Coral Reefs
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REPORT

Amphistegina lobifera foraminifera are excellent bioindicators of heat stress on high latitude Red Sea reefs

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Abstract Coral reefs are in global decline and anomalously hot temperatures shoulder the blame. Foraminferal bioindicators are important because they record historical reef stress over periods of centuries to millennia, as compared to the few decades offered by diver surveys. For a region lacking systematic long-term reef monitoring programs, the use of bioindicators in the Red Sea is compelling. Whereas foraminfera-based indices exist to reconstruct histories of nutrient stress on reefs, there is a paucity of equivalent bioindicators that respond to temperature. Capitalizing on a portfolio of surficial sediment samples collected along the eastern margin of the N. Red Sea and Gulf of Aqaba, this study shows that the relative abundance of Amphisteginidae foraminifera—specifically *Amphistegina lobifera*—closely track heat stress, as has recently been reported for this family in the S. Pacific. This result is consequential for at least three reasons. First, the Red Sea hosts some of the most northerly coral reefs on Earth. Establishment of a thermal bioindicator here confirms the strategy can be deployed on high latitudes reefs, which are disproportionally afflicted with heat extremes. Second, the considered reefs, and the foraminifera they host, are famed for their thermal resilience. Foraminiferal bioindicators have not previously been trialed on reefs that have adapted in this way. Finally, as a restricted offshoot of the Indian Ocean, the level of endemism in the Red Sea is especially high. The bioindicator that we propose is apparently not compromised by endemism. Our findings advocate for an expanded deployment of *Amphistegina*-based reef bioindicators.

Keywords Red Sea · Gulf of Aqaba · Large benthic foraminifera · Bioindicators · Thermal stress · Coral reefs

Introduction

Coral reefs are in rapid decline and ocean heatwaves are primarily to blame (Carpenter et al. 2021; Goreau and Hayes 2021). In the Red Sea, timeseries of corals from traditional diver monitoring, rarely extend back more than ten years (Kotb et al. 2004; De'ath et al. 2012; Flower et al. 2017). This limitation frustrates attempts to distinguish reefs that have consistently endured thermal stress—as is the case on naturally marginal reefs—from those whose condition has only recently been degraded by anthropogenic warming. Faced with this challenge, benthic foraminiferal bioindicators are an emerging solution for reconstructing the stress regime of reefs over centuries to millennia, as opposed to the decadal timescales delivered by diver surveys (Hallock et al. 2003; Uthicke and Nobes 2008; Uthicke et al. 2013; Narayan et al. 2015; Fajemila et al. 2015; Humphreys et al. 2019).

The calcareous shells (hereafter 'tests') of the amoeboid protists known as foraminifera (forams), accumulate in reef sands, preserve well (resist destruction), and can be easily identified. Conveniently, large benthic forams (LBFs) contain photosynthetic endosymbionts analogous to those in

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corals and prosper under the same conditions conducive to healthy reefs—namely low nutrient waters with stable temperatures (Hallock et al. 2003). Pioneered by the FoRAM-Index (FI), the use of foram bioindicators has primarily been to inform on the history of nutrient loading around reefs (Hallock et al. 2003; Schueth and Frank 2008; Uthicke et al. 2012; Humphreys et al. 2018; Prazeres et al. 2020). Near real-time UV photic stress on reefs has also been proxied using forams (Hallock et al., 2006; Spezzaferri et al. 2018; Stainbank et al. 2020).

For reefs in the Pacific, we recently showed how the relative abundance of a group of endosymbiont-bearing LBF from the Amphisteginidae family respond in unison with live coral cover along a gradient of long-term average thermal stress (Fig. 5; Humphreys et al. 2022). Our findings from the Pacific suggested the potential for the development of a new foram bioindicator for heat stress on reefs.

Whereas it is promising that Amphisteginidae forams seem to effectively track thermal loading, the use of this foram family as a bioindicator only really becomes viable if their behavior is consistent over large spatial scales. For instance, the performance of the bioindicator would be diminished if the forams behave differently with regard to temperature along gradients of biodiversity, endemism, latitude, or any other local factors. Hence, the motivation for this paper is to take the indicator presented by Humphreys et al. (2022) in the Pacific and test it in the Red Sea—Gulf of Aqaba system. We consider this system to represent the most challenging case for the bioindicator because it boasts among the most northerly shallow coral reefs on Earth.

Situated in the subtropics, the winter waters in the northern Red Sea and Gulf of Aqaba routinely drop down to 20 °C under the influence of Mediterranean weather systems and rise as high as 35 °C in the summer, under the climate influence of the Indian Ocean (Edwards et al. 1987; Purkis et al. 2010; Berumen et al. 2013; Chaidez et al. 2017; Genevier et al. 2019). Induced by levels of thermal variability not witnessed in the tropics, the reefs of the northern Red Sea and Gulf of Aqaba, and the LBFs that inhabit them, show a greater degree of thermal resistance than observed in the tropics. Corals situated in the northern reaches of the Gulf of Aqaba, for instance, resist bleaching even when exposed to temperatures ≥ 6 °C above their average maximum summer values for up to four weeks (Fine et al. 2013). In the tropics, by contrast, bleaching is triggered when temperature exceeds the summer maximum by as little as 1–2 °C for only two weeks (Riegl and Purkis 2009; Hoegh-Guldberg 2011; Riegl et al. 2015; Grottoli et al. 2017). Just like the corals, the foram species *Amphistegina lobifera* in the northern Red Sea shows tolerance to bleaching (Schmidt et al. 2016). Moreover, in contrast to tropical reefs, the restricted nature of the Red Sea delivers exceptionally high levels of endemism for deep and shallow reef fauna (DiBattista et al., 2016a, b; Sonnewald and El-Sherbiny 2017; Maggioni et al. 2022). For all these reasons, the reefs that inhabit this rift basin represent an extreme case and constitute a possible end member for the successful deployment of a global foram bioindicator.

Methods

Environmental data

Our sample sites span a climatological gradient of thermal stress, as can be emphasized using Degree Heating Weeks (DHW) for the period 1985–2019 (Fig. 1). DHW, which is developed by the National Oceanic and Atmospheric Administration's Coral Reef Watch program, is a well-documented predictor of coral bleaching (Liu et al. 2003, 2018; Van Hooidonk and Huber 2009; Kayanne 2017; Kumagai and Yamano 2018). The DHW metric 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 (Liu et al. 2003; Kumagai and Yamano 2018).

In addition to the DHW climatology for each field sample, we also assembled time series for sea surface temperature (SST) as derived from 0.25 km resolution GHR-L4 monthly averages from 2002 to 2019, in situ depth of each sample, as well as in situ salinity and chlorophyll-a fluorescence measurements collected between 07 October and 15 November 2020, using a Seabird 911plus Conductivity-Temperature-Depth (CTD) probe and a Seabird Eco Fluorometer sensor at sites adjacent to our sediment collections. SBE data processing was used to convert the data files, filter the data, remove wild edits, and bin average the data into 1-m bins. Chlorophyll-a fluorescence values were converted from volts to milligrams per cubic meter using calibration values from Seabird, adjusted for nonzero deep values and divided by a factor of 2 to correct for overestimation (Roesler et al. 2017).

Sampling and counting of forams

The 41 surficial samples used in this project were collected under the auspices of the 2020 OceanX-NEOM 'Deep Blue' Expedition (Purkis et al. 2022). Along a transect spanning the northern Red Sea to northern Gulf of Aqaba, we systematically sampled the uppermost 5 cm of reef sediment situated shallower than 15 m water depth (Fig. 1). Following the protocols of Purkis et al. (2014), each sample consisted of 250 ml of sediment which, so as to not lose fine material, was carefully scooped by a diver into a Nalgene sampling bottle and capped at the seabed. Sample locations were determined via differential GPS. Following the workflow of Prazeres et al. (2020), the samples were

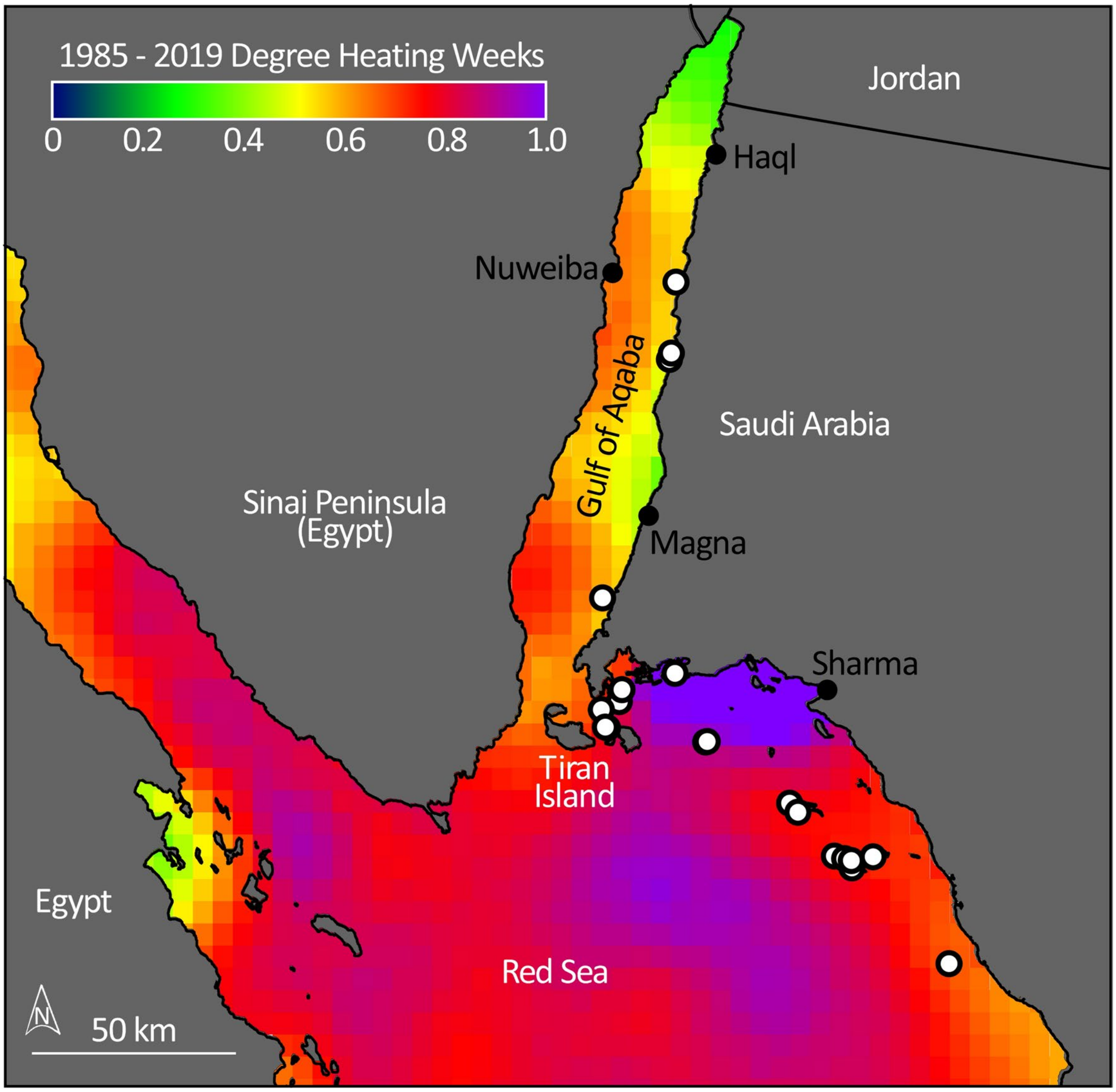

Fig. 1 Degree heating weeks (DHW) for the northern Red Sea and Gulf of Aqaba averaged over 1985–2019. Locations of surficial sediment samples from which foram specimens were extracted and quantified (white dots) fall along a north-to-south gradient of low thermal stress in the Gulf of Aqaba to high stress in the northern Red Sea. The embayment offshore the Saudi city of Sharma is particularly afflicted by the accumulation of excessive summer heat

sieved to determine grainsize, further split into study subsamples, and again sieved with a 125 µm mesh to remove the ultra-fine fraction and unidentifiable small and juvenile foram tests. Of the original collection, only samples with a majority of grains falling between 125 µm and 2 mm were picked, to deliver the 20 samples used in this study (Table 1). Unlike Humphreys et al. (2022) who carefully selected all samples from the same soft sand, back-reef settings, as a proof-of-concept effort to reduce statistical noise, here we decided to forego this level of careful collection, thereby testing whether useful signals can be discerned from time-averaged death assemblages in samples from mixed fore-reef and back-reef sites.

At least 200 foram tests-per-sample were assembled from picking trays using stereomicroscopy. 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: photosymbiont-bearing large benthic, heterotrophic, and stress-tolerant opportunistic, according to the generic classifications of Hallock et al. (2003) (Table 1). In addition to these familial categorizations, all forams from the Amphisteginidae family were further identified

Table 1 Sample locations and associated biophysical variables as determined by analysis of remote sensing climatologies and CTD casts conducted in the field

DHW zone	Lat	Long	Sample	Depth	Avg DHW	Avg SST	Sal	Fluor	Amp	Pen	Sor	Calc	Numm	Alv	Total LBF	Total Het	Total stress Tol
	DD	DD	ID	m	1985–2019, ˚C	2002–2019, °C	PSU	mg/m^3	%	%	%	%	%	%	%	%	%
	28.78963	34.82331	32	8	0.40	24.51	40.78	0.21	42.95	1.31	8.20	0.00	2.62	0.00	55.08	44.59	0.33
0.40–0.49	28.80384	34.82829	34	7	0.40	24.50	40.78	0.21	49.57	1.16	1.16	0.29	0.29	0.00	52.46	46.38	1.16
	28.25508	34.65369	37	8	0.42	25.02	40.56	0.24	54.66	0.00	0.00	0.00	0.00	0.00	54.66	45.34	0.00
	28.96303	34.84018	36	9	0.45	24.46	40.69	0.19	32.68	0.00	20.23	6.23	0.39	0.00	59.53	33.85	6.61
	27.43197	35.52558	11	10	0.54	26.57	40.22	0.17	24.67	3.33	5.00	0.00	1.00	1.00	35.00	63.00	2.00
	27.67277	35.33595	47	12	0.57	26.48	40.19	0.18	20.99	11.11	4.94	0.00	1.85	3.40	42.28	57.10	0.62
	27.67483	35.23825	01	10	0.58	26.46	40.19	0.18	47.39	1.30	10.43	0.00	2.17	3.04	64.35	35.65	0.00
0.50–0.59	27.66897	35.26425	03	10	0.58	26.46 26.46	40.19	0.18	21.10	3.67	3.06	0.31	1.22	0.00	29.36	70.64	0.00
	27.66456	35.28097	04	8	0.58	26.46	40.19	0.18	25.70	12.85	2.23	0.00	4.47	3.91	49.16	50.28	0.56
	27.77338	35.14682	43	8	0.61	26.36	40.22	0.16	22.80	1.20	14.00	0.40	1.20	2.00	41.60	58.40	0.00
	27.79383	35.12588	12	10	0.61	26.34	40.22	0.16	10.20	6.12	18.78	8.57	0.41	1.63	45.71	53.88	0.41
0.60–0.69	28.00415	34.65072	55	8	0.67	25.43	40.18	0.22	26.75	1.91	12.42	0.00	4.78	0.00	45.86	48.41	5.73
	27.96310	34.66647	59	8	0.67	25.62	40.18	0.22	30.95	13.47	12.89	0.00	5.44	4.01	66.76	32.95	0.29
	27.96495	34.66094	62	8	0.67	25.58	40.18	0.22	29.75	4.96	10.74	4.13	0.83	1.65	52.07	47.52	0.41
	27.93149	34.91433	56	8	0.76	26.16	40.21	0.16	11.21	5.45	23.64	7.58	1.21	0.00	49.09	50.91	0.00
	27.93263	34.91825	58	8	0.76	26.16	40.21	0.16	21.85	17.23	9.24	0.00	0.00	0.42	48.74	47.48	3.78
0.70+	28.04862	34.70272	14	10	0.79	25.47	40.18	0.22	15.15	6.40	39.39	0.00	4.04	5.05	70.03	28.96	1.01
	28.02225	34.69635	49	8	0.79	25.59	40.18	0.22	10.47	3.25	11.19	0.00	2.53	1.44	28.88	0.00	2.17
	28.04910	34.70290	50	8	0.79	25.47	40.18	0.22	16.12	32.23	5.49	0.37	1.10	0.73	56.04	43.22	0.73
	28.08562	34.83705	61	8	0.86	25.69	40.29	0.30	13.68	37.74	15.57	0.00	2.83	0.00	69.81	29.72	0.47

Foram family relative abundance data derived from the quantification of at least 200 foram tests-per-sample (max 327)

Lat, latitude; Long, longitude; Sal, salinity; Fluor, Fluorescence; Amp, Amphisteginidae; Pen, Peneroplidae; Sor, Soritidae; Calc, Calcarinidae; Numm, Nummulitidae; Alv, Alveolinidae; LBF, large benthic forams; Het, heterotrophic forams; Stress Tol, stress tolerant forams according to their species classifications, with relative foram abundance reported. Finally, all relative abundance results were averaged according to four distinct DHW zones selected for use in our analyses. The DHW zones, 0.40–0.49; 0.50–0.59; 0.60–0.69; 0.70+, were chosen to create distinct heat-stress delineations for grouping our samples, while aiming to minimize ambiguity in our methodological choices (see Table 1 for details).

As recommended by Legendre and Legendre (1998) and Legendre and Gallagher (2001), a Redundancy Analysis (RDA) was performed on the Hellinger-transformed foram family relative abundance data. A second RDA was performed on relative abundances of *Amphistegina* species identified in our samples. The RDA runs a direct-gradient analysis to summarize relationships between the foram response variables that, in this case, have the potential to be explained by averaged climatologies of DHW, sea surface temperature, fluorescence, and by water depth.

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

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

where γ is relative abundance, γ_{ij}, here, is the relative abundance of foram families j in sample i, and $i+$ is the sum of values over row i. This transformation guarantees that the samples are being compared according to their familial relative abundances, without giving undue importance to double zero counts (Borcard et al. 2011), which could plausibly occur because of the uncertain interpretation of absent counts in our data. For instance, a familial absence at two sampling sites may result from the two sites lying above or below the optimal niche environments for that particular foram group or, alternatively, one site could be above and the other below this ideal niche range (Legendre and Legendre 1998). Relationships between relative abundances of the considered forams—families and *Amphistegina* species—and the environmental climatologies were explored by means of cross plots (Figs. 2, 3) and via RDA (Fig. 4). Analysis of the RDA was performed using a permutation test to inform on the level of significance within each presented dimension of the multivariate plot ($p = 0.05$; Table 2).

Results

LBF family relative abundances and DHW

Six LBF families were identified in our samples (Fig. 2; Table 1). Among the identified families, the relative abundance of forams in the family Amphisteginidae exhibited a strong negative correlation with DHW from lowest to highest DHW zones (Fig. 2a). Specifically, Amphisteginidae average relative abundance decreased from 45 to 15% from the lowest to highest DHW zones, 0.40–0.49 to 0.70+, respectively. This relationship is statistically significant ($p = 0.05$).

By contrast, forams of the Peneroplidae and Soritidae families increased in relative abundance with increasing DHW. For instance, Peneroplidae relative abundance averages significantly increased from 1 to 17% ($p = 0.05$) and those for Soritidae increased from 7 to 17% from the lowest to highest end-member DHW zones, respectively (Fig. 2b, c). The relative abundance of Calcarinidae, Nummulitidae, and Alveolinidae, meanwhile, show no notable trend along our DHW gradient (Fig. 2d–f).

Amphistegina species relative abundances

Results for *Amphistegina* species identified in our samples are plotted according to identified DHW zones of this project (Fig. 3). Three *Amphistegina* species were identified in our Red Sea samples: *A. lobifera*; *A. lessonii; A. bicirculata*. Figure 3a shows significant declines in relative abundances of *A. lobifera* from the low DHW waters of the Gulf of Aqaba to the two highest DHW zone averages in the northeast Red Sea ($p = 0.05$). In contrast, *A. lessonii* relative abundances, averaged according to our four DHW zones, reveal statistical similarity throughout the region, indicating that, while a prominent species in our samples, *A. lessonii* is not swayed by average heat stress in our results (Fig. 3b). *A. bicirculata* did not reveal any significant patterns of relative abundance in our samples (Fig. 3c).

Redundancy analysis (RDA)

Redundancy Analysis (RDA) constructed from the Hellinger-transformed relative abundance data for all LBF families reveals three distinct clusters of samples tracking left-to-right along the horizontal RDA1 dimension from the Gulf of Aqaba throughout the Northeastern Red Sea sites (Fig. 4a). Prominently plotted along this RDA 1 axis, Amphisteginidae exhibits a strong negative correlation ($p = 0.001$) with average DHW and a modest positive trend with salinity in the horizontal RDA dimension. This result is highly significant (see permutation in Table 2). Peneroplidae forams, meanwhile, covary moderately with increasing DHW and increasing average SST, while Soritidae relative abundances align closely with water depth, in the model. RDA for the identified species of *Amphistegina*—*A. lobifera*; *A. lessonii*; *A. bicirculata*—reveals a highly significant negative correlation between *A. lobifera* and average DHW ($p = 0.003$) along the horizontal RDA1 axis (Fig. 4b; Table 2). *A. lessonii* and *A. bicirculata*, meanwhile, plot along the RDA2 axis and show

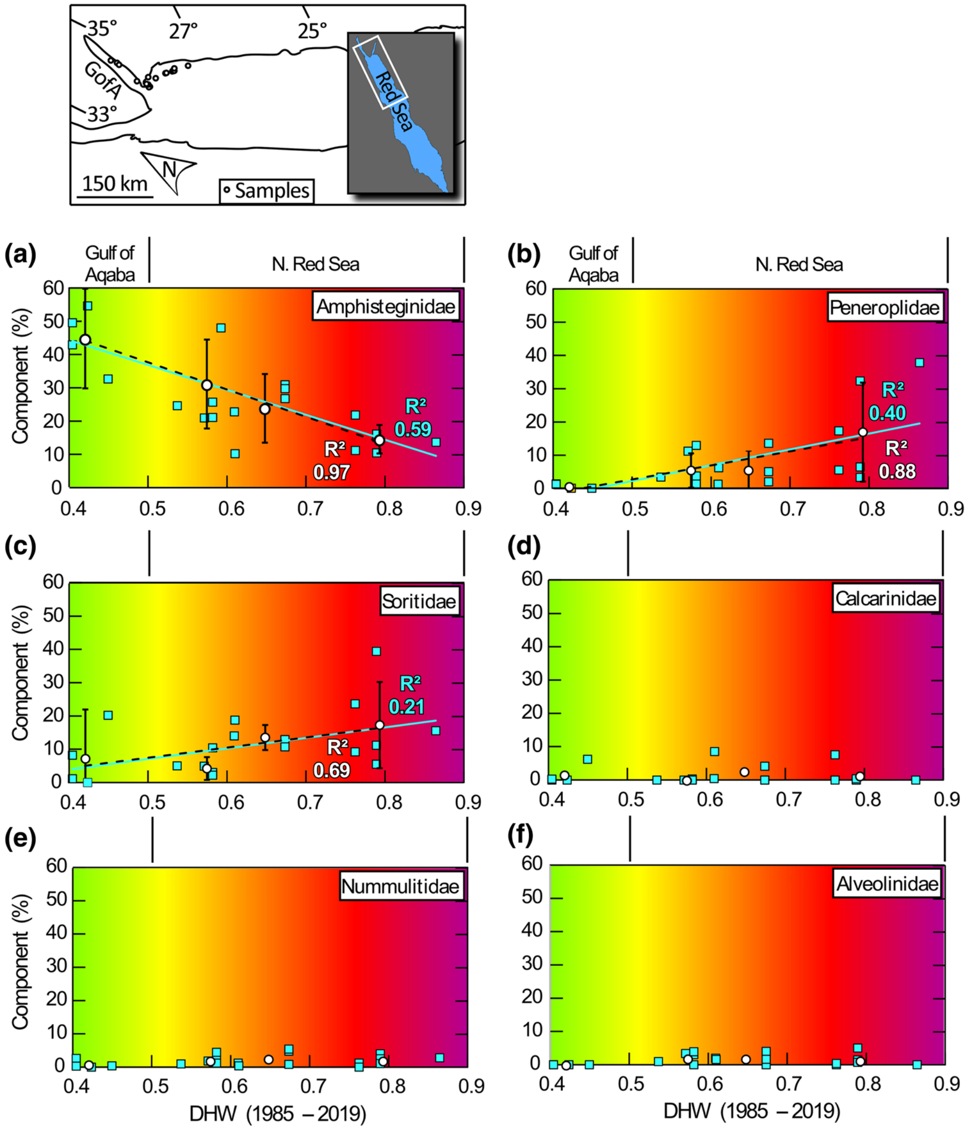

Fig. 2 Plots of foram family relative abundance versus thermal loading as assessed between 1985 and 2019 via Degree Heating Weeks (DHW). Samples as cyan-colored squares, DHW zone-averages as open black circles (95% confidence bars shown for Amphisteginidae averages). DHW zones are as follows: 0.40–0.49; 0.50–0.59; 0.60–0.69; 0.70+, as represented by color-scale shading. Trendlines and R^2 values given for families that show statistically meaningful trends with increasing DHW. R^2 values in cyan font represent raw data, while those in white represent DHW zone averages. Map details geographical distribution of sample sites from low DHW Gulf of Aqaba samples on left to higher DHW waters in the northern Red Sea. GofA = Gulf of Aqaba

no significant correlation among the parameters tested in our model (Table 2).

Permutation test results for the RDA plots are shown in Table 2. Test results of the RDA for identified LBF families in Fig. 4a reveals strong significance in the horizontal RDA1 Axis ($p = 0.001$; Table 2, top). The high level of significance in this axis is further illustrated in the RDA by color coding the individual samples with their respective DHW zone gradation, revealing a low-to-high DHW gradation with declining Amphisteginidae among our samples in this RDA axis (Fig. 4a). Further, the permutation test reveals a lack of significance in the vertical RDA2 dimension ($p > 0.05$), which is interpreted as weak correlations between Nummulitidae, Peneroplidae, Soritidae, and Calcarinidae forams—which plot primarily in this dimension—and the remaining control variables tested in our model. Test results for identified species relative abundances among Amphisteginidae from Fig. 4b (Table 2, bottom) shows the negative correlation between *A. lobifera* and DHW to be highly significant in the Horizontal RDA1 axis along which they lie ($p = 0.003$). All RDA projections in the RDA2 dimension lack significance, for this plot ($p > 0.05$).

Discussion

Relative abundances of Amphistegina track thermal loading in the Pacific and in the Red Sea

Our results of LBF family relative abundances, and RDA reveal that forams from the endosymbiont-bearing Amphisteginidae family vary geographically in a manner consistent with the multi-decadal thermal loading of the reefs with which they are associated (Figs. 2, 4). Specifically,

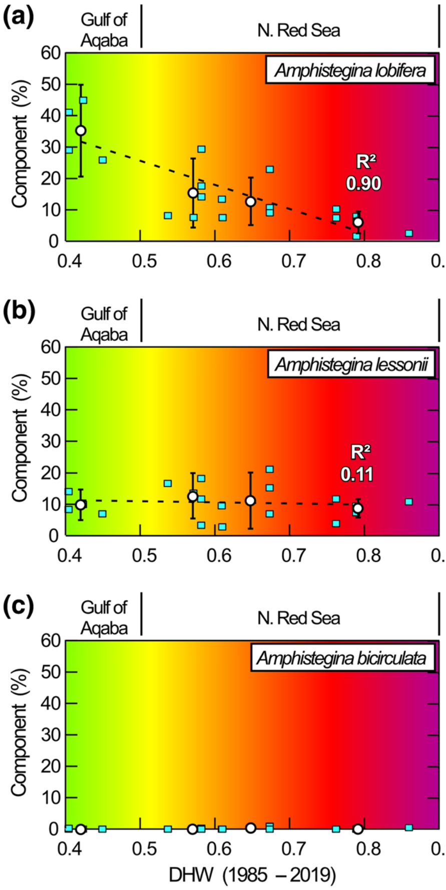

Fig. 3 Plots of average relative abundance for identified *Amphistegina* species according to DHW. Individual samples are plotted as cyan-squares. Relative abundance averages for the four DHW zones: 0.40–0.49; 0.50–0.59; 0.60–0.69; 0.7+ are plotted as white circles. Results indicate significant declines in *A. lobifera* from lowest DHW waters in Gulf of Aqaba to samples collected from two highest DHW zone waters in the northeast Red Sea

we can report that this familial patterning is driven by a significantly negative decline in relative abundance of the species *Amphistegina lobifera* from lowest to highest average heat stress—as catalogued by average DHW for the period 1985–2019—along the eastern Gulf of Aqaba and northeast Red Sea (Figs. 1, 3, 4). The systematic behavior of *A. lobifera*—and its familial averages as a whole—with respect to temperature stress in the Red Sea and Gulf of Aqaba (Fig. 4) therefore mirrors the findings previously reported by Humphreys et al. (2022) in the Solomon Islands and New Caledonia (Fig. 5). Furthermore, the slopes of the lines for Amphisteginidae relative abundance in the N. Red Sea and S. Pacific are – 80.00 and – 90.02, respectively, which are similar and is supported by strong R^2 values for both trends (0.97 and 0.92, respectively). These values correspond to declines in Amphisteginidae relative abundance of 81% and 93% with a 1 °C elevation in average DHW for the N. Red Sea and S. Pacific, respectively. Hence, these comparisons suggest a similar pattern of decline with increasing thermal stress in both regions and reveal this foram bioindicator to express widespread sensitivity to modest increases in thermal loading. These parallel reports are particularly notable given that the Red Sea samples in this study were not collected according to the same rigid sampling methodology of Humphreys et al. (2022). In particular, Humphreys et al. (2022) limited collections to back-reef soft sand environments of the Solomon Islands and New Caledonia, in order to limit statistical noise and enhance potential signaling in their proof-of-concept publication. In contrast, our Red Sea sample collections were expanded to include fore-reef and back-reef sandy environments. While this distinction likely contributes to the higher degree of noise in our results, here, nevertheless we can confidently report a correspondingly significant pattern of decline in relative abundance of *A. lobifera* with temperature stress.

RDA reveals average summer heat stress, as designated by long-term DHW records, followed by salinity, to exert primary sway over Amphisteginidae forams in our samples and to group the samples into three distinct clusters running along the horizontal RDA1 dimension (Fig. 4). Variations in the remaining oceanographic drivers which we consider—fluorescence, average sea surface temperature, and the water depths at which the samples were acquired—are not shown to exert predictive power on the relative abundance of Amphisteginidae forams. To aid interpretation of these results, it should be noted that water temperatures and salinity both covary with latitude within the study area (Fig. 4; Table 1). Further, salinity values only range from 40.18 to 40.78 PSU along the latitudinal gradient of our collection sites. Since long-term DHW is not strictly latitudinal in our study region (see Fig. 1), its predominance over salinity in our RDA models and closer alignment with Amphisteginidae tests and *A. lobifera*, in particular, suggests that it is temperature stress, as opposed to salinity, that is most directly controlling the distribution of *A. lobifera* relative abundances (Fig. 4b).

The effects of temperature and light stress on *Amphistegina* are well-documented (Hallock and Talge 1995; Fitt et al. 2001; Talge and Hallock 2003; Williams and Hallock 2004; Schmidt et al. 2011; Prazeres et al. 2016; Prazeres et al. 2017; Prazeras 2018; Narayan et al. 2022 and others). With respect to temperature, Prazeres et al. (2016) illustrate how in vitro populations of *Amphistegina lobifera* exhibit higher sensitivity to thermal stress when they are adapted to stable temperature and light conditions. Further, working along the Great Barrier Reef, Prazeres (2018) conclude abrupt SST spikes to be the predominant driver of changes to the bacterial microbiome and bleaching in *A. radiata*. However, coinciding with these effects of peak summer temperatures, is the impact of sensitivity among *Amphistegina* (and shallow water coral)

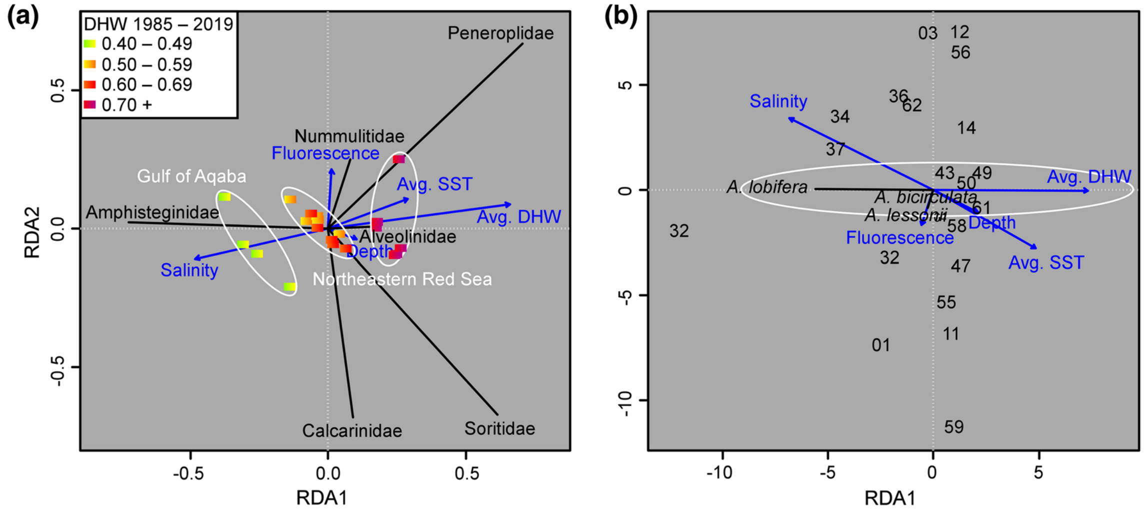

Fig. 4 Redundancy Analysis (RDA). **a** Triplot results for relative abundances of all foram family counts and overriding environmental variables. Foram families plotted as black text, environmental parameters plotted as blue vectors and text, sample groupings and locales as white circles and text, and individual samples as rectangles color coded according to the DHW zones: 0.40–0.49; 0.50–0.59; 0.60–0.69; 0.7+used in this analysis. RDA results indicate a strong negative correlation ($p=.001$; Table 2) for Amphisteginidae forams with long-term average heat stress (DHW; 1985–2019). Further, the analysis displays three distinct sample clusters tracking DHW from low to high along the RDA1 axis. Permutation tests show high significance in the RDA1 axis for both Amphistiginidae forams and DHW (Table 2). RDA model formula = Hellinger transformed LBF relative abundance as response variables, modeled against Depth + Avg DHW + Avg SST + Salinity + Fluorescence data as control variables. **b** Triplot results for *Amphistegina* species relative abundances and overriding environmental variables. Individual samples as numbers corresponding to codes in Table 1. DHW = degree heating week; SST = average sea surface temperature. Salinity and fluorescence measured by CTD casts. RDA model formula = *Amphistegina* spp. relative abundance as response variables, modeled against Depth + Avg DHW + Avg SST + Salinity + Fluorescence data as control variables

Table 2 Permutation test for the RDA results in Fig. 4a, b

	Degrees of freedom	F	Pr(> F)
LBF family (Fig. 4a)			
RDA1	1	12.67	0.001
RDA2	1	3.42	0.253
Amphisteginas pecies (Fig. 4b)			
RDA1	1	30.50	0.003
RDA2	1	0.73	0.994

Number of permutations = 999. Results show high significance in the horizontal RDA 1 axis. Pr(> F) informs on the likelihood that the F statistic is significant ($p=0.05$). A Pr(> F) value < 0.05 is significant and null hypothesis is rejected

populations to high energy (blue to UV wavelength) light (Fitt et al. 2001; Williams and Hallock 2004). For example, field investigations in the 1990s, primarily in the Florida Keys, found *Amphistegina* bleaching to begin in spring, peak in midsummer, and decline in late summer to fall, coinciding with the crescendo of high energy solar irradiance (Hallock et al. 1995, 2006; Williams et al. 1997; Williams 2002). Further, in vitro studies of *Amphistegina* growth, test shape, and bleaching under variable light conditions (Hallock et al. 1986; Williams and Hallock 2004) reveal a high sensitivity among these forams to light stress (Hallock 2011).

However, given that temperature stress and light intensity are seasonally coupled in the world's oceans, it is arguable that they play synergistically detrimental roles in driving instances of bleaching and population declines of Amphisteginidae forams and corals, globally (see Coles and Jokiel 1978; Mumby et al. 2001, 2004 and others). Thus,

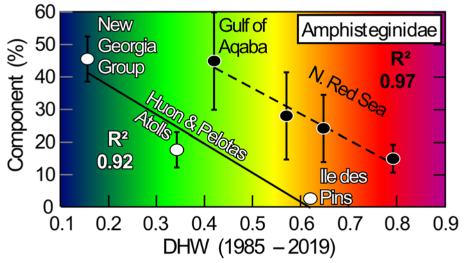

Fig. 5 Comparative plots of average relative abundances for Amphisteginidae tests from Solomon Islands, New Georgia Group, through New Caledonia, Huon and Pelotas Atolls and Ile des Pins (white circles and text; Humphreys et al. 2022) to those from this study (black circles and text). Plots reveal a similar pattern of decline in Amphisteginidae relative abundance along gradations of increasing heat stress

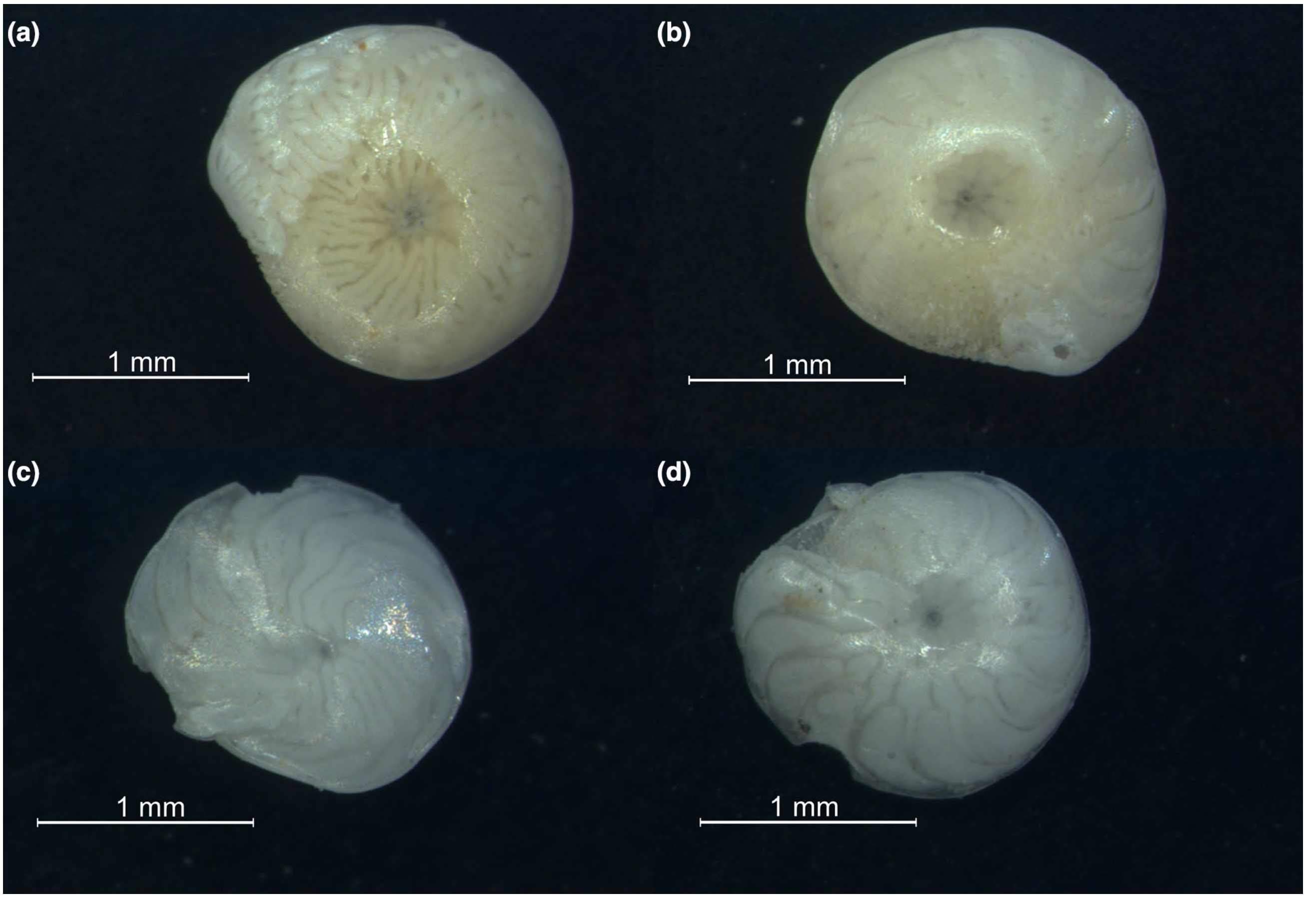

Fig. 6 Specimens of *Amphistegina lobifera* and *Amphistegina lessonii*. **a** *A. lobifera* dorsal view; **b** *A. lobifera* ventral view; **c** *A. lessonii* dorsal view; **d** *A. lessonii* ventral view. Both specimens selected from sample 36, Gulf of Aqaba

discovering a global bioindicator of reef temperature stress could prove doubly invaluable in its potential for helping to identify shallow coral reef ecosystems with histories of long-term thermal and light anomalies. Our report here, connecting long-term histories of temperature stress and Amphisteginidae forams in field collections from the N. Red Sea, buoys a similar finding from the South Pacific (Humphreys et al. 2022). Hence, these results enhance the potential of this cosmopolitan LBF family as a bioindicator of coral reef stress across a spectrum of reef environments spanning the tropics to high latitudes.

Conservative thermal resistance in the Gulf of Aqaba

Coral communities in the Gulf of Aqaba exhibit high temperature resistance (Krueger et al. 2017; Grattoli et al. 2017; Bellworthy and Fine 2017; Bellworthy and Fine 2021; Hammerman et al. 2021), to the point that the Gulf has been pitched as possessing the potential to become a coral refugia in the coming decades (Osman et al. 2018; Bellworthy et al. 2019; and others). Fine et al. (2013), for instance, hypothesized that the elevated heat tolerances of Gulf of Aqaba corals are the result of "selective filtering" during invasion from the Indian ocean. This hypothesis suggests that thermal tolerance expressed by hermatypic corals, in the moderately lower heat stresses of the Gulf of Aqaba, has been conserved for millennia without any obvious functional advantage. Similarly, *Amphistegina lobifera* forams from the Gulf of Aqaba also exhibit strong resistance to ocean heating events (Schmidt et al. 2016). In lab experiments, comparing the genetics and heat tolerance of a population of *A. lobifera* forams from the Gulf to a recently invaded population in the Eastern Mediterranean via the Suez Canal (a "Lessepsian" invasion), Schmidt et al. (2016) reported similar tolerances to high temperature in both the native and the invading populations, indicating that, like Gulf of Aqaba corals, these tolerances in forams are a conservative trait in regional populations of this LBF species. These authors´ findings not only serve to test the "selective filtering" hypothesis of Fine et al. (2013), but also conclude that

A. lobifera from this region have likely experienced similar filtering through high temperature settings in the southern Red Sea (Fine et al. 2013). Buttressing this conclusion are genetic analyses of members of *A. lobifera* from the Red Sea that indicate a similar Indian Ocean origin as that of the region's corals (Schmidt et al. 2016). Here, our report of declining time-averaged *A. lobifera* relative abundances along a gradient of increasing average heat stress, serves to bolster these previous findings by showing evidence of long-term death assemblages thriving in the waters of the Gulf. Our results therefore indicate the potential for *A. lobifera* to continue to find refuge in the Gulf of Aqaba in the near future, as populations continue to decline in the more heat-impacted waters of the Red Sea proper.

The Gulf of Aqaba is inhabited by two dominant species of shallow water forams—*Amphistegina lobifera* and *A. lessonii*—which populate the same habitats and show similar resistances to ocean heating events (Titelboim et al. 2019; Fig. 6). Our results, however, indicate that despite their similar adaptation to thermal stress, only time-averaged *A. lobifera* relative abundances decline with increasing thermal stress. The relative abundance of *A. lessonii*, by contrast, does not exhibit a significant response to heating stress. Reassuringly, our results also suggest that, despite the fact that *A. lobifera* in the northern Red Sea has historically adapted to thermal stress, this resistance does not appear to diminish the systematic response of this species to it, thereby bolstering the use of *A. lobifera* as a bioindicator. Additionally, the thermal tolerance that this species has acquired likely explains why relative abundances of *A. lobifera* in the Red Sea are less affected by heat stress than those from sites in New Caledonia. For example, Humphreys et al. (2022) report the relative abundance of Amphisteginidae death assemblages to average 2.4% of the total foram component, from atoll back-reef sands from New Caledonia, Ile des Pins, where 1985–2019 DHW averaged between 0.60 and 0.70 (Fig. 5). Here in the Red Sea, however, 1985–2019 DHW values of 0.70–0.86 coincide with Amphistiginidae forams averaging a 15% component of sediment foram tests (Fig. 5), likely elevated by the greater thermal resistance of *A. lobifera* (5.9%) and *A. lessonii* (8.8%) on these more thermally-impacted reefs.

Spatial distribution of Soritidae and Peneroplidae families in the Red Sea and Gulf of Aqaba

Soritidae and Peneroplidae relative abundances trend against those of *A. lobifera* (Fig. 2b, c), yet the oceanographic controls on this patterning remain inconclusive. In addition to Amphisteginidae forams, regional populations of *Sorites orbiculus* (Merkado et al. 2013) and *Peneroplis* spp. (Abu Tair and Langer 2010) have also become Lessepsian invaders of the eastern Mediterranean and likely share the same Indo-Pacific origin to that of Amphisteginidae (Merkado et al. 2013). However, except for the Gulf of Aqaba, the diversity and oceanographic relationship of benthic forams in the Red Sea is not extensively known (Schmidt et al. 2015). Hence, these shared migratory and evolutionary characteristics with that of Red Sea *Amphistegina* species could hint at a similar selective filtering of heat resistant Soritidae and Peneroplidae forams into the northern Red Sea. Furthermore, the positive associations for Peneroplidae forams and average SST/DHW in our model may indicate higher heat tolerances for regional genera in this family, than Amphisteginidae at the same sites, and could allow for some niche-filling in response to Amphisteginidae declines (Figs. 2, 4).

While RDA indicates a dimensional alignment of Soritidae and depth (Fig. 4a), the depth range of our samples is too limited to decipher any meaningful conclusion from these results. For instance, the collection depths in this study span 7 and 12 m, which is well within the range of all the taxa identified in this study (Table 1). We acknowledge that our findings for Soritidae and Peneroplidae LBF families are preliminary, and we stress the need for the continued cataloguing of these important protists as it pertains to local oceanography and bathymetry. Such work is required to illuminate how foram populations adjust to geographic temperature variability. Future research, using the collections from this region, aims to analyze all forams to the level of genus and expand the scope of these multivariate models, in an attempt to discern whether our positive Soritidae and Peneroplidae trends with DHW are, indeed, indicative of inter- and intra-generic species shuffling, competition, or opportunism / niche-filling.

Familial identification as a rapid foram assessment methodology

Sorting and fully assessing foram assemblages in laboratory samples takes time, is costly, and requires higher levels of experience. Hence, there has been a push in recent years to provide approaches that remain scientifically robust, while simultaneously reducing the amount of time and taxonomic knowledge required for routine evaluation of foram assemblages in reef samples. For example, Prazeres et al. (2020) discuss the potential use of a 125 µm mesh sieve to remove very fine sand-sized particles as a time-saving measure, as it eliminates small fragments and juveniles that are often difficult to identify (Schönfeld et al. 2012)—a methodology we employ here. Further, in recent years it has become acceptable to reduce identifications to broader taxonomic rankings, where appropriate, or limit the count threshold from the traditional standard of 300 tests-per-sample, as studies show that 150–200 tests are often statistically sound (Prazeres et al. 2020). The advantage of narrow taxonomic assessments is the acquisition of more detailed information related to foram assemblages. The disadvantage, however, is time. For example, identification to the level of species, while necessary in descriptive analyses, can take up to five times longer per sample (Prazeres et al. 2020), whereas classification to genus level can efficiently generate reliable data for statistical analysis, in many cases. In this vein, Humphreys et al. (2022) and this current Red Sea analysis have opted to broaden the initial taxonomic classifications to that of family as a way of rapidly assessing large scale LBF responses to oceanographic controls. Our results indicate that this methodology serves to swiftly reveal robust patterns of response that can help identify candidate forams for more detailed consideration. Ultimately, the successful deployment of any global foram-based bioindicator will benefit from the considerate balancing of scientific robustness and methodological efficiency.

Conclusion

This study of benthic foraminiferal relative abundances in the Red Sea is consequential as it proves that a promising bioindicator that was recently identified in the Pacific Ocean also performs in the some of the most northerly shallow coral reefs on Earth. Specifically, the time averaged relative abundance of *Amphistegina lobifera* in our samples negatively track increasing average thermal stress and drives broad Amphisteginidae familial patterning in our statistical model. This discovery suggests that the Amphisteginidae family responds systematically to thermal stress in both tropical and sub-tropical reef settings, thereby raising the promise of a new and globally applicable bioindicator, in the same vein as that pioneered for nutrient stress by Hallock et al. (2003). Lacking long-term diver records of reef health, the Red Sea is excellently poised for the use of a foram bioindicator to fill this critical data gap.

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Declarations

Competing interests All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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