Coral Reefs
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RESEARCH

Millennial-scale reef assemblage shifts in the Spermonde Archipelago, Makassar Strait, Indonesia

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Abstract The Coral Triangle is the region in the Indo-Pacific with the highest diversity of reef organisms. Coral reefs here have experienced increased anthropogenic stressors since the late 1970s due to destructive fishing, land reclamation, industrialization, and agriculture. Biological observations in the Spermonde Archipelago (SW Sulawesi, Indonesia) started only after large-scale disturbances had begun limiting insights into long-term reef assemblage dynamics. To address this knowledge gap and mitigate shifting baseline bias, we documented assemblage shifts over centennial/millennial timescales using 16 reef sediment cores from two islands in this area. These cores, previously dated using radiocarbon methods, documented the geomorphic history of these islands. We expand upon this by investigating coral, sponge, and foraminifera assemblage shifts over the past 7200 years. Our findings reveal transitions from more mixed growth forms (foliose, massive, and free-living) to predominantly branching Acroporidae over the last 6000 years, likely driven by changing sea-level regimes. The scleractinian species *Palauastrea ramosa* (Yabe and Sugiyama 1941) was represented in several core samples but has never been observed in modern surveys, suggesting a historical shift in coral assemblages. Foraminiferal assemblages on the reef flat transitioned from dominance of coral/rubble-associated taxa to more algal-associated substrates in recent times. Sponge spicule assemblages indicate a persistence of cryptic/excavating sponges over the past 2000 years. Since these sponges are associated with coral rubble, their presence suggests that declining coral cover has created more rubble habitat in recent millennia. These findings demonstrate that assemblage shifts began centuries to millennia before modern anthropogenic stressors accelerated these changes.

Keywords Reef cores · Paleoecology · Paleobiology · Carbonate production · Coral Triangle

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Introduction

Coral reefs occur in the marine subtropical to tropical belt, where they harbor over 25% of all marine species and provide numerous ecological and economic benefits (Hoegh-Guldberg et al. 2019), including protection from storms (Kench et al. 2022). Their biodiversity is highest within the Indo-Pacific region known as the Coral Triangle (CT), which contains over 600 scleractinian coral species. The border of this area has been defined from Central/Eastern Indonesia to Papua New Guinea and northward to include northern Borneo and the Philippines (Hoeksema 2007; Renema et al. 2008; Lane and Hoeksema 2016). This hotspot of diversity has been present in this location since the Pleistocene and earlier and had shifted to this position from the Atlantic and Mediterranean through the former Tethys seaway (Renema et al. 2008) due to shifting tectonics and sea levels. Within the CT there are numerous low-lying islands, many of which are densely populated, that are set to face increased climate change and sea-level rise disturbances in the coming centuries (Kench and Mann 2017). Carbonate sediments needed to maintain these low-lying islands associated with reef complexes are produced by locally occurring organisms, such as corals, foraminifera, and coralline algae (Mann et al. 2016; Ryan et al. 2018; Morgan et al. 2020; Hynes et al. 2025). Climate change is rapidly reshaping coral reefs, with major impacts on the organisms that shape them and accelerating sea-level rise (Lee et al. 2023). It is likely that over the next 70 years global sea levels will rise by at least another 50 cm, threatening the existence of sand cays, either inhabited or not (Khan et al. 2019; Lee et al. 2023). Therefore, it is important to understand how changing climate and environments have impacted these reefs in the past and consequently be able to examine and predict how they may then compensate under varying future environmental conditions.

Coral reefs in the CT have been subjected to increased anthropogenic stressors, such as destructive fishing practices, human population growth, land reclamation, agriculture, and industrialization, since well before the mid-nineteenth century (Haywood et al. 2016; Heery et al. 2018; Plass-Johnson et al. 2018; Bejarano et al. 2019; Cybulski et al. 2020; Hoeksema 2026). This has for example been observed on coral reefs of the Spermonde Archipelago in the Makassar Strait (SW Sulawesi, Indonesia), which have been investigated in much detail since the 1930s (Umbgrove 1928, 1947). However, most studies (like long-term reef organism assemblage data) for Sulawesi, and the CT as a whole, only go back decades (Renema and Troelstra 2001; Becking et al. 2006; de Voogd et al. 2006; Hoeksema 2012b; Razak et al. 2024). As most large-scale disturbances in the Spermonde Archipelago may have begun long before these data were collected, this has resulted in limited insights into long-term reef assemblage dynamics and a more accurate examination of the level of degradation that has occurred, causing an inaccurate (or shifted) baseline of reef health to be determined. To avoid the shifting-baseline syndrome, it is important to examine reef assemblage shifts at longer timescales (centennial to millennial scales) than survey data are available (Cramer et al. 2017, 2020; Lukowiak et al. 2018; Johnson et al. 2019).

A frequently used tool for documenting longer-term assemblage shifts of reef organisms is the use of Holocene (11,700 YBP to modern day) reef matrix/framework cores and measuring the abundances of specific groups contained within (Tager et al. 2010; Cramer et al. 2017, 2018; Lukowiak et al. 2018; Johnson et al. 2019; Morgan et al. 2020; Gischler et al. 2023). This allows for examining controlling factors on community shifts (both anthropogenic and biogenic) throughout the Holocene. In particular, organisms with high preservation potential, including corals (Morgan et al. 2016; Sanborn et al. 2020), foraminiferans (Almeida et al. 2013; Storz et al. 2014; Johnson et al. 2019), sponges (Lukowiak et al. 2018), sea urchins (Cramer et al. 2018), and fishes (Cramer et al. 2017; Sibert et al. 2017), can be examined as models to document the response to shifts in environmental conditions. Stony corals are primary calcium carbonate ($CaCO_3$) producers and reef builders (Polónia et al. 2015; Lange et al. 2020), while foraminifera are also carbonate ($CaCO_3$) producers and are highly specialized to specific environmental conditions, such as water depth/quality and substrate type (Renema and Troelstra 2001; Renema 2018). Further, marine sponges solidify substrates, purify water, and provide other ecological services to reef organisms (de Goeij et al. 2013; Pawlik and McMurray 2020), but also can act as a source of bioerosion of reef carbonates (Lange et al. 2020; Pacheco et al. 2020). Therefore, the presence and abundance of these three different groups together provide important indicators of a reef's environmental parameters, health, and diversity.

To examine millennial-scale development of Spermonde reefs, we have documented coral, foraminiferan, and sponge assemblage shifts from 16 reef cores collected from patch reefs on two reef islands, Samalona and Kudingareng Keke. These cores were already examined to establish the geomorphological history of the reef and islands in conjunction with radiocarbon dating (Hynes et al. 2025). Here, we are interested in determining if the relative abundance of corals, foraminiferans, and sponges can be correlated with changing environmental factors like water depth and turbidity on these patch reefs over the last 7200 YBP. By examining how communities have shifted well before modern anthropogenic stressors had begun, we can determine how these reef communities might evolve in the future under changing environmental conditions.

Methods

Location and setting

The Spermonde Archipelago (Fig. 1A) off SW Sulawesi in the Makassar Strait, Indonesia, comprises a collection of 120 islands, approximately 80 of which see subaerial exposure, on a carbonate shelf called the Spermonde Shelf (Umbgrove 1928). It is situated close to the city of Makassar (1.5 million people) and three river outlets (the Jene Berang in the south, and the Tallo and Maros rivers to the north), as well as several smaller tributaries (de Klerk 1983). These rivers, and the large population in Makassar and surrounding settlements, have influenced the turbidity of the entire shelf system by depositing nutrients and sediments, directly impacting the patch reef complexes. This generates an onshore to offshore gradient of decreasing turbidity and nutrients across the entire system (Parenden et al. 2021).

Between the mainland coast and the barrier reef, there are numerous patch reefs that form islands from the open bottom of the shelf, often at the top of parallel ridges of karst pillars of Eocene to Miocene limestone, likely capped by Pleistocene reefs (de Klerk 1983; Moll 1983), similar to the Great Barrier Reef (Hopley et al. 1983). These islands are sand cay

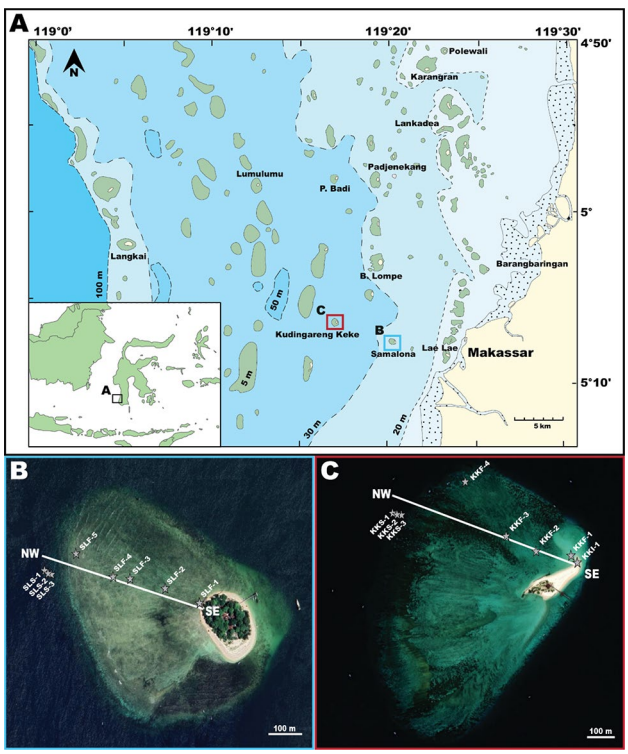

Fig. 1 **A.** Map of the Spermonde Archipelago with labelled isobaths, modified from (Renema and Troelstra 2001). **B.** Satellite image of Samalona (Bing 2024) with coring transect superimposed. **C.** Satellite image of Kudingareng Keke (Bing 2024) with coring transect superimposed

reefs, which follow a general geomorphological outline, with a wide crescent-shaped reef crest (and sometimes rampart) on the Western/Northwestern (seaward) edge protecting a reef flat, and if present, a sand cay (de Klerk 1983). Outside the seaward reef crest is a reef slope, which comprises the majority of coral cover for the complex (Moll 1983; Moll and Borel-Best 1984). The reef flat currently has minimal coral cover, which decreases in quantity toward the island. On the leeward side is a gentle, sandy slope, with minimal coral cover and no defined crest (Hoeksema 1990; Renema and Troelstra 2001; Hynes et al. 2025).

Coral diversity is high due to the position of the Spermonde Archipelago in the center of the CT, seeing some 225 species from 70 genera of Scleractinia, plus a large diversity of octocorals (Moll 1983; Best et al. 1989; Veron 1995, 2000; Mcfadden et al. 2025). Common coral genera include *Acropora*, *Montipora*, *Seriatopora*, *Porites*, and *Pocillopora*, as well as a high species richness of Fungiidae corals (Moll 1983; Moll and Borel-Best 1984; Hoeksema 2012a). Similarly, there is a high diversity of marine sponges in this area, totaling over 175 species from around 80 genera (de Voogd et al. 2006; van Soest and de Voogd 2015; Putra et al. 2024). Large Benthic Foraminifera (LBF) communities also display a remarkable diversity of some 35–40 species (Renema 2002, 2018), with small benthic foraminiferans representing an even larger number of genera (Renema 2002).

These reefs grow upward and then prograde outward. They vary in size, with growth depending on the surrounding depth, which increases with distance from shore (Moll 1983; Hoeksema 2012a). Some patch reefs eventually see limited subaerial exposure. The larger patch reefs develop a sand cay, an island of ~1–3 m above fair-weather high-tide sea level (Kench and Mann 2017). Around half of the islands in the Spermonde Archipelago are densely populated, and have houses, jetties, and other structures covering a large proportion of the island. Recently, in response to rising sea level, low sea walls have been built around the coastline of some of the islands. These large populations have also impacted the diversity of these reef systems (Glaeser et al. 2017). Studies from the last few decades show that coral cover in the Spermonde Archipelago has declined by over 30% compared to that observed in original studies from the 1980s (Moll 1983; Best et al. 1989; Haya and Fujii 2017; Razak et al. 2024).

Samalona and Kudingareng Keke (in the Mid-Shelf to Outer-Shelf Zones) are influenced by their proximity to Makassar. These islands vary in size, with Samalona about 1 ha larger than Kudingareng Keke (Kench and Mann 2017) and the total reef area varying from about 40 ha on Samalona to 55 ha on Kudingareng Keke. Samalona has a permanent human population living on it, as well as frequent tourism use which further raises the degree of human impact. Kudingareng Keke is not permanently inhabited, but in recent

years also sees increased day tourism, and is used as an overnight stay for fisherman and other local inhabitants. The coastal city of Makassar has seen rapid development since the 1950s, with an increase of major coastal reclamation projects (including a new harbor) being built in the last decade (Teichberg et al. 2018; Girard et al. 2022; Estradivari et al. 2025). Further, surrounding land has seen long-term agricultural development and use, which sees sediment runoff and nutrification impacting the river systems, and consequently the nearshore marine ecosystem.

Core collection/radiometric dating

In August of 2022 a suite of 16 cores of 0.41–3.53 m recovered length with a mean recovery percentage (recovery/penetration*100) of 58.3% was collected from Samalona and Kudingareng Keke using push coring techniques (Perry and Smithers 2010; Cramer et al. 2017; Hynes et al. 2025). These cores were collected from a roughly Southeast–Northwest transect across the reef platform (Fig. 1B, C): three from each reef slope, and five from each reef flat/island (Hynes et al. 2025). The cores were subsampled on site to 5 cm sections (with some sections being longer due to large coral pieces present) to compensate for time averaging due to bioturbation, mixing, and compaction (Kidwell et al. 2005; Kidwell 2013). Samples were sieved in the laboratory to > 2 mm and < 2 mm size fractions. Mollusks (39 gastropods, 6 bivalves) from the > 2 mm subsamples were used for radiocarbon dating. Conventional ^{14}C dates (in YBP) were calibrated using Calib version 8.2.0 and the Marine20 curve (Stuiver and Reimer 1993; Heaton et al. 2020; Stuiver et al. 2022). This was done using a local reservation correction value ($\Delta R = -254 \pm 151$) averaged from the ten nearest points around the Makassar Strait within the Marine20 Reservoir Database to account for a lack of an exact local correction factor.

An apparent reef growth Hiatus was determined to exist on both Samalona and Kudingareng Keke, where the island and reef flat experienced low accretion rates during a minor sea-level decline between approximately 2000 and 6000 YBP. However, this does not meet the geological definition of a Hiatus being a gap in geologic continuity (Boggs 2012), but would be better defined as a period of significant reef growth/accretion slowdown. Similar periods of reef accretion slowdown have been found across the Indo-Pacific, with potentially varying mechanisms causing this (Perry and Smithers 2011; Toth et al. 2015; Gischler and Hudson 2019; Leonard et al. 2020; Cybulski et al. 2025). These other studies have already established the nomenclature of reef growth Hiatus, and so for this work, the term Hiatus was also used.

Ultimately due to the period of slow accretion, for this study, three time bins were selected for use. These are classified as: Pre-Hiatus (> 6000 YBP), Hiatus (2000–6000 YBP), and Post-Hiatus (< 2000 YBP) as shown in Supplemental Fig. 1. Core facies were also described and determined by dominant coral morphology and the quantity of the > 2 mm and < 2 mm grain size fractions of the sediment (Hynes et al. 2024, 2025). These size fractions were chosen by geologic standards of pebble/clast (> 2 mm) where the majority of coral pieces are found, and sand, silt, and smaller particles (< 2 mm) where foraminiferans and sponge spicules are concentrated (Boggs Jr. 2012, Hynes et al. 2025).

Coral abundances

To examine stony coral assemblage shifts, we determined the relative abundances of stony coral taxa throughout every core (76 samples from Kudingareng Keke and 111 from Samalona). Here we define stony corals as scleractinian and non-scleractinian corals that produce a carbonate skeleton. The latter includes the octocoral genera *Heliopora* and *Tubipora*, and the hydrozoan genera *Millepora* and *Stylaster*. Corals that preserved sufficient character from the > 2 mm fraction were identified to the lowest taxonomic level possible (often family or genus), using Corals of the World (Veron 2000), Coral Finder (Kelley 2022), and the WoRMS World List of Scleractinia (Hoeksema and Cairns 2025). Broken, and especially abraded, coral fragments could not always be identified at genera-species level due to lack of corallite preservation or other diagnostic features being preserved. These are thus referred to as unidentified coral fragments. For each sample, all identified corals were weighed, which was compared to the total coral identified weight to obtain relative abundance (%) of the identified corals. After calculating the weights, the median weight of identified corals across all samples was calculated, and only subsamples at or above this median weight were used, which reduced our total dataset to 99 samples (55 from Samalona and 44 from Kudingareng Keke) to compensate for some samples having only a few grams of identified corals.

For further analysis corals were reduced to 16 taxonomic groups, including a catch-all 'Others' group comprising about 10% of the average relative abundance (from all samples excluding unidentified corals). The taxonomic groups (Supplemental Figs. 2, 3, 4, Supplemental Table 1) used to create the coral assemblages are as follows: the genera *Acanthastrea*, *Acropora*, *Dipsastraea*, *Echinopora*, *Galaxea, Goniastrea*, *Isopora*, *Montipora*, *Palauastrea*, *Physogyra*, *Pocillopora*, Porites, and Seriatopora. Additionally, two family-level groups were used: Merulinidae (for corals from this family that did not preserve any genus-level characteristics), and Fungiidae (free-living fungiids found in several cores were combined into one group for analysis, but genus-level taxonomy was possible for many of these). All other corals were assigned to the Other group. Further, the dominant coral morphology (branching, foliose, massive, free-living)

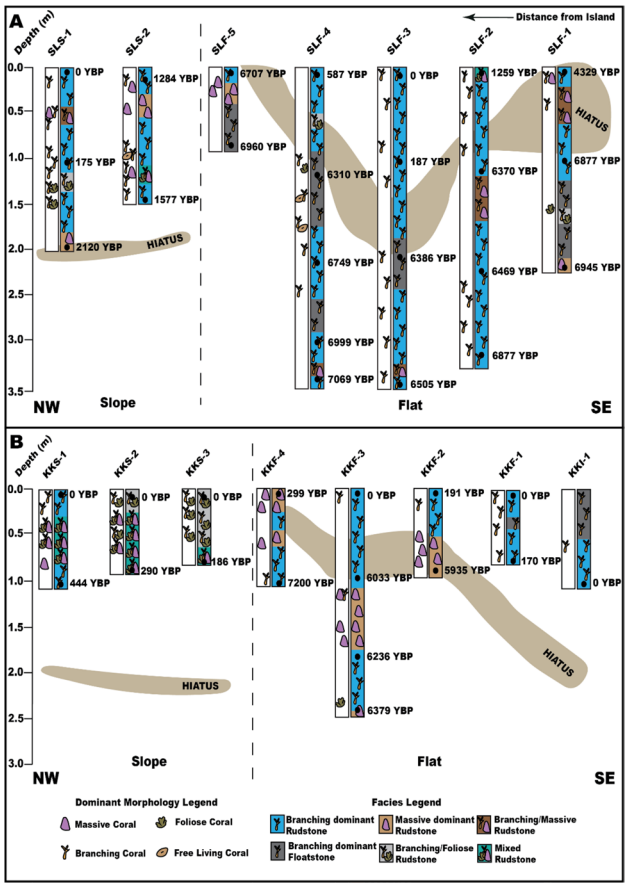

Fig. 2 **A.** Dominant coral morphology (left core image) and facies (right core image) for Samalona. Black dots and values are calYBP ^{14}C dates and core names at the top. Sandy-shaded area represents the Hiatus. Modified from (Hynes et al. 2025) **B** Dominant coral morphology (left core image) and facies (right core image) for Kudingareng Keke. Black dots and values are calYBP ^{14}C and core names at the top. Sandy-shaded area represents the Hiatus

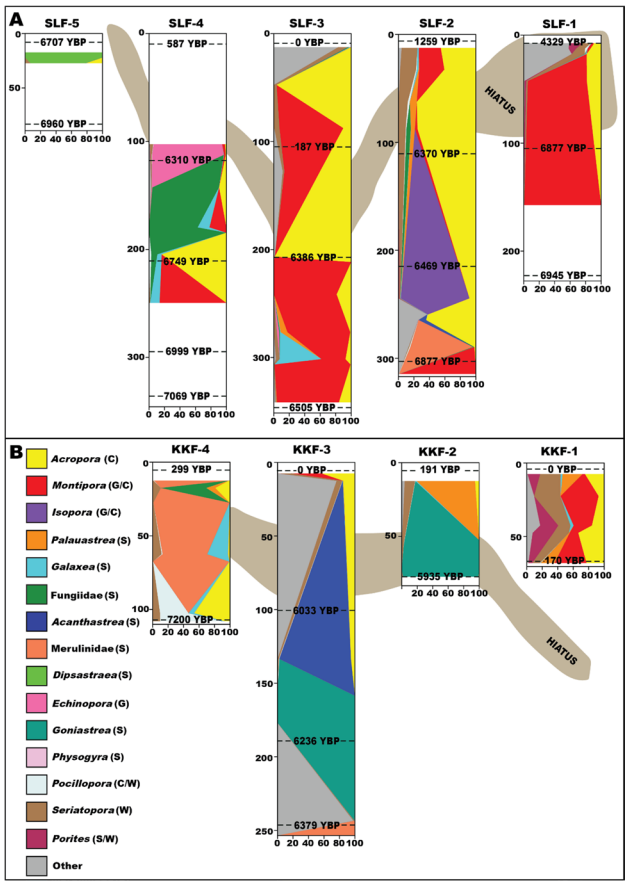

Fig. 3 Stacked line chart of the relative abundance of identified corals from the reef flat cores. The vertical axis of each core is the core depth (cm), and the horizontal axis is the relative abundance (%). Letters in brackets indicate the life history trait (Darling et al. 2012), G—Generalist, C—Competitive, S—Stress-tolerant, W—Weedy. Sandy-shaded area represents the Hiatus. Ages superimposed on each core are calYBP ^{14}C dates. Core names are at the top. A. Samalona reef flat cores. B. Kudingareng Keke reef flat cores

was quantified for each sample by determining which growth morphology formed the majority (> 50%) of the sample's corals (Fig. 2). This was done to gain information regarding facies, as well as to counteract the fact that in many subsamples, over half the corals present were unidentifiable due to taphonomic processes such as erosion and diagenesis (Kidwell 2013). Coral traits, habitats, and morphologies were defined by previous literature and placed into Table 1 (Darling et al. 2012; Veron 2000; Kelley 2022).

Foraminifera abundances

For LBF assemblages, we used approximately 15 g of sediment from the < 2 mm size fraction (sand and smaller), taken roughly every 30 cm downcore for cores SLF-1, SLF-3 (reef flat), and cores SLS-1 and SLS-2 (reef slope) for Samalona, and cores KKF-2, KKF-3, KKF-4 (flat) and KKS-1 and KKS-2 (slope) for Kudingareng Keke. This sediment was then further wet-sieved to 125 µm at the laboratories of Naturalis Biodiversity Center. After sieving, the 125 µm–2 mm fractions were dried in an oven at 55 °C for 24 to 48 h. From here, the first approximately 200 LBFs were identified to the lowest taxonomic level, varying from order to species (Holbourn et al. 2013; Renema 2018). The amount of each identified foraminiferans group in a subsample was divided by the total number of individuals counted to determine relative abundance of foraminiferans for a particular subsample (%).

However, some foraminiferans could only be identified to the family or order level due to the necessity of high-level taxonomic specialty knowledge for further distinctions (such as the family Miliolidae and the order Textulariida). As the genus *Amphistegina* has two readily identifiable species groups (*A. lessonii* group and *A. radiata* group), which show distinct ecological preferences, these have been examined at the species group level (Renema 2002, 2018). For

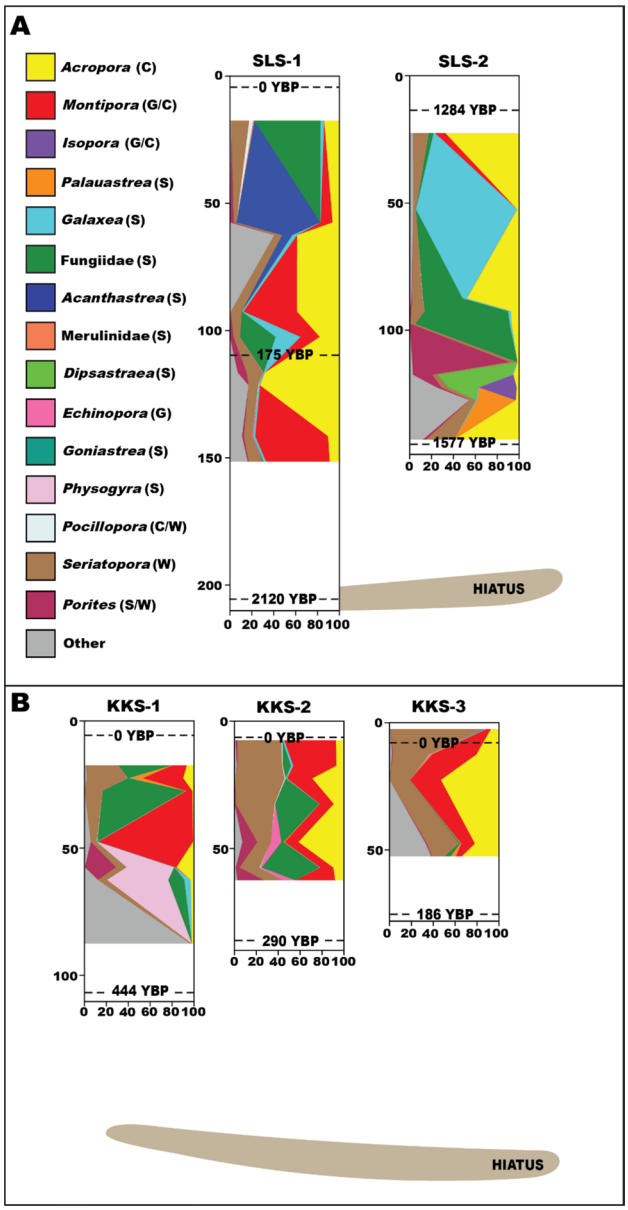

Fig. 4 Stacked line chart of the relative abundance of identified corals from the reef slope cores. The vertical axis of each core is the core depth (cm), and the horizontal axis is the relative abundance (%). Letters in brackets indicate the life history trait (Darling et al. 2012), G—Generalist, C—Competitive, S—Stress-tolerant, W—Weedy. Sandy-shaded area represents the Hiatus. Ages superimposed on each core are calYBP ^{14}C dates. Core names are at the top. **A.** Samalona reef slope cores. **B.** Kudingareng Keke reef slope cores

the LBF assemblages we used the following nine groups based on relative abundances: the species *A. lessonii* and *A. radiata*, the genera *Calcarina, Neorotalia, Heterostegina,* and *Operculina*, the family Soritidae, and the order Textulariida (Supplemental Fig. 5, Supplemental Table 2). All other groups were put into an 'Other' category that only represents on average (across all samples) 8.5% of the total abundance. Foraminiferan traits were defined by previous literature and placed into Table 2 (Renema and Troelstra 2001; Girard et al. 2022).

Sponge spicule abundances

Spicules were isolated from the < 2 mm fraction in 17 Samalona and seven Kudingareng Keke samples. The protocol for processing spicules from marine sediments was adapted from previous studies in the Caribbean (Lukowiak 2016; Lukowiak et al. 2018). This was done by first macerating 3–5 g of < 2 mm sediment in 30% hydrogen peroxide (H_2O_2), with the reaction rate sped up by use of a hot plate, to remove organic materials. The sediments were subsequently rinsed and decanted several times and then dried in an oven at 55 °C. These were then subjected to a 50% acetic acid (CH_3COOH) digestion for 24–48 h to remove all carbonate sediments (with acid topped off as needed). Calcareous sponge spicules were lost in the digestion process, but as the vast majority of sponges on these reefs are Demospongiae or Homoscleromorpha, it still presents an accurate representation of the overall reef assemblages (de Voogd et al. 2006; van Soest and de Voogd 2015). After digestion, samples were again rinsed and decanted several times before a final drying at 40–55 °C. Spicules were taken from roughly every 30 cm downcore from cores SLF-1, SLF-3 (flat) and cores SLS-1, SLS-2 (slope) from Samalona, and core KKF-3 (flat) and core KKS-1 (slope) on Kudingareng Keke.

Digested samples were then analyzed by mounting part of the isolated non-carbonate material onto a glass slide using Ultrabed following previously established protocols (de Voogd et al. 2006). For each slide, the first 200 spicule morphotypes were identified using established nomenclature and taxonomy (Boury-Esnault and Rützler 1997; Hooper and van Soest 2002; de Voogd et al. 2025). The quantity of each morphotype was divided by the total number of spicules in the sample to obtain relative abundance (%) of spicule morphotypes for each sample. For SEM imaging, spicules were handpicked and mounted on a SEM stub with carbon tape. These were then sputter coated using 10 nm of Pt/Pd to reduce backscatter.

Due to the variable difficulty in assigning individual spicules to low-level specific taxonomy (some spicules are diagnostic of a genus or even species, while others can only be used to higher levels such as the order), spicules were grouped into nine broad spicule morphotypes based on recent nomenclature (Lukowiak et al. 2022) to create spicule assemblages for further analysis. These morphotype groups are as follows: monoaxone megascleres, rhabd derived, asters, selenaster/sterraster/aspidaster, long triaenes, ectosomal triaenes, sigma derived, Homoscleromorpha, and Lithistid (Supplemental Figs. 6, 7, Supplemental Table 3). Similar to the corals and LBF, the remaining morphotypes

Table 1 Table of life history traits, preferred environments, and morphologies of dominant coral taxa examined here (Darling et al. 2012; Veron 2000; Kelley 2022)

Coral taxa	Life history strategy (Darling et al. 2012)	Common environment (Veron 2000)	Morphologies (Veron 2000; Kelley 2022)	Notes
Acropora	Competitive	Shallow water (reef flat to upper slope), clear water, often high energy	Dominantly branching, table/plate-like	100s of species, variability in traits is expected
Montipora	Generalist/competitive	Shallow water reef environments, turbid or clear water	All morphologies	
Isopora	Generalist/competitive*	All environments, especially upper reef slopes, high energy water	Branching/columns or encrusting plates	*Inferred life history strategy
Seriatopora	Weedy	Shallow water reef environments (intertidal to subtidal)	Thin branches	
Pocillopora	Competitive/weedy	Shallow water reef environments, turbid or clear water	Branching	
Porites	Stress-tolerant/weedy	Shallow water reef environments, generally clear water	Most frequently massive or branching. Encrusting plates	
Galaxea	Stress-tolerant	Shallow water reef environments, low energy, turbid or clear water	Dominantly branching or massive, encrusting plates	
Acanthastrea	Stress-tolerant	Most reef environments and water clarity	Massive or encrusting	
Echinopora	Generalist	Shallow protected reef environments	All morphologies	
Palauastrea	Stress-tolerant*	Upper reef slopes, turbid water	Branching	*Inferred life history strategy
Merulinidae	Stress-tolerant*	Common all reef environments. Often shallow water, turbid or clear	All morphologies, commonly massive	*Multiple genera, majority of which are stress-tolerant
Goniastrea	Stress-tolerant	Shallow water reef environments (intertidal to subtidal)	Dominantly massive	
Dipsastraea	Stress-tolerant	Common all reef environments	Massive	
Fungiidae	Stress-tolerant*	Lagoons, upper reef slope to inter reef, clear or turbid	Dominantly free-living	*Multiple genera, majority of which are stress-tolerant
Physogyra	Stress-tolerant	Protected reef environments, turbid water	Massive	

were placed into an 'Other' category representing only 1% of the spicules on average from all samples.

Data analysis

To visualize the change in communities throughout a core, each group was plotted using a stacked-line chart comparison of the relative abundance (%) to the core depth. This was done with the areaplot R package (Magnusson 2025), and subsequently all charts were drawn with the Hiatus period shaded, as well as calibrated ^{14}C dates imposed on top for temporal context.

To determine which key members of each assemblage (corals, foraminiferans, and sponges) were the main drivers of changes on both islands spatiotemporally, we conducted principal component analyses (PCAs) on all groups. This was done in R using the ggplot2 package (Wickham 2016) using the relative abundances of coral fragments, LBF, and sponge spicules for the entire system, and each island individually. This was also done by using the reef environmental data (flat, slope, island) as well as the three time bins data to complement the PCAs and determine which organisms were responding to these spatiotemporal shifts. Further, coral relative abundance data were square root transformed prior to conducting the PCA to account for the high occurrence of zero percent relative abundance samples.

To complement this a SIMPER analysis was conducted on the coral (square root transformed) and LBF relative abundance data using 10,000 permutations and the R package vegan (Oksanen et al. 2023). Here we compared between time bins, between islands, and between reef environments (flat or slope) for statistically significant taxa driving changes between said factors. While p values are considered significant when $p < 0.05$, a few select taxa of a slightly higher p value were indicated by the SIMPER analysis as potentially being a driver of variance, and therefore we have

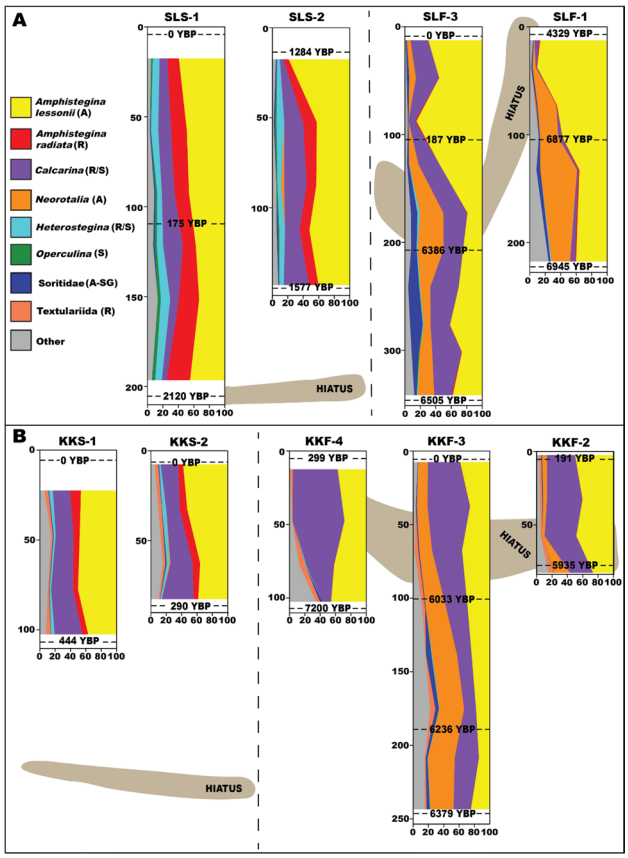

Fig. 5 Stacked line chart of the relative abundance of Large Benthic Foraminifera. The vertical axis of each core is the core depth (cm), and the horizontal axis is the relative abundance (%). Letters in brackets indicate substrate preference (Renema and Troelstra 2001; Girard et al. 2022), A—All substrate types, R—Rubble/hard substrate, S—Sediment substrate, A-SG—Algae/sea grass substrate. Sandy-shaded area represents the Hiatus. Ages superimposed on each core are calYBP ^{14}C dates. Core names are at the top. **A.** Samalona flat and slope cores. **B.** Kudingareng Keke flat and slope cores

Table 2 Table of preferred environments and substrate types of LBF examined here (Renema and Troelstra 2001; Girard et al. 2022)

LBF taxa	Common environment	Substrate type
A. lessonii	Shallow to mid-slope	All
A. radiata	Mid- to deep slope	Hard/rubble
Heterostegina	Mid- to deep slope	Hard/rubble or sediment
Calcarina	Flat or slope	Hard/rubble or sediment
Operculina	Slope	Carbonate sediment
Neorotalia	Flat	All
Textulariida	All	Hard/rubble
Soritidae	Flat	Algae or sea grass

highlighted them in the results. Spicules were not used for SIMPER analysis due to the lack of high-level taxonomy, as well as that only 4 samples examined here are older than

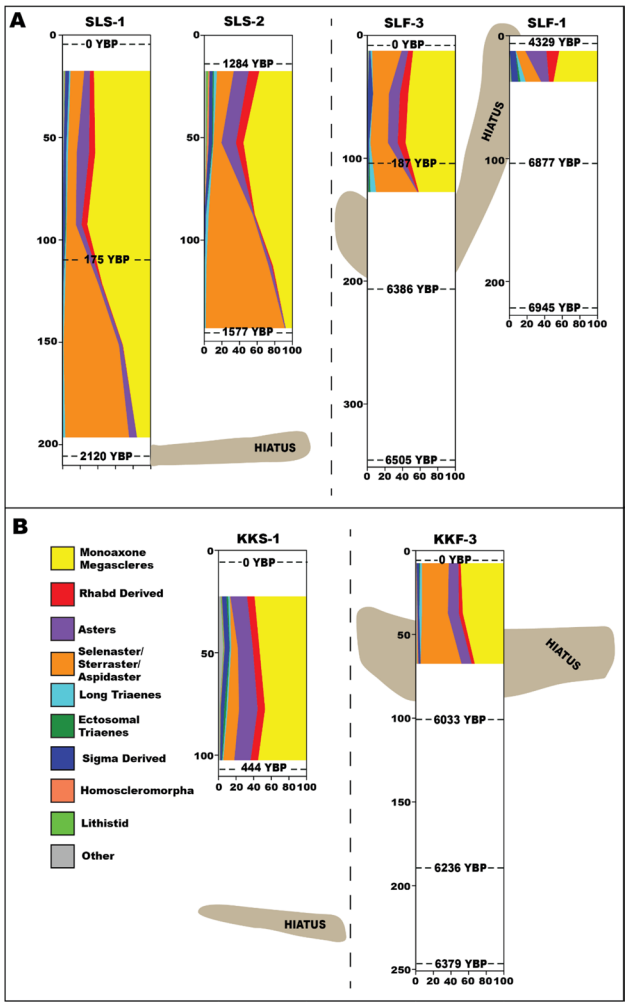

Fig. 6 Stacked line chart of the relative abundance of spicule morphotypes. The vertical axis of each core is the core depth (cm), and the horizontal axis is the relative abundance (%). Sandy-shaded area represents the Hiatus. Ages superimposed on each core are calYBP ^{14}C dates. Core names are at the top. **A.** Samalona flat and slope cores. **B.** Kudingareng Keke cores flat and slope cores

2000 YBP. However, two specific spicule morphotypes representing *Cliona* and *Spiroxya* (groups monoaxone megascleres and rhabd derived, respectively) were subjected to a generalized linear model (GLM) regression with a 95% confidence interval and R^2 values of relative abundance (%) versus core depth using the ggplot2 R package (Wickham 2016) to examine apparent shifts toward the core tops.

Results

Coral assemblage shifts

In general, it was found that the Pre-Hiatus period was frequently dominated by massive and foliose coral

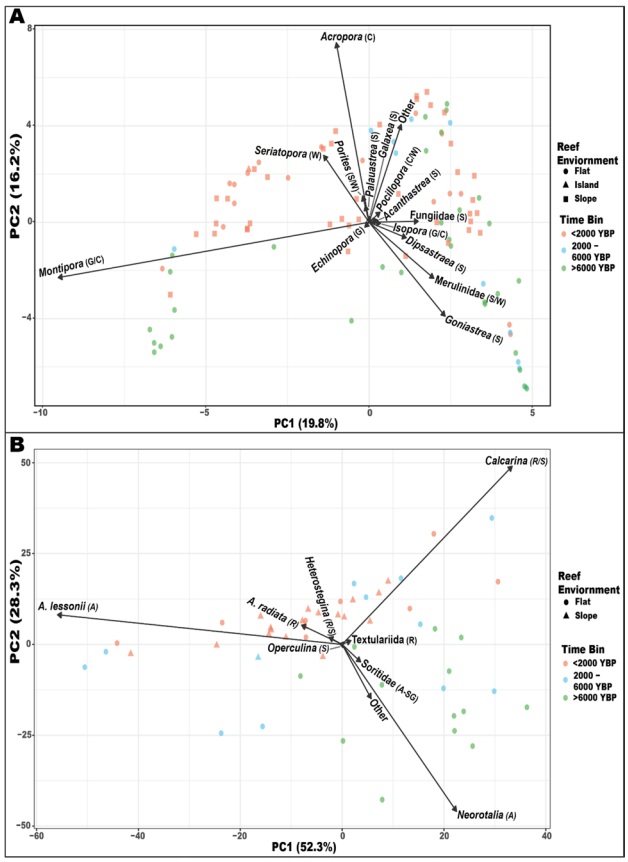

Fig. 7 A. Principal component analysis for the coral taxonomic groups examined. Shapes represent different reef environments (flat, island, slope), and colors represent the time bins. Letters in brackets indicate the life history trait (Darling et al. 2012), G—Generalist, C—Competitive, S—Stress-tolerant, W—Weedy. Coral relative abundance data were transformed using a square root transformation prior to running the PCA. B. Principal component analysis for the Large Benthic Foraminifera taxonomic groups examined. Shapes represent different reef environments (flat, slope), and colors represent the varying time bins. Letters in brackets indicate substrate preference (Renema and Troelstra 2001; Girard et al. 2022), A—All substrate types, R—Rubble/hard substrate, S—Sediment substrate, A-SG—Algae/sea grass substrate

morphologies (Fig. 2; Hynes et al. 2025), with a shift to predominantly branching coral species by the Post-Hiatus (< 2000 YBP). However, this shift occurred much earlier, from Pre-Hiatus to Hiatus, on the nearshore Samalona, whereas on Kudingareng Keke it occurred during the transition from the Hiatus (2000–6000 YBP) to the Post-Hiatus. While the reef slopes of both islands show a high diversity of coral, the reef flat of Kudingareng Keke has a higher diversity than Samalona, the latter of which is predominantly corals of the Acroporidae family (especially in the Hiatus and Post-Hiatus periods). PCA and SIMPER analysis (Fig. 7A, Supplemental Table 4) shows that the Pre-Hiatus is driven by a higher occurrence of *Montipora* ($p = 0.0100$) and lesser so the statistically non-significant *Dipsastraea* ($p = 0.0560$) and *Echinopora* ($p = 0.0762$), compared to the higher Post-Hiatus occurrences of *Acropora* ($p = 0.001$) and *Seriatopora* ($p = 0.0001$) especially on the reef slope. The Hiatus period differs from both the Post-Hiatus and Pre-Hiatus due largely to *Goniastrea* ($p = 0.0161$) and lesser so Merulinidae (which *Goniastrea* is a member of, $p = 0.0013$). Differences between islands can be explained largely due to the more frequently occurring occurrences of massive corals on Kudingareng Keke reef flat, such as *Goniastrea* ($p = 0.0010$), Merulinidae ($p = 0.0083$), and *Physogyra lichtensteini* ($p = 0.0416$) but also by higher occurrences of *Palauastrea ramosa* and *Pocillopora* (Supplemental Table 4).

Across all 16 cores, we identified 44 genera of scleractinian stony corals, as well as four genera of non-scleractinian corals (*Heliopora*, *Tubipora*, *Stylaster*, and *Millepora*). Competitive *Acropora* (19.7%) and the generalist *Montipora* (19.1%) are the two most frequently encountered groups in terms of relative abundance, across all time bins and both islands (Table 1). Both of these groups show a higher occurrence on Samalona than Kudingareng Keke, especially on the reef flat. The next most common groups across all samples were the weedy *Seriatopora* (an average relative abundance of 10.7%) and those of the stress-tolerant Fungiidae (8.8%). Stress-tolerant Merulinidae and two specific genera of Merulinidae, *Goniastrea* and *Dipsastraea,* occur frequently throughout the Pre-Hiatus and Hiatus periods. Interestingly, these corals can often take up 80–99% of the relative abundance of a 5 cm subsample as they were massive corals which spatially filled the entire width of the coring tube. *Palauastrea ramosa* is present with an average abundance of 2.2% which, while not a large amount of the overall abundance, is interesting as this coral species has not been reported from the region during earlier studies going back to the 1980s (Moll 1983; Hoeksema 2012a; Yusuf et al. 2021) even though it is known to be stress-tolerant especially in regard to turbidity. Further, *Palauastrea ramosa* is present in cores from both islands and all three time bins, including in the last 100 to 200 YBP, suggesting this coral has been present in the area in both the distant and recent past, and possibly remains there cryptically today.

From the reef flat of Samalona (Fig. 3A), there is a dominance of branching coral growth forms, especially in the Hiatus (2000–6000 YBP) and Post-Hiatus (< 2000 YBP) periods. In the Pre-Hiatus (> 6000 YBP), however, massive, foliose, and free-living corals also appear more frequently during this time period (Fig. 2A). This is sustained by a dominance of *Montipora*, present as both foliose and branching morphologies. There also are occurrences of massive corals like *Acanthastrea, Galaxea, Dipsastraea*, and Merulinidae in the Samalona reef flat cores. The Samalona flat during the Hiatus and Post-Hiatus periods shows an almost total dominance of branching corals, mostly driven by a high dominance of branching *Acropora.* Individual subsamples

can consist of high occurrences of specific stress-tolerant or weedy taxa such as: *Heliopora*, *Cyphastrea*, and *Pachyseris*. These corals have a low average abundance across all samples, but due to their dominant abundance in select subsamples and their stress-tolerant/weedy life traits are worth highlighting. Coral data from the reef slope of Samalona are entirely from the Post-Hiatus period (Fig. 4A). Here there is both a much more varied diversity of corals and coral morphologies across the cores (Fig. 2A), although branching corals are still the most common type with a prevalence of the branching rudstone facies (with other facies intermixed). There is a high abundance of stress-tolerant Fungiidae corals, as well as some massive *Porites* colonies (as well as other non-statistically significant stress-tolerant massive colonies like *Acanthastrea* and *Galaxea)*.

Comparatively, on the less turbid-influenced (further offshore) island of Kudingareng Keke (Fig. 3B) the Pre-Hiatus (> 6000 YBP) and Hiatus (2000–6000 YBP) periods are marked by a high abundance of massive corals, mostly consisting of stress-tolerant *Goniastrea,* and Merulinidae from the reef flat cores (as well as other non-significant massive corals such as *Acanthastrea* and *Galaxea*). This is further evidenced by a more frequent occurrence of the massive rudstone facies during this period. There is also a non-significant dominance of stress-tolerant and weedy corals like *Pocillopora* and *Pavona* in the Pre-Hiatus. During the Post-Hiatus of Kudingareng Keke, branching corals dominate, driven by occurrences of *Acropora*, as well as *Palauastrea ramosa*. The reef slope of Kudingareng Keke only dates back about 450 YBP and therefore is all Post-Hiatus (Fig. 4B). The slope is much more varied in morphologies with the most dominant facies being a mixed rudstone of massive, foliose, and branching morphologies (Fig. 2B). There is a high abundance of Fungiidae in these cores, as well as commonly *Seriatopora*, especially when compared to Samalona (Supplemental Table 4). Unlike the reef flat, there is a more common occurrence of *Acropora* and *Montipora*, more akin to the Samalona reef slope. The bottom of KKS-1 is dominated by large fragments of a massive stress-tolerant *Physogyra lichtensteini* skeleton, which both is a significant driver in the difference between the flat and the slope on Kudingareng Keke, as well as one of the major differences to Samalona (Supplemental Table 4, Fig. 7A).

Foraminifera assemblage shifts

The overall trend identified is that the diversity of LBF species observed has reduced over time, from a higher variability in the Pre-Hiatus period to a dominance of the *A. Lessonii* group by the Post-Hiatus period (especially on the reef flat). However, on the less turbid island Kudingareng Keke, a second group, *Calcarina*, appears to compete with *A. Lessonii* and at times is more dominant in terms of abundance. PCA and SIMPER analysis of LBF abundances (Fig. 7B, Supplemental Table 5) shows that the Pre-Hiatus (> 6000 YBP) is being driven by the groups *Neorotalia* ($p = 0.0001$), Soritidae ($p = 0.0001$), and others ($p = 0.0002$) as opposed to the Hiatus (2000–6000 YBP) having a higher (but statistically non-significant) presence of *Calcarina* ($p = 0.0790$) and *A. lessonii* ($p = 0.0501$). The Post-Hiatus (< 2000 YBP) differs from the Pre-Hiatus due to the more common appearance of the non-significant reef slope group *A. radiata* ($p = 0.0918$) and the Hiatus also sees variance from the Post-Hiatus due to *A. radiata* ($p = 0.0136$), and lesser so *Heterostegina* and *Calcarina* (Supplemental Table 5). Differences between islands are largely driven by a dominance of *A. lessonii* ($p = 0.0354$) and non-significant *Heterostegina* ($p = 0.0603$) on the slope of Samalona, whereas Kudingareng Keke sees *Calcarina* ($p = 0.0002$) and Textulariida ($p = 0.0001$) as the key contributors to variance.

In total we identified 28 genera of Foraminifera across all 51 samples (27 from Samalona, 24 from Kudingareng Keke). Three groups, *Amphistegina*, *Calcarina*, and *Neorotalia,* are the most dominant genera across all time bins and represent statistically significant drivers between time bins and islands. Soritidae and *Heterostegina* both represent significant contributors to the variance in time bins, islands, and reef environment. *Amphistegina radiata* is predominantly found on the reef slope of both locations and therefore is significant to the Post-Hiatus period of both islands, while *Calcarina* and *Neorotalia* are abundant on the reef flat, which is in line with other studies from the region (Renema and Troelstra 2001; Girard et al. 2022). *Amphistegina lessonii* is the only group that was found across all samples and is the most abundant group over almost all cores. This observation is consistent with a study of twelve islands from the Spermonde Archipelago from 1997 to 2018 which also showed a dominance of *A. lessonii* across the entire archipelago (Girard et al. 2022).

On the Samalona reef flat (Fig. 5A), the Pre-Hiatus (> 6000 YBP) period has a high variability and a larger diversity of Foraminifera groups. The most significantly dominant groups are a mixture of *A. lessonii* and *Neorotalia. Heterostegina* is present in very rare amounts in this period likely due to a deeper water level over 6000 YBP. Soritidae also occurs here, which then all but disappears in the subsequent time periods. The Hiatus (2000–6000 BP) period shifts toward *A. lessonii* dominance, while *Calcarina* decreases in abundance, it still is an important driver of the shift to the Hiatus (Fig. 7B). The Post-Hiatus (< 2000 YBP) period, which on the Samalona reef flat is only represented by a single core, SLF-3, contains a complete dominance of *A. lessonii*, accompanied by a decrease in *Neorotalia* and an almost complete lack of any other LBF. The Samalona reef slope demonstrates a fairly consistent LBF assemblage across the entire Post-Hiatus period (the only time period the

slope LBF assemblages represent). There is a slight increase in the relative abundance of *A. lessonii* moving toward the modern day. Here there is also a relatively consistent significant abundance of *Heterostegina* and *A. radiata*, both of which represent deeper water (reef slope) species (Table 2).

On Kudingareng Keke (Fig. 5B), the Pre-Hiatus reef flat also has *A. lessonii*, *Calcarina,* and *Neorotalia* dominance but with a higher proportion of *Calcarina* compared to the Samalona flat. Further, there are minor amounts of Textulariida present throughout all of the Kudingareng Keke cores which were almost completely absent from all Samalona cores. Similar to Samalona, Soritidae is significantly present in the Pre-Hiatus, which is all but absent in more subsequent time periods. Moving into the Hiatus period, there is a decrease in *A. lessonii*, while simultaneously *Calcarina* becomes the most dominant group of Foraminiferans. The reef flat during the Post-Hiatus displays a slight recovery of *A. lessonii*, with *Calcarina* in roughly equal proportions of the relative abundance (though SIMPER results show no significance of these groups). Due to this, the overall Foraminifera diversity for Post-Hiatus of Kudingareng Keke is quite low. On the reef slope (which is all Post-Hiatus with the oldest recovered ^{14}C date being 444 YBP), an apparent high diversity is seen, similar to the reef slope of Samalona. *Heterostegina* and *A. radiata* are present across all samples, but are not as abundant as on the Samalona reef slope, but still are driving the variance to the reef flats. Instead, Textulariida is present across all time periods in small but significant abundances, which are not present in the Samalona slope cores and therefore is the driver of variance between islands.

Sponge assemblage shifts

Here we identified a total of 88 spicule morphotypes from 24 samples from six cores (two cores each from Samalona flat and slope, one core each from Kudingareng Keke flat and slopes). The four most common morphotypes recorded here are oxea, selenaster, subtylostyle, and spheryoxyaster. Further, as older, and deeper samples from the reef flat cores tended to have a majority of broken (and therefore unidentifiable) spicules, we were unable to count the requisite 200 individuals to be able to include them for analysis. Due to this, the spicule data almost entirely consist of the Post-Hiatus (< 2000 YBP) period, with only four samples from the Hiatus (2000–6000 YBP) period (Fig. 6). However, this still allows us to examine sponge assemblage shifts over the last 2000 years, since the Hiatus, by looking at changes over the core depth. Of the three assemblage types examined, sponges were the most challenging to quantify due to spicule preservation and a lack of high taxonomic identification. However, during the Post-Hiatus period (< 2000 YBP) it can be seen that there are key differences in assemblage compositions between the two islands, with an increase in the dominant monoaxone megascleres being observed toward the present day on the more turbid Samalona, whereas this population is consistent throughout the same period on Kudingareng Keke. A high presence of cryptic species was also observed, especially those of boring/excavating sponges, increasing in relative abundance toward the present.

In all cores except KKS-1, monoaxone megascleres and selenaster/sterreaster/aspidaster (the vast majority of which are selenasters) are the most common morphotype groups encountered. In all reef flat cores, and the Kudingareng Keke slope core, monoaxone megascleres are relatively consistent across the cores, while on the Samalona slope these go from less than 20% relative abundance at the core bottom (and in SLS-1 the end of the Hiatus period) to the most common morphotype identified toward the modern day. Inversely, the selenaster/sterreaster/aspidaster decreases toward the present on the Samalona slope. In all cores spicule diversity is seemingly higher at the core tops. Lithistid and Homoscleromorpha spicules combined represented less than 1% of the average relative abundance (Fig. 6). These two groups were more commonly identified from the reef slope than on the reef flat for both islands.

Cryptic species of sponges (many of which are excavating with a preferred coral rubble habitat) were also found throughout the spicule assemblages. Spicules from the genera *Acanthotetilla*, *Alectona*, *Rhabdermia*, *Samus, Triptolemma*, *Spiroxya,* and *Cliona mucronata* were found in varying samples across all cores examined. Specifically, mucronate subtylostyles from *C. mucronata* (from the monoaxone megascleres group) and spiral microstrongyles of S*piroxya* (from the rhabd derived group) were found in relative abundances of up to 11.5% and 4%, respectively. However, these were not statistically significant with R^2 values of 0.42 for *C. mucronata* and 0.23 for *Spiroxya* sp. Interestingly for both of these genera, the relative abundance of their spicules appears to increase toward the modern day, with the tops of each core showing 9% or higher relative abundance of *C. mucronata* (Supplemental Fig. 8). *Cliona* sp. with similar mucronate subtylostyles are also found cryptically in the Eastern Pacific and Caribbean, likely as new species (Pacheco et al. 2020). Despite this lack of significance, it is certain that spicules of excavating sponges are present throughout the entire Post-Hiatus period.

Discussion

The 48 genera of stony corals found in the cores of the present study represent well over half of the known diversity of genera reported from the Spermonde Archipelago (Moll 1983; Moll and Borel-Best 1984; Hoeksema 2012a). Given that many corals were too degraded for identification, it is

likely that more genera are also represented within these cores. Additionally, 28 genera of LBF were also identified, which represents over 2/3 of all known LBF genera for the region (Renema 2002, 2018). Further, a total of 88 varying spicule morphotypes were also identified here, though it cannot be said how much of the sponge diversity is captured by these morphotypes (de Voogd et al. 2006; Putra et al. 2024). After reducing these into larger taxonomic groups for further analysis, shifts in the coral and LBF assemblages from the Pre-Hiatus (> 6000 YBP) to the Post-Hiatus (< 2000 YBP) show a change in coral morphology and diversity from more massive, foliose, and free-living morphologies and mixed diversity to predominantly branching *Acropora* (especially on the reef flat). Further, the presence of *Palauastrea ramosa* on both islands and all time bins shows that cryptic diversity can also be captured by these reef cores. LBF assemblages shift from higher diversity in the Pre-Hiatus to dominantly *A. lessonii* group and *Calcarina* on both the slope and the flat. Samalona contains a higher abundance of *A. lessonii*, while Kudingareng Keke has a higher abundance of *Calcarina*, with *Heterostegina* (Samalona) and Textulariida (Kudingareng Keke) further driving the difference between islands. Finally, 2000 years of sponge spicule assemblage data shows an apparent increase in the relative abundance of cryptic excavating sponges like *Cliona* and *Spiroxya*. Here we then examine how potential environmental conditions have impacted these reef assemblage shifts over 7200 years.

Reef communities in a changing sea-level regime

Coral reefs and their associated low-lying islands are set to face increased sea-level change in the coming decades (Morgan et al. 2020; Walker et al. 2021). Further, it is known that the Early to Mid-Holocene was a time of rapid sea-level rise, followed by a period of slow decline in the region (Bender et al. 2020; Hynes et al. 2025). Therefore, we can examine past reef assemblage shifts in the context of a changing sea-level regime to help understand what the future of these species may hold (Table 1). For the reef flat during the Pre-Hiatus (> 6000 YBP) on both islands, massive, foliose, and free-living corals are much more common, especially on Kudingareng Keke where there is a dominance of stress-tolerant massive corals during this period (Figs. 2B, 3B, 7A). This is especially of interest, as many core studies in the Indo-Pacific region have an underrepresentation of massive corals in percussion/push cores, due to the challenges associated with coring through and collecting them, especially when compared to the relative ease of sampling thinner and more fragile branches and foliose forms (Cybulski et al. 2020; Diers et al. 2025). However, a recent core study from Singapore (a natural and anthropogenic turbid reef system) also shows a higher capture rate of stress-tolerant massive corals (Chan et al. 2025) especially in the Early to Mid-Holocene. Kudingareng Keke is dominated by stress-tolerant and massive Merulinidae corals (including *Goniastrea*) and *Acanthastrea,* while Samalona reef flat has a dominance of the generalist *Montipora*, present frequently in its foliose morphology, as well as more free-living Fungiidae corals, and occurrences of *Dipsastraea,* submassive *Galaxea,* and Merulinidae, all of which are stress-tolerant. The more common presence of these coral morphologies is likely largely driven by deeper water depths than exist on the modern reef flat (with depths of 1.0–1.5 m MSL), as sea level during this period was approaching a Mid-Holocene high stand and was rapidly increasing up to this point (Mann et al. 2019; Bender et al. 2020). Corals during this period had much higher accretion rates as part of a 'catch up/keep up' phase with this sea-level rise (Hynes et al. 2025).

During the Hiatus (2000–6000 YBP) period, while *Goniastrea* is statistically driving the changes compared to the Hiatus, the dominant coral morphology begins to shift to more commonly branching corals during this period ($p = 0.0161$). Samalona especially shifts to dominantly branching *Acropora* from the Hiatus to the recent, in part due to the shift to keep up as the Mid-Holocene sea-level high stand occurred (Diers et al. 2025). This continues into the Post-Hiatus (< 2000 YBP) as sea level declines until only the last few decades and is accompanied by increase in coral diversity. Competitive *Acropora* tends to favor the shallower and clearer waters seen on reef flats and upper reef slopes (Table 1; Veron 2000). Further, we have seen extremely low accretion rates throughout the Hiatus period (average mean accretion rate of 0.20 mm/yr from both islands), and this low accretion continues until the last few centuries (Hynes et al. 2025). By the Post-Hiatus (< 2000 YBP), the relative abundance of the weedy *Seriatopora* (a common shallow water/intertidal coral) is higher and more common on the flat. The reef slopes, which are almost entirely Post-Hiatus, show a higher diversity of corals and include common reef slope corals like Fungiidae and *Seriatopora* as well as more mixed coral morphologies. This shows that the Pre-Hiatus reef flat was somewhat similar to the deeper water upper slope coral communities seen in these slope cores. As mentioned, *Palauastrea ramosa* is present in all three time periods, and even close to the modern day, but this coral has never been recorded in the Spermonde Archipelago, although the coral fauna of this region has been extensively studied over the past 50 years. (Moll 1983; Best et al. 1989; Razak et al. 2024). This shows that reef assemblage shifts occurred long before industrialization in the area, as well as being a potential tool for capturing cryptic diversity. The nearest locality where *P. ramosa* has been found alive is Selayer Island off the southernmost tip of South Sulawesi (Best et al. 1989), which is only 150 km away from the Spermonde Archipelago. Since this species is known to occur in shallow, lagoonal habitats with turbid water (Best et al.

1989; Veron 2000), it is unclear why this species was present in the past and appears to have become locally extinct in the Spermonde Archipelago.

The reef flat foraminifera assemblages on both islands show an assemblage of LBF that prefer deeper water (shallow to mid-slope) as well as reef flat-preferring LBF in the Pre-Hiatus (Figs. 5, 7B, Table 2). This is shown by the consistent appearance of *A. lessonii* across all reef flat samples of both islands. This observation is consistent with a study of 12 islands in the Spermonde Archipelago from 1997 to 2018 which also showed a dominance of *A. lessonii* across the entire archipelago (Girard et al. 2022). Further, there is a high relative abundance of *Calcarina* which is especially significant during the Hiatus ($p = 0.0790$), which has some species preferential to the flat and others to the reef slope (Renema and Troelstra 2001; Renema 2002; Girard et al. 2022). In both cores from the reef flat of Samalona examined for LBF during this period, there are minor abundances of *A. radiata*, and on both islands minor occurrences of *Heterostegina*, both of which have a preference for the mid-slope (Renema 2018; Girard et al. 2022). Further, there is a higher diversity of LBF groups in the Pre-Hiatus flat (> 6000 YBP), which decreases to a dominance of only three groups into the Post-Hiatus (*A. lessonii*, *Calcarina*, and reef flat significant, $p = 0.0036$, *Neorotalia)* as the water depth on the flat was only 1.0–1.5 m on average in this period and into the modern (Hynes et al. 2025). The reef slopes, which only have one data point from the Hiatus period on Samalona, show a higher diversity of LBF throughout the cores on both islands. Further, much higher occurrences of slope-preferring foraminiferans such as *A. radiata*, *Heterostegina*, and *Operculina* are noted from the slope. Diversity and relative abundances of LBF on the reef slope are consistent and steady throughout the last 2100 YBP and 450 YPB on Samalona and Kudingareng Keke, respectively.

Sponge spicule assemblages are almost entirely from the Post-Hiatus (< 2000 YBP) and therefore offer little insight to their assemblages prior to the past 2100 YBP (Fig. 6, Supplemental Fig. 9). Despite these limitations, there are apparent changes in the dominant abundant spicule morphotype groups across this time period. On the reef flats of both islands, an increase in monoaxone megascleres appears to occur toward the present, which simultaneously comes with a decrease in selenaster/sterraster/aspidaster (with selenasters present in the genus *Placospongia* representing most of this group). It cannot be ruled out that the high prevalence in selenasters in the past is due to taphonomic mechanisms (Kidwell et al. 2005; Lukowiak 2016). The selenaster/sterraster/aspidaster preserves well due to their round shape and robust construction, as well as the fact that even when broken they can be readily identified compared to monoaxone/triaene/rhabd derived. For example, spicules with broken ends are often not identifiable to a specific morphology group. However, as the Asters group, which shows similar robustness and identifiable broken spicules, either increase slightly or stay stable moving toward the recent, it is likely this pattern is not entirely taphonomic in nature. Interestingly, the trend of decreased selenasters/sterrasters and increasing monoaxone megascleres, especially oxeas, is the opposite as was observed in a core study from Panama where increasing presence of *Placospongia* (selenasters) and *Geodia* (sterrasters) was possibly due to the overhunting of Hawksbill turtles (*Eretmochelys imbricata*) in the region (Lukowiak et al. 2018). Although it is often difficult to assign taxonomy to individual spicules, there appears to be an increase in diversity and a more even spread of abundance at the core tops. This sub-recent to recent material has a higher occurrence of monoaxone megascleres, especially oxeas, which are present in many classes of Demospongiae and therefore their high relative abundance is to be expected. Many of these oxeas do come from the order Haplosclerida, which is common across the Spermonde Archipelago with long-term sponge studies going back to 1997 (de Voogd et al. 2006). Mucronate subtylostyles from the excavating *Cliona* also contribute to the increased presence of monoaxone megascleres reported here. Further, the appearance of cryptic species in these sediments shows an additional benefit of identifying the presence of cryptic/excavating sponge species within spicule assemblages.

Reef substrate changes

As LBF shows a high preference of reef substrate alongside their water depth specializations (Table 2), we can examine how the reef substrate has changed over the last 7200 YBP through their presence. On the reef flats of both islands, the Pre-Hiatus (> 6000 YBP) suggests an algal-dominated rubble substrate, as shown by the more significant abundance of *Neorotalia* and Soritidae over *A. lessonii* (Holbourn et al. 2013; Renema 2018). Moving into the Hiatus period, the flat becomes a more evenly mixed algae and coral rubble substrate as *A. lessonii* and *Calcarina* become the dominant LBF groups. This rubble algal-mixed substrate continues into the Post-Hiatus (< 2000 YBP) period, with a recovery of rubble on the flat (likely driven by high coral coverage on the flat contributing to the rubble) until the last few decades where algae starts to dominate again, likely an indication of more severe anthropogenic influences (Renema 2018; Girard et al. 2022). Interestingly this rubble-dominant substrate in the Hiatus to Post-Hiatus is being driven largely by *A. lessonii* and *Heterostegina* on Samalona compared to *Calcarina* and Textulariida on Kudingareng Keke. The Post-Hiatus reef slope shows a mostly coral rubble-dominant substrate with some periods of higher algae cover driven largely by the *A. radiata* group. This is to be expected due to the higher coverage of coral on the slope Post-Hiatus, as the reef complex

progrades outward on the slope during this period and still has accommodation space (Girard et al. 2022; Hynes et al. 2025). Both reef slopes have a more consistent substrate throughout the cores, but mostly only represent the Post-Hiatus and therefore cannot tell us what longer-term changes may have occurred.

Corals also contribute to the reef substrate through continued growth and coverage of the substrate, competition with algae, and the creation of additional rubble through breakage and erosion. The Samalona reef flat in the Pre-Hiatus is a mixture of branching, massive, and free-living growth forms (with minor foliose), and this shifts to almost dominantly branching in the Post-Hiatus. Similarly, on Kudingareng Keke the Pre-Hiatus flat is dominantly massive with some branching and minor foliose, but is almost entirely branching in the Post-Hiatus. As branching corals are more fragile and likely to break than massive ones, this shift would have also contributed to an increase in coral rubble on the reef substrate in the Post-Hiatus (Rasser and Riegl 2002). This is further evidenced by the rapid decline of coral cover on the reef flats in Spermonde in the last century (Umbgrove 1928, 1947; Haya and Fujii 2017; Razak et al. 2024), while rubble and algae do cover large parts of the reef flat in the modern. However, accretion rates have begun to increase toward the modern day, likely sustained by the rapid growth of the Acroporidae corals on the flat and slope, as well as other carbonate producers, to keep carbonate production in pace with increased erosion/breakage (Hynes et al. 2025). The single island core from Kudingareng Keke is entirely branching coral, much of which is eroded, and where many subsamples are more sand particles than large coral clasts (floatstone facies, Fig. 2B), showing that this erosion/breakage is also responsible for the continued sedimentation of the islands and the accumulation on the leeward slope.

The Late Hiatus (2000–6000 YBP) to Post-Hiatus (< 2000 YBP) periods frequently have spicules from cryptic sponge species, many of which are cryptic due to their excavating nature where they bore into coral rubble and other hard substrates. These cryptic species (specifically *C. mucronata* and *Spiroxya* sp.) seemingly are more frequently present toward modern day, though are not analyzed here with SIMPER. These specific sponges (as well as other cryptic sponges such as *Acanthotetilla celebensis)* have not been observed in previous sponge surveys of the region (de Voogd et al. 2006; van der Windt et al. 2020) and represent an expansion of their known range. As these cryptic excavating sponges have a habitat preference of coral rubble and crevices in rocks (Hooper and Van Soest 2002), this would suggest that throughout the Post-Hiatus coral rubble or hard substrates have been present in large enough amounts for these sponges to inhabit both the flat and the slope of both islands. Also, given that the relative abundance of spicules from *C. mucronata* and *Spiroxya* visually increases toward the modern day (especially *C. mucronata* subtylostyles represent upward of 11% of the relative abundance) this could be an indicator of further coral degradation and a subsequent increase in dead coral rubble assemblages in recent decades–centuries (Lukowiak et al. 2018; Pacheco et al. 2020; Diers et al. 2025), though without a more robust statistical analysis this cannot be said for certain. Further, the presence of excavating sponges would also contribute to an increase in bioerosion, which in turn would add to the creation of sand or smaller-sized carbonate sediment for continued expansion of the island and progradation/accumulation of the reef complexes margins (Lange et al. 2020; Kench et al. 2024).

Natural turbidity and tolerant corals

As many areas in SE Asia (and the Indo-Pacific as a whole) are experiencing increased natural and anthropogenic turbidity (as well as other anthropogenic stressors), coral communities are facing stressors related to this, such as sediment smothering of corals and increased eutrophication/algae outcompeting corals (Kleypas 1996; Morgan et al. 2020; Dimitrijevic et al. 2024). The Spermonde Archipelago also has had its turbidity influenced by large-scale land clearing and reclamation from the nearshore and other factors (Teichberg et al. 2018; Girard et al. 2022; Estradivari et al. 2025). Other reefs in the region are seeing shifts from competitive/generalist corals (such as *Acropora* and *Montipora*) to more stress-tolerant and weedy corals (Darling et al. 2012) such as *Euphyllia, Goniopora, Porites,* and *Turbinaria* (Johnson et al. 2017; Cybulski et al. 2020; Morgan et al. 2020). In this study, on the Samalona reef flat as well as the tops of KKF-1 and KKF-3 reef flat cores there is a shift from more stress-tolerant corals in the Pre-Hiatus to dominantly competitive *Acropora* in the Hiatus and especially the Post-Hiatus (Table 1, Supplemental Table 4). Kudingareng Keke is dominantly stress-tolerant massive corals (*Acanthastrea*, *Goniastrea,* and Merulinidae) until the Post-Hiatus. This is the inverse of what is shown in other studies (Pandolfi and Minchin 1996; Edinger et al. 2001; Cybulski et al. 2020), but interestingly matches that of a recent study from Singapore, another area though to be influenced heavily by modern anthropogenic turbidity (Chan et al. 2025).

This suggests that Spermonde has always seen some level of natural turbidity, going back to at least 7000 YBP. Other stress-tolerant genera are visually found in relatively common abundances in some subsamples (10% or more relative abundance) in the reef flat cores (Darling et al. 2012; Veron 2000; Johnson et al. 2017; Morgan et al. 2020). The Pre-Hiatus of Samalona has subsamples with high occurrences of *Palauastrea*, *Turbinaria,* Fungiidae, and Merulinidae (many genera of both groups are stress-tolerant), while the same time period on Kudingareng Keke has subsamples with occurrences of *Goniastrea*, *Pavona,* and also Merulinidae.

Interestingly, on these islands there is a persistence of stress-tolerant genera into the Hiatus (*Palauastrea* and *Heliopora* on Samalona, *Goniastrea* on Kudingareng Keke). The Samalona Post-Hiatus (when including the reef slope) has some samples with frequent appearances of *Euphyllia, Australogyra, Palauastrea,* and *Pachyseris*, while Kudingareng Keke (slope and flat) in the same period has samples containing *Palauastrea, Physogyra, Goniopora,* and *Porites*. Both islands on the reef slope also harbor some abundance of stress-tolerant Fungiidae corals. This helps to confirm that the region has also seen varying levels of natural turbidity, which likely has been exacerbated by anthropogenic turbidity in the last decades and even centuries of the Post-Hiatus period (Renema 2018; Girard et al. 2022).

Foraminiferan assemblages during the Hiatus show a high abundance of *A. lessonii* especially on Samalona, which shifts to a significant dominance of *Calcarina* by the Post-Hiatus demonstrating additional evidence that Samalona has always seen some level of turbidity (Renema and Troelstra 2001; Girard et al. 2022), even 7200 YBP. Kudingareng Keke has a high abundance of *Calcarina* and some abundance *A. lessonii* which are capable of handling turbidity, but, due to the higher presence of *Neorotalia* and Textulariida, shows that although some turbidity has persisted here, Kudingareng Keke is overall less turbid than Samalona throughout all three time periods (which holds true to this day, due to the proximity of Samalona to shore). Further evidence for this is supported by the grain size analysis previously conducted on these cores (Hynes et al. 2025). Here in all cores, there is a fining-downwards sequence, with oldest samples often containing high amounts of calcium carbonate mud and very poor sorting of grains. If the turbidity was largely driven by anthropogenic causes, then a fining-up sequence, with the Post-Hiatus especially being finer-grained, would be expected due to the increased terrestrial input over time. Further, all core samples analyzed for spicular analysis had portions of non-carbonate material left post-digestion, some of which is due to terrestrial input (as well as other biogenic silica material) present throughout this system's history.

Conclusions

This study shows that reefs in the Spermonde Archipelago were already experiencing large-scale assemblage shifts at centennial to millennial scales, predating modern anthropogenic stressors from the last few centuries. From 7200 to 6000 YBP these reefs saw more massive, foliose, and free-living corals (Fungiidae) sustaining the accretion and growth of the reef under the final stages of rapid sea-level rise that occurred in the Early to Mid-Holocene (Hynes et al. 2025). A reef growth Hiatus of low accretion occurred from 6000 to 2000 YBP during a sea-level highstand, with a shift to dominantly branching corals (especially those of the Acroporidae family on Samalona), which continues toward the present day. Large benthic foraminifera assemblages also saw shifts with changing sea levels, including substrate changes from more commonly coral rubble to more algal-dominant mixed substrates in the Post-Hiatus. Sponge communities also have seen temporal shifts; however, due to the difficulty in high-level taxonomy of individual spicules, the true assemblage shifts are not inherently clear.

However, spicules from reef core sediments are shown here as a way to find and identify the presence of cryptic species of sponges throughout a reef's history. The spicular assemblages examined here seem to demonstrate that there has been an apparent increase in cryptic sponges (especially excavating sponges) over the last few centuries, and these excavating sponges occur consistently throughout the Post-Hiatus period. This also indicates that substrates during the last 2000 YBP are more frequently coral rubble and other hard substrates. This is likely due to declining coral coverage and reef health over the last few decades and even centuries. Foraminiferan communities also show a shift toward less coral and more coral rubble and algal-dominant substrates, further highlighting the potential reef degradation occurring. The detection of cryptic species is also revealed in the coral communities with the presence of *Palauastrea ramosa* throughout all time periods. The presence of *P. ramosa* until the sub-recent, also shows that shifts occurred well before modern surveys were able to quantify these shifts, potentially due to more recent anthropogenic stressors. Finally, coral and LBF assemblages show us that the Spermonde Archipelago has always experienced some level of natural turbidity (especially on the more nearshore Samalona), and the earliest corals were often stress-tolerant and/or weedy species (Darling et al. 2012), which allowed them to keep growing in the face of added anthropogenic turbidity.

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Data availability All data supporting the findings of this study are available within the paper and its Supplementary Information.

Declarations

Conflict of interest The authors declare no competing interests.

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