Marine Environmental Research 211 (2025) 107437

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Foraminifera record historical coral-algal phase shifts on Caribbean coral reefs

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ARTICLE INFO

Keywords:
Foraminifera
Bioindicator
Caribbean
Coral reefs
Phase shifts

ABSTRACT

Healthy Caribbean reefs are coral-dominated. When disturbed, however, they can slide into a degraded state, characterized by few live corals and abundant macroalgae. Timeseries collected by SCUBA divers are valuable in tracking these coral-algal phase shifts, but their temporal scope is typically limited to decades—insufficient to capture long-term ecosystem dynamics. To address this limitation, we integrate vintage aerial photography, fieldwork, and foraminiferal counts to develop a new bioindicator capable of identifying historical coral-algal phase shifts in eight Caribbean reef provinces. Our bioindicator leverages the contrasting life habits of two foraminifera genera: *Archaias*, which thrives in coral-dominated environments, but is replaced during a phase-shift by *Quinqueloculina*, which benefits from an algal canopy. This ecological bifurcation is excellently captured by the ratio in the abundance of these two genera in the seabed foraminiferal death assemblage, which is easily sampled. We propose that our new foraminiferal bioindicator provides a valuable tool for reconstructing the historical trajectories of Caribbean reefs, even in the absence of historical monitoring data.

1. Introduction

Caribbean coral reefs are particularly vulnerable to phase shifts (Bellwood et al., 2004; Gardner et al., 2005; Eakin et al., 2010; Cramer et al., 2012; Webb et al., 2021; Bove et al., 2022; Molina-Hernández et al., 2022; Rivas et al., 2023). Once corals die, their skeletons gradually erode, leading to a loss of reef structural complexity (Johannes, 1975; Bozec et al., 2015) and a subsequent collapse in fish and invertebrate populations (Feary et al., 2007; Przeslawski et al., 2008; Graham and Nash, 2013; Webb et al., 2021; Wolfe et al., 2021; Najeeb et al., 2025). In this degraded state, the reef becomes vulnerable to macroalgal overgrowth, which inhibits the settlement of juvenile corals, further hindering recovery (Hughes, 1994; McManus and Polsenberg, 2004; Mumby and Steneck, 2008; Mumby, 2009; Clements and Hay, 2019; Smith et al., 2022; Isdianto et al., 2023). Coral-algal phase-shifted reefs therefore rarely recover to their original healthy state, though reversals have been documented (Quinn et al., 2005; Graham et al., 2013).

Evidence for phase-shifting Caribbean coral reefs is not restricted to the modern era. Fossil coral assemblages and sediment cores indicate at least two pronounced shifts over the past millennium (Jackson, 1997; Jackson et al., 2001; Cramer et al., 2017, 2020). The earliest episode, which times to approximately 1000 years ago, was likely driven by natural disturbances (Cramer et al., 2020). The second pre-modern phase shift occurred approximately 250 years ago and was driven by historical fishing pressure and land-clearing activities—disturbances from which many Caribbean reefs have yet to fully recover (Cramer et al., 2017, 2020).

In the modern era, the timing and severity of coral-algal phase shifts are primarily inferred from monitoring timeseries collected by SCUBA divers (Gardner et al., 2003; Côté et al., 2005; Palandro et al., 2008; Hughes et al., 2010; Obura et al., 2019; Nocerino et al., 2020). These data have limitations. The longest Caribbean diver timeseries only extend back three decades, and the majority of reefs in the region have only been monitored for less than half that duration (Obura et al., 2019). Longer timeseries would be exceptionally valuable to understand the cadence of phase shifts and to put the current demise of Caribbean reefs in a temporal context. To achieve that goal, we propose that benthic foraminifera can serve as bioindicators of historical macroalgal

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https://doi.org/10.1016/j.marenvres.2025.107437
Received 2 June 2025; Received in revised form 6 August 2025; Accepted 7 August 2025

dominance on Caribbean reefs.

Due to their rapid and predictable responses to changing environment, foraminifera have been widely used as bioindicators to assess reef health. These tiny protists provide historical insight into key environmental parameters, including nutrient levels, light availability, pH, temperature, salinity, turbidity, and heavy metal pollution (Hallock et al., 2003; Schueth and Frank, 2008; Uthicke et al., 2012; Humphreys et al., 2018; Prazeres et al., 2020). One such bioindicator is the FoRAM Index (FI), developed by Hallock et al. (2003), which is widely used to assess water quality and reef health based on the abundance of symbiont-bearing, opportunistic, and stress-tolerant foraminifera picked from seabed sediment samples (e.g., Oliver et al., 2014; Prazeres et al., 2020; Rosa Marín et al., 2024; Chadda-Harmer et al., 2025). What has not yet been tested, however, is whether a foraminiferal bioindicator can be developed to track historical coral-algal phase shifts – the motivation for this study.

Large Benthic Foraminifera (LBF) are particularly abundant on reefs (Martin, 1986; Dawson et al., 2014; Mateu-Vicens et al., 2014). Like corals, some LBF genera host photosynthetic endosymbionts and are thus favored in oligotrophic, high-clarity waters that support photosynthesis (Doo et al., 2014). In contrast, turbid and shaded environments tend to support genera which lack endosymbionts, which are not disadvantaged by light attenuation and can persist where photosymbiotic taxa would be excluded (Nash et al., 2010; Narayan and Pandolfi, 2010; Wilson et al., 2010; Mendes et al., 2012; Kelmo and Hallock, 2013). We hypothesize that reefs which have undergone a coral-algal phase shift will exhibit a time-averaged assemblage of LBFs distinct from that hosted by reefs unaffected by algal overgrowth.

To test this hypothesis, we quantified foraminiferal assemblages in 161 surficial sediment samples which we collected at eight Caribbean study areas between 2010 and 2023 (Fig. 1). We reconstructed the history of macroalgal overgrowth on those reefs by analyzing vintage aerial photographs, modern satellite imagery, and historical diver surveys spanning 1936 to 2025 and linked them with time-averaged foraminiferal abundances. Conveniently, reefs darken in color when colonized by algae, allowing algal phase shifts to be remotely sensed.

2. Methods

2.1. Collection of surficial seabed sediments

Under the auspices of the Living Oceans Foundation Global Reef Expedition (Purkis et al., 2019), we collected 161 surficial sediment samples across eight Caribbean reef provinces (Fig. 1). Between 2010 and 2012, we worked in the Bahamas, sampling Andros Island and the Berry Islands on Great Bahama Bank (samples collected (*N*) = 16), Cay

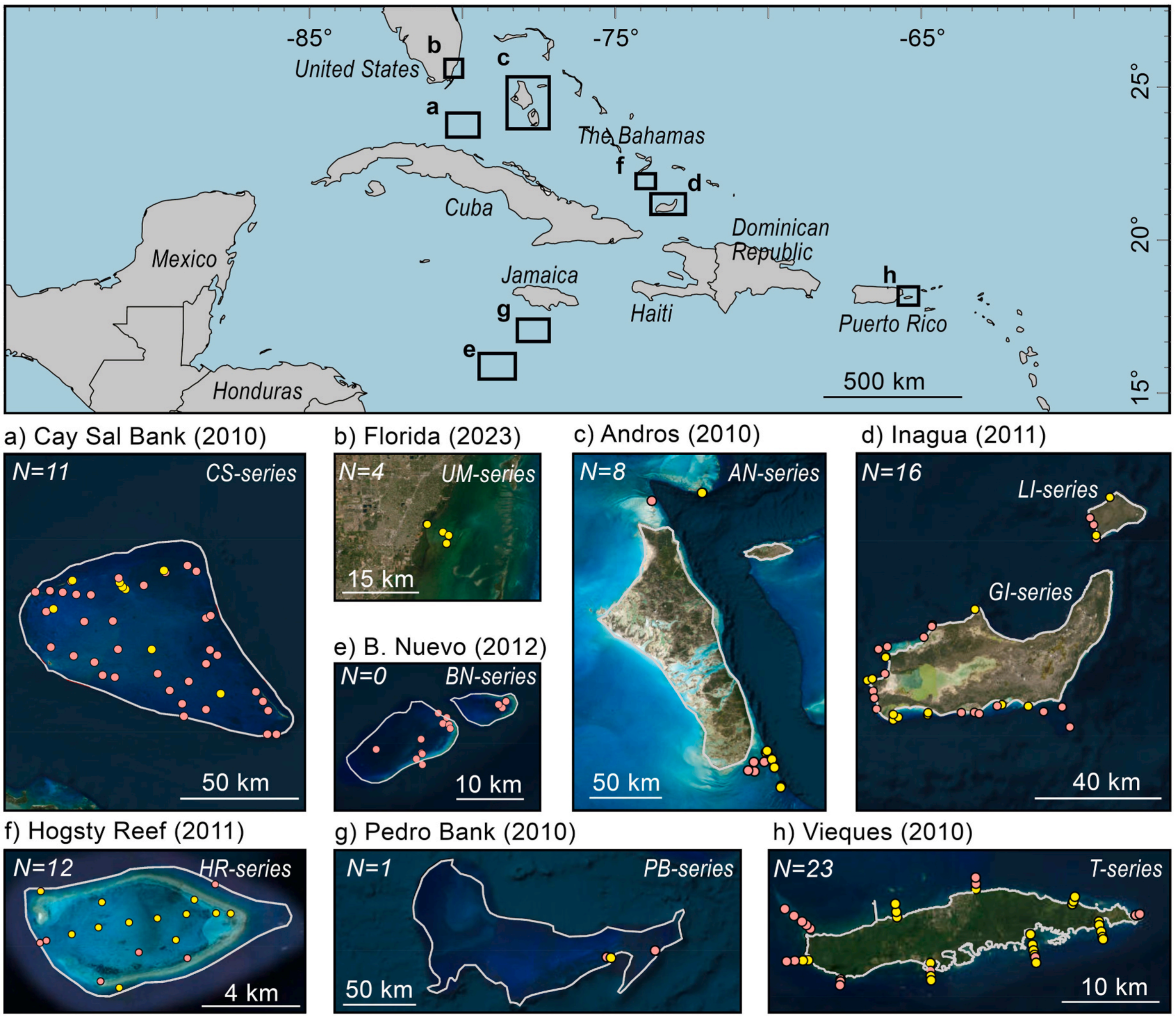


Fig. 1. Locations of 161 reef sediment samples collected across the Caribbean as part of the Living Oceans Foundation Global Reef Expedition. Foraminiferal assemblages were initially quantified from all samples. However, 86 samples (*red dots*) were excluded from further analysis because they were collected outside the accepted 3–15 m depth range, in high-energy settings prone to transport of tests, or from sites lacking historical remote sensing coverage. The remaining 75 samples (*yellow dots*), which met all criteria, were retained for analysis. North up in all maps.

Sal Bank (*N*=*38*), Hogsty Reef (*N* = 18), Great Inagua (*N* = 28) and Little Inagua (*N* = 5). In the same timeframe, we also sampled Vieques, Puerto Rico (*N* = 53), and Bajo Nuevo (*N* = 14), a carbonate platform offshore Colombia, and the Pedro Banks (*N* = 3), offshore Jamaica. Our final set of four samples were collected in 2023 from Biscayne Bay, Florida (U.S. A).

Although staining with a protein-binding dye such as Rose Bengal is routinely used in paleoecological studies to distinguish live from dead foraminifera at the time of collection, we did not apply this method. Our samples were part of a broader project focused on bulk-sample geochemistry (Oehlert et al., 2023; Purkis et al., 2023; Lopez-Gamundi et al., 2025), which precluded staining. As a result, we could not differentiate living foraminifera from fossil or subfossil specimens. However, this limitation does not undermine our primary goal of detecting historical coral–algal phase shifts, as we did not aim to resolve the precise timing of macroalgal overgrowth events.

Samples were collected by divers at sites representing a range of exposure regimes (backreefs, forereefs, etc.). Following the sampling protocol of Purkis et al. (2015) and Kalman et al. (2025), each sediment sample was collected by penetrating vertically from the sediment–water interface to a depth of 5 cm below the seafloor. Sampling continued laterally until approximately 500 ml of material was obtained. The sediment was transferred into Nalgene bottles, which were sealed underwater at the seafloor to prevent the loss of fine-grained particles. The benthic character at the location of each sample was recorded by digital underwater photographs.

2.2. Foraminiferal counts

Following (Prazeres et al., 2020), each of the sediment samples was wet-sieved using a 125-μm mesh to remove small, broken, and juvenile foraminifera. The sieved samples were dried at 60 °C in preparation for foraminifera collection. Once dried, the samples were split into 3-g subsamples using a sediment micro-splitter. Under stereomicroscopy, 200 foraminifera-per-subsample were picked using fine-tipped brushes and glued to micropaleontological slides using an organic glue comprising gum tragacanth with a drop of clove oil as an antifungal. In samples with fewer than 200 foraminifera-per-subsample, all specimens were picked. Because foraminiferal abundances were variable among our samples, a minimum of 100 specimens-per-subsample was accepted for further analysis.

To align our sampling with the well-documented FoRAM Index (Hallock et al., 2003) and the recommendation of Prazeres et al. (2020), only samples collected between 3 and 15 m water depth were carried forward for analysis. Next, we also removed samples from our dataset which satisfied the requirement for water depth, but had been collected in high-energy settings, such as reef passes and shoals, where there was an obvious risk that foraminiferal tests originating from far away could be brought into a location by currents. Finally, we excluded samples from sites lacking historical remote sensing and literature observations, as the absence of these records precluded reconstruction of past algal dynamics.

These exclusions delivered a curated set of 40 reef samples and 35 off-reef soft-sediment samples for statistical analysis (Table S1). We consider the foraminifera picked from our seabed samples to comprise the so-called sedimentary “death assemblage”. That is, this assemblage is the product of the time-averaged cumulative input of successive foraminiferal generations through time.

2.3. Separating samples collected on stable versus phase-shifted reefs

Key to the methods of our study is to distinguish sediment samples

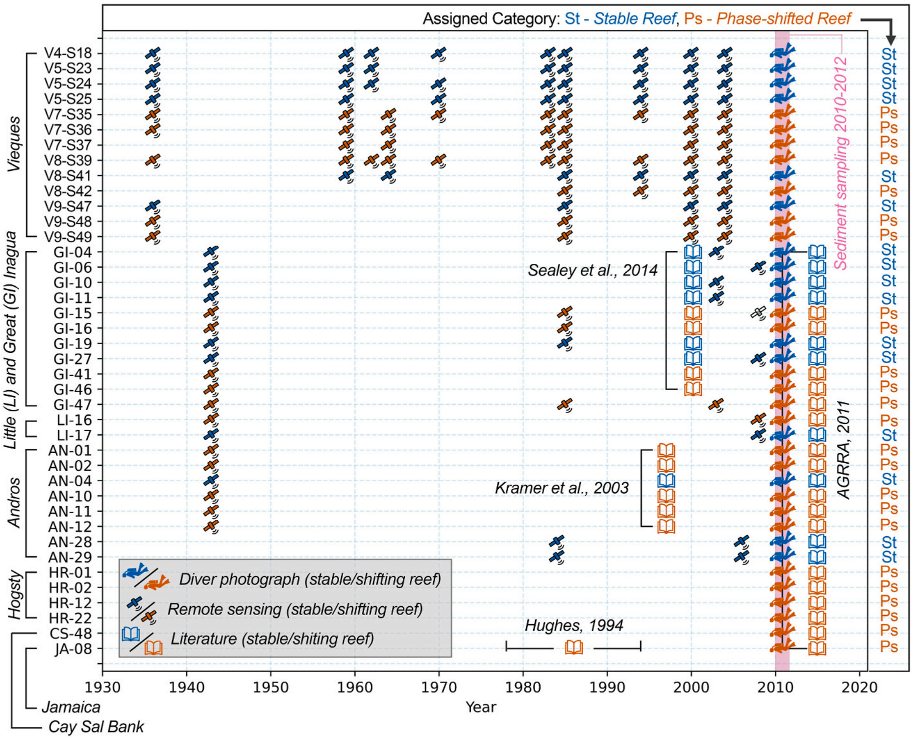


Fig. 2. Application of the three data sources used to classify each sediment sample as originating from a “stable” (St) or “phase-shifted” (Ps) reef. Diver photographs taken during sample collection were the first diagnostic tool: Samples from reefs with abundant algal overgrowth (*orange diver symbols*) were assigned to the phase-shifted class. Samples from reefs lacking visible algae (*blue divers*) required further diagnosis, as absence of algae at the time of sampling does not preclude a prior phase shift followed by recovery. To reconstruct reef history, we conducted a literature analysis, which documented past algal dominance at Great Inagua, southern Andros Island and offshore Jamaica, leading to their classification as “phase-shifted”. Finally, time-separated remote sensing was used to detect persistent algal cover; sites exhibiting the spectral signature of macroalgae at any point (*orange satellite symbols*) were classified as “phase-shifted”. Only those with no evidence of overgrowth across the entire timeseries (*blue satellites*) were classified as “stable reefs”.

collected from reefs that have experienced pronounced algal overgrowth within the past half century from those collected on reefs that have remained stable—i.e., not having undergone an ecological phase shift. As developed in Fig. 2, we drew from three complementary data sources to achieve this classification.

First, we examined our own diver photographs taken contemporaneously with sediment sampling. Following criteria established by Hughes (1994) and Mumby et al. (2007), reefs were classified as phase-shifted if macroalgae occupied more than 50 % of the benthic surface in these images. Second, we conducted a meta-analysis of published literature pertaining to our Caribbean study sites to reconstruct temporal trajectories in macroalgal cover. Several key studies informed this synthesis, each providing insights into the benthic state of specific reefs. Long-term changes in benthic community composition, especially the relative cover of live coral versus macroalgae, have been used to differentiate stable from phase-shifted reefs (Hughes, 1994). In this framework, reefs that maintain high coral cover and resist or recover from disturbances are considered stable, while those that transition to persistent macroalgal dominance following perturbations are regarded as coral-algal phase-shifted. Complementing this ecological perspective, Kramer et al. (2003) categorized reef condition across the wider Caribbean using standardized AGRRA (Atlantic and Gulf Rapid Reef Assessment) survey data, incorporating indicators such as coral and algal cover, coral recruitment, fish biomass, and *Diadema antillarum* densities (a keystone herbivorous sea urchin). Their classification scheme highlighted gradients of reef degradation, with many Jamaican sites identified as severely impacted due to low coral cover and herbivore abundance. Building on the understanding of reef condition, Sealey et al. (2014) demonstrated how terrestrial alterations can exacerbate reef degradation. In the western portion of Great Inagua (which we sampled), for instance, they identified the area as "severely altered" due to historical coastal modifications that disrupted natural hydrology, increased turbidity and sedimentation, and ultimately impacted coral recruitment and benthic community structure. Finally, the third data source used to classify reef state involved time-separated remote sensing, as described in the following section.

2.4. Time-separated remote sensing

To test our hypothesis that LBF assemblages developed under algal canopies differ from those developed in the absence of algae, we pursued two strategies to assemble time-separated remote sensing datasets capable of documenting historical coral-algal phase shifts. For Vieques (Puerto Rico), the archive is particularly rich. For that island, we downloaded aerial photographs from the archive curated by the US Fish and Wildlife Service (https://costavispr.org/; accessed June 2024). This

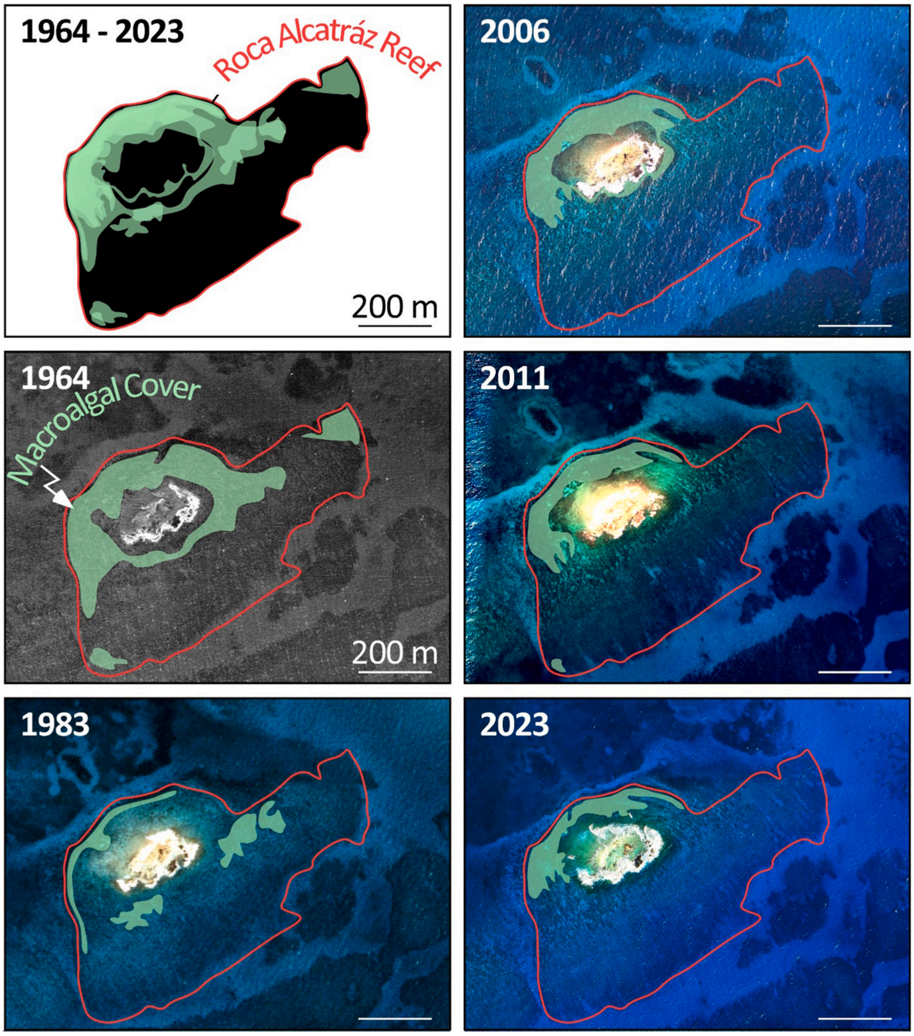


Fig. 3. Time-separated remote sensing imagery showing the dynamics of algal overgrowth at Roca Alcatráz Reef, south of Vieques, for 1964, 1983, 2006, 2011, and 2023. A continuous halo of macroalgae in 1964 becomes fragmented by 1983, reestablishes north of the reef by 2006, persists through 2011, and retreats by 2023. Based on our criteria, Roca Alcatráz is classified as a phase-shifted reef. Additional case studies are shown in Supplementary Fig. S1 (Bahia Yoye and Jalova, Vieques) and Fig. S2 (southern Great Inagua).

remote sensing time series spans from 1936 to 2000, allowing nearly 75 years of benthic change to be tracked (Hernández-Cruz et al., 2006). The spatial resolution of these aerials was exceptionally high—finer than 50 × 50 cm. Unlike modern digital imagery, the spatial fidelity of these vintage analog aerial photography is determined by the silver-halide bonds in the original photographic negatives. Similar aerial photographs dating to 1943 also exist for our Bahamian sites, Great and Little Inagua, and also Andros Island, as utilized by Wu et al. (2021). For all other sites, aerial photographs from 1984 and later were obtained from the USGS EarthExplorer platform (https://earthexplorer.usgs.gov/; accessed June 2024).

To demonstrate how remote sensing can be used to track macroalgae dynamics in the Caribbean, we assemble a timeseries for Roca Alcatráz Reef, located off the south coast of Vieques, spanning the years 1964, 1983, 2006, 2011, and 2023 (Fig. 3). In the earliest image from 1964, a continuous halo of macroalgae surrounds Roca Alcatráz, which becomes fragmented by 1983. Algae reestablish north of the reef by 2006, a pattern that persists through 2011, before retreating in the most recent scene from 2023. Based on our classification criteria, Roca Alcatráz qualifies as a phase-shifted reef. Two additional case studies are developed in our Supplemental Figures: S1 presents changes in two bays (Bahia Yoye and Jalova) along Vieques' southeast coast; S2 examines the southwestern tip of Great Inagua.

Lacking such a rich archive as offered by Vieques, Great and Little Inagua, and Andros for the remaining five Caribbean study areas, we used the imagery assembled in Google Earth Timelapse. This online database provides a record dating back to 1984, primarily based on imagery from the Landsat Program, a mission boasting a long pedigree in reef remote sensing (Andréfouët et al., 2001; Purkis et al., 2002; Palandro et al., 2003; Purkis and Pasterkamp, 2004), and still used to this day (Wei et al., 2018; Andréfouët and Paul, 2023). Despite the differences in spectral and spatial resolution between the analog photographs assembled for Vieques and the Google Earth Timelapse images for our other sites, standard criteria could be established to track the state of the seabed through time. Note, because our study focuses on detecting historical coral-algal phase-shifts, it was not necessary to map the benthos into a large number of habitat classes, as done, for instance, by the Living Oceans Foundation Global Reef Expedition (Purkis et al., 2019) and the Allen Coral Atlas (Lyons et al., 2020). To meet our objectives, we instead required only two “ecological states” to describe changes in benthic condition through time – “stable reef”, and “phase-shifted reef”.

In the remote sensing data, coral reefs densely overgrown by macroalgae appear dark in color and homogeneous in texture. Reefs unincumbered by macroalgae, by contrast, are bright in color and texturally heterogeneous. Accordingly, “stable reefs”—those which have not phase-shifted during the period of observation—showed no change, or darkening in color or in texture, through successive entries in the remote sensing timeseries. Following Violette et al. (2024), “phase-shifted reefs”, by contrast, were identified by systematic changes in color and texture through time. Fig. 2 captures the three sources of information (benthic photographs, literature, and remote sensing) used to separate our seabed samples into stable versus phase-shifted reefs. These data advocate that we sampled 16 stable reef sites and 24 reef sites which had undergone a phase shift within the last 75 years.

The remaining 35 samples in our dataset were not collected on coral reefs but rather from unconsolidated off-reef sandy areas that are episodically occupied by dense meadows of seagrass and/or macroalgae. These sites were classified as a third category, which we refer to as “dynamic SAV” (Submerged Aquatic Vegetation; Table S1). Following Hernández-Cruz et al. (2006), SAV presence was readily identified in our remote sensing timeseries, where these habitats appear as uniformly dark patches, in stark contrast to the high reflectivity of unvegetated sand. We propose that the sediment samples collected from these “dynamic SAV” environments are ecologically informative for the purpose of this study, as they likely contain endmember LBF accumulations shaped by persistent canopy cover and associated light-limited conditions.

2.5. *Clustering of foraminiferal counts*

Following Rey et al. (1994) and Parker and Arnold (2003), we applied Linear Discriminant Analysis (LDA) to identify the linear combinations of foraminiferal genera that most effectively discriminate among our three predefined ecological states: Stable reefs, phase-shifted reefs, and dynamic SAV (Fig. 5A). LDA is a supervised ordination technique that reduces dimensionality while retaining the features that best separate groups. It does so by maximizing the variance between classes relative to the variance within classes, thereby enhancing class separability in a reduced number of axes. We assessed classification performance using a confusion matrix (Fig. 5B), which summarizes how well samples are assigned to their true groups based on the LDA model. All analyses were performed in PAST (v.4.06; Hammer et al., 2001).

3. Results

3.1. *Diversity of foraminifera genera across the Caribbean*

We identified a total of 43 foraminiferal genera in our 161 samples collected across the Caribbean (Fig. 1). The relative abundances of the 13 genera which exceeded 1 % of the total foraminiferal assemblage are graphed in Fig. 4. Then, Table S2 captures the abundances of all 43 genera identified in our study and our full global foraminiferal dataset is made available in Kalman et al. (2025). Of the 13 genera exceeding 1 % of the total assemblage, 24 % of all counted foraminifera belong to the genus *Archaias* and 22 % to the genus *Quinqueloculina*. Two

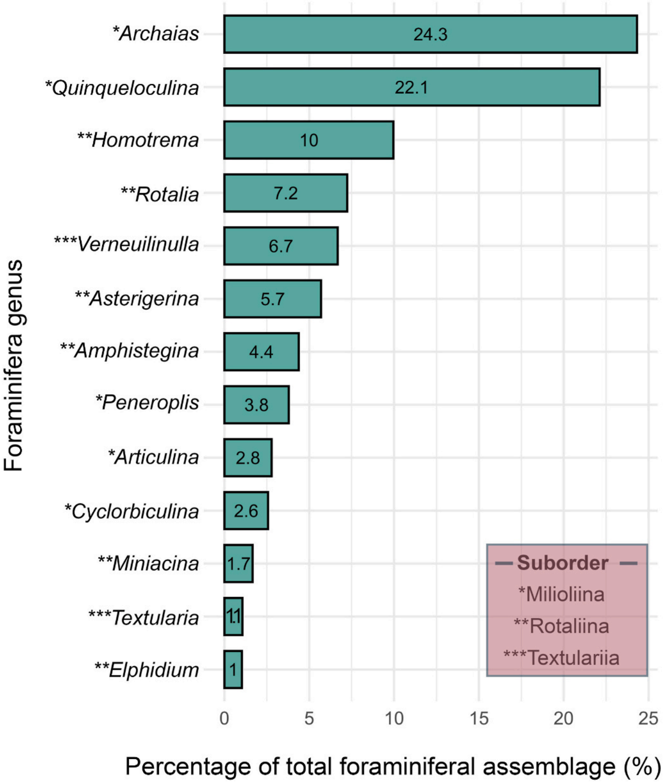
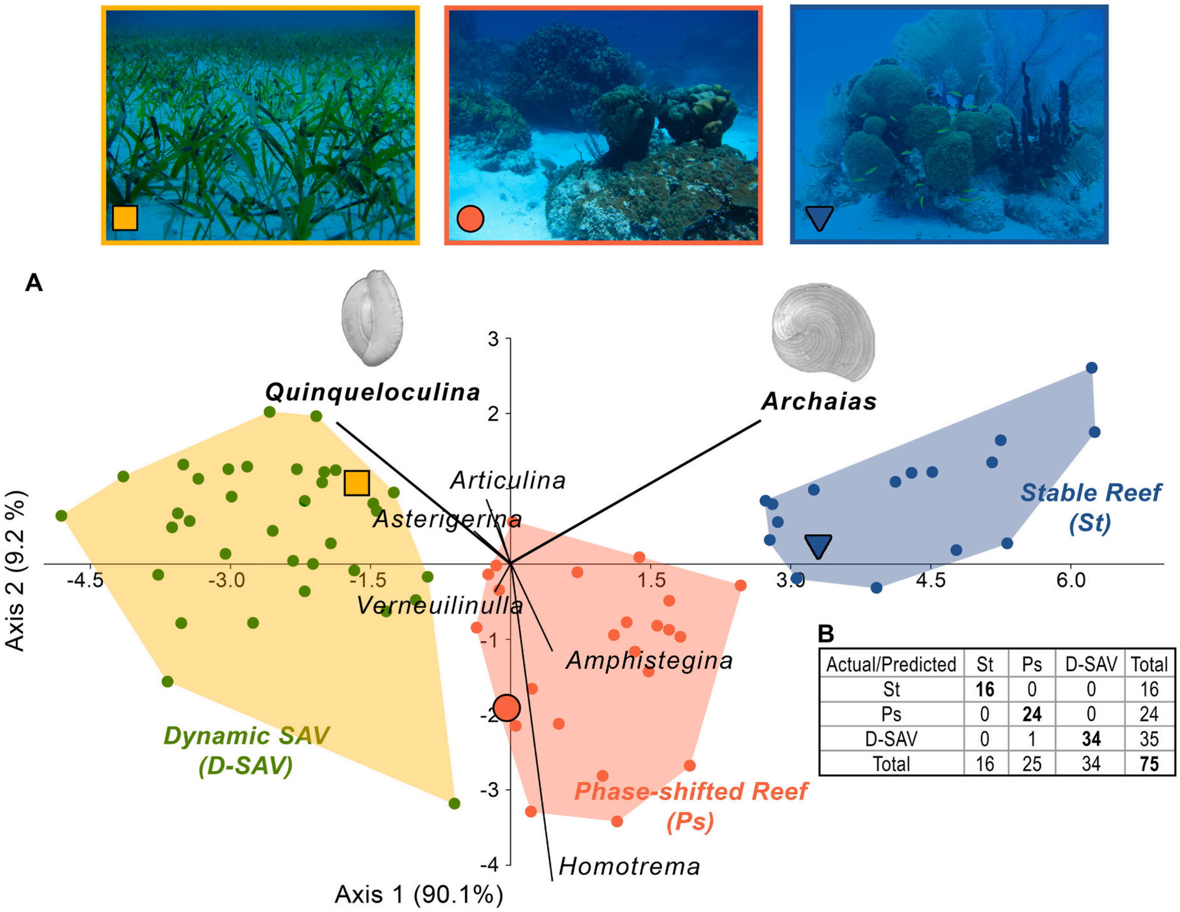


Fig. 4. Relative abundance of the 13 genera which account for >1 % of the foraminifera identified in our Caribbean samples. Note the dominance of two genera; *Archaias* (24 %) and *Quinqueloculina* (22 %), which together account for nearly half (46 %) of all foraminifera. These 13 genera aggregate under three suborders: Milioliina, Rotaliina, and Textulariina (denoted by asterisks).



Actual/Predicted	St	Ps	D-SAV	Total
St	**16**	0	0	16
Ps	0	**24**	0	24
D-SAV	0	1	**34**	35
Total	16	25	34	**75**

Fig. 5. Linear Discriminant Analysis (LDA) of the 13 most common genera of foraminfera identified in our samples. (A) LDA biplot of foraminiferal assemblages separates samples into three distinct ecological groups: Phase-shifted reef, stable reef, and dynamic SAV. The primary axis, explaining 90.1 % of the variance, reflects a gradient from high *Archaias* (stable reefs) to high *Quinqueloculina* (dynamic SAV). The secondary axis (9.2 % of variance), driven by *Homotrema* abundance, further distinguishes phase-shifted reefs, which are often associated with reef rubble. The LDA confusion matrix **(B)** quantifies classification performance. All stable and phase-shifted reef samples were correctly identified by the LDA. One misclassification occurred in the dynamic SAV group, yielding an overall classification accuracy of 98.7 % across the three ecological states.

foraminiferal suborders dominated our samples: Milioliina, (56 % of all counted foraminifera) and Rotaliina (37 %). The suborder Textulariina was less common, comprising ~8 % of all foraminifera, with only a single individual from the planktonic suborder Globigeriina observed.

3.2. Remotely–sensed benthic habitat dynamics

Time-separated remote sensing reveals changes in algal cover across our sample sites throughout the study period. To illustrate these dynamics, we present three case studies of phase-shifting reefs (Fig. 3, S1, and S2), demonstrating how vintage aerial photographs and Google Timelapse imagery can be combined into timeseries to track the expansion and retreat of macroalgal canopies at sites off Vieques (Puerto Rico) and Great Inagua (Bahamas).

Of the 40 samples collected atop reefs, 24 were from sites exhibiting episodic spectral darkening in remote sensing imagery—indicative of macroalgal overgrowth. These same sites also hosted abundant macroalgae at the time of sampling (Fig. 2), supporting their classification as “phase-shifted reefs.” In contrast, the remaining 16 reef sites remained spectrally bright throughout the remote sensing timeseries and were free of macroalgae during field visits, and were therefore classified as “stable reefs.” Additionally, following the classification protocol of Hernández-Cruz et al. (2006), the 35 samples collected from soft-sediment habitats away from reefs were categorized as “dynamic SAV,” reflecting their episodic occupation by seagrass and/or macroalgal meadows as resolved in the remote sensing data.

3.3. A foraminifera bioindicator for historical coral–algal phase-shifts on Caribbean reefs

Linear Discriminant Analysis (LDA) was applied to the relative abundances of foraminiferal genera to distinguish among the three predefined ecological states: “Phase-shifted reefs”, “stable reefs”, and “dynamic SAV”. When projected into the resulting discriminant space, the samples form three distinct clusters corresponding to their ecological classifications (Fig. 5A).

The primary axis of separation which accounts for 90 % of the variance in the dataset is driven by the relative abundance of foraminifera in the photosymbiont-bearing *Archaias* genus – dominant on stable, coral-dominated reefs – and the *Quinqueloculina* genus of heterotrophs, which thrive under macroalgal canopies. A secondary axis of separation accounts for only 9 % of the variance and is driven by the relative abundance of encrusting foraminifera belonging to the genus *Homotrema*. As foraminifera in this genus are often associated with reef rubble, samples from phase-shifted reefs trend along this second axis of separation. Samples from dynamic SAV habitats cluster farthest from those collected on stable reefs in the ordination, reflecting their increasing abundance of *Quinqueloculina,* decreasing *Archaias,* and low *Homotrema* abundance.

Classification performance of the LDA was assessed using a confusion matrix (Fig. 5B). All 16 samples determined to have been collected on stable reefs were correctly identified in the ordination, as were the 24 samples collected on phase-shifted reefs. In just one case, the LDA assigned a sample collected in an off-reef dynamic SAV environment to the phase-shifted reef class. The remaining 34 dynamic SAV samples were correctly classified. Overall, the LDA achieved a classification accuracy of 98.7 % across the three predefined ecological states.

These patterns confirm that foraminferal assemblages capture the ecological history of our sampled sites and support their use as bioindicators of reef condition. Given that 90 % of the separation among the three ecological states is explained by the relative abundances of *Archaias* and *Quinqueloculina*, we propose that these two genera alone can serve as a robust bioindicator for distinguishing between phase-shifted and stable reef histories. Fig. 6A shows how the relative abundances of *Archaias* [A] versus *Quinqueloculina* [Q] are adequate to delineate the three ecological states, confirming that it is unnecessary to audit the abundance of *Homotrema*.

Table 1 presents the mean, minimum, and maximum values of *Archaias* and *Quinqueloculina* abundances corresponding to our samples collected in “phase-shifted reefs”, “stable reefs”, and “dynamic SAV” environments. Over 35 % of the foraminifera accumulating under stable coral reef conditions belong to the genus *Archaias*, with local abundances reaching up to 80 %. In contrast, *Quinqueloculina* is consistently rare on stable reefs—accounting for less than 20 % of the death assemblage even at its peak and dropping as low as 1 %. On average, *Archaias* comprises 49 % of the assemblage on stable reefs, whereas *Quinqueloculina* averages just 9 %.

This pattern reverses in samples from reefs classified as phase-shifted. *Archaias* becomes subordinate, with abundances ranging from 6.3 % to 36.5 % (mean = 20.5 %), while *Quinqueloculina* is marginally more abundant, ranging from 1 % to 27.1 % (mean = 12.9 %). *Quinqueloculina* is even more dominant in the “Dynamic SAV” samples—soft sediments accumulating beneath seagrass and macroalgae meadows—where its abundance ranges from 8.5 % to 70.3 % (mean = 33.0 %). In contrast, *Archaias* is often absent from these samples, with several zero counts, a mean of just 8.9 %, and a maximum of 22.5 %.

Clearly, the contrasting ecological preferences of *Archaias* and *Quinqueloculina* result in divergent death assemblages over time, depending on how long a reef remains under an algal canopy. This divergence is well illustrated by the ratio of their mean abundances across our three substrate scenarios (the A:Q ratio, Fig. 6B). On stable reefs, the *Archaias*:*Quinqueloculina* ratio is 5.7:1. In phase-shifted reefs, the ratio drops to 1.58:1, and declines further to just 0.23:1 in dynamic SAV environments, where *Quinqueloculina* greatly outnumbers *Archaias*.

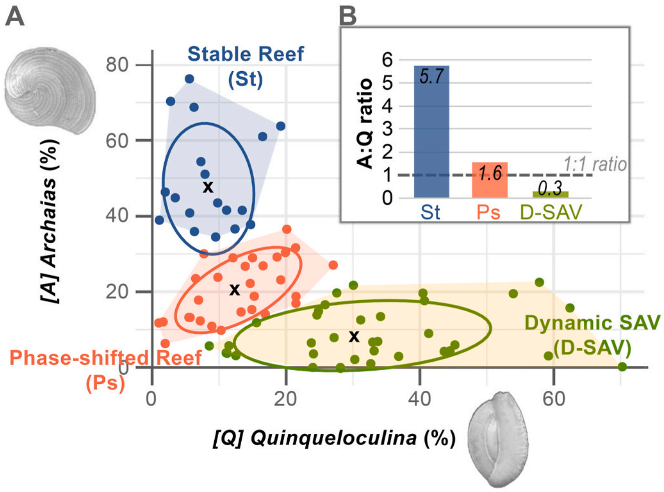


Fig. 6. The relative abundance of foraminifera in the genus *Archaias* and *Quinqueloculina* separate phase-shifted reefs from stable reefs, and soft-sediment off-reef areas occupied by dynamic submerged aquatic vegetation (SAV). (A) Scatter plot of the relative abundances of *Archaias* and *Quinqueloculina*, the two dominant genera in our Caribbean sample set. *Black crosses* denote mean abundances for each of the three ecological states and *colored ellipses* define one standard deviation around the means. **(B)** Presents the ratio of abundances of *Archaias*:*Quinqueloculina* (the A:Q ratio) in the three ecological states. A:Q declines across reef states, from 5.7:1 on stable reefs to 1.6:1 on phase-shifted reefs, and 0.2:1 in dynamic SAV habitats.

Table 1

Mean, minimum, and maximum abundances of *Archaias* (A) and *Quinqueloculina* (Q) across phase-shifted reefs, stable reefs, and dynamic SAV environments.

Temporal Class	A_{mean}	A_{min}	A_{max}	Q_{mean}	Q_{min}	Q_{max}
Stable Reef	49.3 %	34.5 %	76.3 %	8.6 %	1.1 %	19.2 %
Phase-shifted Reef	20.5 %	6.3 %	36.5 %	12.9 %	1.0 %	27.1 %
Dynamic SAV	8.9 %	0.0 %	22.5 %	33.0 %	8.5 %	70.3 %

4. Discussion

4.1. Limitations to remote sensing historical coral-algal phase shifts

We acknowledge several caveats in our classification of reefs as “stable” or “phase-shifted” (Fig. 2). First, the temporal depth of available remote sensing imagery is limited. Even the earliest aerial photographs allow us to examine sites in Vieques, Great and Little Inagua, and Andros Island only as far back as the 1940s. As emphasized by Cramer et al. (2020), coral–algal phase shifts may have occurred on these reefs centuries, even millennia, before our observations, imparting canopy-associated foraminifera into the sediment.

As we cannot control for such historical events, it is possible that some reefs we classified as “stable” had in fact undergone earlier shifts. Nevertheless, large-scale Caribbean coral–algal phase shifts were likely rare prior to the major decline in herbivory that began in the 1970s, which reached a crescendo in the 1980s (Lessios et al., 1984; Bellwood et al., 2004; Gardner et al., 2005; Eakin et al., 2010; Cramer et al., 2012; Webb et al., 2021; Bove et al., 2022; Molina-Hernández et al., 2022; Rivas et al., 2023). At several of our sites—Hogsty Reef, Cay Sal Bank, and Jamaica—remote sensing data are unavailable. However, this did not impede classification, as all samples from these locations were collected from reefs with conspicuously high macroalgal cover at the time of fieldwork, justifying their assignment as “phase-shifted.”

A second caveat concerns the lack of historical *in situ* ground-truth data to validate our remote sensing interpretations of algal overgrowth. Despite this, we argue that substantial macroalgal dominance alters the spectral and textural signatures of reefs—changes that are detectable even in vintage aerial photographs (Hernández-Cruz et al., 2006; Violette et al., 2024). This permits phase-shift dynamics to be reliably tracked across the remote sensing timeseries, as illustrated in Fig. 2, and Supplemental Figs. S1 and S2.

The fact that ordination of foraminifera; abundances by genus separates our “stable” and “phase-shifted” reef samples into distinct groups (Fig. 5) suggests that our combined approach—integrating time-series remote sensing, field observations, and literature review—was effective in distinguishing between these reef states.

4.2. Limitations of the foraminiferal death assemblages

Another caveat of our study is the lack of direct temporal constraint on the foraminiferal death assemblages. In principle, the timespan of these assemblages could be constrained using radiocarbon or uranium-series dating; however, both methods lack precision for material younger than a few centuries. Furthermore, dating the large number of individual foraminifera required would be prohibitively expensive and logistically impractical.

Given these limitations, the age span of the death assemblages is better constrained indirectly. Each 500 ml sample penetrated from the sediment–water interface to 5 cm below the seafloor. Sedimentation rates in coral reef sand pockets are generally low, typically ranging from 0.5 to 1 mm/yr depending on local conditions such as wave energy, bioturbation, and carbonate production. Relevant to our study, Gischler and Hudson (2019) estimated average lagoonal sedimentation rates of 0.89 mm/yr from cores in Belize, the Maldives, and French Polynesia—broadly consistent with the ~1 mm/yr reported by Hubbard (1986) from St. Croix. Applying a conservative rate of 1 mm/yr, the 5 cm sampled likely represents several decades of accumulation.

This timespan aligns with taphonomic studies showing that porcelaneous taxa such as *Archaias* and *Quinqueloculina* preserve intact and remain recognizable within reef sediment over decadal to low centennial timescales (Martin et al., 1996; Belanger, 2011). We therefore assume that the death assemblages curated for this study span a similar timeframe – broadly comparable to the multidecadal remote sensing and literature records of historical phase shifts used in our calibration.

4.3. Large Benthic Foraminifera as bioindicators for phase-shifted reefs

Of the 38 genera identified in our sample set, the abundance ratio of just two—*Quinqueloculina* and *Archaias*—was sufficient to distinguish between samples from stable and phase-shifted reefs (Fig. 6A). This pairing is especially convenient – together, they represent nearly 50 % of all foraminifera identified in our sample set, and their test morphologies are conspicuously different. *Quinqueloculina* possesses an elongate, porcelaneous test with distinct chambers arranged in a triserial to quinqueloculine (five-chambered) pattern, whereas *Archaias* lacks this structure and instead presents a large, flattened, discoidal test with a complex architecture. As such, the two can be reliably separated using basic stereomicroscopy. Our results suggest that a robust bioindicator can be developed using only this genus pair (Fig. 6B), offering a streamlined alternative to more complex indices, such as that proposed by Hallock et al. (2003) for evaluating water quality and overall reef ecosystem health, which requires identification of numerous genera, including symbiont bearing, opportunistic, and other smaller taxa.

We contend that the contrasting abundances of *Archaias* and *Quinqueloculina* reflect their differing ecological preferences. *Archaias* hosts photosynthetic endosymbionts (Mateu-Vicens et al., 2014) and thrives under the high-light conditions typical of healthy coral reefs (Waters and Hallock, 2017), where it often dominates the foram assemblage. A shift from coral to macroalgae dominance triggers ecological succession within the LBF community. This transition is unlikely to be driven solely by substrate type—*Archaias* is cosmopolitan in this regard, capable of colonizing both hard substrates and algal fronds. Rather, we propose that reduced light availability beneath the algal canopy is the primary driver. As a symbiont-bearing genus, *Archaias* is disadvantaged when photosynthetically active radiation is limited. In contrast, *Quinqueloculina* lacks symbionts and is therefore less sensitive to light attenuation. Moreover, many species within *Quinqueloculina* are motile epiphytes (Mateu-Vicens et al., 2014), well adapted to colonizing macroalgae canopies (Hallock, 2012; Weinmann and Goldstein, 2016).

While our data cannot directly confirm it, we infer that the proliferation of *Quinqueloculina* closely tracks the onset of macroalgal dominance, aided by its short lifespan of only a few months (Hallock et al., 2003). By contrast, with a lifespan of 1–2 years (Martin, 1986; Mateu-Vicens et al., 2014), *Archaias* likely recovers more slowly in the rare case that a reef shifts back toward coral dominance.

4.4. Utility of the Archaias:Quinqueloculina bioindicator on Caribbean Reefs and beyond

Given that *Archaias* and *Quinqueloculina* are widely reported across the Caribbean (Culver and Buzas, 1982; Cottey and Hallock, 1988; Hallock et al., 2003; Rosa Marín et al., 2024), we see no barrier to broader application of their abundance ratio as a bioindicator of coral–algal phase shifts in this region. Indeed, the *Archaias*:*Quinqueloculina* ratio (Fig. 6B) could potentially be refined to the point where *Quinqueloculina* functions as a temporal proxy. Two promising avenues emerge. First, the abundance of *Quinqueloculina*—the genus associated with macroalgal canopies—may correlate with the duration of algal dominance on the reef. Second, the preservation state of its tests, their so-called "taphonomic grade" (Berkeley et al., 2009), could indicate the time elapsed since algal retreat; a higher proportion of pristine tests might imply more recent overgrowth. Trialing these refinements would require more precise constraints on the timing of algal episodes than were available at our study sites. Nonetheless, this concept opens exciting prospects for developing the foraminifera bioindicator to not only detect historical phase shifts, but also constrain their timing.

Another compelling question also presents itself. Could our approach be extended beyond the Caribbean? While *Quinqueloculina* is globally distributed, *Archaias* is regionally restricted to the Caribbean, posing a challenge for direct application elsewhere. The key to adapting the indicator lies in identifying substitute genera that, like *Archaias*, are symbiont-bearing and thus similarly disadvantaged under algal canopy. Several candidate taxa exist among other symbiont-bearing LBFs, including members of the Calcarinidae (*Calcarina*, *Baculogypsina*), Amphisteginidae (*Amphistegina*), and Nummulitidae (*Heterostegina*, *Operculina*), all of which occur on Indo-Pacific reefs (Lobegeier, 2002; Uthicke and Nobes, 2008; Fajemila et al., 2015; Pam and Mohan, 2022; Makled et al., 2024). These genera may serve as suitable substitutes for *Archaias* in extending the bioindicator to other reef provinces.

It is important to note that Indo-Pacific and Caribbean coral reefs differ markedly in how they undergo and respond to coral–algal phase shifts, largely due to contrasts in biodiversity, herbivory, and disturbance regimes. Indo-Pacific reefs generally support higher coral and herbivore diversity, providing greater functional redundancy and conferring resilience to phase shifts and enhanced capacity for recovery following disturbance (Bellwood et al., 2004; Hughes et al., 2005; Roff and Mumby, 2012). In contrast, Caribbean reefs are comparatively species-poor—especially in herbivorous taxa and key reef-building corals—making them more vulnerable to ecological shocks. This vulnerability was starkly illustrated in the early 1980s, when a mass mortality event eliminated the urchin *Diadema antillarum* (Lessios et al., 1984). With no functional replacement available, and compounded by widespread overfishing of herbivorous fishes (Jackson et al., 2001), many Caribbean reefs transitioned to algal dominance (Mumby et al., 2007).

Despite these ecological differences, a bioindicator similar to the A:Q ratio developed here may still prove useful in the Indo-Pacific. While reduced herbivory alone is less likely to trigger algal overgrowth in that region, other mechanisms—such as cyclone damage (Roff et al., 2015), coral bleaching (Diaz-Pulido et al., 2009), and historical land-use changes (Fong and Todd, 2021)—can similarly promote macroalgal proliferation. In such cases, nutrient enrichment often precedes the phase shift, suggesting that a ratio-based indicator like ours could complement the FoRAM-Index (Hallock et al., 2003), which is sensitive to water quality via the relative abundances of symbiont-bearing, stress-tolerant, and opportunistic foraminifera.

5. Conclusions

Coral-algal phase shifts are a hallmark of reef degradation in the Caribbean, yet their long-term dynamics often elude conventional monitoring. To address this gap, we developed a bioindicator based on the ecological preferences of two foraminiferal genera: *Archaias* and *Quinqueloculina*. By integrating remote sensing timeseries with field-collected sediment samples, we show that the relative abundances of these foraminifera track the multidecadal history of algal overgrowth across eight Caribbean reef systems. This bioindicator offers a retrospective lens to assess reef condition beyond the temporal limits of diver-based surveys, enhancing our capacity to interpret past ecological baselines and inform conservation strategies.

CRediT authorship contribution statement

Akos Kalman: Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Alex F. Humphreys:** Supervision, Project administration, Methodology, Conceptualization. **Zach Adams:** Investigation, Data curation. **Riley Ames:** Investigation, Data curation. **Angelique R. Marín:** Methodology, Data curation. **Alex C. Dempsey:** Project administration, Conceptualization. **Sam J. Purkis:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization.

Funding sources

This study was funded by National Science Foundation (NSF) award No. EAR-2035135.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Sam Purkis reports financial support was provided by National Science Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We owe a debt of gratitude to the host nations of the Global Reef Expedition who not only permitted our team to work in their countries but also provided both logistical and scientific support. We are similarly indebted to the crew of the M/Y Golden Shadow, through the generosity of HRH Prince Khaled bin Sultan, for their inexhaustible help in the field. We are grateful to Roy Armstrong and Tania Lopez Marrero for their advice on Puerto Rican vintage aerial photographs, and to Jeremy Gabriel for his valuable lessons in data ordination. We also thank Zsofia Adam-Kalman for her insights into visualization and graph design. We are especially thankful for the thorough and meticulous work of Sofia Sherman, Sadie Cox, Emma Rosen, Bianca Banato, and the many other U. Miami undergraduate students who contributed to sampling the seafloor, as well as picking, gluing, organizing, and identifying the foraminifera in the samples. The quality of our manuscript was improved substantially by the thoughtful critique of two anonymous reviewers.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107437.

Data availability

Data will be made available on request.

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