Journal of Earth Science, *Vol. XX*, *No. XX*, *p. 1−9*, *Online 2022* *ISSN 1674-487X*
Printed in China
https://doi.org/10.1007/s12583-021-1543-7

A New Foraminiferal Bioindicator for Long-Term Heat Stress on Coral Reefs

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ABSTRACT: Coral reefs are in terminal decline. For conservation to be effective, naturally depauperate reefs must be distinguished from those recently degraded by humans. Traditional reef monitoring is time consuming and lacks the longevity to make this distinction. Success in using foraminifera as bioindicators for reef health has hitherto levered their response to nutrients. Because ocean heat waves are the dominant driver of coral bleaching and death, there is compelling motivation to develop new foraminiferal bioindicators that inform on temperature stress over meaningful timescales. This study focuses on identifying which foraminifera respond systematically to the temperature stress that kills corals. Statistical models were used to compare endosymbiont-bearing foraminiferal families, collected along a heat-stress gradient spanning the Solomon Islands and New Caledonia, to live coral cover at the same sites. Results indicate that Amphisteginidae foraminifera and coral cover show a significant decline in abundance as heat stress increases along the transect sites. Furthermore, ocean productivity and salinity, both recognized environmental influences on foraminifera, are shown to be subordinate to temperature in their sway of this ecological patterning. These findings indicate the potential for using foraminifera to develop new indices capable of quantifying long-term thermal impacts on reefs.

KEY WORDS: foraminifera, bioindicator, corals, bleaching, degree heating week, FoRAM Index.

0 INTRODUCTION

Coral reefs are in global decline. Humans have been damaging coral ecosystems since their first interactions with them (McClenachan et al., 2017; Pandolfi et al., 2003), but it is only in the last forty, or so, years that impacts such as overfishing, pollution, and anthropogenic climate change have precipitated their global collapse (Bellwood et al., 2004; Jackson et al., 2001). Conservation and restoration are tools that can stem this crisis, but to be effective, they must be applied to reefs that were healthy prior to being exposed to human stress. Importantly, the geologic record shows that, prior to any human interference, some reefs are naturally depauperate because they are situated in so called ‘marginal’ environments, such as those episodically too hot, too cold, or compromised by other natural inconveniences to optimal reef growth (Humphreys et al., 2016; Riegl et al., 2015, 2012; Purkis et al., 2011; Purkis and Riegl, 2005; Perry, 2003; Riegl, 2003; Riegl and Piller, 2000; Kleypas et al., 1999; Glynn et al., 1979). Time series from traditional diver-monitoring of corals rarely extend back more than ten years (Gardner et al., 2003; Aronson et al., 2002), and therefore cannot adequately separate recently damaged reefs from those which are naturally marginal and have been so for a long time. Bioindicators are an emerging solution for understanding reef health over meaningful timescales and benthic foraminifera (forams) show excellent promise in assessing whether average conditions conducive to healthy reefs have existed over centuries to millennia (Humphreys et al., 2019; Fajemila et al., 2015; Narayan et al., 2015; Uthicke et al., 2013; Uthicke and Nobes, 2008; Hallock et al., 2003).

Despite their excellent potential for guiding reef conservation, foram bioindicators have been examined in a limited number of sites. Therefore, their global performance as proxy indicators remains largely unknown, while their continued and accelerated study is important. These tiny, testate (shelled) protists accumulate abundantly in reef sediments and, because they preserve well, can be easily identified. Large benthic forams (LBF), which contain similar photosynthetic endosymbionts to corals, prosper in the same conditions conducive to healthy reefs—excellent water quality and stable temperatures—whereas small-

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Manuscript received August 3, 2021.
Manuscript accepted September 8, 2021.

Alexander F. Humphreys, Sam J. Purkis, Chuyan Wan, Matthew Aldrich, Sarah Nichols, Jazmin Garza, 2022. A New Foraminiferal Bioindicator for Long-Term Heat Stress on Coral Reefs. *Journal of Earth Science*, XX(XX): 1–9. https://doi.org/10.1007/s12583-021-1543-7. http://en.earth-science.net

er heterotrophic and opportunistic benthic forams proliferate in conditions which are stressful to reefs, such as elevated nutrients and turbidity (Hallock et al., 2003). Because death assemblages of forams accumulate on the seabed and are mixed in the sediment over centuries to millennia, these organisms provide a time-averaged overview of prevailing environmental conditions, which stretches far beyond the decade or so offered by diver monitoring. Hence, it follows that indices, which capture details about the abundance of large benthic, heterotrophic, and opportunistic forams provide invaluable insight into the environmental history of their host reefs. Time-averaged foram assemblages therefore have the potential to be used to distinguish recently-damaged reefs, which have the capacity to respond to conservation intervention, from naturally depauperate reefs, which do not.

One index that assesses if trophic conditions are suitable for coral reef photosymbiosis in LBF and corals is the Foram in Reef Assessment and Monitoring Index (FoRAM Index), hereafter shortened to ‘FI’. This index was developed as a water quality-based reef assessment tool in Florida and the Caribbean (Prazeres et al., 2020; Uthicke et al., 2012; Schueth and Frank, 2008; Hallock et al., 2003). At the time that it was proposed, however, Hallock et al. (2003) foresaw the need to evolve the FI to tune its performance beyond the region where it was created; a premonition supported by some subsequent data collection (Barbosa et al., 2012, 2009; Renema, 2010, 2008). Furthermore, the FI was created using three functional groups of forams, whose relative abundance primarily responded to nutrients—a highly relevant parameter for reef health, but, in an age of rapidly warming seas inducing catastrophic coral bleaching, not always predominant. Hence, there is ample scope to increase the relevance of foram-based indices to the global reef crisis by tuning them to detect historical thermal stress.

In addition to water quality, forams systematically respond to other reef-degrading influences, including (but not limited to) temperature, UV, salinity, turbidity, and pH stress (Kelmo and Hallock, 2013; Schmidt et al., 2011; Martinez-Colón et al., 2009; Hallock, 2000; Schafer, 2000). Based on work by Beccari et al. (2020), mass coral bleaching has the potential to indelibly alter foram assemblages. Literature also shows that changing environmental conditions can cause shifts in the mosaic of bacterial—and reef—endosymbiont algal communities, resulting in a reorganization of the communal test micriobiome, including the appearance of new taxa (Prazeres, 2018; Prazeres et al., 2017a; Webster et al., 2016, 2013). Finally, the lab-controlled settings of Webster et al. (2016) demonstrate that these microbial changes can be associated with shifting temperature regimes. We propose that this sensitivity to environmental conditions should be discernable in time-averaged foram assemblages influenced by long-term (centuries to millennia) oceanographic patterning.

Herein, we investigate the effects of multi-decadal averages for temperature stress (as measured by Degree Heating Week—*DHW*; see Methods) and other predominant oceanographic parameters, as well as depth on the abundance of LBF families and percent coral cover, from oligotrophic reefs along a geographic *DHW* gradient spanning the Solomon Islands through New Caledonia, southwestern Pacific (Fig. 1).

1 METHODS

All of the samples for this project were collected under the auspices of the Global Reef Expedition accomplished by

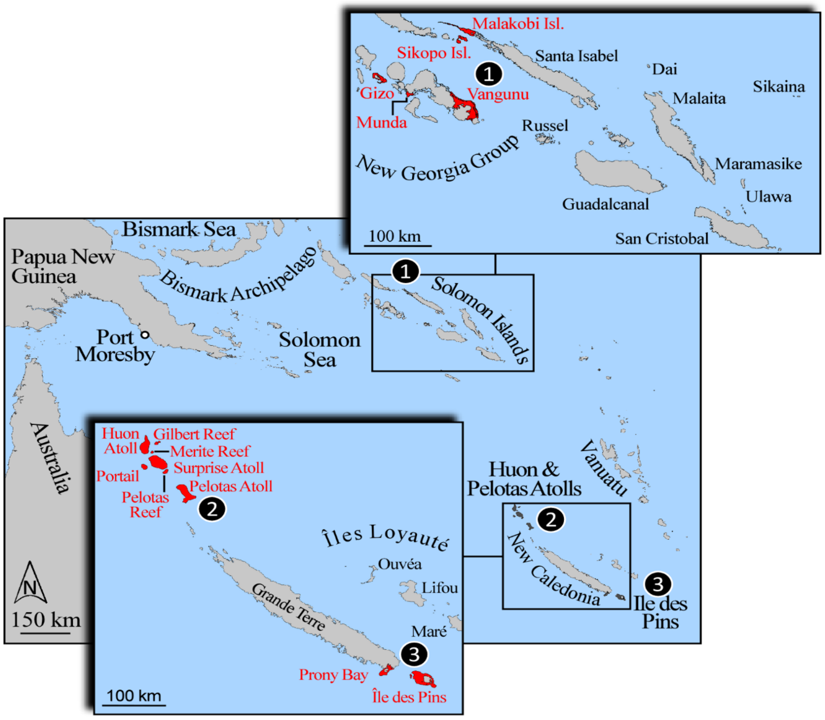


Figure 1. Map of study location detailing relative geographic location of the Solomon Islands and New Caledonia. (1) Solomon Islands, New Georgia Group; (2) New Caledonia, Huon and Pelotas Atolls; (3) New Caledonia, Ile des Pins. Sites at which foram samples were collected and *in situ* coral cover audited are emphasized in red.

the Khaled bin Sultan Living Oceans Foundation—a ten-year survey of a broad selection of Earth's remotest reef sites (Purkis et al., 2019). In 2013 and 2014, 240 surficial (upper 5 cm) samples were collected from 1 to 25 m water depth, within the associated islands and atolls of New Caledonia (130 samples) and Solomon Islands (110 samples; Fig. 2a). The sediment samples were collected by SCUBA divers. Each sample consisted of 250 mL of sediment which, so as not to lose fine material, was carefully scooped into a Nalgene sampling bottle and capped at the seabed. Sample locations were determined via differential GPS and sufficient underwater digital photographs were taken to characterize each sample site and surrounding environment in terms of benthic cover and morphology. At the same depth as each sediment sample, the benthic cover of major functional groups and substrate type were assessed along 10 m transects using both diver-recorded observations, point-intercept counts, and 1 m^2 digital photo-quadrats. A minimum of four transects were completed at each sample site. Initially, these collections were part of a larger set of 2 500 samples from >1 000 reefs spanning a global reef transect, but were isolated for use in the current investigation because New Caledonia and the Solomon Islands span a climatological spectrum of thermal stress as quantified by average Degree Heating Week (*DHW*) for the period 1985–2019 (Fig. 2a). *DHW*, which is developed by the National Oceanic and Atmospheric Administration Coral Reef Watch (NOAA CRW), is a well-documented predictor of coral bleaching (Kumagai et al., 2018; Kayanne, 2017; van Hooidonk and Huber, 2009; Liu et al., 2003; and others). *DHW* is based on satellite-derived climatologies of sea surface temperature (*SST*) and computed as the sum over a period of 12 weeks of temperatures exceeding 1 °C above the historical summer monthly *SST* (Kumagai et al., 2018; Liu et al., 2003).

The sediment samples were washed, oven dried at 35 °C, and stored in Nalgene jars. In order to maintain consistency in the sampling environment, mitigate depth influence, and reduce statistical noise, only samples collected at water depths shallower than 15 m (per Prazeres et al., 2020), within distinct average 1985–2019 *DHW* brackets (0.1–0.2, 7 samples; 0.3–0.4, 11 samples; 0.6–0.7, 6 samples; Fig. 2b), and from backreef sandy substrates, situated away from high islands and lagoon centers, were carried forward for analysis. Following the workflow of Prazeres et al. (2020), these samples were further split into subsamples, sieved with a 125 μm mesh to remove the ultra-fine fraction and unidentifiable small and juvenile foram tests, to deliver the 24 samples used in this study (Table S1).

Following the widely-adopted standard for statistical significance proposed by Schönfeld et al. (2012), at least 300 tests-per-sample were collected from picking trays using stereomicroscopy (min 301; max 386), which were converted to percentages for analysis. These tests were transferred to 60-cell micropaleontology slides for further analysis. All large benthic forams (LBF) were identified to the level of family and all foram tests were separated into three functional groups: [1] photosymbiont-bearing large benthic, [2] heterotrophic, and [3] stress-tolerant opportunistic, according to the generic classifications of Prazeres et al. (2020). The functional groups were used to calculate the FI, following the methods outlined in Hallock et al. (2003). This calculation was performed to test the utility of FI in the strictly oligotrophic environments of the study setting.

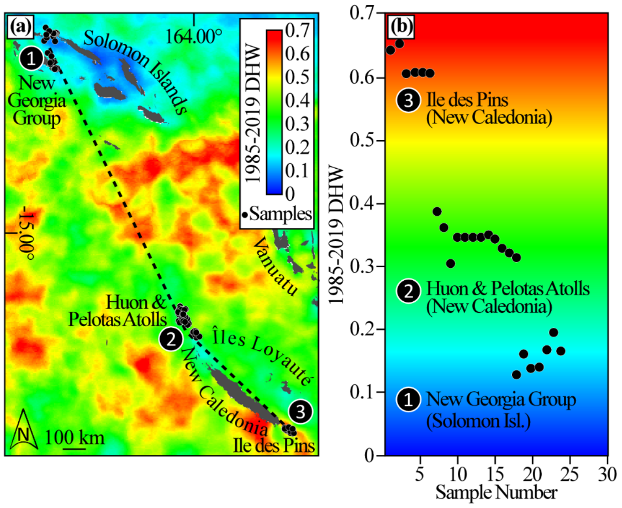


Figure 2. (a) Detailed map of study region indicating three study locations according to their 1985–2019 average Degree Heating Week (*DHW*): (1) Solomon Islands, New Georgia Group; (2) New Caledonia, Huon and Pelotas Atolls; (3) New Caledonia, Ile des Pins. Sample sites are shown as black dots. (b) Plots of study samples and their respective place within distinct *DHW* brackets. Ile des Pins, 0.6–0.7 *DHW*, 6 samples; Huon and Pelotas Atolls, 0.3–0.4 *DHW*, 11 samples; New Georgia Group, 0.1–0.2 *DHW*, 7 samples.

A Redundancy Analysis (RDA) was performed for percent coral percent cover data (Fig. 4a), according to three predetermined coral depth ranges—d2: 8–12 m; d3: 12–18 m; d4: 18–24 m (Table S2)—and a second RDA was performed on the Hellinger-transformed foram-family percent count data, as recommended by Legendre and Gallagher (2001). Full coral cover data and site coordinates can be found in Table S2. RDA operates by running a direct-gradient analysis, which summarises linear relationships between the coral and foram response variables that, in this case, are explained by *DHW*, sea surface temperature, sea surface salinity, chlorophyll-a, and depth (Legendre and Legendre, 1998).

The Hellinger transformation (γ'_{ij}) is defined by

$$\gamma'_{ij} = \sqrt{\frac{\gamma_{ij}}{\gamma_{i+}}}$$

where γ is abundance, γ_{ij} is the abundance of foram families j in sample i, and $i+$ is the sum of values over row i (Legendre and Gallagher, 2001). This transformation guarantees that the samples are being compared according to their familial abundances, without giving undue importance to double zero counts (Borcard et al., 2011; Legendre and Gallagher, 2001; Legendre and Legendre, 1998). The double-zero problem occurs as a result of the uncertain interpretation of absent counts. For instance, a familial absence at two sampling sites may result from the two sites lying above or below the optimal niche zone for that particular group or, alternatively, one site could be above and the other below the ideal niche range (Legendre and Legendre, 1998).

The environmental parameters used in the construction of the RDA are averages from a larger master set of regional physical and environmental data (see the ESM for full dataset). These data include average sea surface temperature (*SST*; MODIS-

Aqua; 2002–2019; monthly avg; 4 km), average chlorophyll-a (*CHL-A*; MODIS-Aqua; 2002–2019; monthly avg; 4 km; collected from NASA Giovanni: https://giovanni. gsfc. nasa. gov/giovanni/), sea surface salinity (*SSS*) from the Simple Ocean Data Assimilation (SODA; July 2002–December 2015), average *DHW* (1985 to 2019), sample depth in meters, and count data.

2 RESULTS

Site-averaged percent coral cover, for the visited reefs, plotted according to water-depth ranges that overlap our foram sample depths (d2, 8–12 m), reveal declining coral cover with increasing *DHW* (95% confidence; Fig. 3a; Table S2).

Redundancy Analysis (RDA) results, constructed from the percent coral cover data for all depths, are plotted as a triplot (Fig. 4a). The RDA reveals a highly significant negative correlation (p = 0.001) between *DHW* and percent live coral cover for the sample sites in waters shallower than 12 m, with no other oceanographic variables explanatorily aligning with coral abundance (Fig. 4a; RDA1 axis in the permutation test).

Six LBF families are identified from samples collected at Solomon Islands and New Caledonia (Figs. 3a–3f, respectively; Table S1). Among the identified families, members of Amphisteginidae and Calcarinidae (Figs. 3a and 3b) dominate all samples and show notable correlations with *DHW*. For example, Amphisteginidae displays a significant decline (95% confidence) in % component from low to high average *DHW* sites (avg. 45.6%; 17.5%; 2.4%; Fig. 3a). In contrast, Calcarinidae exhibits a significant increase (95% confidence) in % component from low to high *DHW* (avg. 15.7%; 47.8%; 72.5%; Fig. 3b; 95% confidence). Furthermore, at each *DHW* end-member (New Georgia Group, Solomon Islands and Ile des Pins, New Caledonia; Fig. 2a) Amphisteginidae and Calcarinidae are the dominant foram families, respectively.

Redundancy Analysis (RDA) results, constructed from the Hellinger-transformed percent abundance data for all of the identified foram families, are plotted as a triplot (Fig. 4b). The RDA reveals a significant negative correlation (p = 0.001) between Amphistegenidae and *DHW* (RDA1 axis in the permutation test). Furthermore, Calcarinidae is closely correlated with increasing *DHW*. The other foram families show no significant correlation to any of the overriding physical and oceanographic parameters considered (Fig. 4b; RDA2 axis in the permutation text).

Site-averaged and individual sample FI values, as well as their ecological interpretations, are plotted in Figs. 5a and 5b, respectively. Interpretations are based on the definitions of Hallock et al. (2003), where FI > 4 is characteristic of oceanographic conditions suitable for endosymbiosis, coral reef framework development, and coral recovery following disturbances, FI between 2 and 4 indicates environments that are marginal to strong reef growth and not suitable for coral recovery following ecological disturbance, and FI values <2 are indicative of environments that are stressed, and not conducive to extensive coral reef development of any kind.

Site-averaged FI values (Fig. 5a) for the Solomon Islands

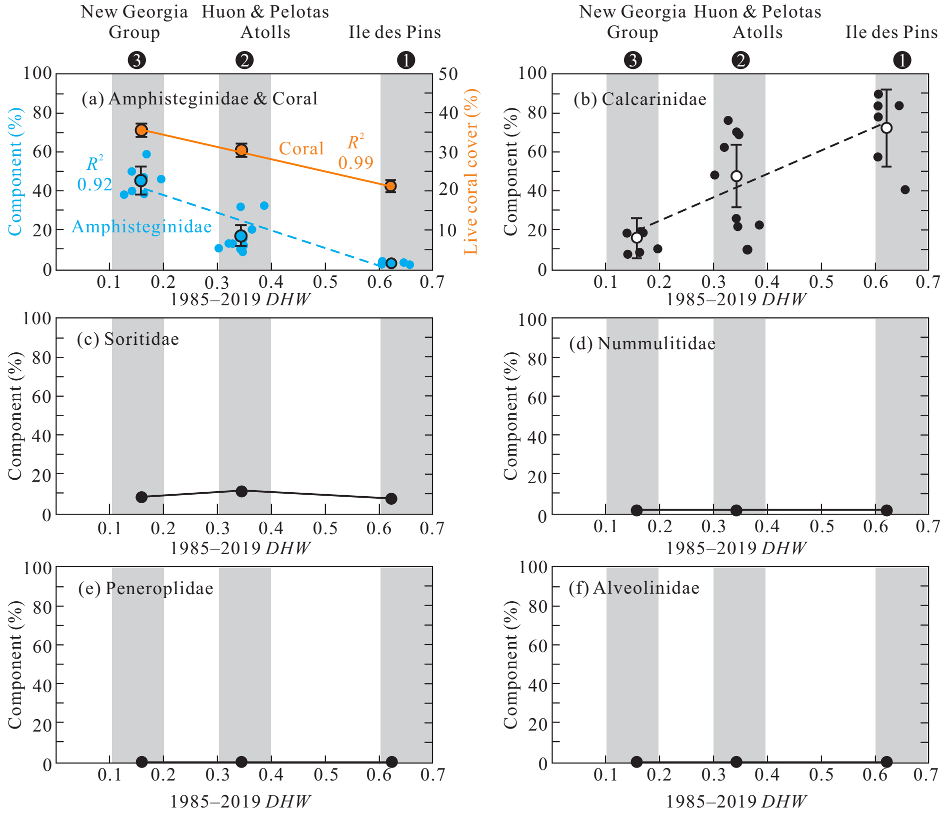
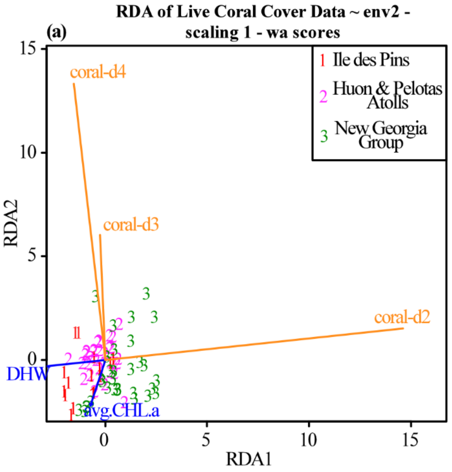


Figure 3. Plots of foram family % component and live coral % cover, by Degree Heating Week (*DHW*). (a) Comparison of coral percent cover (orange; 8–12 m) and Amphistiginidae % component (blue; 1–15 m) at each study site: (1) New Caledonia, Ile des Pins; (2) New Caledonia, Huon and Pelotas Atolls; (3) Solomon Islands, New Georgia Group; see Fig. 2a. Individual foram samples as blue and black scattered dots; site averages as circles with 95% confidence bars shown for the averages. Individual samples only added for Amphisteginidae and Calcarinidae as other families indicated no significant pattern of change.

(New Georgia Group; Fig. 5a1), New Caledonia (Huon and Pelotas Atolls; Fig. 5a2), and New Caledonia (Ile des Pins; Fig. 5a3) indicate no significant difference (p = 0.05) among sampling locations. Furthermore, Fig. 5b hints at individual samples, from the three respective sampling locations, settling well within trophic environments that are suited to coral reef development—a result that is consistent with field observation.

3 DISCUSSION

Mass coral bleaching events and associated coral die-offs are predicted to accelerate in the coming years as ocean temperatures continue to rise (Goreau and Hayes, 2021; DeCarlo et al., 2020; Glynn, 1984; and others). Traditionally, field studies that consider the effect of temperature stress on reefs have relied on costly, and time consuming, diver-collected timeseries data of live coral cover. These timeseries rarely extend beyond a few decades, with the majority considerably shorter. LBF, meanwhile, contain similar photosynthetic endosymbionts to corals, prosper in the same conditions conducive to healthy reefs, and accumulate as century to millennial assemblages (Hallock et al., 2003). For all these reasons, benthic forams, and LBF, in particular, provide a time-averaged overview of prevailing environmental conditions, which stretches far beyond that offered by divers. It follows, then, that indices, which capture details about the relative abundances of different groups of forams, can provide insight into the environmental history of surrounding reefs, including temperature stress. Hence the benefit of identifying sensitive bioindicators that can be used as proxies for long-term temperature stress on reefs. Here, results of foram family counts, coupled with Redundancy Analysis (RDA), show endosymbiont-bearing forams from the Amphisteginidae family to exhibit a significant negative correlation with average heat stress (*DHW*), along a latitudinal gradient from the Solomon Islands through New Caledonia (Figs. 3



```
Permutation test
Number of permutations: 999

Model: rda(formula = Coral ~ DHW + avg.CHL.a +
avg.SST + avg.SSS, data = env2)
          Df Variance       F Pr(>F)
RDA1       1   115.71 12.2349  0.001 ***
RDA2       1    23.85  2.5215  0.078 .
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Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘
’ 1
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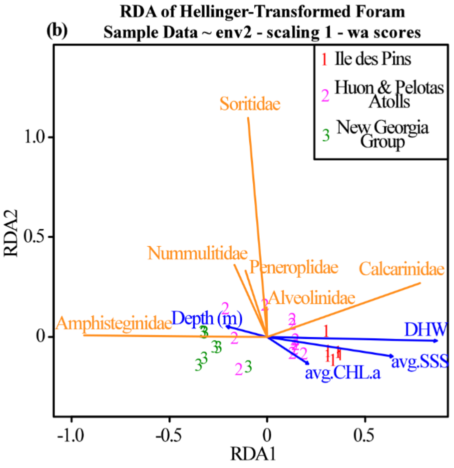

```
Permutation test
Number of permutations: 999

Model: rda(formula = Foram.hel ~ Depth..m. + DHW +
avg.CHL.a + avg.SSS + avg.SST, data = env2)
          Df Variance       F Pr(>F)
RDA1       1 0.100715 49.9783  0.001 ***
RDA2       1 0.002639  1.3095  0.754
```

Figure 4. Redundancy Analysis (RDA) triplot results for coral cover and forams. (a) RDA of % coral cover for 8–12 m (coral-d2), 12–18 m (coral-d3) and 18–24 m (coral-d4), modeled against environmental variables from Table S1. Coral reef sites overlap those of foram counts in our three DHW collection zones. Coral depth zones plot as orange vectors, overriding environmental parameters plot as blue vectors, and individual sites numbered and colored according to the three collection locations in Fig. 2a: (1) New Caledonia, Ile des Pins [red]; (2) New Caledonia, Huon and Pelotas Atolls [pink]; (3) Solomon Islands, New Georgia Group [green]. (b) RDA constructed from percent abundance of all foraminiferal family counts and overriding environmental variables. Foram families plotted as orange vectors, environmental parameters plotted as blue vectors, and individual samples numbered and color coded as in (a). RDA results indicate a strong negative correlation (p = 0.001) for both corals and Amphisteginidae forams with long-term average heat stress (DHW; 1985–2019 avg.). Permutation tests show high significance in the RDA1 axis for both corals and Amphistiginidae forams. DHW, Degree Heating Week; avg.SSS, average surface salinity; avg.CHL.a, average chlorophyll-a (Table S1).

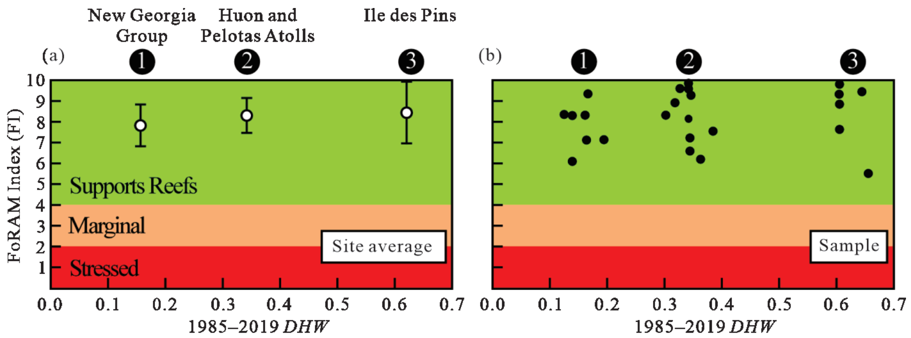

Figure 5. Charts of FoRAM Index (FI; Hallock et al., 2003) for all samples, based on functional group data in Table S1. (a) Site average; (b) samples. All samples show values well above 4, indicating trophic conditions suitable for photosymbiont activity, reef development, and post-disturbance recovery. FI values between 2 and 4 indicate marginal trophic conditions with no true reef framework development, and poor recovery post-disturbance. FI < 2 indicates stressed conditions and no significant coral development.

and 4). When coupled with percent coral cover data for these three locations and among overlapping depths, time-averaged assemblages of Amphisteginidae align with live shallow water coral abundances along the same long-term *DHW* gradient. Our findings suggest that these shallow water coral reef environments, with histories of higher long-term average summer heat stress, negatively affect members of this cosmopolitan foraminiferal family in ways that mirror the centuries to millennial temperature effects on neighboring corals.

The FI is intended as a coral-independent measure of whether water quality (nutrient concentrations and pollution) in the local environment is adequate for coral reef framework development, photosymbiont activity, and post-disturbance recovery (Prazeres et al., 2020; Hallock, 2012; Hallock et al., 2003). Since Hallock et al. (2003) first developed the FI, it has since been successfully implemented in numerous studies for predicting coral reef health, in reefs with natural and anthropogenic trophic sourcing (Sreenivasulu et al., 2019; Humphreys et al., 2018; Pisapia et al., 2017; Fabricius et al., 2012; Narayan and Pandolfi, 2010; Uthicke and Nobes, 2008; and others); Narayan et al. (2022) uses the FI as part of their investigation of benthic foraminifera from the carbonate dominated reefs off the west coast of Zanzibar. In strictly oligotrophic environments, however, such as those among our Solomon Islands and New Caledonia sites, FI is expected to plot values well above 4, coral suitable habitats, because of the perpetually low nutrient concentrations in the water column—and hence high abundance of time-averaged LBF tests—even if the environments are not suitable for healthy coral reef development, as a result of non-trophic parameters, like temperature. Thus, Fig. 5, which reveals FI values indicating strong suitability for coral symbiosis and post-disturbance recovery at our three strictly oligotrophic sites is a predicted outcome. Additionally, temperature appears to be a significant controller of coral health in the shallowest sites within our study region (Fig. 4a), and thus relying on the FI, as a proxy index for coral reef health, could misidentify coral reefs as healthy, when they may be showing a time-averaged pattern of repeated heat stress in relative abundances of LBF. Hence, these results underscore the importance of discovering forams in primarily temperature and UV affected environments, that can be used to develop new proxy indices of long-term—centuries to millennia—coral reef health, based on environmental factors in addition to nutrient concentration.

In addition to the FI, the *Amphistegina* Bleaching Index (ABI) is another developing reef analysis tool that uses the percent of live bleaching in *Amphisteginia* species to inform on whether water quality supports calcifying symbioses, and if damaging photo-inhibitory stress is occuring in the reef environment (Stainbank et al., 2020; Spezzaferri et al., 2018; Hallock et al., 2006; and others). This index offers a snapshot of near real-time stressors on coral reefs and has the potential to inform on coral UV stress before corals respond (Spezzaferri et al., 2018)—an important tool for reef monitoring, but one which lacks the ability to discern these historic conditions on the reef.

Our results indicate Amphisteginidae to be the sole LBF family to express strongly negative impacts from long-term average temperature stress, in our study region (Fig. 4). Reports of temperature and light stress on *Amphistegina* species are not new (see Narayan et al., 2022; Stainbank et al., 2020; Prazeres, 2018; Spezzaferri et al., 2018; Prazeres et al., 2017b, 2016; Stuhr et al., 2017; Reymond et al., 2012; Schmidt et al., 2011; Talge and Hallock, 2003; Hallock and Talge, 1995; and others). However, many of these studies are constrained by controlled laboratory settings, with some concluding UV light over temperature as the primary driver of foram bleaching (Talge and Hallock, 2003). In recent years, it has become increasingly clear that temperature plays a major role in the abundances of Amphisteginidae spp., since they are often attached to reef rubble and can control UV exposure through phototaxic behavior (Prazeres, 2018; Fujita, 2004). For example, Prazeres (2018) concludes a rapid increase in *SST* as the likely driver of bacterial microbiome changes and bleaching in *A. radiata* during the bleaching event across the GBR in 2016. Furthermore, Prazeres et al. (2016) show that when in-vitro populations of *Amphistegina lobifera* are adapted to stable temperature and light conditions, they exhibit higher sensitivity to temperature stress. The current study is the first time that a controlled field collection of forams, along a multi-decadal gradient of average temperature stress, shows a strong correlation between average temperature disturbance and time-averaged development of Amphisteginidae foram assemblages.

Calcarinidae abundances trend against those of Amphisteginidae (Fig. 3b), however the causal mechanism for this result is inconclusive. Dominance of Calcarinidae in Indo-western Pacific reef sands is common (Prazeres et al., 2020). Species of this family are known to thrive in waters of variable trophic levels, including the mesotrophic reefs of Indonesia, as a result of their ability to live epiphytically on the surfaces of a variety of macroalgae and seagrass (Renema, 2010). Furthermore, temperature effects on *Calcarina* spp. in the literature is variable. On one hand, for instance, Schmidt et al. (2011) concluded that lab-controlled temperature elevations negatively impact some species of *Calcarina*, while leaving others unaffected. Our RDA results for Calcarinidae, meanwhile, clearly indicate that elevated nutrient concentrations (avg. CHL.a; Chlorophyll-a; Fig. 4b) do not account for the distribution of tests from this family, but they do reveal a moderate association—close vector alignment—among abundances of this foram family and increasing *DHW* in the first RDA axis (Fig. 4b). We acknowledge, though, that our findings are preliminary and stress the need for the continued cataloguing of Calcarinidae species as it pertains to local oceanography and bathymetry. Such work is required to illuminate how foram populations adjust to geographic changes in trophic and temperature variability. Future research using the collections from this study aims to identify LBF forams to the level of species, in an attempt to discern whether our positive Calcarinidae trends with *DHW* are indicative of intrafamilial species shuffling or opportunism/niche-filling in response to Amphistiginidae absence.

Aside from those of Amphistegidae and Calcarinidae forams, our results indicate no clear geographic trends among other LBF, with respect to the considered oceanographic parameters. These results may become clear with more focused identifications, but reveal the need to expand research into the role that oceanography and geography play on these sensitive endosymbiont-bearing protists. Additionally, we recommend these findings be compared to those of similar settings, to tease out potential regional-scale patterns to oceanographic gradients.

Along with clear declines in Amphisteginidae abundances from Solomon Islands to New Caledonia (Ile des Pins), coral communities exhibit diminishing percent live cover for the same reefs and depths. RDA for percent coral cover, modeled against regional oceanographic parameters, reveal negatively correlated temperature stress (*DHW*) to be the overriding driver of patterns of coral cover in our multivariate analysis. The shallowest reef communities (Fig. 4a: coral-d2; 8–12 m) show a strong negative correlation with *DHW* in the RDA1 axis. However, coral communities at depths of 13 to 24 m exhibit no alignment with our modeled explanatory variables, which may indicate parameters other than temperature stress to predominate at these depths. Ultimately, this disparity with respect to reef depth and foram distribution may indicate long-term exposure to temperature and light extremes, in our study region, to be moderately buffered at depths greater than 12 m, and hence reef depth may offer temporary climate refugia for sensitive LBF and corals in the coming decades. Thus, these results add to growing evidence of the deep reef refugia hypothesis, as first posited by Riegl and Piller (2003).

4 CONCLUSION

This study represents the first comparative analysis of benthic foraminiferal abundances and coral percent cover along a multi-decadal gradient of temperature stress at a regional scale. Our results indicate long-term patterns of past temperature stress to suppress percent coral cover and the time-averaged assemblages of LBFs in the Amphisteginidae family. With time running out to solve the coral reef crisis, new uses of foram bioindicators, especially as barometers of temperature stress that extend far beyond diver records, have immediate value. We hope that our results offer a road map for continued research into foram bioindicators for reef health, building forward from the current FoRAM Index, which relies on three broad functional groups of forams that are primarily sensitive to nutrients. Additionally, we hope that this work be considered a step towards harnessing intra-familial shifts in LBFs as a tool for the development of indices of coral reef temperature stress.

ACKNOWLEDGMENTS

We owe a debt of gratitude to the host nations of the Khaled bin Sultan Living Oceans 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. The project would have been impossible without the 200 scientists who participated in the Global Reef Expedition. Finally, special thanks go to Anna Bakker for her assistance compiling *DHW* data for the Pacific. This project is based upon work supported by the National Science Foundation (NSF) (No. EAR-2035135). The final publication is available at Springer via https://doi.org/10.1007/s12583-021-1543-7.

Electronic Supplementary Materials: Supplementary materials (Tables S1–S2) are available in the online version of this article at https://doi.org/10.1007/s12583-021-1543-7.

REFERENCES CITED

Aronson, R., Precht, W., Toscano, M., et al., 2002. The 1998 Bleaching Event and Its Aftermath on a Coral Reef in Belize. *Marine Biology*, 141(3): 435–447. https://doi.org/10.1007/s00227-002-0842-5

Barbosa, C. F., de Freitas Prazeres, M., Ferreira, B. P., et al., 2009. Foraminiferal Assemblage and Reef Check Census in Coral Reef Health Monitoring of East Brazilian Margin. *Marine Micropaleontology*, 73(1/2): 62–69. https://doi.org/10.1016/j.marmicro.2009.07.002

Barbosa, C. F., Ferreira, B. P., Seoane, J. C. S., et al., 2012. Foraminifer-Based Coral Reef Health Assessment for Southwestern Atlantic Offshore Archipelagos, Brazil. *The Journal of Foraminiferal Research*, 42(2): 169–183. https://doi.org/10.2113/gsjfr.42.2.169

Beccari, V., Spezzaferri, S., Stainbank, S., et al., 2020. Responses of Reef Bioindicators to Recent Temperature Anomalies in Distinct Areas of the North Ari and Rasdhoo Atolls (Maldives). *Ecological Indicators*, 112: 106128. https://doi.org/10.1016/j.ecolind.2020.106128

Bellwood, D. R., Hughes, T. P., Folke, C., et al., 2004. Confronting the Coral Reef Crisis. *Nature*, 429(6994): 827 – 833. https://doi. org/10.1038/nature02691

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. Springer, New York. https://doi.org/10.1007/978-1-4419-7976-6

DeCarlo, T. M., Gajdzik, L., Ellis, J., et al., 2020. Nutrient-Supplying

Ocean Currents Modulate Coral Bleaching Susceptibility. *Science Advances*, 6(34): eabc5493. https://doi.org/10.1126/sciadv.abc5493

Fabricius, K. E., Cooper, T. F., Humphrey, C., et al., 2012. A Bioindicator System for Water Quality on Inshore Coral Reefs of the Great Barrier Reef. *Marine Pollution Bulletin*, 65(4/5/6/7/8/9): 320–332. https://doi.org/10.1016/j.marpolbul.2011.09.004

Fajemila, O. T., Langer, M. R., Lipps, J. H., 2015. Spatial Patterns in the Distribution, Diversity and Abundance of Benthic Foraminifera around Moorea (Society Archipelago, French Polynesia). *PLoS One*, 10(12): e0145752. https://doi.org/10.1371/journal.pone.0145752

Fujita, K., 2004. A Field Colonization Experiment on Small-Scale Distributions of Algal Symbiont-Bearing Larger Foraminifera on Reef Rubble. *The Journal of Foraminiferal Research*, 34(3): 169–179. https://doi.org/10.2113/34.3.169

Gardner, T. A., Côté, I. M., Gill, J. A., et al., 2003. Long-Term Region-Wide Declines in Caribbean Corals. *Science*, 301(5635): 958 – 960. https://doi.org/10.1126/science.1086050

Glynn, P. W., 1984. Widespread Coral Mortality and the 1982-83 El Niño Warming Event. *Environmental Conservation*, 11(2): 133–146. https://doi.org/10.1017/s0376892900013825

Glynn, P. W., Wellington, G. M., Birkeland, C., 1979. Coral Reef Growth in the Galapagos: Limitation by Sea Urchins. *Science*, 203(4375): 47–49. https://doi.org/10.1126/science.203.4375.47

Goreau, T. J. F., Hayes, R. L., 2021. Global Warming Triggers Coral Reef Bleaching Tipping Point. *Ambio*, 50(6): 1137 – 1140. https://doi. org/10.1007/s13280-021-01512-2

Hallock, P., 2000. Symbiont-Bearing Foraminifera: Harbingers of Global Change? *Micropaleontology*, 46(1): 95–104

Hallock, P., 2012. The FoRAM Index Revisited: Uses, Challenges, and Limitations. In: Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia. 9–13

Hallock, P., Lidz, B. H., Cockey-Burkhard, E. M., et al., 2003. Foraminifera as Bioindicators in Coral Reef Assessment and Monitoring: The FoRAM Index. *Environmental Monitoring and Assessment*, 81(1/2/3): 221–238. https://doi.org/10.1023/a:1021337310386

Hallock, P., Talge, H. K., 1995. Symbiont Loss (“Bleaching”) in the Reef-Dwelling Benthic Foraminifer Amphistegina Gibbosa in the Florida Keys in 1991-92. *Oceanographic Literature Review*, 42(8): 977. https://digitalcommons.usf.edu/msc_facpub/977

Hallock, P., Williams, D. E., Fisher, E. M., et al., 2006. Bleaching in Foraminifera with Algal Symbionts: Implications for Reef Monitoring and Risk Asessment. *Anuário do Instituto de Geociências-UFRJ*, 29(1): 108–128. https://doi.org/10.11137/2006_1_108-128

Humphreys, A. F., Halfar, J., Ingle, J. C., et al., 2018. Effect of Seawater Temperature, pH, and Nutrients on the Distribution and Character of Low Abundance Shallow Water Benthic Foraminifera in the Galápagos. *PLoS One*, 13(9): e0202746. https://doi. org/10.1371/journal.pone.0202746

Humphreys, A. F., Halfar, J., Ingle, J. C., et al., 2019. Shallow-Water Benthic Foraminifera of the Galápagos Archipelago: Ecologically Sensitive Carbonate Producers in an Atypical Tropical Oceanographic Setting. *Journal of Foraminiferal Research*, 49(1): 48–65

Humphreys, A. F., Halfar, J., Rivera, F., et al., 2016. Variable El Niño-Southern Oscillation Influence on Biofacies Dynamics of Eastern Pacific Shallow-Water Carbonate Systems. *Geology*, 44(7): 571 – 574. https://doi.org/10.1130/g37745.1

Jackson, J. B. C., Kirby, M. X., Berger, W. H., et al., 2001. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science*, 293(5530): 629–637. https://doi.org/10.1126/science.1059199

Kayanne, H., 2017. Validation of Degree Heating Weeks as a Coral Bleaching Index in the Northwestern Pacific. *Coral Reefs*, 36(1): 63 – 70. https://doi.org/10.1007/s00338-016-1524-y

Kelmo, F., Hallock, P., 2013. Responses of Foraminiferal Assemblages to ENSO Climate Patterns on Bank Reefs of Northern Bahia, Brazil: A 17-Year Record. *Ecological Indicators*, 30: 148 – 157. https://doi. org/10.1016/j.ecolind.2013.02.009

Kleypas, J. A., McManus, J. W., Menez, L. A., 1999. Environmental Limits to Coral Reef Development: Where do We Draw the Line? *American Zoologist*, 39(1): 146–159. https://doi.org/10.1093/icb/39.1.146

Kumagai, N. H., Yamano, H., Sango-Map-Project, C., 2018. High-Resolution Modeling of Thermal Thresholds and Environmental Influences on Coral Bleaching for Local and Regional Reef Management. *PeerJ*, 6: e4382. https://doi.org/10.7717/peerj.4382

Legendre, P., Gallagher, E. D., 2001. Ecologically Meaningful Transformations for Ordination of Species Data. *Oecologia*, 129(2): 271–280. https://doi.org/10.1007/s004420100716

Legendre, P., Legendre, L. F., 1998. Numerical Ecology, 2nd Edition. Elsevier

Liu, G., Strong, A. E., Skirving, W., 2003. Remote Sensing of Sea Surface Temperatures during 2002 Barrier Reef Coral Bleaching. *Eos, Transactions American Geophysical Union*, 84(15): 137 – 141. https://doi.org/10.1029/2003eo150001

Martinez-Colón, M., Hallock, P., Green-Ruiz, C., 2009. Strategies for Using Shallow-Water Benthic Foraminifers as Bioindicators of Potentially Toxic Elements: A Review. *The Journal of Foraminiferal Research*, 39(4): 278–299. https://doi.org/10.2113/gsjfr.39.4.278

McClenachan, L., O’Connor, G., Neal, B. P., et al., 2017. Ghost Reefs: Nautical Charts Document Large Spatial Scale of Coral Reef Loss over 240 Years. *Science Advances*, 3(9): e1603155. https://doi. org/10.1126/sciadv.1603155

Narayan, Y. R., Pandolfi, J. M., 2010. Benthic Foraminiferal Assemblages from Moreton Bay, South-East Queensland, Australia: Applications in Monitoring Water and Substrate Quality in Subtropical Estuarine Environments. *Marine Pollution Bulletin*, 60(11): 2062 – 2078. https://doi.org/10.1016/j.marpolbul.2010.07.012

Narayan, Y. R., Lybolt, M., Zhao, J. X., et al., 2015. Holocene Benthic Foraminiferal Assemblages Indicate Long-Term Marginality of Reef Habitats from Moreton Bay, Australia. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, 420: 49–64. https://doi.org/10.1016/j.palaeo.2014.12.010

Narayan, G. R., Reymond, C. E., Stuhr, M., et al., 2022. Response of Large Benthic Foraminifera to Climate and Local Changes: Implications for Future Carbonate Production. *Sedimentology*, 69(1): 121 – 161. https://doi.org/10.1111/sed.12858

Pandolfi, J. M., Bradbury, R. H., Sala, E., et al., 2003. Global Trajectories of the Long-Term Decline of Coral Reef Ecosystems. *Science*, 301(5635): 955–958. https://doi.org/10.1126/science.1085706

Perry, C. T., 2003. Coral Reefs in a High-Latitude, Siliciclastic Barrier Island Setting: Reef Framework and Sediment Production at Inhaca Island, Southern Mozambique. *Coral Reefs*, 22(4): 485 – 497. https://doi.org/10.1007/s00338-003-0339-9

Pisapia, C., Kateb, A. E., Hallock, P., et al., 2017. Assessing Coral Reef Health in the North Ari Atoll (Maldives) Using the FoRAM Index. *Marine Micropaleontology*, 133: 50 – 57. https://doi.org/10.1016/j.marmicro.2017.06.001

Prazeres, M., 2018. Bleaching-Associated Changes in the Microbiome of

Large Benthic Foraminifera of the Great Barrier Reef, Australia. *Frontiers in Microbiology*, 9: 2404. https://doi. org/10.3389/fmicb. 2018.02404

Prazeres, M., Roberts, T. E., Pandolfi, J. M., 2017a. Variation in Sensitivity of Large Benthic Foraminifera to the Combined Effects of Ocean Warming and Local Impacts. *Scientific Reports*, 7: 45227. https://doi. org/10.1038/srep45227

Prazeres, M., Ainsworth, T., Roberts, T. E., et al., 2017b. Symbiosis and Microbiome Flexibility in Calcifying Benthic Foraminifera of the Great Barrier Reef. *Microbiome*, 5(1): 38. https://doi. org/10.1186/ s40168-017-0257-7

Prazeres, M., Martínez-Colón, M., Hallock, P., 2020. Foraminifera as Bioindicators of Water Quality: The FoRAM Index Revisited. *Environmental Pollution*, 257: 113612. https://doi.org/10.1016/j. envpol. 2019.113612

Prazeres, M., Uthicke, S., Pandolfi, J. M., 2016. Influence of Local Habitat on the Physiological Responses of Large Benthic Foraminifera to Temperature and Nutrient Stress. *Scientific Reports*, 6: 21936. https:// doi.org/10.1038/srep21936

Purkis, S. J., Riegl, B., 2005. Spatial and Temporal Dynamics of Arabian Gulf Coral Assemblages Quantified from Remote-Sensing and *in situ* Monitoring Data. *Marine Ecology Progress Series*, 287: 99–113. https:// doi.org/10.3354/meps287099

Purkis, S. J., Gleason, A. C. R., Purkis, C. R., et al., 2019. High-Resolution Habitat and Bathymetry Maps for 65, 000 sq. km of Earth’s Remotest Coral Reefs. *Coral Reefs*, 38(3): 467 – 488. https://doi. org/10.1007/ s00338-019-01802-y

Purkis, S. J., Renegar, D. A., Riegl, B. M., 2011. The Most Temperature-Adapted Corals have an Achilles’ Heel. *Marine Pollution Bulletin*, 62(2): 246–250. https://doi.org/10.1016/j.marpolbul.2010.11.005

Renema, W., 2008. Habitat Selective Factors Influencing the Distribution of Larger Benthic Foraminiferal Assemblages over the Kepulauan Seribu. *Marine Micropaleontology*, 68(3/4): 286–298. https://doi.org/10.1016/j. marmicro.2008.06.002

Renema, W., 2010. Is Increased Calcarinid (Foraminifera) Abundance Indicating a Larger Role for Macro-Algae in Indonesian Plio-Pleistocene Coral Reefs? *Coral Reefs*, 29(1): 165 – 173. https://doi.org/ 10.1007/s00338-009-0568-7

Reymond, C. E., Uthicke, S., Pandolfi, J. M., 2012. Tropical Foraminifera as Indicators of Water Quality and Temperature. In: Proceedings of the 12th International Coral Reef Symposium, July 9 – 13, 2012, Cairns, Australia

Riegl, B., 2003. Climate Change and Coral Reefs: Different Effects in Two High-Latitude Areas (Arabian Gulf, South Africa). *Coral Reefs*, 22(4): 433–446. https://doi.org/10.1007/s00338-003-0335-0

Riegl, B., Piller, W. E., 2000. Biostromal Coral Facies: A Miocene Example from the Leitha Limestone (Austria) and Its Actualistic Interpretation. *PALAIOS*, 15(5): 399–413. https://doi.org/10.2307/3515512

Riegl, B., Piller, W. E., 2003. Possible Refugia for Reefs in Times of Environmental Stress. *International Journal of Earth Sciences*, 92(4): 520–531. https://doi.org/10.1007/s00531-003-0328-9

Riegl, B., Glynn, P. W., Wieters, E., et al., 2015. Water Column Productivity and Temperature Predict Coral Reef Regeneration across the Indo-Pacific. *Scientific Reports*, 5: 8273. https://doi.org/10.1038/srep08273

Riegl, B. M., Purkis, S. J., Al-Cibahy, A. S., et al., 2012. Coral Bleaching and Mortality Thresholds in the SE Gulf: Highest in the World. In: Riegl, B., Purkis, S., eds., Coral Reefs of the Gulf. Coral Reefs of the World, vol. 3. Springer, Dordrecht. 95 – 105. https://doi. org/10.1007/ 978-94-007-3008-3_6

Schafer, C. T., 2000. Monitoring Nearshore Marine Environments Using Benthic Foraminifera: Some Protocols and Pitfalls. *Micropaleontology*, 46: 161–169

Schmidt, C., Heinz, P., Kucera, M., et al., 2011. Temperature-Induced Stress Leads to Bleaching in Larger Benthic Foraminifera Hosting Endosymbiotic Diatoms. *Limnology and Oceanography*, 56(5): 1587 – 1602. https://doi.org/10.4319/lo.2011.56.5.1587

Schönfeld, J., Alve, E., Geslin, E., et al., 2012. The FOBIMO (Foraminiferal Bio-Monitoring) Initiative—Towards a Standardised Protocol for Soft-Bottom Benthic Foraminiferal Monitoring Studies. *Marine Micropaleontology*, 94/95: 1 – 13. https://doi. org/10.1016/j. marmicro.2012.06.001

Schueth, J. D., Frank, T. D., 2008. Reef Foraminifera as Bioindicators of Coral Reef Health: Low Isles Reef, Northern Great Barrier Reef, Australia. *The Journal of Foraminiferal Research*, 38(1): 11–22. https:// doi.org/10.2113/gsjfr.38.1.11

Spezzaferri, S., El Kateb, A., Pisapia, C., et al., 2018. *In situ* Observations of Foraminiferal Bleaching in the Maldives, Indian Ocean. *Journal of Foraminiferal Research*, 48(1): 75 – 84. https://doi. org/10.2113/gsjfr. 48.1.75

Sreenivasulu, G., Praseetha, B. S., Daud, N. R., et al., 2019. Benthic Foraminifera as Potential Ecological Proxies for Environmental Monitoring in Coastal Regions: A Study on the Beypore Estuary, Southwest Coast of India. *Marine Pollution Bulletin*, 138: 341 – 351. https://doi.org/10.1016/j.marpolbul.2018.11.058

Stainbank, S., Spezzaferri, S., Beccari, V., et al., 2020. Photic Stress on Coral Reefs in the Maldives: The Amphistegina Bleaching Index. *Ecological Indicators*, 113: 106257. https://doi.org/10.1016/j.ecolind.2020.106257

Stuhr, M., Reymond, C. E., Rieder, V., et al., 2017. Reef Calcifiers are Adapted to Episodic Heat Stress but Vulnerable to Sustained Warming. *PLoS One*, 12(7): e0179753. https://doi.org/10.1371/journal.pone.0179753

Talge, H. K., Hallock, P., 2003. Ultrastructural Responses in Field-Bleached and Experimentally Stressed Amphistegina Gibbosa (Class Foraminifera). *Journal of Eukaryotic Microbiology*, 50(5): 324–333. https://doi. org/10.1111/j.1550-7408.2003.tb00143.x

Uthicke, S., Momigliano, P., Fabricius, K. E., 2013. High Risk of Extinction of Benthic Foraminifera in this Century due to Ocean Acidification. *Scientific Reports*, 3: 1769. https://doi.org/10.1038/srep01769

Uthicke, S., Nobes, K., 2008. Benthic Foraminifera as Ecological Indicators for Water Quality on the Great Barrier Reef. *Estuarine*, *Coastal and Shelf Science*, 78(4): 763–773. https://doi.org/10.1016/j.ecss.2008.02.014

Uthicke, S., Patel, F., Ditchburn, R., 2012. Elevated Land Runoff after European Settlement Perturbs Persistent Foraminiferal Assemblages on the Great Barrier Reef. *Ecology*, 93(1): 111 – 121. https://doi. org/ 10.1890/11-0665.1

van Hooidonk, R., Huber, M., 2009. Quantifying the Quality of Coral Bleaching Predictions. *Coral Reefs*, 28(3): 579 – 587. https://doi. org/ 10.1007/s00338-009-0502-z

Webster, N. S., Negri, A. P., Botté, E. S., et al., 2016. Host-Associated Coral Reef Microbes Respond to the Cumulative Pressures of Ocean Warming and Ocean Acidification. *Scientific Reports*, 6: 19324. https:// doi.org/10.1038/srep19324

Webster, N. S., Negri, A. P., Flores, F., et al., 2013. Near-Future Ocean Acidification Causes Differences in Microbial Associations within Diverse Coral Reef Taxa. *Environmental Microbiology Reports*, 5(2): 243–251. https://doi.org/10.1111/1758-2229.12006