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Photic stress on coral reefs in the Maldives: The *Amphistegina* bleaching index

Stephanie Stainbank^{a,*}, Silvia Spezzaferri^a, Valentina Beccari^a, Pamela Hallock^b,
Arthur Adams^{c,1}, Aurelie Angeloz^d, Daniela Basso^e, Annalisa Caragnano^f, Nicolo Del Piero^d,
Patrick Dietsche^a, Ines Eymard^d, Nicholas Farley^d, Marine Fau^a, Anneleen Foubert^a,
Bruno Lauper^a, Anael Lehmann^g, Marine Maillat^d, Haileyesus Negga^a, Luis Ordonez^d,
Giovan Peyrotty^d, Valentin Rime^a, Andres Rüggeberg^a, Iris Schoellhorn^g, Lucas Vimpere^d

^a University of Fribourg, Department of Geosciences, Chemin du Musée 6, 1700 Fribourg, Switzerland

^b University of South Florida, College of Marine Science, St Petersburg, United States

^c University of Bern, Institute of Geological Sciences, Baltzerstrasse 1 + 3, 3012 Bern, Switzerland

^d University of Geneva, Department of Earth Sciences, Rue des Maraîchers 13, 1205 Geneva, Switzerland

^e Università degli Studi di Milano-Bicocca, Dipartimento di Scienze dell'Ambiente e della Terra, Piazza della Scienza 4, 20126 Milano, Italy

^f Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche, via Brecce Bianche, 60131 Ancona, Italy

^g University of Lausanne, Faculty of Geosciences and Environment, Géopolis, 1015 Lausanne, Switzerland

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ABSTRACT

The *Amphistegina* Bleaching Index (ABI) was applied to three Maldivian reefs in the Rasdhoo and North Ari Atolls in 2018, during normal sea surface temperature conditions. This dataset was then compared with a 2015, pre-coral bleaching study. The results provide a context for the verification and application of the ABI in outlining the photo-inhibitory stress status of coral reefs outside of the Florida Reef Tract where it was originally developed. The sampling periods encompass different seasons and temperature regimes. The 2015 field sampling preceded the El Niño induced, mass coral-bleaching events of 2015 and 2016. It was carried out in late April and early May, during the dry season, when temperatures exceeded 31.5 °C and photosynthetically active radiation (PAR) was high. The 2018 sampling took place near the September equinox, towards the end of the monsoon, when PAR was again high, though water temperatures were ~30 °C. Although there were slightly higher percentages of bleached *Amphistegina* in 2018, there were also higher percentages of juveniles, indicating either that (1) the chronic stress was insufficient to impact asexual reproduction or (2) the onset of stress was within the past few weeks; the latter hypothesis was supported by an increase in PAR and temperature coinciding with the time of sampling. From the ABI plots it is possible to distinguish between the 2015 (high data scatter), highly stressed pre-bleaching conditions with elevated photo-oxidative stress levels, and the near-baseline conditions represented by the 2018 dataset (tight data clustering). Overall, this study thus shows the potential of *Amphistegina* populations and the ABI in forecasting bleaching events, and contributing to the question of the resilience potential of the coral reefs as a whole. It also highlights the usefulness and suitability of the ABI, within Maldivian coral reefs, as an indicator of photo-inhibition through photo-oxidative stress that can increase susceptibility to coral bleaching as water temperatures approach or exceed the bleaching threshold.

1. Introduction

Coral reefs are biodiversity hotspots which are under increasing stress from climate-related pressures. These ecosystems host a wide array of species, with great biological, economic and recreational significance. Their survival and health is thus paramount, particularly for the development of small island states such as the Maldives, Mauritius and Bahamas. The establishment of long-term monitoring programs is one of the first steps in

coral reef conservation. Through global initiatives by the International Union for Conservation of Nature (IUCN), National Oceanic and Atmospheric Administration (NOAA), World Wide Fund for Nature (WWF), among others, monitoring programs have gained traction over the last few decades, yet their scope and ease of implementation is paramount to their overall success. With an increase in frequency of climate-induced coral-bleaching events, from every 25–30 years in the 1980s to approximately every 6 years in recent years (Hughes et al., 2018), this is particularly

* Corresponding author.

E-mail address: stephanie.hayman@unifr.ch (S. Stainbank).

¹ Current address: École polytechnique fédérale de Lausanne, 1015 Lausanne, Switzerland.

important now more than ever.

The term “bleaching”, in relation to symbiont-bearing organisms, is typically denoted as a temporary or permanent loss of the symbiotic microalgae or pigments (Glynn, 1996). Causes of bleaching can include a combination of abiotic factors such as drastic changes in seawater temperatures or salinity (both high or low) (Jokiel and Coles, 1990), visible or ultraviolet solar irradiance (e.g., Gleason and Wellington, 1993; Glynn, 1996) and heavy metal concentrations or sedimentation rates (Hoegh-Guldberg and Smith, 1989), as well as biotic factors such as disease. Yet, the main drivers of coral-bleaching events are thermal, with the inclusion of its associated photo-inhibitory stresses. Thermal stress makes endosymbionts more susceptible to photo-inhibition through photo-oxidative reactions, resulting in a subsequent loss of symbionts (Coles et al., 1976; Goreau and Hayes, 1994; Glynn, 1996; Hoegh-Guldberg, 1999; Talge and Hallock, 2003).

Conventional coral-reef monitoring programs are typically oriented towards the assessment of the health and diversity of coral and fish communities, which can include *in situ* counts as well as photographic or videographic transects (e.g. Rogers et al., 1994; Hill and Wilkinson, 2004; Cruz et al., 2008; Ruzicka et al., 2013; Wartenberg and Booth, 2015; Roberts et al., 2016). In this way, assemblage changes and the visual health of selected indicator species/groups can be established and monitored. While we acknowledge the importance of this approach, species-level identification of corals and fish requires specialist knowledge. Additionally, the visual reflection of stress in corals (i.e., bleaching) is known to be a delayed response (e.g. Gardner et al., 2017; Krueger et al., 2015; Stimson, 1997). With this in mind, a low-cost, simple biotic index, the *Amphistegina* Bleaching Index (ABI), was proposed by Hallock et al. (2006) and Ramirez (2008) for assessing coral reef photo-inhibitory stress using symbiont-bearing, unicellular protists called foraminifera. This index uses the reef-dwelling larger benthic foraminiferal genus *Amphistegina*, which hosts diatom endosymbionts. *Amphistegina* spp. are sensitive to environmental stress over days to weeks (Hallock et al., 2006) and, as such, their populations are able to respond more rapidly, in comparison to corals, to changes in the environment. In particular, *Amphistegina* specimens bleach when exposed to photo-inhibitory stress, the susceptibility to which can be independently induced by increases in light and/or temperature (Hallock et al., 2006; Prazeres et al., 2016). Schmidt et al., (2011) demonstrated that temperatures above 31 °C have a negative effect on *Amphistegina*, while temperatures around 30 °C significantly impact the photosynthetic activity of symbionts (Sinutok et al., 2011; Uthicke et al., 2012).

The ABI was developed on *Amphistegina gibbosa* populations living

on the Florida Reef Tract (Hallock et al., 2006; Ramirez, 2008) and first implemented by Spezzaferri et al. (2018) in the Maldivian Archipelago located in the northern equatorial Indian Ocean. However, the establishment of this Index within long-term coral-reef monitoring programs requires testing by comparison with baseline conditions outside of Florida. Importantly, Spezzaferri et al. (2018) observed bleaching in Maldivian *Amphistegina* populations a few weeks before the first observed coral bleaching in June 2015 and, as such, their dataset represents a disturbance period, a deviation from baseline conditions.

Pisapia et al. (2016) demonstrated a decadal recovery time for the Maldivian reefs following the 1998 mass coral-bleaching event. Their compilation of data from 1993 to 2016 showed that, while the Maldivian reefs had an eventual, yet protracted recovery time, a shift in coral assemblage cover was noted and the future resilience of these ecosystems was questioned with the prospect of future bleaching events. This is particularly true considering the extensive El Niño related coral-bleaching event in 2015–2016, which, in relation to the level of thermal stress, was more severe than expected (NOAA Coral Reef Watch., 2015; Spezzaferri et al., 2018).

Within this context, the purpose of our study was to (1) use our 2018 (post-disturbance, baseline) dataset to verify the use and potential of the ABI within the Maldives; (2) to use both the *Amphistegina* populations and ABI to explore the resilience of three Maldivian island coral reefs in response to this 2015–2016 El Niño induced mass-bleaching event and (3) as human pressures (e.g., local settlements, tourist resorts) are evident in the Maldives, we utilise the ABI to further facilitate the distinction between water quality (local) and photo-oxidative (global) stresses. The overall significance for the incorporation of this biotic index within long-term coral-reef monitoring programs was thus assessed.

2. Materials and methods

2.1. Study site

The Maldivian Archipelago is located in the equatorial Indian Ocean between 7°07'N to 0°40'S and 72°33'E to 73°45'E. It encompasses 16 complex atolls, which include > 1100 islands. In 2018, within the framework of a Training Through Research Cruise sponsored by the “Conférence Universitaires de Suisse Occidentale” (CUSO), three of these islands from the Rasdhoo and North Ari Atolls (Rasdhoo, Vihamaafaru and Maayafushi), were surveyed, each representing an example of different island management plans (i.e., uninhabited, resort and community, Fig. 1). All three were

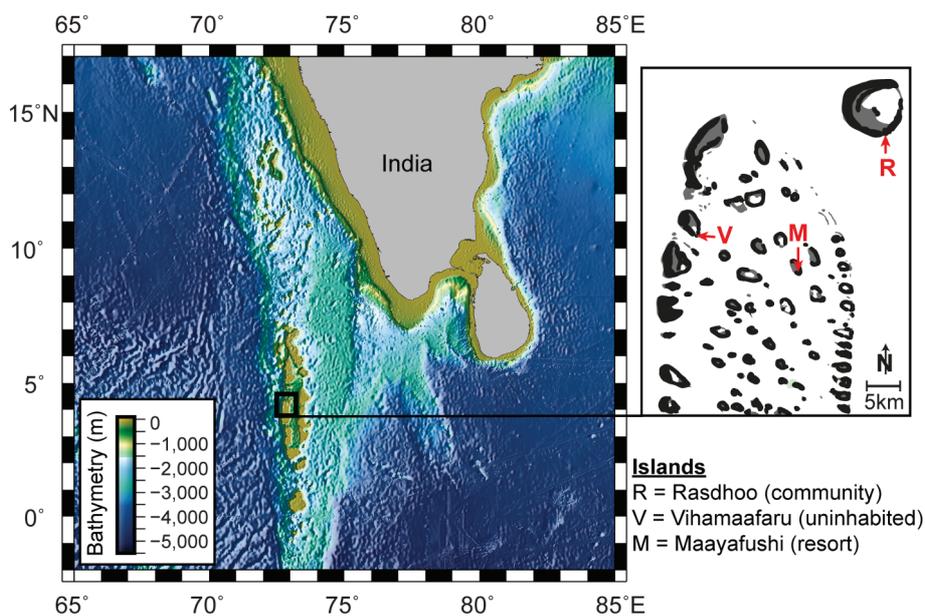


Fig. 1. Location map of the Maldives in the northern equatorial Indian Ocean, showing the three investigated islands, Rasdhoo (R), Vihamaafaru (V) and Maayafushi (M). (CEBCO Compilation Group, 2010)

Table 1
Amphistegina classification categories.

Species	Size	Degree of bleaching
<i>A. lessonii</i>	Juvenile	Normal (N)
<i>A. lobifera</i>	Adult	Partially bleached (BP)
<i>A. radiata</i>		Bleached (B)

previously sampled in 2015 during the International Union for Conservation of Nature (IUCN) REGENERATE Cruise and thus the 2018 sampling campaign served as the next step in establishing a time-series to monitor the recovery and resilience status of these reefs following a mass-bleaching event (Pisapia et al., 2017a; Beccari et al., 2020; Caragnano et al., submitted). Whilst the REGENERATE cruise aimed to establish if different island management strategies impacted the health of the reef, this was not the

primary focus of the 2018 sampling campaign. Nevertheless, representatives from the same island classification groups were included in the 2018 sampling, albeit with a reduced subset, to facilitate a more comprehensive long-term monitoring regime.

2.2. Sampling strategy

Rasdhoo represents a community-managed island, Vihamaafaru is an uninhabited island, and Maayafushi is a resort island. At each of these islands' reefs, two sites at 10 m water depth were chosen in 2018 to correspond to sites previously sampled in 2015 (Moritz et al., 2017; Pisapia et al., 2017a,b). At each site, two to three coral rubble pieces were collected by SCUBA divers at three locations approximately 50 m apart. Once collected, the rubble was processed immediately on board according to the protocol outlined in Ramirez (2008) and used in 2015

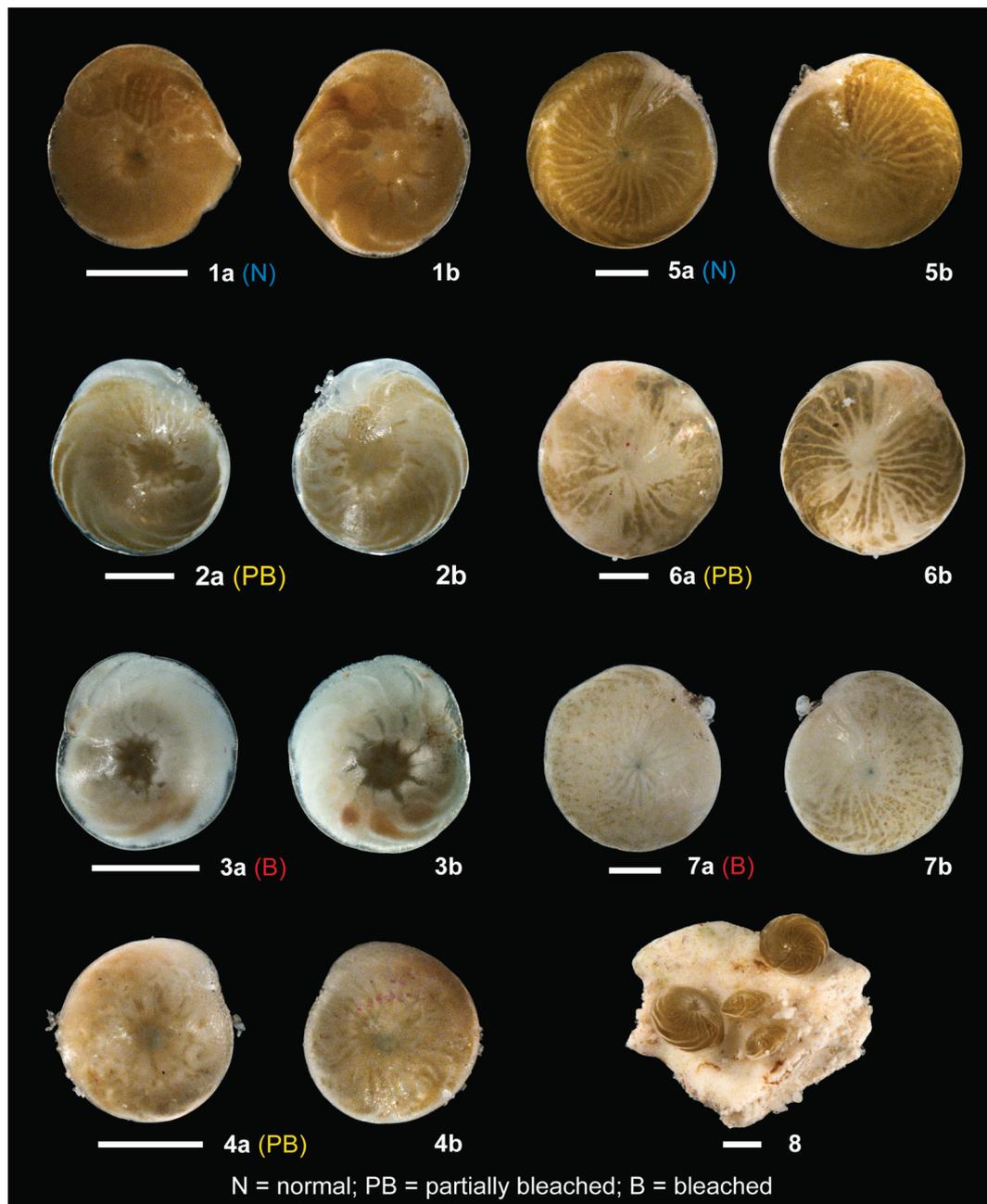


Fig. 2. Representative specimens for each bleaching class: Normal (N), Partially Bleached (PB) and Bleached (B) for *A. lessonii* (1–3); *A. lobifera* (4) and *A. radiata* (5–7) with an example of *A. lessonii* individuals attached to a coral rubble fragment (8). Scale bars = 500 μm.

by Spezzaferri et al. (2018), ensuring avoidance of exposure to bright lights and temperature extremes at all times. Briefly, the rubble pieces were gently scrubbed with a small brush to remove all biogenic material and the resultant slurry stored in petri dishes and allowed to settle for at least two hours. While the temperature was not monitored during this interval, care was taken to store the samples in an air-conditioned room out of direct sunlight to ensure the organisms were not subjected to any further stress.

Subsequently, all living *Amphistegina*, identified by the presence of coloured protoplasm together with a visual check for pseudopodial activity, were classified according to three criteria: species, size and degree of bleaching (Table 1). While this is not in the original ABI protocol, three typical Indo-Pacific species, *Amphistegina lessonii*, *Amphistegina lobifera* and *Amphistegina radiata*, were distinguished to provide supplementary data. As previously mentioned, the ABI was originally developed on *Amphistegina gibbosa*, a species which is restricted to the Atlantic and Caribbean. Similarly, juvenile and adult size classes were distinguished according to Mateu-Vicens et al. (2009), with the former being $\sim < 1$ mm in size and the latter $\sim 1-3$ mm. The customary ABI bleaching categories evaluated were: Normal (N) = with no observable bleaching; partially bleached (PB) = $< 50\%$ of bleached surface and bleached (B) = $> 50\%$ of bleached surface. The PB category includes slightly mottled and mottled individuals whereas the B category is defined by individuals which are very mottled, pale or white. Representative examples for each bleaching class for *A. lessonii* and *A. radiata*, and, when possible for *A. lobifera*, are displayed in Fig. 2. Each rubble piece was photographed on a gridded tray to estimate its planar area, which was calculated using the Carl Zeiss Axio Vision 4.8 software (Supplementary Material 1).

The obtained *Amphistegina* data (Supplementary Material 2) were used to generate the ABI graphs. The ABI plots the density rank (number of living *Amphistegina* per 100 cm^2 rubble area) into three categories: $< 10/100\text{ cm}^2$, $100-1000/100\text{ cm}^2$, $> 1000/100\text{ cm}^2$ against the bleaching rank (relative abundance of bleached specimens in three categories: $< 5\%$, $5-40\%$ and $> 40\%$). The resultant matrix is divided into nine quadrants, each accounting for a different ecological status (for further explanation on the allocation of the ecological statuses please see the original ABI publications by Hallock et al. (2006) and Ramirez (2008)).

Seawater samples and photosynthetically active radiation (PAR) light readings were collected in conjunction with the benthic samples at the sea surface (0 m) and at 10 m water depth (Note the collection times at each sampling site varied). Immediately after collection, pH, temperature and salinity of the water samples were measured using a multiparameter meter OrionTM Star A325. The PAR readings were measured using a Li-COR LI-193SA Spherical Underwater Quantum Sensor.

3. Results

3.1. Abiotic water parameters

Some variability in the two main bleaching-related abiotic variables, PAR and seawater temperature, was noted (Fig. 3). Due to different sampling times (Supplementary Material 3), light readings were not all taken at the same time of day, furthermore cloud conditions varied (according to Copernicus Climate Change Service (C3S), 2017 cloud cover varied between 0.25 and 1 over the study period, where 0 = no cloud cover and 1 = full cloud cover). As such, some variability was seen in the PAR readings (e.g., the high PAR readings at

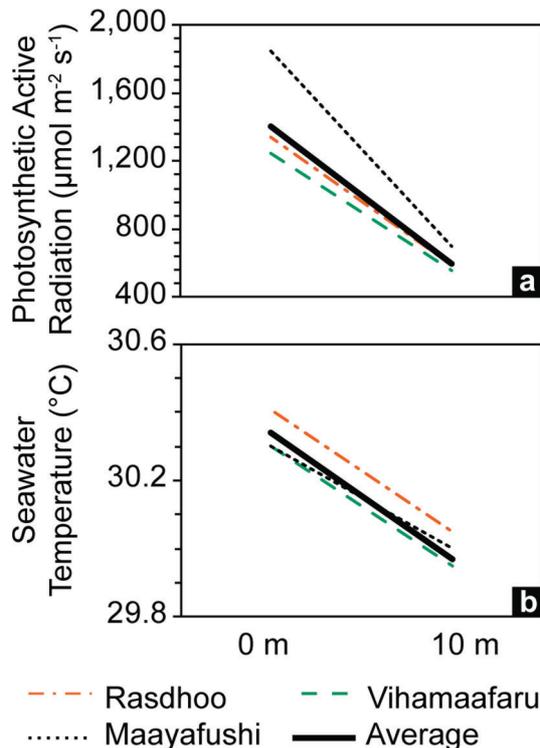


Fig. 3. Mean *In situ* photosynthetic active radiation (PAR) and seawater temperature measurements from 0 m and 10 m water depth for each of the three investigated islands in 2018 (i.e. Rasdhoo, Vihamaafaru and Maayafushi).

Maayafushi), however, PAR extinction coefficients were quite consistent, averaging 0.086 (range 0.075–0.097; Supplementary Material 3, Fig. 3). Temperature marginally decreased with depth (mean $\Delta = 0.34\text{ }^\circ\text{C}$) while salinity and pH, 35.03 ± 0.09 PSU and 8.18 ± 0.05 , respectively, were both consistent between islands and within normal seawater values for the Indian Ocean (Ramamirtham, 1968; Spezzaferri et al., 2018).

3.2. Changes in *Amphistegina* spp. populations

The 2015 and 2018 data on bleaching in *Amphistegina* were marginally different, with a mean decline in normal, healthy individuals from 70% to 64% (Fig. 4). The mean proportion of bleached individuals increased from 7% in 2015 to 10% in 2018 (Fig. 4). The abundance of *Amphistegina* (ind/100 cm^2) varied somewhat among sample sites across the three islands in both years. Mean abundances in 2015 were 214 ± 199 , 111 ± 43 and 186 ± 116 (ind/100 cm^2), whereas mean abundances in 2018 were 205 ± 72 , 217 ± 76 and 139 ± 76 (ind/100 cm^2), for Rasdhoo, Vihamaafaru and Maayafushi, respectively (Fig. 4). Considering the overall community composition, juvenile specimens were much less abundant in 2015, with an average of 16% overall across the islands in comparison to 30% in 2018.

The ABI plot shows more scatter in the combined bleaching and abundance data from 2015 than in 2018 (Fig. 5). In 2015, the ABI plots for Rasdhoo were most variable in abundance and in bleaching rank, with data points scattered among four quadrats: BA, CA, BB and CB. In 2018, the data points also fell in those four quadrats, but were more

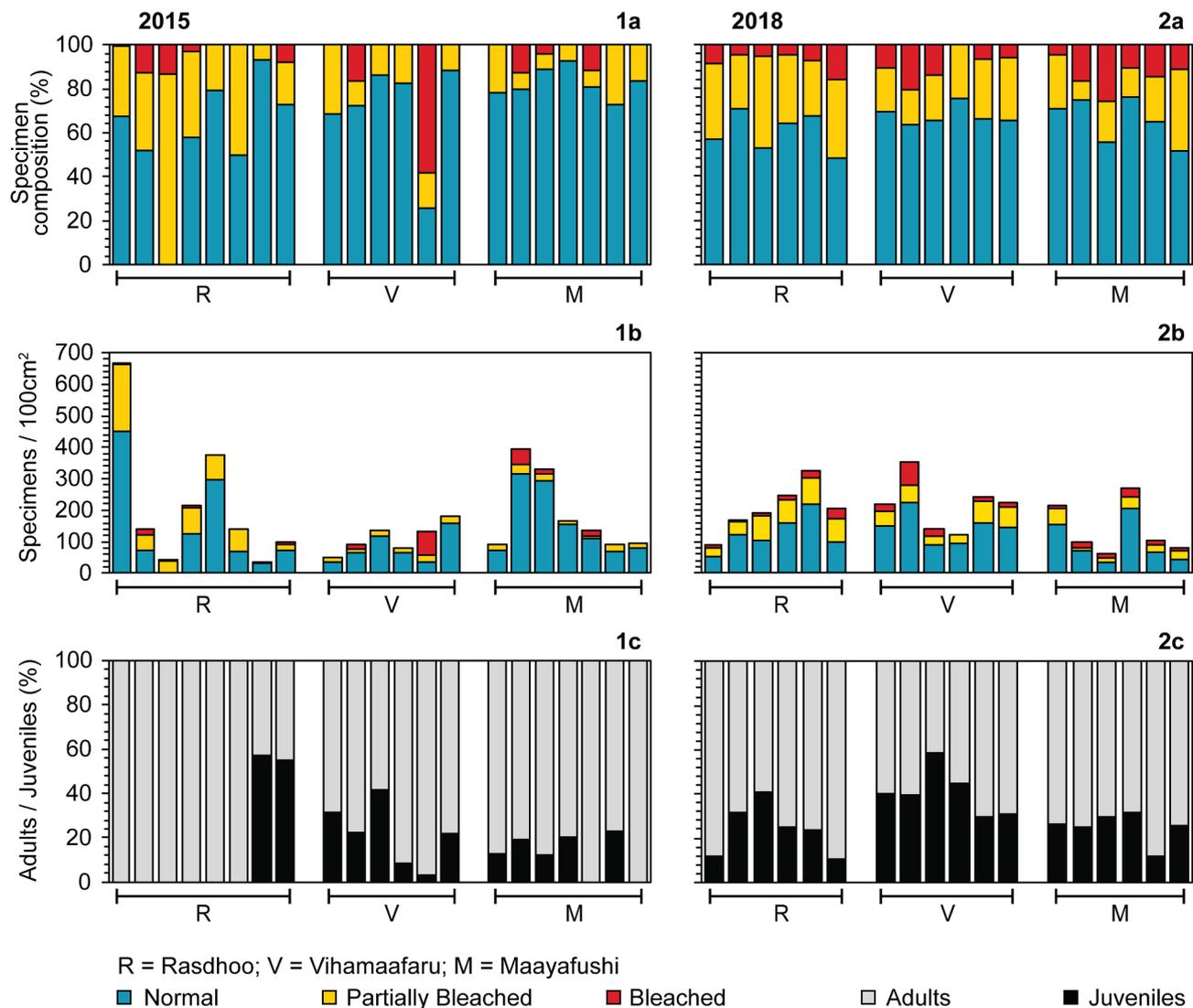


Fig. 4. Data composition comparison: (1) 2015 and (2) 2018 showing (a) specimen composition, (b) specimen abundance and (c) adult/juvenile proportions for all sites at each of the three island reefs, Rasdhoo (R), Vihamaafaru (V), Maayafushi (M) (Note: 2015 sites which had < 15 specimens are not shown as they were not used in the ABI interpretations).

tightly clustered, with two-thirds falling in the lower left of the BA quadrante denoting ‘photo-inhibitory stress either chronic and mild or recent and moderate’.

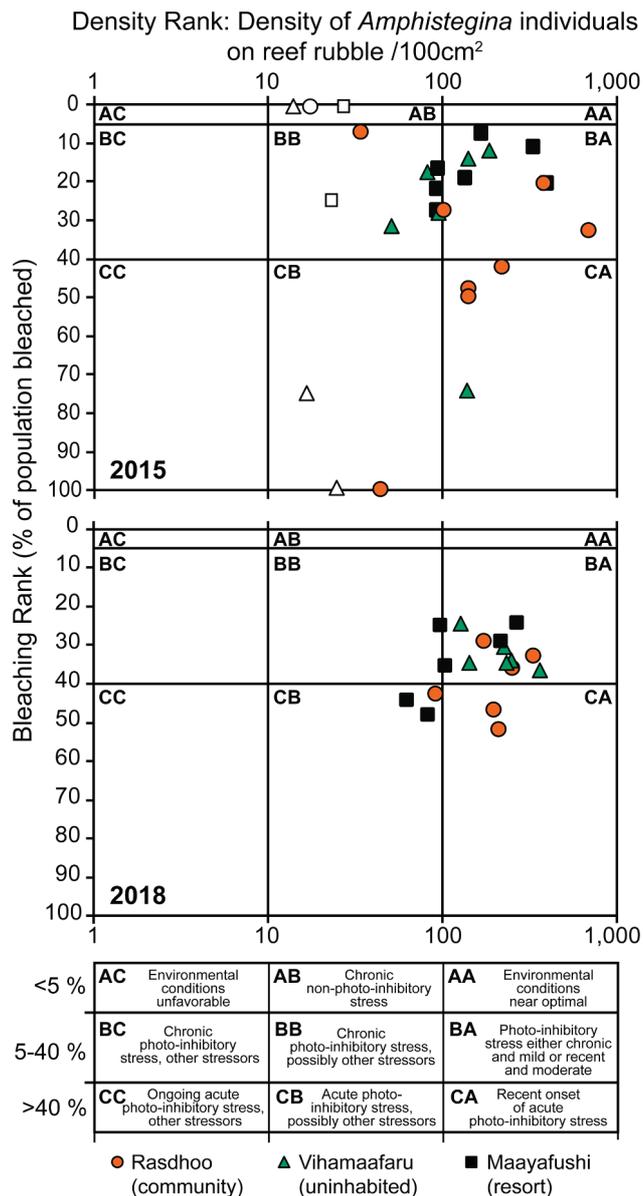
4. Discussion

Maldivian coral reefs have among the highest diversity in the Indian Ocean (Naseer and Hatcher, 2004) and their remote location implies only local anthropogenic stresses and reduced continental influence. As such, they provide the perfect framework for the ABI to be used in a time-series study to assess the response of reefs in the context of our current changing climate. However, as this index has only previously been applied in a single study in the Maldives in 2015 (Spezzaferri et al., 2018), which preceded (by two weeks) a major coral-bleaching event, prior to its routine implementation in long-term monitoring programs the verification of the suitability of its application is required. Baseline conditions are subsequently provided by our 2018 dataset, however differences and influences of island management regimes, sampling months (in 2015 versus 2018), as well as reproductive timing are important considerations.

In 2015, most water parameters measured (salinity, dissolved oxygen, pH) were within the range typically reported in Indian Ocean

tropical environments and coral reefs during the warm, dry season (Ramamirtham, 1968; Wild et al., 2010; Zweng et al., 2013; Lauvset et al., 2015; Spezzaferri et al., 2018). The only deviations from standard water parameters were the exceptionally high seawater temperatures recorded at some sites (Spezzaferri et al., 2018). Benthic foraminiferal assemblages were also typical of tropical coral reefs, with minimal changes among sites with different management regimes (Pisapia et al., 2017b).

In 2018, the two main bleaching-related abiotic variables, PAR reaching the seafloor and seawater temperature, were relatively consistent among the investigated sites (Fig. 3), indicating that management regime was not detectably influencing water characteristics such as turbidity. For example, at Rasdhoo, as it is a community island, there is the probability of sewage discharge into the sea, yet the PAR extinction coefficients revealed that water clarity is comparable to clarity at the resort and uninhabited island sites (Note: while Maayafushi has slightly higher PAR readings, which can be attributed to the measurements being taken near midday in conjunction with limited cloud cover at the time of sampling, these readings are still representative as noted by the comparable PAR extinction coefficients). Even though no PAR readings were measured in 2015, considering the coherence and normality of the measured water parameters (salinity, dissolved oxygen,



(open symbols indicate sites which had specimens < 15; too few for interpretation)

Fig. 5. *Amphistegina* Bleaching Index (ABI) plot of 2015 vs 2018. An explanation for the ecological condition of each quadrant is given in the bottom panel (Samples with < 15 specimens were excluded to avoid misinterpretation as the distribution of foraminifera is not homogenous and is related to food availability on the rubble, the relative position of the rubble within the sediments as well as its exposure to light amongst others).

pH) across all sites, differing management regimes among the investigated islands was not likely a contributing factor to *Amphistegina* densities and bleaching ranks in either 2015 or 2018.

The 2015 and 2018 sampling campaigns were carried out in different months. In 2015, sampling occurred in late April and early May as temperatures were ~31 °C at the end of the dry season, following the spring peak in solar irradiance that occurs with the equinoxes at this latitude. In 2018, sampling occurred in early September, as the autumnal equinox was approaching, the monsoon was waning, and seawater temperatures were ~30 °C (Fig. 6). Therefore, seasonal differences in photo-oxidative stress and consequent reproductive success

were possible influences on *Amphistegina* bleaching and density rankings in the ABI plots (Fig. 5).

The abundances of juvenile *Amphistegina* were somewhat different between the 2015 and 2018 datasets. Temperature has been reported as a pivotal factor controlling reproduction in this genus (Gruber et al., 2007; Prazeres et al., 2016). In subtropical regions such as Eilat, Florida, and Hawaii, bi-annual reproduction has been reported. Gruber et al. (2007) noted June and January reproduction in *A. lobifera* in the Gulf of Aqaba (Red Sea), in contrast to only summer reproduction in the Mediterranean. This difference was attributed to the winter seawater temperatures in the Mediterranean being below the reproductive tolerance of this species. In Florida, Hallock et al. (1995, 2006) and Williams et al. (1997) reported predominantly spring-early summer peaks in juvenile abundances in *A. gibbosa*, indicating asexual reproduction, with evidence for sexual reproduction in the autumn. Similarly, in *A. lobifera* in Hawaii, Muller (1977) found peak juvenile abundances, indicating asexual reproduction, in May–August, with evidence for sexual reproduction in October–November. She also found juvenile *A. lessonii* to be common throughout the year, with strong peaks in abundance in March and April (Muller, 1977). Based upon both field and culture studies, she interpreted the typical life span of asexually-produced *A. lobifera* to be about 6 months and of *A. lessonii* to be 3–4 months.

Although no data are available on the reproductive strategy of *A. lessonii*, *A. lobifera* and *A. radiata* for the Maldives, the equatorial position, tropical climate and limited variations in seasonal sea surface temperature (SST) are more similar to Palau, in the Western Caroline Islands in the Pacific Ocean (Muller, 1977; Hallock, 1984), than to the subtropical localities noted above. In Palau, Muller (1977) reported juvenile size classes present throughout the year in both *A. lessonii* and *A. lobifera*, with small positive deviations from the overall size-frequency distributions at roughly 3–4 month intervals. Thus, in the Maldives, juvenile *A. lessonii* and *A. lobifera* could be expected to be relatively abundant year-round.

However, the Palau study was carried out long before the discovery of bleaching in *Amphistegina*. Hallock et al. (1995) documented the profound impact of bleaching on reproduction in *A. gibbosa* in Florida. Following the onset of acute bleaching in June 1991, >80% of adult specimens exhibited some degree of bleaching when sampled in September that year. By the following May, the densities of *A. gibbosa* had declined by >90%, indicating failure of individuals that had experienced bleaching to successfully reproduce. The relatively few specimens found in May were exhibiting some degree of bleaching and juveniles were uncommon. In subsequent years, Hallock et al. (1995) and Williams et al. (1997) reported low juvenile abundances in spring and summer months when bleaching was most acute. However, in years when higher percentages of normal-appearing specimens were found in spring and summer, higher densities of *A. gibbosa* and higher percentages of juveniles were also recorded.

Comparisons of overall densities and juvenile densities, together with bleaching prevalence from the samples from the Maldives in April – May 2015 and September 2018, appear somewhat contradictory. Although there were somewhat higher percentages of specimens exhibiting bleaching in 2018, overall densities were sufficient to place most samples in the BA range, indicating either chronic bleaching or recent onset of more acute bleaching. The relatively high percentages of juveniles are consistent with that assessment, that is, either the intensity of bleaching was insufficient to seriously impact reproductive success or reproduction occurred before the onset of more acute bleaching. The timing near the end of the monsoon, with elevated PAR reported in September 2018 (Fig. 7), along with the abundance of juveniles, are consistent with an interpretation of normal reproduction prior to a more recent, moderate photo-oxidative stress that induced

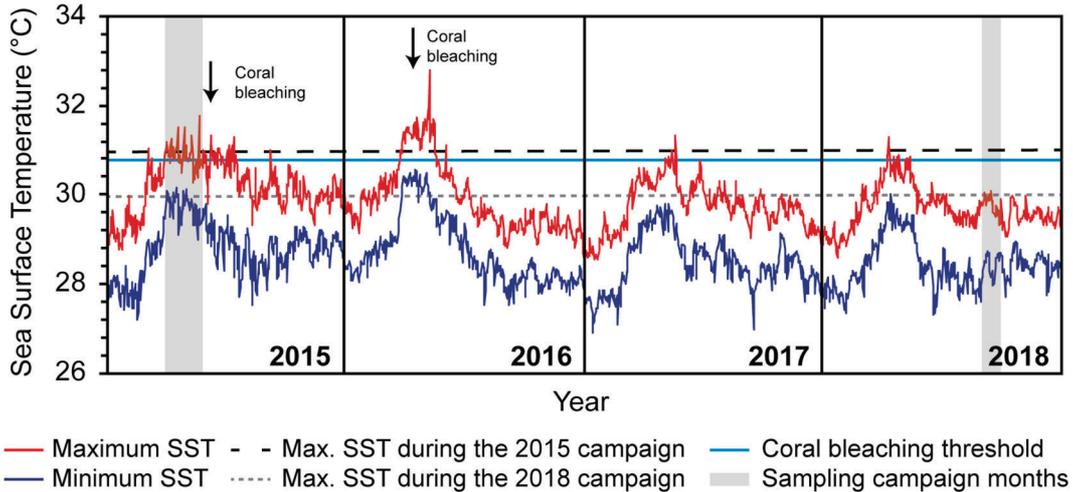


Fig. 6. Sea surface temperature (SST) time-series (2015–2018) for the Maldives. The 2015 and 2018 sampling campaign months are illustrated together with their mean maximum SSTs. The Maldives coral bleaching threshold is also shown for comparison (NOAA Coral Reef Watch., 2018).

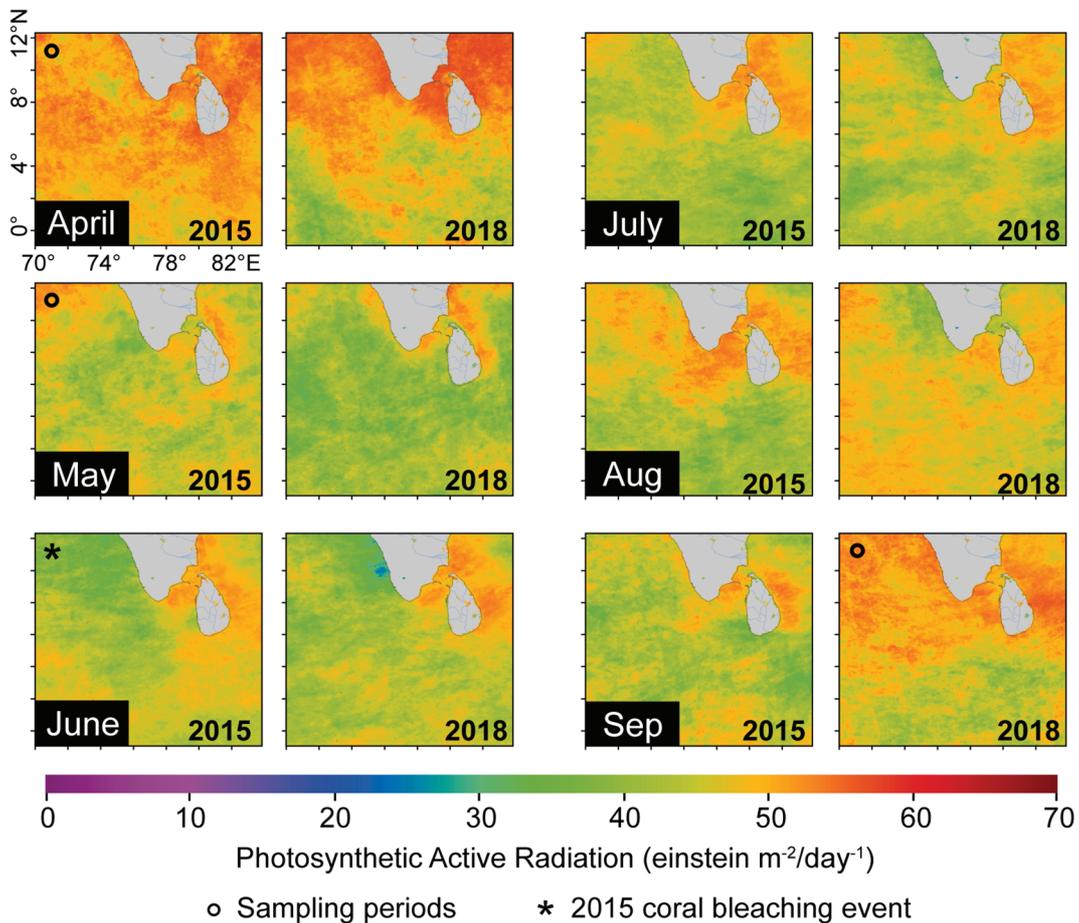


Fig. 7. Photosynthetic active radiation (PAR) graphs for the 2015 vs 2018 sampling periods (NASA/GSFC/OBPG, accessed 25-02-2019) for the surface ocean: 2015 (April–May) and 2018 (September) sampling periods are indicated (circles) together with the timing of the first coral bleaching observed in June 2015 (black star). (Note: $1 \mu\text{mol s}^{-1} \text{m}^{-2} \equiv 1 \mu\text{E s}^{-1} \text{m}^{-2} \equiv 6.02 \times 10^{17} \text{photons s}^{-1} \text{m}^{-2}$, LI-COR, 1991).

bleaching in the near-adult individuals that had not yet reproduced. In contrast, the sampling in April–May 2015 was during an interval of rising seawater temperatures that prompted a NOAA coral-bleaching alert (NOAA Coral Reef Watch., 2015; Fig. 6). Furthermore, the sampling occurred a few weeks before the June onset of an extensive El

Niño-related coral-bleaching event that was unexpectedly severe for this region. Spezzaferri et al. (2018) suggested that the proportions of bleached specimens in April–May 2015 were related to photo-inhibitory stress resulting from both seawater temperatures exceeding 30°C , and even reaching up to 32°C , during the peak of seasonal solar

irradiance and water transparency (Figs. 6 and 7). Moreover, the data show lower juvenile counts than in 2018, which was sampled during an interval of lower (<30 °C) seawater temperatures (Figs. 4 and 6). This increased stress status is indicative in the scatter on the 2015 ABI plot (Fig. 5).

Overall, based on the SST data (Fig. 6), 2017 and 2018 appear to be representative of baseline conditions with marginal seasonal variations, as opposed to that observed in 2015 and 2016. The ABI dataset for September 2018, which is unaffected by differing island management regimes, revealed some bleaching in *Amphistegina*, which was likely induced by photo-oxidative stress that was either chronic and mild, or recent and moderate. While this indicates the ecosystem as a whole is still in a stressed state, following the 2015 and 2016 bleaching events, the higher abundance of juveniles in 2018 indicates that the *Amphistegina* populations are resilient. This conclusion is consistent with the Maldivian coral and benthic foraminiferal assemblage studies by Caragnano et al. (submitted) and Beccari et al. (2020), conducted on the same reefs and sites. They found that, while high proportions of the reef cover were dominated by sediment and coral rubble (dead coral skeletons), small (<5 cm) coral colonies were abundant, supporting a natural resilience and possible recovery for these reefs back to their pre (2015 and 2016) bleaching state.

5. Conclusions

The *Amphistegina* Bleaching Index (ABI) can be an effective indicator of photo-inhibitory stress affecting coral reefs and as shown is applicable for use in the Maldives in the Indian Ocean. The sampling protocol for the ABI is non-destructive and has the potential to be easily included into preexisting monitoring programs (Hallock et al., 2006). The ABI, if assessed one to two months prior to peak seasonal temperatures, can indicate potential for coral bleaching when temperature peaks. That is, the greater the photo-oxidative stress in the months preceding peak temperature, the more stressed the corals will be when peak temperature occurs. Peak photic stress occurs around the summer solstice at subtropical latitudes, while it occurs with the equinoxes in equatorial latitudes such as the Maldives. Other than the similarities in solar irradiance associated with proximity to an equinox, environmental conditions preceding the two sampling events were somewhat different, which is reflected in the ABI plots. As such, the results highlight the potential of this biotic index for broader Maldivian coral-reef monitoring applications, especially in the context of current global climate changes and the prospect of future bleaching events.

Author contributions

SS participated in the cruise, contributed to sample collection, processed samples, analysed and interpreted the data, wrote the paper. SS participated in the cruise, processed samples, analysed and interpreted the data, wrote the paper. VB participated in the cruise, contributed to sample collection, processed samples, analysed and interpreted the data, wrote the paper. PH participated in the cruise, processed samples, analysed and interpreted the data, wrote the paper. MF participated in the cruise and contributed to sample collection. AA, AA, DB, AC, NDP, PD, IE, NF, AF, BL, AL, MM, HN, LO, GP, VR, AR, IS, LV participated in the cruise and contributed to data collection regarding seawater geochemistry.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.106257>.

References

- Beccari, V., Spezzaferri, S., Stainbank, S., Hallock, P., Basso, D., Caragnano, A., Pisapia, C., Adams, A., Angeloz, A., Del Piero, N., Dietsche, P., Eymard, I., Farley, N., Fau, M., Foubert, A., Lauper, B., Lehmann, A., Mailet, M., Negga, H., Ordonez, L., Peyrotty, G., Rime, V., Rüggeberg, A., Schoellhorn, I., Vimpera, L., 2020. Responses of reef bioindicators to recent temperature anomalies in distinct areas of the North Ari and Rasdhoo atolls (Maldives). *Ecol. Indic.* 112, 106128.
- Caragnano, A., Basso, D., Spezzaferri, S., Hallock, P., Adams, A., Angeloz, A., Beccari, V., Piero, N., Del, Dietsche, P., Eymard, I., Farley, N., Fau, M., Foubert, A., Lauper, B., Lehmann, A., Mailet, M., Negga, H., Ordonez, L., Peyrotty, G., Rime, V., Rüggeberg, A., Schöllhorn, I., Stainbank, S., Vimpera, L., submitted for publication. North Ari Atoll (Maldives): Coral decline following the 2016 bleaching event. *Mar. Fr. Res.*
- Coles, S.L., Jokiel, P.L., Lewis, C.R., 1976. Thermal tolerance in tropical versus subtropical Pacific reef corals. *Pacific Sci.* 30, 159–166.
- Copernicus Climate Change Service (C3S), 2017. ERA5: Fifth generation of ECMWF atmospheric reanalyses of the global climate. Copernicus Climate Change Service Climate Data Store (CDS), date of access. <https://cds.climate.copernicus.eu/cdsapp#!/home>.
- Cruz, I.C.S., Kikuchi, R.K.P., Leão, Z.M.A.N., 2008. Use of the video transect method for characterizing the Itacolomis reefs, eastern Brazil. *Brazilian J. Oceanogr.* 56, 271–280.
- Gardner, S.G., Raina, J.B., Nitschke, M.R., Nielsen, D.A., Stat, M., Motti, C.A., Ralph, P.J., Petrou, K., 2017. A multi-trait systems approach reveals a response cascade to bleaching in corals. *BMC Biol.* 15, 117. <https://doi.org/10.1186/s12915-017-0459-2>.
- GEBCO Compilation Group, 2019. GEBCO 2019 Grid. <https://doi:10.5285/836f016a-33be-6ddc-e053-6c86abc0788e>.
- Gleason, D.F., Wellington, G.M., 1993. Ultraviolet radiation and coral bleaching. *Lett. Nat.* 365, 836–838.
- Glynn, P.W., 1996. Coral reef bleaching: facts, hypotheses and implications. *Glob. Chang. Biol.* 2, 495–509. <https://doi.org/10.1111/j.1365-2486.1996.tb00063.x>.
- Goreau, T.J., Hayes, R.L., 1994. Coral bleaching and ocean “hot spots” *Ambio* 23, 176–180.
- Gruber, L., Almogi-Labin, A., Sivan, D., Herut, B., 2007. The life cycle of the symbiont-bearing foraminifera *Amphistegina lobifera*, a new arrival at the Israeli shelf. *Rap. Comm. int. Mer Médit.* 38, 491.
- Hallock, P., 1984. Distribution of selected species of living algal symbiont-bearing foraminifera on two Pacific coral reefs. *J. Foraminif. Res.* 14, 250–261.
- Hallock, P., Talge, H.K., Cockey, E.M., Muller, R.G., 1995. A new disease in reef-dwelling foraminifera: Implications for coastal sedimentation. *J. Foraminif. Res.* 25, 280–286.
- Hallock, P., Williams, D.E., Fisher, E.M., Toler, S.K., 2006. Bleaching in foraminifera with algal symbionts: implications for reef monitoring and risk assessment. *Anu. do Inst. Geociencias* 29, 108–128.
- Hill, J., Wilkinson, C., 2004. Methods for ecological monitoring of coral reefs. Australian Institute of Marine Science, Townsville doi: 10.1017/CBO9781107415324.004.
- Hoegh-Guldberg, O., 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshw. Res.* 50, 839–866. <https://doi.org/10.1071/MF99078>.
- Hoegh-Guldberg, O., Smith, J.G., 1989. The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. *J. Exp. Mar. Bio. Ecol.* 129, 279–303. [https://doi.org/10.1016/0022-0981\(89\)90109-3](https://doi.org/10.1016/0022-0981(89)90109-3).
- Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., Baird, A.H., Baum, J.K., Berumen, M.L., Bridge, T.C., Claar, D.C., Eakin, C.M., Gilmour, J.P., Graham, N.A.J., Harrison, H., Hobbs, J.-P.A., Hoey, A.S., Hoogenboom, M., Lowe, R.J., McCulloch, M.T., Pandolfi, J.M., Pratchett, M., Schoepf, V., Torda, G., Wilson,

- S.K., 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359, 80–83. <https://doi.org/10.1126/science.aan8048>.
- Jokiel, P.L., Coles, S.L., 1990. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs* 8, 155–162.
- Krueger, T., Hawkins, T.D., Becker, S., Pontasch, S., Dove, S., Hoegh-Guldberg, O., Leggat, W., Fisher, P.L., Davy, S.K., 2015. Differential coral bleaching-Contrasting the activity and response of enzymatic antioxidants in symbiotic partners under thermal stress. *Comp. Biochem. Physiol. Part A* 190, 15–25. <https://doi.org/10.1016/j.cbpa.2015.08.012>.
- Lauvset, S.K., Gruber, N., Landschützer, P., Olsen, A., Tjiputra, J., 2015. Trends and drivers in global surface ocean pH over the past 3 decades. *Biogeosciences* 12, 1285–1298. <https://doi.org/10.5194/bg-12-1285-2015>.
- LI-COR, 1991. LI-COR Radiation Sensors Instruction Manual. <https://www.licor.com/documents/w7yjhknnesn0191hpew4ty53lvcadu>.
- Mateu-Vicens, G., Hallock, P., Brandano, M., 2009. Test-Shape variability of *Amphistegina* d'Orbigny, 1826 as a paleobathymetric proxy: Application to two Miocene examples. *Geol. Probl. Solving with Microfossils A Vol. Honor Garry D. Jones. SEPM Special Publication*, doi: 10.2110/sepm093.067.
- Moritz, C., Ducarme, F., Sweet, M.J., Fox, M.D., Zgliczynski, B., Ibrahim, N., Basheer, A., Furby, K.A., Caldwell, Z.R., Pisapia, C., Grimsditch, G., Abdulla, A., 2017. The “resort effect”: can tourist islands act as refuges for coral reef species? *Divers. Distrib.* 23, 1301–1312. <https://doi.org/10.1111/ddi.12627>.
- Muller, P.H., 1977. Some aspects of the ecology of several large, symbiont-bearing foraminifera and their contribution to warm shallow-water biofacies. University of Hawaii, Ph.D Dissertation.
- NASA/GSFC/OBPG, Photosynthetically Available Radiation (PAR), Aqua MODIS - Monthly, 2002-present. v.2018.0. Accessed: 25-02-2019.
- Naseer, A., Hatcher, B.G., 2004. Inventory of the Maldives' coral reefs using morphometrics generated from Landsat ETM+ imagery. *Coral Reefs* 23, 161–168. <https://doi.org/10.1007/s00338-003-0366-6>.
- NOAA Coral Reef Watch., 2015. Bleaching Event Continues, June 2015 Update [WWW Document]. URL http://coralreefwatch.noaa.gov/satellite/analyses_guidance/global_bleaching_update_20150602.php.
- NOAA Coral Reef Watch., 2018. Maldives 5-km Bleaching Heat Stress Gauges (Version 3.1). Data Accessed: 20.05.2019 at <https://coralreefwatch.noaa.gov/vs/gauges/maldives.php>.
- Pisapia, C., Burn, D., Yoosuf, R., Najeeb, A., Anderson, K.D., Pratchett, M.S., 2016. Coral recovery in the central Maldives archipelago since the last major mass-bleaching, in 1998. *Sci. Rep.* 6, 34720. <https://doi.org/10.1038/srep34720>.
- Pisapia, C., Abdul Rahman, M., Abdulla, A., Basheer, A., Caldwell, Z., Ducarme, F., El Kateb, A., Fox, M., Furby, K., Ibrahim, M., Moritz, C., Schmidt, A., Spezzaferri, S., Sweet, M., Yoosuf, R., Zgliczynski, B., Grimsditch, G., 2017a. Baseline assessment of coral reefs of North Ari Atoll. IUCN and Government of Maldives, Maldives, Gland, Switzerland.
- Pisapia, C., El Kateb, A., Hallock, P., Spezzaferri, S., 2017b. Assessing coral reef health in the North Ari Atoll (Maldives) using the FORAM Index. *Mar. Micropaleontol.* 133, 50–57. <https://doi.org/10.1016/j.marmicro.2017.06.001>.
- Prazeres, M., Uthicke, S., Pandolfi, J.M., 2016. Changing light levels induce photo-oxidative stress and alterations in shell density of *Amphistegina lobifera* (Foraminifera). *Mar. Ecol. Prog. Ser.* 549, 69–78. <https://doi.org/10.3354/meps11698>.
- Ramamirtham, C.P., 1968. Vertical distribution of temperature, salinity and dissolved oxygen in the Maldivian region of the Indian Ocean. *Indian J. Fish.* 15, 27–39.
- Ramirez, A., 2008. Patch reefs in Biscayne National Park, FL: Sediments, foraminiferal distributions and a comparison of three biotic indicators of reef health. Unpublished Graduate Theses and Dissertations, <https://scholarcommons.usf.edu/etd/465/>.
- Roberts, T.E., Bridge, T.C., Caley, M.J., Baird, A.H., 2016. The point count transect method for estimates of biodiversity on coral reefs: Improving the sampling of rare species. *PLoS One* 11. <https://doi.org/10.1371/journal.pone.0152335>.
- Rogers, C.S., Garrison, G., Grober, R., Hillis, Z.-M., Franke, M.A., 1994. *Coral Reef Monitoring Manual for the Caribbean and Western Atlantic. National Park Service, Virgin Islands National Park*, pp. 114.
- Ruzicka, R.R., Colella, M.A., Porter, J.W., Morrison, J.M., Kidney, J.A., Brinkhuis, V., Lunz, K.S., MacAulay, K.A., Bartlett, L.A., Meyers, M.K., Colee, J., 2013. Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. *Mar. Ecol. Prog. Ser.* 489, 125–141. <https://doi.org/10.3354/meps10427>.
- Schmidt, C., Heinz, P., Kucera, M., Uthicke, S., 2011. Temperature-induced stress leads to bleaching in larger benthic foraminifera hosting endosymbiotic diatoms. *Limnol. Oceanogr.* 56, 1587–1602. <https://doi.org/10.4319/lo.2011.56.5.1587>.
- Sinutok, S., Hill, R., Doblin, M.A., Wuhrer, R., Ralph, P.J., 2011. Warmer more acidic conditions cause decreased productivity and calcification in subtropical coral reef sediment-dwelling calcifiers. *Limnol. Oceanogr.* 56, 1200–1212. <https://doi.org/10.4319/lo.2011.56.4.1200>.
- Spezzaferri, S., El Kateb, A., Pisapia, C., Hallock, P., 2018. In situ observations of foraminiferal bleaching in the Maldives, Indian Ocean. *J. Foraminif. Res.* 48, 75–84.
- Stimson, J., 1997. The annual cycle of density of zooxanthellae in the tissues of field and laboratory-held *Pocillopora damicornis* (Linnaeus). *J. Exp. Mar. Bio. Ecol.* 214, 35–48. [https://doi.org/10.1016/S0022-0981\(96\)02753-0](https://doi.org/10.1016/S0022-0981(96)02753-0).
- Talge, H.K., Hallock, P., 2003. Ultrastructural responses in field-bleached and experimentally stressed *Amphistegina gibbosa* (Class Foraminifera). *J. Eukaryot. Microbiol.* 50, 324–333. <https://doi.org/10.1111/j.1550-7408.2003.tb00143.x>.
- Uthicke, S., Vogel, N., Doyle, J., Schmidt, C., Humphrey, C., 2012. Interactive effects of climate change and eutrophication on the dinoflagellate-bearing benthic foraminifer *Marginopora vertebralis*. *Coral Reefs* 31, 401–414. <https://doi.org/10.1007/s00338-011-0851-2>.
- Wartenberg, R., Booth, A.J., 2015. Video transects are the most appropriate underwater visual census method for surveying high-latitude coral reef fishes in the southwestern Indian Ocean. *Mar. Biodivers.* 45, 633–646. <https://doi.org/10.1007/s12526-014-0262-z>.
- Wessel, P., Smith, W.H., 1991. Free software helps map and display data. *Eos. Trans. AGU* 72 (41), 441–446.
- Wild, C., Niggli, W., Naumann, M.S., Haas, A.F., 2010. Organic matter release by Red Sea coral reef organisms—Potential effects on microbial activity and in situ O₂ availability. *Mar. Ecol. Prog. Ser.* 411, 61–71. <https://doi.org/10.3354/meps08653>.
- Williams, D.E., Hallock, P., Talge, H.K., Harney, J.N., McRae, G., 1997. Responses of *Amphistegina gibbosa* populations in the Florida Keys (U.S.A) to a multi-year stress event (1991–1996). *J. Foraminif. Res.* 27, 264–269.
- Zweng, M.M., Reagan, J.R., Antonov, J.I., Locarnini, R.A., Mishonov, A. V., Boyer, T.P., Garcia, H.E., Baranova, O.K., Johnson, D.R., Seidov, D., Biddle, M.M., 2013. World Ocean Atlas 2013, Volume 2: Salinity, in: Levitus, S. (Ed.), NOAA Atlas NESDIS 74. pp. 39.