" (Norström et al., 2009; Roff and Mumby, 2012). These alternative, degraded states on reefs are often reinforced by feedback loops (Nyström et al., 2012). Specific and local contexts will determine the recovery of coral reefs to return to their initial state (Roff and Mumby, 2012) or to another coral cover-dominated state with altered species composition and structural complexity (McWilliam et al., 2020). However, with ongoing large-scale stressors, most reefs are likely to remain in a degraded state (Wilkinson, 2008).

To predict ecological regime shifts, a range of techniques have been developed. Nonparametric methods, such as the analysis of variance and diffusion, are particularly efficient when parameters are consistently and frequently measured over long time windows (Brock and Carpenter, 2012; Carpenter and Brock, 2006). Such statistical approaches can be applied to a wide range of environments, from coral reefs to forests. However, noise related to external phenomena may interfere with the true variance signal of the indicator parameter as well as the pace at which their changes occur (Boettiger and Hastings, 2012; Carpenter and Brock, 2006). Given the urgency imposed by worldwide reef degradation, research towards identifying good proxies to detect early signs of coral reef regime shifts has been flourishing in the last 30 years (Crosby et al., 1996; Sammarco et al., 2007). Among others, changes in sediment load and fish grazing rate (Crosby et al., 1996; Goatley et al., 2016) and, more recently, the sensitive behaviour of free-living microbes (Glasl et al., 2019) have been suggested as indicators for signs of coral reef degradation. These proxies are useful as soon as the regime shift is triggered and changes of the benthic habitat are already visible. To detect impending coral reef regime shifts before transformation of the benthic habitat has happened, it is necessary to develop simple tools for future monitoring programs.

Large benthic foraminifera (LBF) have been suggested as proxies for coral reef condition (see e.g., Cockey et al., 1996; Hallock, 1996) because of their sensitivity to physico-chemical conditions. For example, the Foraminifera in Reef Assessment and Monitoring (FoRAM) Index (Hallock et al., 2003) has been widely applied, with those applications reviewed and recommendations given for standardization (Prazeres et al., 2020). LBF are calcifying protists (size >0.5 mm) living in warm and shallow marine environments (Renema, 2018). Similar to reef-building corals, LBF host eukaryotic photosymbionts as well as a complex prokaryotic microbiome (Prazeres and Renema, 2019). Therefore, they are constrained by similar conditions to reef-building corals to thrive (Hallock et al., 2003; Prazeres and Renema, 2019). Furthermore, they are less impacted by destructive weather events and are widely distributed (Hallock et al., 2003). Renema (2018) further hypothesized that the assemblage composition of LBF follows a transformation on two levels leading up to and during a regime shift: (1) associated with a change in water quality and (2) transition of benthic habitats (Fig. 1). With their short community turnover (few months to at most two years), the first response of the foraminiferal assemblage is faster than that of reef-building corals (Hallock et al., 2003). If this gradual environmental change persists, a threshold might be reached and the benthic habitat drastically changes following a disturbance event reducing the coral cover. The regime shift happens as, here, fleshy algae begin to dominate the benthic habitat (Fig. 1). At this time, a second shift in the assemblage composition of LBF is predicted to occur. Hence, predicting regime shifts might become possible by yearly surveying the living assemblage of LBF or, at least, every few years (Hallock, 2012).

Herein, the objective is to explore the hypothesis suggesting that assemblage composition of LBF can be used as a tool to warn against imminent coral reef degradation (Fig. 1), using a 20-year time series of living large benthic foraminiferal assemblages from the Spermonde Archipelago (South Sulawesi, Indonesia) as a case study. The Spermonde Archipelago, located in the Coral Triangle – the world's marine biodiversity hotspot (Veron et al., 2009) – is exposed to various anthropogenic disturbances, including intensive and destructive fishing, mariculture and coastal urbanization (Edinger et al., 1998; Halpern et al., 2007; Hoeksema, 2004). These chronic stressors accentuate the risk of regime shifts in the reefs spread around the Spermonde Archipelago, via eutrophication, pollution and ecosystem imbalance (Hempson et al., 2018). The Spermonde Archipelago is also a good example of a turbid coral reef ecosystem, characterized by higher dissolved inorganic nutrients, particulate organic matter and sedimentation and lower light penetration due to decreased water transparency, with spatial inshore-offshore gradients (Fabricius, 2005; Polónia et al., 2015; Renema, 2019). Previous studies provide precious information on the benthic habitat changes in the Spermonde Archipelago since the 1990s. In 1997, the benthic habitat had very little fleshy algal components, with a coral-dominated reef slope and a sandy reef flat (Renema, 2010). From 2010 to 2014, the coral cover ranged from 4% to 82% depending on the location and turf algae cover peaked in 2013 on the reef slope (Polónia et al., 2015; Teichberg et al., 2018). Additionally Renema et al. (unpublished report) confirmed that profound benthic habitat changes have happened on the reef flat, from a sand- to an algae-dominated habitat. These observations provide a solid reference in time for our analysis. Moreover, we hold the longest record of the living large benthic foraminiferal assemblage from the Indo-West Pacific, ranging from 1997 to 2018.

2. Material and methods

2.1. Study site

The Spermonde Archipelago is characterized as a carbonate shelf harboring ca. 120 reef islands and shoals, located at the southwest coast of Sulawesi province in Indonesia, the middle of the Coral Triangle. The shelf (Fig. 2) has been divided into zones according to the average depth (zones 1–5: nearshore, 20, 30, 50 m, offshore) to facilitate data analysis and to group samples from similar environmental and physical conditions (Renema and Troelstra, 2001). The climate in the Spermonde Archipelago is monsoonal (Erftemeijer and Herman, 1994; Kench and Mann, 2017). The southeastern monsoon (from May to October; referred to as "dry season") with prevailing SE winds generates upwelling at the outer shelf rim (zone 5), where water temperature and dissolved oxygen decrease and salinity increases. The northwestern monsoon (from November to April; referred to as "wet season") with prevailing NW winds accentuates freshwater inputs nearshore (zone 1) by fluvial discharges (e.g., from Jene Berang and Maros rivers) onto the shelf, increasing silts, terrigenous sands and pollutant inputs, and decreasing salinity. However, the wet season has lately become less predictable, shifting in time and intensity.

2.2. Sample collection and identification of LBF

Living assemblages of LBF were collected on 12 islands (of which four are uninhabited) during five field campaigns in August/September 1997, 2010, 2012, 2013 and April/May 2018 (Fig. 2; see appendix Table A.1). Foraminiferal assemblages were collected uniformly by sampling a circular surface of approximately 1000 cm^2 of the substratum.

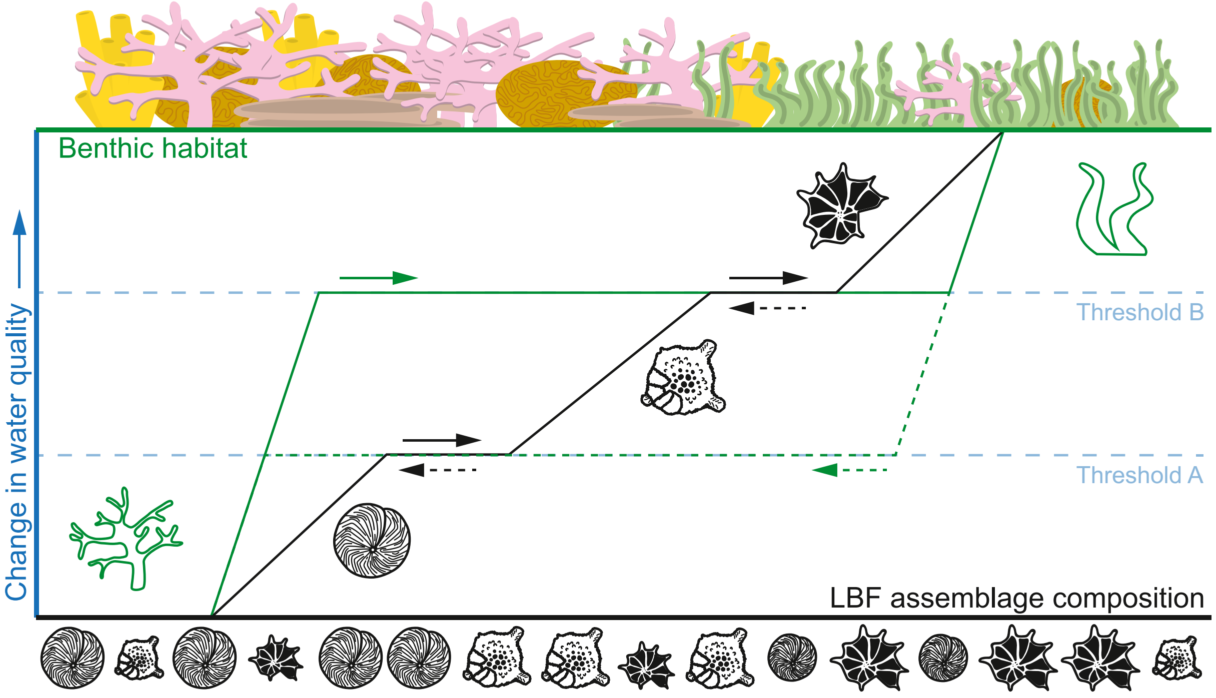

Fig. 1. Hypothetical model after Renema (2018) of the assemblage response of LBF to a changing environment (e.g., change in water quality over time) on the reef flat. As threshold A is reached, a first transformation in foraminiferal assemblage happens, not yet apparent in the benthic habitat. If the disturbance continues, then threshold B is reached and the benthic habitat changes drastically (from coral- to algae-dominated) together with a second transformation in the assemblage of LBF.

On the reef flat, samples were collected at ca. 1 m water depth. On the reef slope, samples were collected in depth transects on the northwest side of the island, perpendicular to the permanent transect measured for benthic habitat, at 2–3 m depth intervals from the reef base to reef crest. Each substrate sampled was classified into the following categories: sand (S), coral rubble (R; most LBF were attached to coral rubble), coral rubble with sand (RS; open spaces between rubble were filled with fine carbonate sand), coral rubble with seagrass (RG), coral rubble with *Halimeda* (RH), coral rubble with sand and algae (RSA; open space between rubble filled with sand, LBF attached to both rubble and macroalgae attached to the rubble), coral rubble with algae (RA; open space between rubble, LBF attached to both rubble and macroalgae attached to the rubble), seagrass with algae (GA) and algae (A; most LBF attached to macroalgae). LBF specimens were isolated from the substrate samples, sieved over a 0.5 mm mesh, and dried. Living LBF were sorted from dead ones based on their color (presence of photosymbionts). LBF were identified to the species level using morphological characteristics of their tests using a stereomicroscope following Renema et al. (2001), Renema (2018), Macher et al. (2021) and the World Foraminifera Database (http://www.marinespecies.org/foraminifera/index.php). Macher et al. (2021) found two morphotypes for the genus *Amphisorus* based on genetic and morphological evidence referred to as follows: *Amphisorus* Spermonde Small (abbreviated *A.* SpS) and Large (abbreviated *A.* SpL), which have been included here.

2.3. Data treatment and analyses

To standardize for differences in sample size, species abundances (number of specimens for a given species) were transformed into relative abundances, where the relative abundance equals the number of specimens for a given species in sample X divided by the sum of all specimens in the sample X. With a low species richness (< 12 species) and a high sample size (between 154 (1st quantile) and 313 (3rd quantile)), species absent from the samples were confidently considered as truly absent from the assemblages. Therefore, in all analyses where the mean relative abundance was calculated, zeros were included to account for absent species. The standard error of the mean relative abundance was calculated as follows: the standard deviation of the relative abundance of a species divided by the square root of the number of samples. All *Elphidium* species (i.e., *E.* sp1, *E.* sp2, *E.* sp3, *E.* sp4 and *E. craticulatum*) were merged together, because they were found at the same locations and substrates, dominated by *Elphidium craticulatum*. Since major foraminiferal assemblage trends through time are the main focus in this study, foraminiferal taxa that have their highest relative abundance below 0.05 or were found in less than 10% of the samples were considered rare. Rare species were disregarded because their presence included a stochastic element (Plass-Johnson et al., 2018). All analyses were performed in R version 3.6.3 (Team and others, 2013) to assess the spatial and temporal dynamics of large benthic foraminiferal assemblages. The effects of multiple variables were considered: habitats (flat, slope), zones (1 to 5), years (1997, 2010, 2012, 2013, 2018) and substrate types (RS, S, R, GA, RA, RSA, A, RG, RH).

Analysis of similarity (ANOSIM) was used to assess the significance (p-value <0.05) of foraminiferal assemblage differences among habitats, zones and years. The indicator species analysis permits the identification of species significantly associated with a group (De Cáceres et al., 2010), performed with the “indicspecies” package (De Cáceres and Jansen, 2016). The significance (p-value <0.05) of the association of a species to a group (indicator value >0.7) was calculated with a permutation test (De Cáceres et al., 2010). Moreover, an Analysis of Variance, one-way ANOVA, was performed to assess the impact of all variables (habitat, year, zone, location, distance from Makassar city, island population, habitat, depth, and substrate) on each species. The analysis was performed three times: on the whole dataset, on the reef flat dataset, and on the reef slope dataset. Species co-occurrence matrices (presence-absence) for years 1997, 2012, 2013 and 2018 were computed using the “cooccur” package (Griffith et al., 2016). The year 2010 was not used because of the absence of reef flat samples for that year. A positive relation between two species means that both species are significantly co-occurring in the samples, whereas a negative correlation means that the species significantly do not occur together. A random

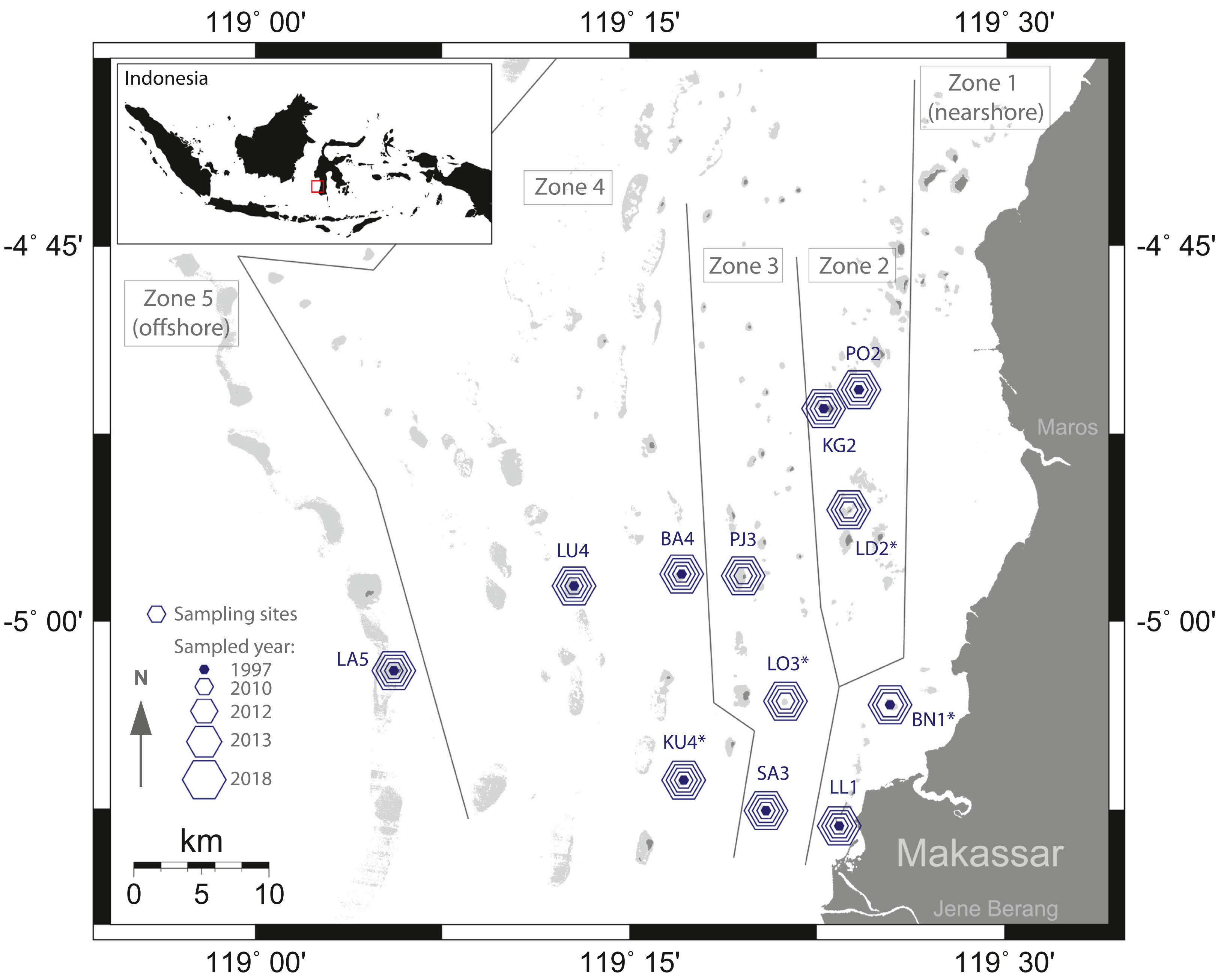

Fig. 2. Map of the Spermonde Archipelago, South Sulawesi, Indonesia, with the geographic location (dark blue hexagons) of the 12 islands in five zones sampled between 1997 (smallest filled hexagon) and 2018 (largest empty hexagon) for foraminiferal assemblage change analysis. Island codes: LL1 (Laelae), BN1 (Barangbaringan), LD2 (Langkadea), KG2 (Karanrang), PO2 (Polewali), SA3 (Samalona), LO3 (Bone Lola), PJ3 (Pajenekang), KU4 (Kudingarengkeke), BA4 (Badi), LU4 (Lumulumu) and LA5 (Langkai). Asterisks indicate uninhabited islands.

relation means that no significant correlation between the two species is found.

Additionally, a non-metric multidimensional scaling (NMDS) analysis was performed to analyze the correlation between spatial distribution of the samples in the ordination and the variables zone and year. It was done using the "vegan" package (Oksanen et al., 2007); the ordination clustering was performed following the Bray-Curtis distance method. A simple linear regression analysis enabled the identification of globally increasing (positive regression) and decreasing (negative regression) species in the time period 1997–2018. The slope was estimated by fitting a linear model to the data points with in-built R functions. The strength of the results was measured using Pearson's correlation coefficient with in-built R functions. Diversity indexes (species richness, Shannon-Wiener, Simpson's diversity (1-D) and Pielou's evenness) were calculated with the "vegan" package. The R code and primary dataset, including specific functions used here, have been deposited on the GitHub online platform (https://github.com/EBGirard/ForamDynamics).

2.4. Limitations of the study

For this global study, 439 samples were collected from 12 islands in the Spermonde Archipelago at five time-points between 1997 and 2018. We acknowledge the presence of a spatial and temporal imbalance in the sampling design; for example, zone 5 is underrepresented with only one island (Fig. 2). However, here we aim to document long term regional assemblage shifts. Additionally, our dataset allows a better understanding of the temporal trends in foraminiferal assemblage composition and how it correlates with the changes in substrates in the Indo-West Pacific region.

3. Results

In 439 samples (109 reef flat; 330 reef slope) spread over 12 islands in the Spermonde Archipelago (South Sulawesi, Indonesia; Fig. 2), we identified 26 species of LBF. Following data treatment, 17 taxa (*Amphisorus* SpL, *A.* SpS, *Amphistegina lessonii, A. lobifera, A. radiata, Baculogypsinoides spinosus, Calcarina mayori, C. spengleri, C. hispida, Elphidium* spp., *Heterostegina depressa, Neorotalia calcar, N. gaimardi, Operculina ammonoides, Peneroplis planatus, Sorites orbiculus* and *Sphaerogypsina globulus*) were the most abundant ones and their abundance and distribution were further analyzed (Table 1). The remaining nine species were characterized as rare (*Alveolinella quoyii, Dendritina ambigua, Laevipeneroplis malayensis, Nummulites venosus, Parasorites* sp1, *Parasorites* sp2, *Peneroplis pertusus, Peneroplis* sp2, *Peneroplis* sp3), and were not included in further analyses.

Taxa dominantly occurring in shallow environments (reef flat and shallow reef slope) were *A. lobifera, C. hispida, N. calcar, N. gaimardi, P. planatus* and *S. orbiculus.* Other taxa were found on the reef slope, distributed along a depth gradient: *A. lessonii* on the shallow and mid slope, *A. radiata, C. mayori, C. spengleri, H. depressa* and *S. globulus* on the mid slope, and *B. spinosus* and *O. ammonoides* on the deep slope. Despite their preference for a habitat and depth range, all species were also found outside their optimal environmental conditions, in lower abundance, owing to the diversity of microhabitats (e.g., shaded area on the reef flat). Foraminiferal assemblages living on the reef flat and the reef slope significantly differed from one another (ANOSIM: *p*-value = 0.001; $R = 0.682$), and indicator species analysis detected different taxa for each of the habitats. Therefore, temporal dynamics of reef flat and reef slope assemblages were analyzed separately.

3.1. Temporal dynamics of large benthic foraminiferal assemblages

Assemblages of LBF were significantly different from one year to the next in every habitat and zone in the Spermonde Archipelago (see appendix Fig. A.1). However, reef flat assemblages had a higher variability among the years (ANOSIM: *p*-value = 0.001; R range = 0.374–0.684, grouping with little overlap) compared to the reef slope assemblages, which had a higher similarity among the years (ANOSIM: *p*-value = 0.001; R range = 0.105–0.478, grouping with high overlap) (see appendix Table A.2). Results from the performed analyses highlight the spatial and temporal variability in species assemblage composition, suggesting that multiple drivers, such as substrate type, island population, zonation and location, shape the assemblages (see appendix Tables A.3, A.4). Calculated diversity indices were generally stable through time on both the reef flat and the reef slope. Nonetheless, the species richness appears lower on the reef flat in 2018 likely due to the dominance of *N. gaimardi*, in line with a lower Shannon-Wiener and Simpson indices (see appendix Fig. A.2).

Several temporal patterns are observed, for both the reef flat and the reef slope foraminiferal assemblages. For example, *A. lobifera* declined by a factor of four, whereas *N. gaimardi* increased seven fold on the reef flat over the studied time window (Fig. 3a, see appendix Fig. A.4). On the reef slope, *C. mayori* increased 13 fold, whereas *A. radiata*, *C. spengleri* and *H. depressa* decreased by factors of two, four and eight, respectively (Fig. 3b, see appendix Fig. A.4). The species temporal trends

Table 1
Species distribution of the most abundant species ($n = 17$) in the Spermonde Archipelago. All taxa are symbiont-bearing Foraminifera, however Elphidium is kleptoplastic. Zone 1 is the closest to the mainland (nearshore) and zone 5 the furtherest away (offshore).

Species	Reference description	Preferred habitat	Optimal depth range (m) per zone					Highest relative abundance	Mean relative abundance	Number of samples	% of samples
			1	2	3	4	5				
Amphisorus Spermonde Large (SpL)	Fig. 3 in Macher et al. (2021)	none				1–15	1–18	0.64	0.10	121	27.6
Amphisorus Spermonde Small (SpS)	Fig. 3 in Macher et al. (2021)	none		1–6	1–6	6–18		0.48	0.05	154	35.1
Elphidium spp.	Fig. 15 in Renema et al. (2001)	none	1–9	1–12	1–18	12–24	15–18	1.00	0.05	216	49.2
Amphistegina lobifera	Fig. 8 in Renema (2018)	Flat	1–3	1–3	1–3	1–3	1–3	0.97	0.35	165	37.6
Calcarina hispida	Fig. 18 in Renema (2018)	Flat	1–3	1–6	1–6	1	1	0.68	0.19	154	35.1
Neorotalia calcar	Fig. 26 in Renema (2018)	Flat	3	1	1	1–6	1–3	0.14	0.02	64	14.6
Neorotalia gaimardi	Fig. 26 in Renema (2018)	Flat	1–6	1–3	1–3	1	1–3	0.98	0.21	179	40.8
Peneroplis planatus	Fig. 7 in Renema et al. (2001)	Flat	1	1	1	1	1	0.54	0.04	251	57.2
Sorites orbiculus	Fig. 10 in Renema et al. (2001)	Flat		1	1	1	1	0.65	0.05	187	42.6
Amphistegina lessonii	Fig. 7 in Renema (2018)	Slope	3–9	3–12	3–18	6–18	6–18	0.94	0.31	401	91.3
Amphistegina radiata	Fig. 10 in Renema (2018)	Slope	3–6	6–12	6–18	6–24	9–18	0.66	0.15	289	65.8
Baculogypsinoides spinosus	Fig. 29 in Renema (2018)	Slope		6–15	9–18	15–24		0.67	0.09	114	26.0
Calcarina mayori	Fig. 23 in Renema (2018)	Slope	3–9	3–12	3–18	9–24	9–21	0.68	0.14	247	56.3
Calcarina spengleri	Fig. 15 in Renema (2018)	Slope	1–3	3–12	6–18	6–21	6–18	0.82	0.11	237	54.0
Heterostegina depressa	Fig. 35 in Renema (2018)	Slope	3–9	6–12	6–18	9–24	9–18	0.33	0.07	281	64.0
Operculina ammonoides	Fig. 31 in Renema (2018)	Slope	9	9–15	12–18	15–24		0.24	0.04	131	29.8
Sphaerogypsina globulus	(Hayward et al., 2021)	slope	1–9	1–12	1–18	1–24	6–18	0.06	0.01	97	22.1

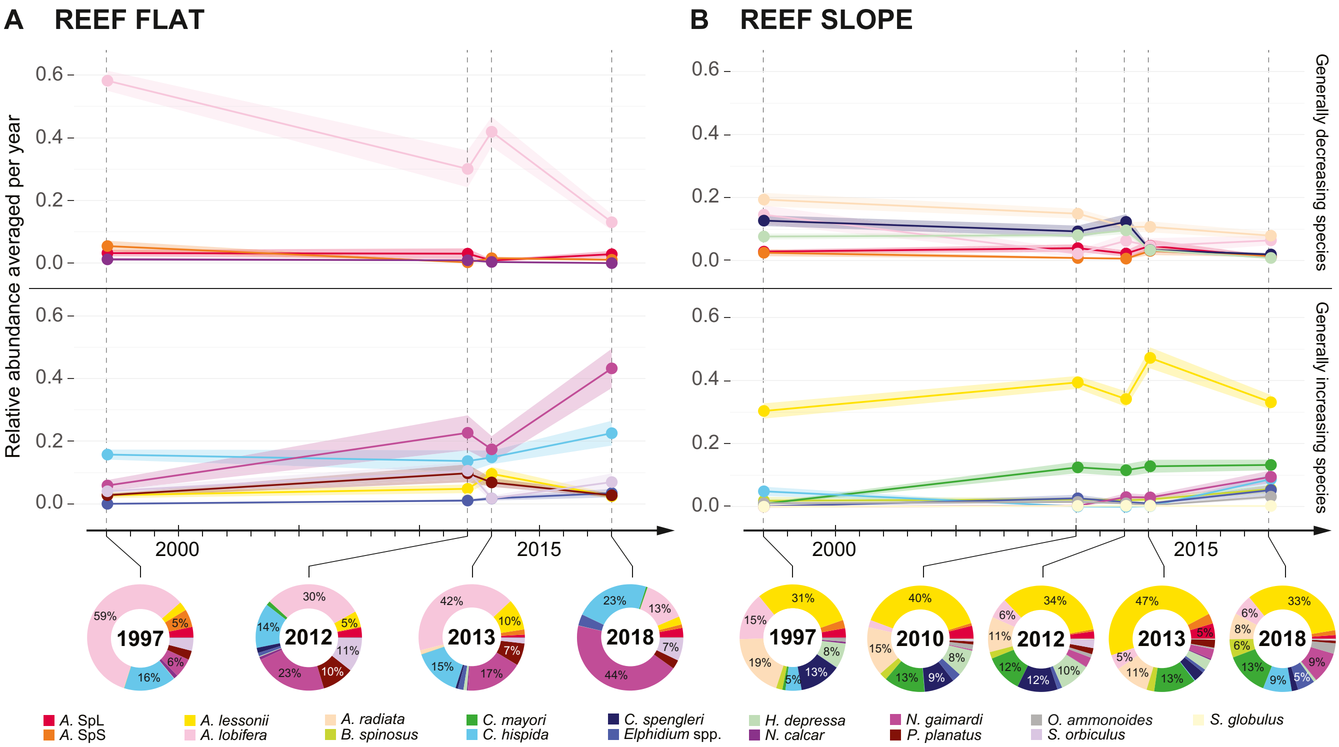

Fig. 3. Assemblages of LBF change through time. Time series of the species relative abundance on the reef flat (A) and the reef slope (B). The shaded area indicates the standard error of the mean relative abundance. Pie charts show the species ratio for each year, respectively for the reef flat and the reef slope.

described above were spatially stable throughout the Spermonde Archipelago. For instance, *N. gaimardi* increased in abundance at all sampling sites on the reef flat (see appendix Fig. A.3). A considerable shift happened in the species time series especially between 2010 and 2013 in both habitats, suggesting some short-term environmental disturbances. Indeed, many species either increase or decrease drastically during that period (e.g., *Amphisorus* spp., *A. lobifera, C. hispida, S. orbiculus*) (Fig. 3). On the contrary, *A. lessonii* was consistently the most abundant species on the reef slope, with little variation in its relative abundance throughout the study period.

3.2. Temporal changes in species co-occurrences

A total of 136 species combinations were compared for co-occurrences, of which only six significantly changed from one year to another. Species with lower abundances (e.g., *P. planatus*, *S. orbiculus, S. globulus* and *B. spinosus*), together with species that have no preferences for habitat (*Elphidium* spp., *A.* SpS and *A.* SpL), had the most temporally variable co-occurrence patterns (Fig. 4). For example, *P. planatus* was rarely found with *B. spinosus* and *H. depressa* in 1997, but consistently found in the same samples in 2013. Nevertheless, there is a clear distinction between species living predominantly on the reef flat versus the reef slope. These species do not share the same optimal living conditions and therefore rarely occurred together (negative co-occurrence). The habitat pattern is strongly illustrated in foraminiferal assemblages from 1997, still recognizable in 2012 and 2018, but less obvious in the samples from 2013 (Fig. 4).

3.3. Temporal changes in substrate and associated species

A clear shift of the substratum happened especially on the reef flat. In 1997, the dominant sampled substrate types were coral rubble, coral rubble with algae, and coral rubble with seagrass, whereas in 2018 only fleshy-algae-dominated substrates (algae, coral rubble with algae, and seagrass with algae) were sampled (Fig. 5a, see appendix Fig. A.5). The species *A. lobifera* prefers coral rubble, coral rubble with algae, and coral rubble with seagrass. *N. gaimardi, C. hispida, P. planatus* and *S. orbiculus* were found mostly on algal-dominated substrates.

This trend is not observed in the data collected on the reef slope. All substrate types were found in almost all years, except for *Halimeda*-associated substrates that were sampled only in 1997 and 2010 (Fig. 5b, see appendix Fig. A.5). The species *A. lessonii* was identified on all substrate types, indicating no preferences. Other species, for example, *O. ammonoides* and *B. spinosus* were found only on rubble with sand (and algae).

4. Discussion

Our results provide a promising example for an early signal of a regime shift in a marine system. Data on living large benthic foraminiferal assemblages were gathered between 1997 and 2018 from turbid reefs of the Spermonde Archipelago (Indonesia). A clear shift in assemblage composition was observed. On the reef flat, assemblages rich in *A. lobifera* in 1997 shifted to assemblages mainly dominated by *N. gaimardi* and *C. hispida* in 2018. On the reef slope, assemblages rich in *H. depressa, A. radiata* and *C. spengleri* in 1997 shifted to *C. mayori* in 2010–2018.

4.1. Factors triggering temporal changes in assemblages of LBF

Changes in foraminiferal assemblages in the Indo-West Pacific region were previously observed to be driven especially by water quality and benthic habitat (Renema, 2006, 2018). In the western Atlantic (i.e., Florida Keys), however, the main distribution factors were habitat depth and symbiont type (Baker et al., 2009). Our data demonstrate a clear relationship between change in substrate types and transformation of the foraminiferal assemblage composition through time. In fact, the change in substrate types on the reef highlights a transition from algal-depauperate to algal-dominated substrates over the time window studied. The abundance of most large benthic foraminiferal species

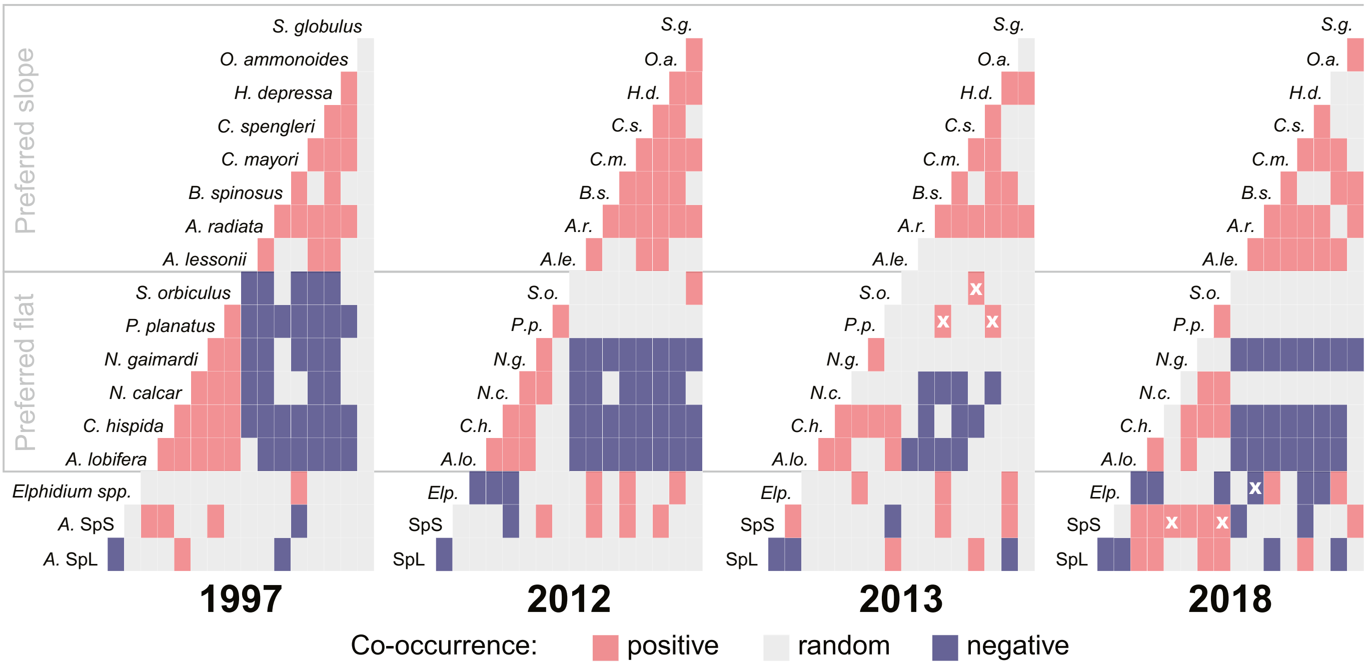

Fig. 4. Temporal changes in species co-occurrence matrices. For each year, the matrix represents the likelihood that two species occur together in a sample. Positive co-occurrence (red): significantly co-occur. Negative co-occurrence (blue): significantly do not occur together. Random co-occurrence (gray): no significant positive nor negative co-occurrence. White crosses on specific co-occurrences in 2013 and 2018 mean that the co-occurrence shifted from a positive to a negative one or vice versa. Note: in 2010, no reef flat samples were taken and therefore no co-occurrence matrix is given for that year.

(e.g., *A. lobifera, A. radiata, C. mayori, C. spengleri, H. depressa, N. gaimardi*) is significantly correlated with substrate types. The same was observed for *B. spinosus* and *O. ammonoides*, but these two species were consistently found at the deepest part of the reef slope. Consequently, their significant association to the substrate type (i.e., rubble with sand) mirrors their preferred depth range and habitat. Importantly however, the variation of some species does not significantly correlate with any changes in substrate type, suggesting that the water quality acts as a main triggering factor. For example, chlorophyll-a and turbidity proxies were identified as water quality drivers for variations in the large benthic foraminiferal assemblage composition (Polónia et al., 2015). The change in substrate type can be a response to local and global environmental changes. On the reef slope, for example, *A.* SpS, *A. lessonii, Elphidium* spp., *P. planatus* and *S. globulus* mainly varied according to location (zones and islands), the year of sampling, and whether an island was inhabited or not. These species were indicators for certain zones (e.g., *Elphidium* spp. indicator taxon for zone 1) or for certain years (e.g., *S. orbiculus* indicator taxon for 2012). Furthermore, they might reflect a spatial and temporal gradient of turbidity and anthropogenic pollution from local inhabited islands and ongoing urban development in the mainland (Johnson et al., 2019). A similar pattern was observed in Moreton Bay, Australia, where *Elphidium* spp. also characterized the near-shore foraminiferal assemblages (Narayan et al., 2015; Narayan and Pandolfi, 2010). Another factor to consider is the sampling time (e.g., wet vs dry season) that potentially triggers changes in the assemblage composition of LBF. Depending on the location, seasonality indeed affects benthic foraminiferal communities and single taxa differently. For example, studies from the Arabian Gulf and West India found a decrease in foraminiferal diversity post-monsoon (Arslan et al., 2016; Buragohain and Ghosh, 2021), and two studies from Japan show higher reproduction rates during the wet monsoon season (Eder et al., 2019; Hohenegger et al., 2019). The abundance of some species can reach extreme variations from one month to the next in Palau Islands (Hallock, 1984), but be resilient over the seasonal cycle in the Adriatic sea, Italy (Melis et al., 2019). Moreover, seasonal variations in Brazil were shown to influence the benthic foraminiferal community more than human impacts (Belart et al., 2019). These previous studies show no consensus on the effect of seasons on LBF around the globe. Additionally, such seasonal data are scarce in turbid ecosystems and the Coral Triangle region. Without continuous sampling and targeted experimental design, we can therefore not fully disentangle benthic habitat and water quality as drivers of foraminiferal assemblage change. Data loggers and standard substrate options, such as autonomous reef monitoring structures (ARMS) (Toonen, 2009; Zimmerman and Martin, 2004), deployed along a known water quality gradient will be used in a future survey design to better understand the effects of seasonality, water quality, and related factors (e.g., island population, local runoff, water transparency and chlorophyll levels) on foraminiferal communities.

4.2. Factors triggering algal growth on the reef

The temporal and spatial distribution of the algal communities is primarily shaped by an imbalance between algal productivity and herbivory-induced disturbances (Figueiredo and Creed, 2009; Steneck and Dethier, 1994). Algal growth may correlate with eutrophication (increased nutrient concentration in the water, especially phosphorus and nitrogen) and light intensity, more than the substrate type the algae develop on (Erftemeijer, 1994; Han et al., 2021; Steneck and Dethier, 1994). On reefs, fleshy algae thrive better in shallow water due to higher light intensity and sediment inputs, coupled with decreased grazing intensity (Fox and Bellwood, 2007; Gordon et al., 2016; Munubi et al., 2018; Purcell, 2000). Increased algal growth on the substrate was observed at all sampling sites, which may be caused by local (at the reef scale) or regional (Spermonde wide) drivers, or both. For example, nutrient-rich influxes resulting from the important hydrological network in South Sulawesi Province intensively affect nearshore islands in the Spermonde Archipelago with higher nutrient availability and sediment inputs. Shallow reefs have been dominantly covered by turf algae, reaching up to 90% on the slope in 2013 near-shore (zones 1 and 2), with a steep decrease in algal cover off-shore (zones 3 to 5) (Teichberg et al., 2018). Further away from the mainland, sewage from inhabited islands is disposed directly on the reef flat, leading to a local increase of nutrient concentrations (Baum et al., 2015; Lamb et al., 2017) and likely affecting the composition of benthic reef flat

Fig. 5. Temporal change of substrate type (top) and foraminiferal relative abundances to different substrate types (bottom) on A) the reef flat and B) the reef slope. Size of the circles are related to the mean relative abundance of a species in a sample. Colors are related to substrate types: sand (S), coral rubble (R), coral rubble with sand (RS), coral rubble with seagrass (RG), coral rubble with Halimeda (RH), coral rubble with sand and algae (RSA), coral rubble with algae (RA), seagrass with algae (GA) and algae (A).

and adjacent shallow reef slope communities (Ford et al., 2017). Together with the higher light intensity, the latter hypothesis explains the transformation of the benthic habitat on the reef flat and the drastic shift in foraminiferal assemblages (from *A. lobifera* dominated to *N. gaimardi* dominated) between 1997 and 2018. Similar patterns were not visible on the reef slope. Until 2013, algal components increased on the reef slope, but drastically decreased in 2014 with a slight increase in coral cover (Teichberg et al., 2018). This short episode led to a complex disturbance in the associated foraminiferal assemblage composition; nonetheless, the reef slope assemblage dynamics shows signs of initial, persistent changes.

4.3. A tool to foreshadow reef degradation?

Our findings support the hypothesis that the reefal large benthic foraminiferal assemblage composition transforms following changes in water quality and substrate type as posited by Renema (2018) (see also Fig. 1). In 1997, the samples collected on the reef flat and reef slope were mostly void of algae in line with a coral-dominated reef ecosystem (Polónia et al., 2015; Renema, 2010); associated large benthic foraminiferal species were highly abundant (*A. lobifera*, *H. depressa*, *A. radiata* and *C. spengleri*). In 2018, most substrates had algal components, reflecting the nature of the benthic habitat, (see Fig. 5) and thus the assemblage composition of LBF shifted to abundant *N. gaimardi*, *C. hispida*, *Elphidium* spp. and *C. mayori*. These findings are compatible with the two extreme assemblages from the tested hypothesis. We observed variations in the foraminiferal assemblage composition (Figs. 3, 4) between 2010 and 2013, likely linked to some short-term disturbances, such as Crown-of-Thorns outbreaks (Baird et al., 2013; Plass-Johnson et al., 2015). Our dataset does not however allow for the interpretation of an intermediate foraminiferal assemblage during the disturbance due to the lack of understanding of the independent effects of water quality and substrate type on the assemblage.

According to the results from our study and previous research conducted in the western Atlantic (Baker et al., 2009; Belart et al., 2019; Hallock et al., 2003; Oliver et al., 2014) and Indo-West Pacific region

(Eder et al., 2019; Hallock, 1984; Hohenegger et al., 2019; Renema, 2018), large benthic foraminiferal assemblages indeed show great sensitivity to both water quality and the substrate type. Hence, LBF are in a good position to consistently adapt to persistent, gradual shifts in environmental conditions. Due to their longer lifespan and generation times compared to microbial communities (Webster and Hill, 2007), LBF are not affected by ephemeral disturbances while being more sensitive to water quality gradients than reef-building corals (Hallock et al., 2003; Prazeres et al., 2020). The FoRAM index has proven itself useful as a proxy for reef condition, especially for the Caribbean and western Atlantic (Prazeres et al., 2020 and citations herein). In short, it suffices to classify benthic foraminifera into three functional groups (large symbiont-bearing, opportunistic and small heterotrophic) and to apply a formula using group proportions to calculate the index (Hallock et al., 2003).

Our study suggests that monitoring large benthic foraminiferal assemblages in reef habitats to detect early stages of reef degradation may be sufficient, instead of looking into all three benthic foraminiferal functional groups. When applying the FoRAM Index, large benthic foraminiferal taxa have equal weights, regardless that some of these species thrive better in degraded reefal environments. In the Spermonde Archipelago, *N. gaimardi* and *C. mayori* are good examples of extremely abundant taxa that prefer settling on fleshy algae substrata, an indication that the reef is degrading, irrespective of the number of small and opportunistic taxa in the assemblage. Förderer and Langer (2019) also reported that *C. mayori* is among the most common taxa in Philippine shallow reefs, where the coral cover has decreased by a third the past decades (Förderer and Langer, 2019; Licuanan et al., 2019). The FoRAM index was developed for Caribbean and western Atlantic foraminiferal assemblages, which are less diverse, and groups that we find sensitive to environmental change (e.g. calcarinids) are missing (Baker et al., 2009; Langer and Hottinger, 2000). Therefore, the FoRAM index is not directly applicable in the Indo-West Pacific, where the diversity of key benthic foraminifera is higher (Förderer et al., 2018), and some large benthic foraminiferal species are abundant even in degraded environments (Förderer and Langer, 2019; Prazeres et al., 2020; Renema, 2018). Our methodology suggesting the use of LBF as warning signals to reef degradation can be applied in the Indo-West Pacific regions with sufficient LBF species richness, such as the Coral Triangle and the Great Barrier Reef (Förderer et al., 2018), but requires regional calibration to the species pool.

5. Conclusion

Studying the dynamics of large benthic foraminiferal assemblages has strengthened our understanding of potential factors triggering composition changes. It has also proven the sensitivity of these small protists to their surrounding conditions. Moreover, our analysis underlines the complexity in isolating and associating stressors to their effects. Additional work is needed to contribute to and enhance our understanding on seasonal dynamics and true effects of water quality on foraminiferal assemblage composition in the Indo-West Pacific region. Besides being an indicator for actual reef condition, closely monitoring assemblages of LBF may alert us of early coral reef degradation, in time to take action against identified stressor (e.g., eutrophication or intensive fishing). The circumtropical distribution of LBF is such that they can be included worldwide in coral reef monitoring programs, conditional to calibration to the regional species pool, to support local and regional reef environmental management.

CRediT authorship contribution statement

Elsa B. Girard: Conceptualization, Methodology, Writing – original draft, Formal analysis, Visualization. **Estradivari:** Writing – original draft, Writing – review & editing. **Sebastian Ferse:** Writing – review & editing. **Rohani Ambo-Rappe:** Resources, Project administration. **Jamaluddin Jompa:** Resources. **Willem Renema:** Conceptualization, Investigation, Data curation, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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