Coral Reefs
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RESEARCH

The *Amphistegina* bleaching index as a tool for evaluating reef-ecosystem health: new data from the Maldives & Australia provide updated insights

Torin Cannings[1] · Daniela Basso[2] · Sebastian Flöter[1] · Pamela Hallock[3] · Chiara Pisapia[4] · Benjamin J. Ross[5] · Stephanie Stainbank[1] · Silvia Spezzaferri[6] · Elias Samankassou[1]

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Abstract The *Amphistegina* bleaching index (ABI) provides a simple, low-cost method for assessing photo-oxidative stress in reef-dwelling foraminifera. The ABI, developed for Florida reefs, has been applied to assess the extent of such stress in several regions globally, including the Maldives, and now in Australia. Here, we assess the application of the ABI for capturing variability in photo-inhibitory stress across contrasting reef settings and temporal scales. We applied the ABI at four sites in the central Maldivian archipelago, adding a new assessment point to previous surveys conducted in 2015 and 2018, and at two sites at Lizard Island on the northern Great Barrier Reef, comparing austral winter (2022) and summer (2024) conditions. In the Maldives, comparisons with previously published data from the same sites collected in 2015 and 2018 indicate very low levels of bleaching in 2025, with the geometric mean of bleached specimens at 2%, compared to 7% in 2015 and 10% in 2018. Mean abundances of *Amphistegina* remained broadly consistent, although slight reductions may reflect local environmental differences or residual effects of recent stress events. At Lizard Island, Australia, seasonal variation was pronounced, with austral summer 2024 samples showing elevated bleaching relative to winter 2022. ABI scores reflected these differences in bleaching and population structure across sampling intervals. Combined with environmental measurements, the ABI provides a repeatable approach for assessing photo-oxidative stress and detecting differences between baseline conditions and periods of elevated bleaching risk.

Highlights

- The *Amphistegina* bleaching index (ABI) has now been applied at the same Maldivian sites in 2015, 2018, and 2025, recording the lowest levels of foraminiferal bleaching in 2025, with some residual evidence of earlier stress.
- We applied the ABI for the first time in the Great Barrier Reef, sampling in austral winter 2022 and austral summer 2024 and observing seasonal shifts in bleaching and size structure.
- The ABI is confirmed as a robust, repeatable, and cost-effective biomonitoring tool.
- Responses of *Amphistegina* populations support long-term assessments of reef health.

Silvia Spezzaferri: Deceased

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✉ Torin Cannings
torincannings@unige.ch

[1] Department of Earth Sciences, University of Geneva, Rue Des Maraîchers 13, 1205 Geneva, Switzerland

[2] Department of Earth and Environmental Sciences, University of Milano-Bicocca; CoNISMa, ULR of Milano-Bicocca, Piazza Della Scienza 4, 20126 Milano, Italy

[3] College of Marine Science, University of South Florida, 140 Seventh Ave. S, St. Petersburg, FL 33701, USA

[4] SHAMS, General Organization for Conservation of Coral Reef and Sea Turtles in Red Sea, 23412 Jeddah, Saudi Arabia

[5] Rosenstiel School of Marine, Atmospheric, and Earth Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

[6] Department of Geosciences, University of Fribourg, Chemin Du Musée 6, 1700 Fribourg, Switzerland

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Introduction

Coral reefs are among the most biodiverse ecosystems on Earth; however, their vulnerability has become increasingly apparent over recent decades (e.g. Bove et al. 2022; Sully et al. 2022; Virgen-Urcelay and Donner 2023). Coral reef ecosystems face increasing environmental pressures, which threaten their biodiversity and the ecosystem services they provide, including food security, livelihoods, and coastal protection for millions of people (Woodhead et al. 2019; Bindoff et al. 2022; Sing Wong et al. 2022; Najeeb et al. 2025).

Threats to coral reef ecosystems include a range of global, regional, and local stressors, including rising sea surface temperatures, changes in seawater pH, and changes in water quality, such as nutrient enrichment and declining water transparency (e.g. Wilkinson 1999; Harborne et al. 2017; Hoegh-Guldberg et al. 2023; Bieg et al. 2024). Many of these stressors affect photosymbiotic reef organisms, including corals, giant clams, and larger benthic foraminifera, which rely on algal symbionts for a substantial proportion of their energy requirements (Douglas 2003; Baker et al. 2008). Bleaching refers to the loss or reduction of algal symbionts and/or their photosynthetic pigments from host tissues, resulting in the characteristic paling of host tissues (Brown 1997; Douglas 2003). Symbiont loss can reduce growth and reproduction, increase mortality, and contribute to the degradation of coral reef ecosystems through the loss of reef-building corals. During mass bleaching events, this process is primarily driven by prolonged marine heatwaves, often exacerbated by high irradiance, which disrupt photosynthesis and promote the production of reactive oxygen species, ultimately leading to symbiont loss (e.g. Downs et al. 2002; Weis 2008; Rädecker et al. 2021). Although oxidative stress is a widely supported mechanism of bleaching, the cellular pathways leading to symbiont loss remain an active area of research and involve multiple interacting processes (e.g. Rädecker et al. 2021; Helgoe et al. 2024). Loss of symbionts can also be triggered by darkness, changes in salinity, pollution, sedimentation, and biotic factors (e.g. disease and parasitism) (e.g. Glynn 1996; Hoegh-Guldberg 1999). Since the 1980s, marine heatwaves and associated mass bleaching events have increased markedly in frequency, duration, and severity (Bove et al. 2022; Sully et al. 2022; Virgen-Urcelay and Donner 2023).

Observing and monitoring bleaching in coral reefs can be challenging (Madin et al. 2019; Obura et al. 2019), often relying on costly aerial surveys and underwater surveys, which may be limited in spatial coverage. Assessing the health of populations of the abundant larger benthic foraminifer, *Amphistegina,* can provide a cost-effective method for monitoring some stressors, particularly elevated heat and light intensity, in reef ecosystems (Hallock et al. 2006; Ramirez 2008). These protists are abundant in tropical and subtropical reef environments, contribute significantly to carbonate production, and host algal symbionts that are sensitive to photo-oxidative stress (Hallock et al. 2006). Because *Amphistegina* responds rapidly to photo-oxidative stress generated through the interaction of elevated temperature and irradiance (e.g. Hallock et al. 1986, 1995; Downs et al. 2005), visible *Amphistegina* bleaching can develop within days of exposure, often preceding visible bleaching in corals. Consequently, *Amphistegina* bleaching status has been proposed as an early indicator of environmental stress and bleaching-related conditions (Spezzaferri et al. 2018; Stainbank et al. 2020).

These characteristics formed the basis for the development of the *Amphistegina* bleaching index (ABI), a standardised approach for quantifying visible bleaching in *Amphistegina* populations. Early observations demonstrated that visible bleaching in *Amphistegina* was associated with chlorophyll loss and deterioration of diatom symbionts (Hallock et al. 1995; Talge and Hallock 1995). Subsequent observations from reef systems across the Caribbean and Indo-Pacific demonstrated that bleaching responses were widespread within the genus, supporting the development of the ABI as a practical indicator of photo-oxidative stress and reef condition (Hallock et al. 2006; Ramirez 2008). The ABI is based on two parameters: the density of living *Amphistegina* (individuals cm^{-2}) and the proportion of individuals exhibiting partial or complete bleaching. The combined position of these factors within the ecological condition matrix of Ramirez (2008) is used to assess reef conditions. Independent of the ABI framework, *Amphistegina* abundance has been suggested as a bioindicator for longer-term thermal stress in the Red Sea and tropical Pacific (Humphreys et al. 2022a, 2022b). Despite the demonstrated sensitivity of *Amphistegina* to thermal and photo-oxidative stress, the application of the ABI remains geographically restricted, having only been used in the Maldives (Spezzaferri et al. 2018; Stainbank et al. 2020) and Florida Keys (Hallock et al. 2006; Ramirez 2008). Expanding the application of the ABI across contrasting reef systems, and across multiple temporal resolutions, is therefore important for evaluating its broader utility as a reef monitoring method.

This study presents new ABI results from two reef regions. In the Maldives, we extend the previously published ABI record (from 2015 and 2018) with a new sampling campaign conducted in May 2025, resulting in three surveys spanning a decade. The 2015 sampling (Spezzaferri et al. 2018), conducted in late April and early May, occurred prior

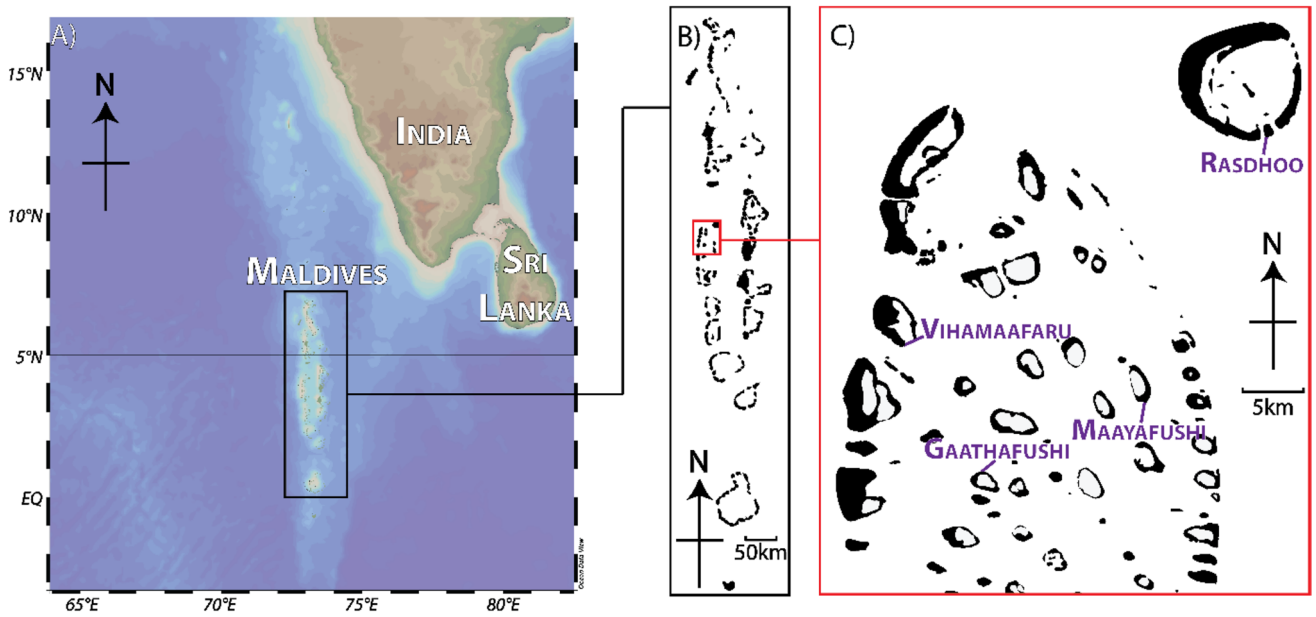


Fig. 1 The location of the Maldivian study sites. **A** Location of the Maldives relative to the Indian subcontinent. **B** The location of Alifu Alifu (North Ari) Atoll within the Maldivian archipelago. **C** The location of sites sampled in this study within Alifu Alifu Atoll

to an El Niño–related bleaching event that caused extensive coral mortality globally, including in the Maldives, where coral bleaching was observed in June 2015. The 2018 sampling (Stainbank et al. 2020), carried out in early September, documented conditions following recovery from the 2015–2016 bleaching event. In 2025, sampling was conducted in early May, temporally similar to the 2015 dataset, but in this case the year following widespread coral bleaching in 2023–2024 (Reimer et al. 2024; Byrne et al. 2025).

In addition, we present ABI data for the first time from Lizard Island on the northern Great Barrier Reef, a long-established focal site for coral bleaching research. Samples were collected during August 2022 (austral winter) and February 2024 (austral summer), capturing conditions representative of both baseline and disturbed states associated with the 2023–2024 global coral bleaching event (Byrne et al. 2025; Reimer et al. 2024). These data provide an initial ABI reference for the Great Barrier Reef and a foundation for any future long-term applications of the method in this region.

The aims of this study were to (1) extend the existing Maldives ABI record with post-bleaching observations from 2025, allowing comparison with the previously published 2015 and 2018 surveys, and (2) apply the ABI for the first time on the Great Barrier Reef by establishing baseline and bleaching-period datasets from Lizard Island. The two regions are treated as independent case studies rather than being compared directly, allowing the applicability and limitations of the ABI to be assessed across contrasting reef settings.

Methods

Study design

Study area-Maldives

The Maldivian sampling sites are located within Alifu Alifu (North Ari) Atoll in the central Maldives (Figs. 1 and 2). The remote location of the archipelago in the Indian Ocean limits continental influence (e.g. riverine runoff and terrestrial sediment input), making the reefs well suited for long-term ABI studies investigating climate-related reef change (Spezzaferri et al. 2018; Stainbank et al. 2020). The reefs are also characterised by high coral diversity (Naseer and Hatcher 2004).

Alifu Alifu (North Ari) Atoll is one of 16 complex atolls in the Central Maldivian Archipelago (Equatorial Indian Ocean) (Fig. 1). In this study, we also include Rasdhoo Atoll as part of Alifu Alifu Atoll. Rasdhoo Atoll is a geologically discrete small atoll to the northeast of Alifu Alifu Atoll but is often included in the Alifu Alifu Atoll for geographic and administrative reasons (Fig. 1). The reefs at these sites form part of the atoll structures, with shallow reef flats and fore-reef slopes ranging from 1 to 10 m depth.

This study revisited three islands (Maayafushi, Rasdhoo, and Vihamaafaru) within the Alifu Alifu Atoll that were previously sampled in both 2015 (Spezzaferri et al. 2018) and 2018 (Stainbank et al. 2020; Fig. 2). These sites were originally selected to represent three different management categories: resort (Maayafushi), community (Rasdhoo),

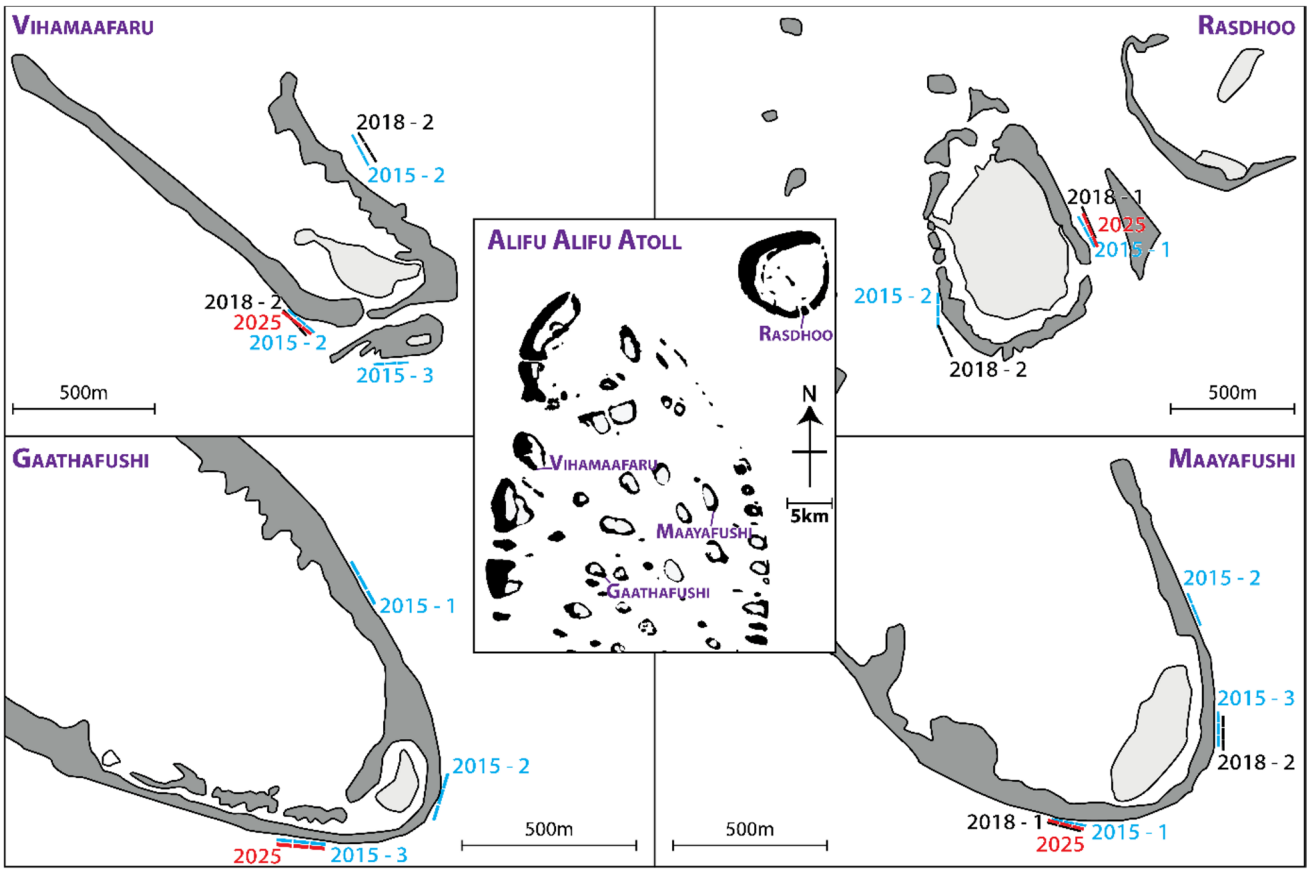


Fig. 2 The location of transects sampled at each site sampled in 2015, 2018, and 2025 within Alifu Alifu (North Ari) Atoll

and uninhabited (Vihamaafaru). During the 2025 survey, Vihamaafaru was found to support agricultural activity and could therefore no longer be considered fully uninhabited. Consequently, Gaathafushi, an uninhabited island that had also been sampled in 2015 but not in 2018 (Spezzaferri et al. 2018), was included to retain an example of an uninhabited island within the study design.

Both previous studies applying the ABI in the Maldives (Spezzaferri et al. 2018; Stainbank et al. 2020) found no relationship between land use and ABI. However, to maintain consistency with the earlier work and to ensure that ABI scores remain unaffected by land use, we again selected sites spanning a range of island management profiles. However, during sampling in 2025, it was noted that Gaathafushi, while an uninhabited island, is now used for some leisure activities from a hotel on the nearby island of Fesdhoo (*c.* 1.7 km S), which underwent substantial renovation in 2024–2025. This may mean that this island is not completely unaffected by local anthropogenic influence (Table 1).

Study area – Australia

The Australian sampling sites are located at Lizard Island (also known as Jiigurru or Dyiigurra), 27 km from the Australian mainland on the northern Great Barrier Reef (Fig. 3). Here, a granitic island group is enveloped by a fringing reef with a semi-enclosed lagoon system (2–15 m deep). The influence of tide and wind drives hydrodynamics at Lizard Island, with wind strongly influencing current speeds across the shallow reef environment occupied by most reef-dwelling organisms (Philipps and Bellwood 2024). Conditions at Lizard Island have supported high coral diversity and reef complexity, and the reef system is well studied, with documented responses to environmental disturbances (e.g. Pratchett 2010; Madin et al. 2018; Raoult et al. 2025). Sampling took place at two sites, North Point and Watson Bay (Fig. 3). Watson Bay is close to the island's only hotel, whereas North Point is located on the more remote northern tip of the island.

Sampling was conducted at two separate time intervals to capture different solar and thermal conditions. The first collection occurred in August 2022 (austral winter), representing baseline/low stress conditions. The second

Table 1 Summary of the Maldivian study sites, island management categories, geographic coordinates and survey years. All study sites are fringing house reefs within Alifu Alifu (North Ari) Atoll, with Rasdhoo included for geographical and administrative consistency. *Indicates that the island management category changed between sampling periods; see text for details

Site	Island management	Latitude	Longitude	Survey period
Maayafushi	Resort	4°04′15.7″ N	72°53′09.8″ E	April/May 2015, September 2018, May 2025
Rasdhoo	Community	4°15′51.3″ N	72°59′38.3″ E	April/May 2015, September 2018, May 2025
Vihamaafaru	Uninhabited*	4°07′39.2″ N	72°44′39.3″ E	April/May 2015, September 2018, May 2025
Gaathafushi	Uninhabited*	4°01′27.6″ N	72°48′42.9″ E	April/May 2015, May 2025

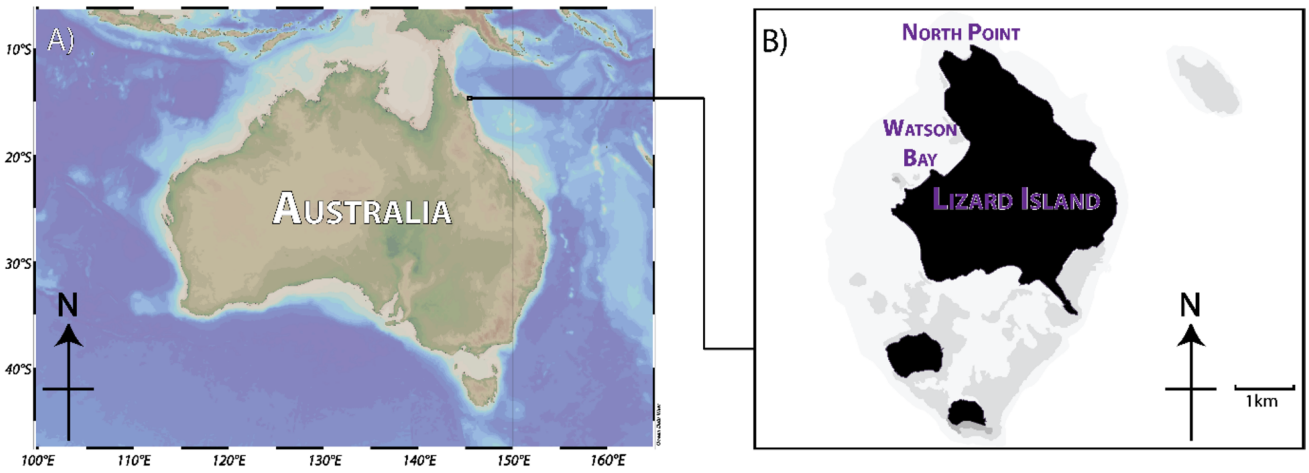


Fig. 3 The location of the Australian study sites. **A** Location of the Lizard Island system relative to Australia. **B** The location of sites sampled in this study at Lizard Island

Table 2 Summary of the Lizard Island study sites, reef settings, geographic coordinates, and survey periods. Both sites are located on fringing reefs surrounding Lizard Island (Jiigurru/Dyiigurra) on the northern Great Barrier Reef

Site	Reef setting	Latitude	Longitude	Survey period(s)
Watson Bay	Leeward fringing reef	14°39′45.7″ S	145°26′58.4″ E	August 2022, February 2024
North Point	Exposed fringing reef	14°38′41.7″ S	145°27′14.1″ E	August 2022, February 2024

collection took place in February 2024 (austral summer), during the 2023–2024 global bleaching event, when the northern Great Barrier Reef experienced prolonged marine heat stress (Raoult et al. 2025). During February 2024, Degree Heating Weeks (DHW) exceeded 6 °C-week at Lizard Island (NOAA 2026). These time points allowed assessment of ABI performance under both relatively stable and heat-stressed conditions (Table 2).

ABI sampling

At each site, three 50-m transect lines were laid at an approximate depth of 10 m, orientated roughly parallel to the reef crest to maintain consistent depth profiles and minimise variability in light availability and associated environmental conditions among sampling locations. Along each transect, coral rubble samples were collected at 0, 25, and 50 m, with 2–3 rubble pieces taken per sample point for ABI assessment. Samples were collected during one dive per site, with each dive lasting 45–60 min. Immediately after surfacing and reaching the dive boat, samples were placed into covered buckets containing ambient seawater to minimise exposure to elevated temperature and light prior to processing. Previous studies in the Maldives used three transects across three separate sites for each island location. However, as no significant differences were identified among sites within islands (Spezzaferri et al. 2018; Stainbank et al. 2020), the 2025 survey design consisted of three transects within a single representative site at each island (Fig. 2).

At all sites, several environmental parameters were recorded at the time of sampling. One bottom water (from the depth of sampling) sample and one surface water sample were taken and measured at each site. Surface temperature, salinity, and pH were measured using Hanna Reef Tester meters (manufacturer-reported accuracy: ± 0.5 °C for temperature, ± 0.1 for pH, and ± 2% for salinity). In the Maldives, Hanna HI781 low-range nitrate testers (manufacturer-reported accuracy of ± 0.25 ppm, resolution of 0.01 ppm) were used to detect any substantial differences in nitrate concentrations between sites. Sampling in the Maldives occurred at the onset of the monsoon season and on different days (one site per day), during which rainfall was variable prior to sampling. Sampling at Lizard Island in 2024 took place over multiple days; therefore, water samples were taken and analysed at each site during each day of sampling. Two bottom water samples (from the depth of sampling), one taken at each site during 2022 sampling at Lizard Island, were also sent to the Tropwater laboratory at James Cook University for analysis to determine nutrient concentrations at each site (see Supplementary Material). Overall, nutrient concentrations were low across all sites, with no consistent differences observed between locations (Supplementary Table 7). As a result, nutrient analyses were not repeated during the 2024 sampling.

ABI sample processing and scoring

Rubble samples were processed following the method of Williams et al. (1997). Each piece was gently brushed to dislodge encrusting organisms, including *Amphistegina*. The resulting slurry was poured into large petri dishes and left undisturbed for at least 2 h, giving living foraminifers time to migrate to the surface. This step was carried out in a dimly lit room maintained at 20–22 °C to minimise any additional stress on the specimens.

All live *Amphistegina*, identified by the presence of pigmentation and/or pseudopodia, were then picked manually under a stereomicroscope using a fine paintbrush and forceps, identified to species level, separated into size categories, and assessed for visible bleaching. Specimens were sorted according to their bleaching status and size category prior to ABI assessment. Processing (identification, picking, and categorisation) time varied depending on specimen abundance but generally required approximately 15–30 min per sample following initial sample preparation (i.e. brushing rubble and waiting for foraminifera to rise to the surface). In previous studies from the Maldives, individuals were categorised as juvenile if they were < 1 mm in diameter and as adult if >1 mm (Spezzaferri et al. 2018; Stainbank et al. 2020). However, these size thresholds do not necessarily correspond to published developmental categories, where juveniles are defined as <0.6 mm in diameter, pre-adults range from 0.6–1 mm, and adults exceed 1 mm (e.g. Hallock et al. 1995; Williams et al. 1997; Cannings et al. 2026). To maintain consistency with previous Maldivian datasets, the same size categories were retained in this study for both Maldivian and Australian samples. Therefore, specimens are referred to only as <1 mm and >1 mm categories, with the former encompassing juvenile and pre-adult stages and the latter generally representing adult individuals.

Once picked, each living individual was examined under a stereomicroscope and assigned to one of three bleaching categories based on the visible loss of the characteristic golden-brown symbiont colour. Specimens with no evidence of symbiont loss were considered normal; those with ≤50% of their test surface showing visible symbiont loss were classed as partially bleached; and those with >50% of the test surface showing visible symbiont loss were deemed bleached. The surface area of each rubble piece was measured using photographs taken on a gridded tray and analysed in ImageJ to estimate the density of living *Amphistegina* (individuals/100 cm^2).

For each sample, population density (the number of individuals per 100 cm^2 of rubble) and bleaching prevalence (the percentage of all individuals showing any sign of bleaching) were then interpreted using the ecological condition matrix of Ramirez (2008) (see results), which is based on the premise that healthy reef environments support high densities of living *Amphistegina*, whereas chronically stressed reefs support lower population densities. The proportion of bleached individuals provides an indication of the severity of recent photo-oxidative stress, with low bleaching prevalence indicating little or no photo-inhibitory stress, intermediate bleaching suggesting chronic or mild recent stress, and high bleaching prevalence indicating recent or ongoing acute photo-inhibitory stress. The combination of these two parameters was used to classify ecological condition.

Data were analysed descriptively to assess patterns in *Amphistegina* bleaching prevalence and population density among survey periods and locations. Comparisons among years and sites were based on observed differences in bleaching prevalence, size structure, and population density. Formal statistical analyses were not applied because the study was designed primarily as a multi-year observational assessment of bleaching patterns rather than a hypothesis-testing study with replicated experimental sampling.

As discussed in detail by Stainbank et al. (2020), the original ABI protocol was established for only *A. gibbosa,* the western Atlantic–Caribbean counterpart of *A. lessonii*. However, in previous studies using the ABI in the Maldives, all three species of *Amphistegina* present were included in bleaching analysis. Therefore, in this study, as with previous studies in the Maldives, the species composition of *Amphistegina* assemblages was recorded, but not discussed further. Counts of species, including size and bleaching

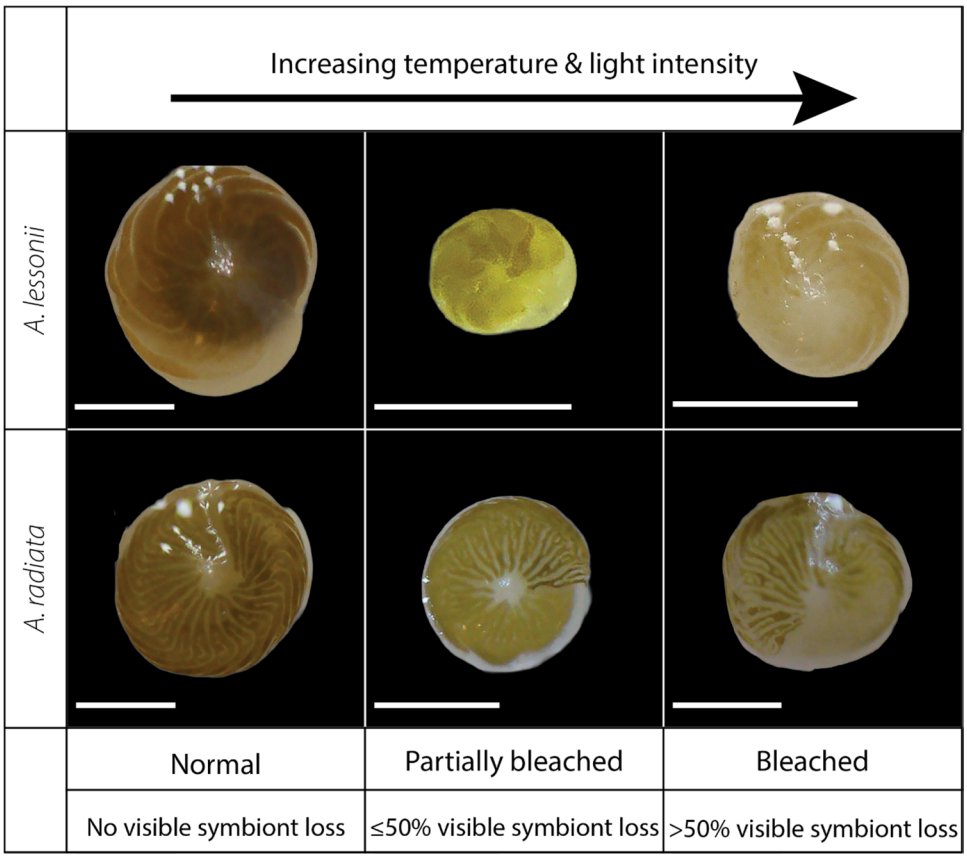


Fig. 4 Representative examples of the bleaching categories. All specimens were collected from the Maldives in May 2025. Scale bars = 500 µm

status, are provided for all samples in the supplementary material. Samples containing <15 *Amphistegina* specimens were excluded from analyses in accordance with previous studies using the ABI (e.g. Stainbank et al. 2020). Low densities of *Amphistegina* can be related to bleaching mortality, rubble position (within sediment), and light exposure.

Results

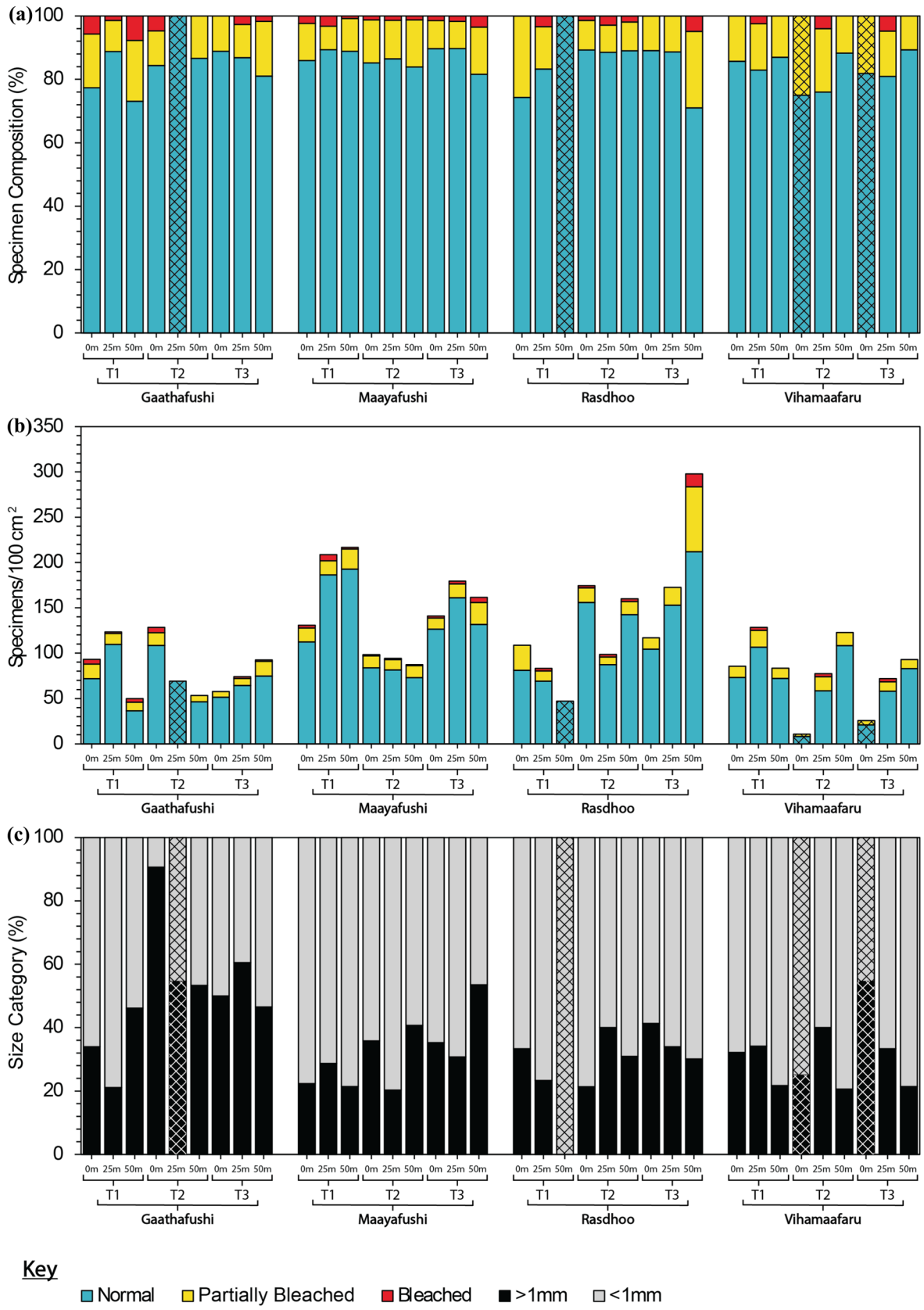
Maldives-abiotic water parameters

Nitrate concentrations were below the detection limit at all sites, except for single measurements of 0.1 ppm in bottom water at Vihamaafaru and surface water at Rasdhoo. Given the accuracy (±0.25 ppm) and detection limits of the Hanna HI781 low-range nitrate checker, these measurements are interpreted as indicating uniformly low nitrate concentrations across all sites rather than meaningful differences. Salinity, pH, and temperature measurements were generally consistent across all sites. Salinity ranged from 40.1 to 40.7 in both surface and bottom waters; a lower salinity value was recorded for the Maayafushi surface water sample (38.1). Measured pH values were uniformly 8.0 across all samples. Recorded temperatures ranged from 29.7 to 30.1 °C. No vertical temperature stratification was detected over the sampled depth range (~ 10 m), with temperatures at depth equivalent to those measured at the surface.

Maldives-bleaching and size of living Amphistegina assemblages

In total, 36 rubble samples (each of which included several pieces of rubble per sample) were collected and processed for assessment of bleaching in *Amphistegina*. All samples hosted living *Amphistegina (A. lessonii, A. radiata, and A. lobifera)*. Of the 36 samples examined, four samples with fewer than 15 *Amphistegina* specimens were excluded from further interpretation (see methods). Benthic foraminiferal assemblages from all samples were dominated by *A. lessonii* (*c.* 87–95% of total assemblage). Living *A. radiata* were identified in samples from all four sites, living *A. lobifera* were absent from samples collected at Vihamaafaru but present (*c.* 0.1–1.1% of total assemblage) in samples from the other three sites.

Of the 1832 specimens analysed, 65% were <1 mm in diameter. Samples from Gaathafushi had the lowest proportion of small specimens (50%), while 68% of specimens from Maayafushi, Vihamaafaru, and Rasdhoo were <1 mm (Fig. 4).


(a)
Specimen Composition (%)
0
20
40
60
80
100
(b)
Specimens/100 cm²
0
50
100
150
200
250
300
350
(c)
Size Category (%)
0
20
40
60
80
100
0m 25m 50m
T1
T2
T3
Gaathafushi
Maayafushi
Rasdhoo
Vihamaafaru
Key
Normal
Partially Bleached
Bleached
>1mm
<1mm

◂**Fig. 5** Bar charts showing the composition of *Amphistegina* populations collected from rubble samples. **A** Percentage levels of bleaching state per sample. **B** Specimen abundance for each site and bleaching state. **C** Size distribution of *Amphistegina* per sample. Samples with < 15 specimens are indicated with a hatched pattern; these samples are excluded from further discussion

Overall, 15% of specimens showed signs of bleaching, including 13% partially bleached and 2% bleached individuals. Bleaching prevalence was highest at Vihamaafaru (18%), followed by Gaathafushi (15%), Rasdhoo (14%), and Maayafushi (13%) (Fig. 5).

Maldives-ABI

The ABI data plotted exclusively within two regions BB and BA of the ABI matrix (Fig. 6). According to Ramirez (2008), these regions indicate chronic non-photo-oxidative stress (BB), chronic mild stress (BA), or recent moderate stress (BA). Higher density ranks are reported from samples collected at Rasdhoo and Maayafushi, with Maayafushi also showing the lowest data scatter. Samples from all four locations plot across both sections BB and BA. Both sections are within the same percentage range of population bleaching, with density rank being the factor that distinguishes the two interpretations. Vihamaafaru had the highest proportion of samples within BB (5/7), followed by Gaathafushi (5/8), Maayafushi (3/9), and Rasdhoo (2/8).

Australia-abiotic water parameters

During the 2022 sampling interval, surface salinity and pH were 35 and 7.9 at North Point and 34 and 7.9 at Watson Bay, respectively. Surface temperatures were 27.9 °C at North Point and 29.5 °C at Watson Bay, with bottom water temperatures of 25.3–25.4 °C, respectively.

During the 2024 sampling interval, North Point surface waters had a temperature of 29.9 °C, salinity of 32.5, and pH 7.9–8.0. Watson Bay surface waters were 29.8–30.4 °C, salinity was 32.0–32.7, and pH was 7.8–7.9. Bottom water measurements at 10 m depth recorded temperatures of 29.8 °C, salinity 32.7, and pH 7.8–7.9.

Australia-bleaching and size of living Amphistegina assemblages

In total, 36 (18 in 2022 and 18 in 2024) coral rubble samples (which included several pieces of rubble per sample) were collected and processed for assessment of bleaching in *Amphistegina* from reefs at Lizard Island. All samples produced 15 living *Amphistegina* specimens; therefore, all samples were included in further analyses.

In August 2022, three species of *Amphistegina* were identified at both North Point and Watson Bay: *A. lessonii*, *A. radiata*, and *A. lobifera*. Assemblages were dominated by *A. lessonii*, comprising 85% of the total assemblage at North Point and 74% at Watson Bay. *A. radiata* accounted for 10% of the assemblage at North Point and 13% at Watson Bay, while *A. lobifera* comprised 5–13%, respectively.

In February 2024, the same three species were present, with assemblages remaining dominated by *A. lessonii* (94% at North Point and 86% at Watson Bay), while *A. radiata* accounted for 2 and 1%, and *A. lobifera* comprised 5 and 13%, respectively. Species level counts, including size and bleaching status, are provided in the supplementary material.

Across all analysed samples, 3152 *Amphistegina* specimens were examined (1612 in 2022; 1540 in 2024). Overall, 28% of specimens were <1 mm in diameter, but size distributions differed markedly between sampling intervals (Fig. 7). In August 2022, small specimens comprised 9% of the assemblage at North Point and 6% at Watson Bay, compared with 56–48%, respectively, in February 2024.

Bleaching prevalence varied between sampling intervals and sites (Fig. 7). In August 2022, 21% of specimens at North Point and 15% at Watson Bay showed signs of bleaching, compared with 39–54%, respectively, in February 2024. Bleached individuals remained uncommon, representing ≤3% of assemblages except at Watson Bay in 2024, where 12% were bleached. Partial bleaching accounted for the majority of observed bleaching across sites and sampling intervals.

Australia-ABI

The ABI scores were calculated for all samples and plotted (Fig. 8) using the ecological condition matrix of Ramirez (2008). The ABI values from both sampling intervals spanned several regions of the matrix. No samples plotted in regions AC, BC, or CC due to density ranks >10 specimens per 100 cm^2, or in regions AC, AB, or AA due to bleaching prevalence >5%. In 2022, samples from North Point and Watson Bay plotted exclusively within BB and BA (North Point: 4/9 BB, 5/9 BA; Watson Bay: 3/9 BB, 6/9 BA). In 2024, samples shifted toward regions of greater stress, with North Point samples predominantly in BB (6/9) and three samples in CB, while Watson Bay samples were concentrated in CB (6/9) and CA (3/9). Minimal overlap occurred between sampling intervals, with 2024 samples distinguished by higher bleaching proportions and generally lower density ranks compared with 2022.

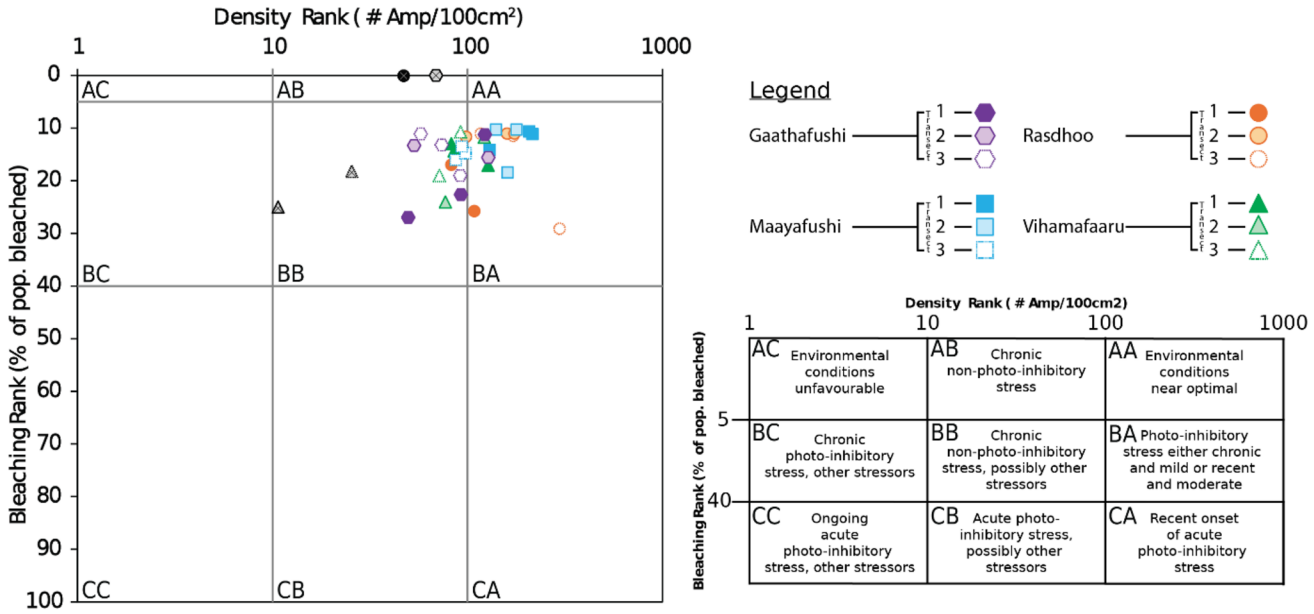


Fig. 6 *Amphistegina* bleaching index (ABI) plot showing the density rank relative to the extent of bleaching in each sample, with the matrix for determining ecological status (Ramirez 2008). Four samples with <15 specimens were excluded. Pop. = population. Amp. = *Amphistegina*

Discussion

Maldives-extent of bleaching and comparison with past studies

The extent of *Amphistegina* bleaching in 2025 was very low. The geometric mean of bleached specimens in 2025 was 2%, compared to 7% in 2015 and 10% in 2018. In 2018, 36% of specimens showed some signs of bleaching, an increase from 30% in 2015. The proportion of specimens showing any bleaching in 2025 (15%) was markedly lower than values in previous years.

The ABI results recorded in 2025 also indicated low levels of photo-oxidative stress, based mainly on the low proportions of bleaching observed. Mean *Amphistegina* abundances (ind/100 cm^2) were generally similar to or lower in 2025 than in previous studies. In 2025, mean abundances (ind/100 cm^2) were 82 ± 29 (Gaathafushi), 146 ± 49 (Maayafushi), 140 ± 73 (Rasdhoo), and 78 ±39 (Vihamaafaru). Corresponding values were 139 ± 76 (Maayafushi), 205 ± 72 (Rasdhoo) and 217 ± 76 (Vihamaafaru), in 2018, and 58 ± 26 (Gaathafushi), 111 ± 43 (Maayafushi), 186 ± 116 (Rasdhoo), and 214 ± 199 (Vihamaafaru) in 2015. Variation (standard deviation) between transects was high for all sites sampled during all years, indicating high variability in living *Amphistegina* abundance. Such variability is commonly observed and is likely related to episodic asexual reproduction (e.g. Buzas et al. 2002). During asexual reproduction, a single *Amphistegina* can produce large numbers of offspring, substantially increasing local population density and altering size-frequency distributions over short timescales (Hallock et al. 1995). Seasonal fluctuations in both abundance and test size have also been documented in natural populations (Muller 1974).

Gaathafushi showed relatively stable abundances between 2015 and 2025, with a slight decline. Maayafushi and Rasdhoo also showed similar abundances between the first and most recent surveys, although both recorded higher abundances in 2018. The 2015 and 2025 surveys were both conducted in spring under similar sea surface temperatures, whereas the 2018 survey took place in late summer/early autumn when SSTs were lower (Stainbank et al. 2020). However, the 2015 sampling occurred during a NOAA Coral Reef Watch (2015a) warning alert in the Maldives and preceded extensive coral bleaching by a few weeks (Spezzaferri et al. 2018). The correspondence between elevated thermal stress identified by satellite monitoring and increased ABI-derived photo-oxidative stress supports the value of integrating biological indicators such as the ABI with remote sensing approaches. Similar stress and bleaching were not reported in 2025, though coral bleaching was extensively reported in 2023–24 (Byrne et al. 2025; Reimer et al. 2024). Relative abundances of *Amphistegina* are generally related to temperature, time of year, and their reproductive cycle (Stainbank et al. 2020), but abundances and low incidences of bleaching may also reflect carryover effects from bleaching events in a previous year (e.g. Hallock et al. 1995), such as the 2023–2024 event. Low abundances of *Amphistegina* have also been related to long-term thermal stress in the Red Sea and tropical Pacific (Humphreys et al. 2022a, 2022b).

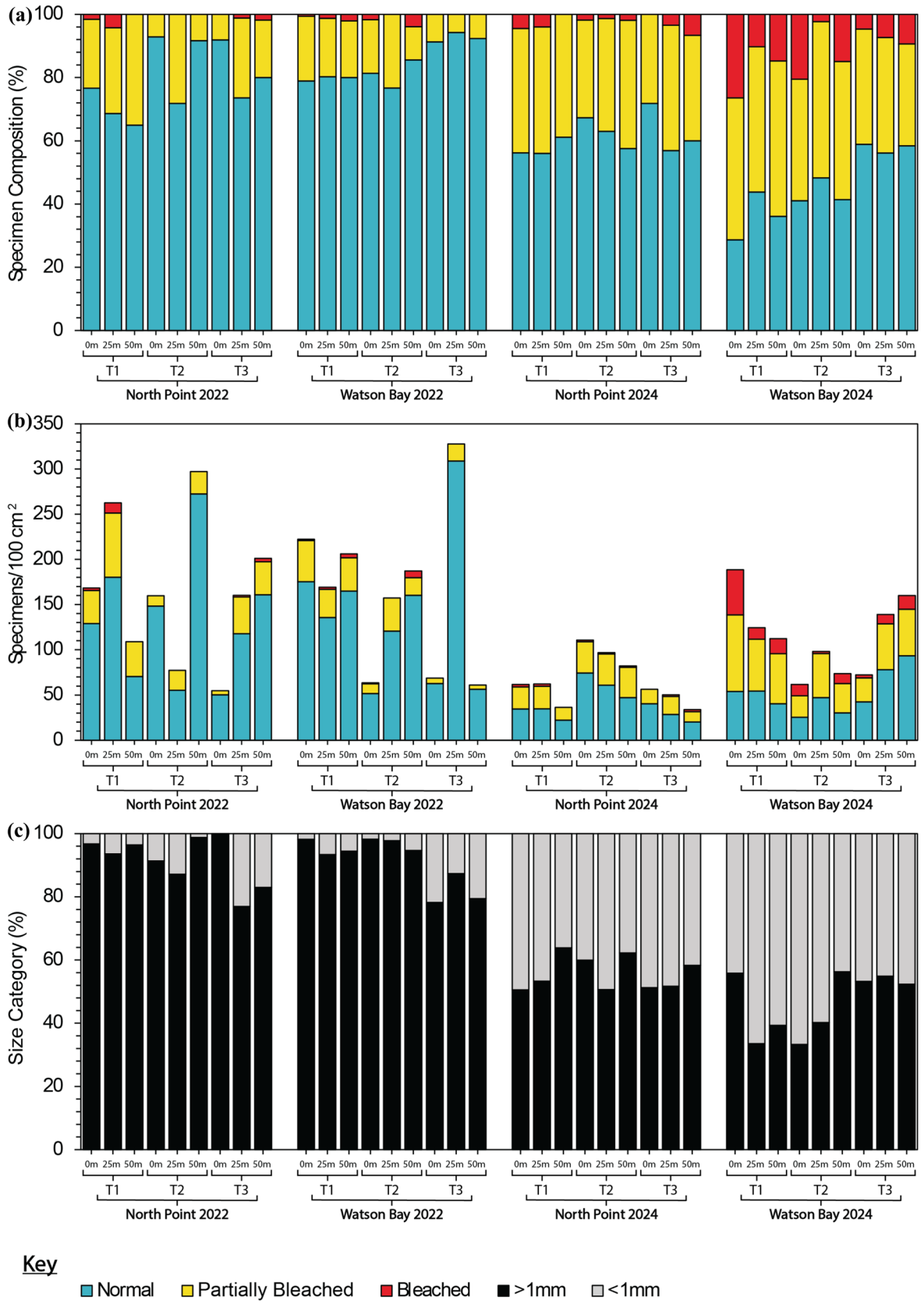


Fig. 7 Bar charts showing the composition of *Amphistegina* populations collected from rubble samples at Lizard Island. **A** Percentage of bleaching state per sample. **B** Specimen abundance by site and bleaching state. **C** Size distribution of *Amphistegina* specimens per sample

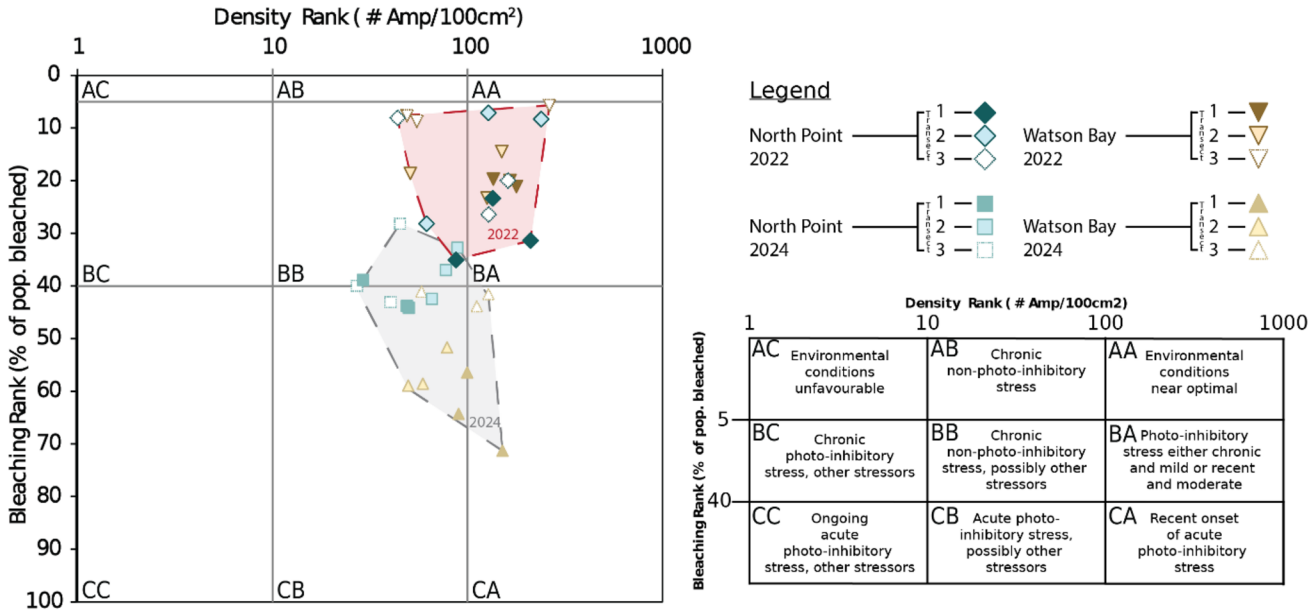


Fig. 8 *Amphistegina* bleaching index (ABI) plot showing density rank relative to bleaching prevalence for samples collected at Lizard Island in August 2022 and February 2024, plotted against the ecological condition matrix of Ramirez (2008). Sampling seasons are grouped using a shaded convex hull. Samples with fewer than 15 specimens were excluded. Pop. = population

In the absence of bleaching, *Amphistegina* density has also been linked to water quality and the suitability of conditions for reef growth (Hallock et al. 2003).

The mean *Amphistegina* abundances at Vihamaafaru ('semi-uninhabited') remained relatively stable (albeit with larger standard deviations) between 2015 and 2018; however, a notable decrease in abundance was recorded in 2025. The reason for this apparent decrease is unclear but could reflect the residual effect of severe bleaching in 2024, or changes in land use (see more detailed discussion below).

Minor discrepancies between bleaching prevalence and *Amphistegina* density underscore the value of integrating both parameters within a single biotic index. Combining these parameters within the ABI allows more direct assessment of photo-oxidative stress. While several samples from 2015 and some from 2018 plotted within sectors indicative of acute photo-oxidative stress, no 2025 samples plotted within sectors CB or CA (Fig. 9), indicating the absence of acute photo-oxidative stress. Likewise, the greater scatter observed in the 2015 ABI results, previously interpreted as evidence of increasing photo-oxidative stress (Spezzaferri et al. 2018; Stainbank et al. 2020), was not evident in the 2018 or 2025 datasets, supporting the inference of lower ongoing stress.

Maldives – land use impacts

Coastal modifications (reclamation and man-made infrastructure), pollution, and sand mining have all been linked to degradation in the Maldives (Dhunya et al. 2017; Dryden et al. 2020; Hilmi et al. 2023). No significant differences in ABI were observed among islands with contrasting land use or management profiles, consistent with previous work at these sites. Nevertheless, slightly lower *Amphistegina* population densities were observed at Gaathafushi and Vihamaafaru, the two originally uninhabited islands with increasing amounts of human use. While these patterns coincide with increased local development and agricultural activity at these islands, no corresponding differences in measured abiotic water parameters were detected, and previous studies have likewise found no relationship between land use and ABI results. As such, the drivers of these site-specific differences remain unresolved. Application of complementary indices, such as the FoRAM Index for assessing water quality (Hallock et al. 2003; Prazeres et al. 2020) and the SEDCON Index for assessing sediment composition and carbonate production (Lidz and Hallock 2000; Daniels 2005; Ramirez et al. 2008), could provide a more direct approach for evaluating the potential impacts of land use change on reef ecosystems.

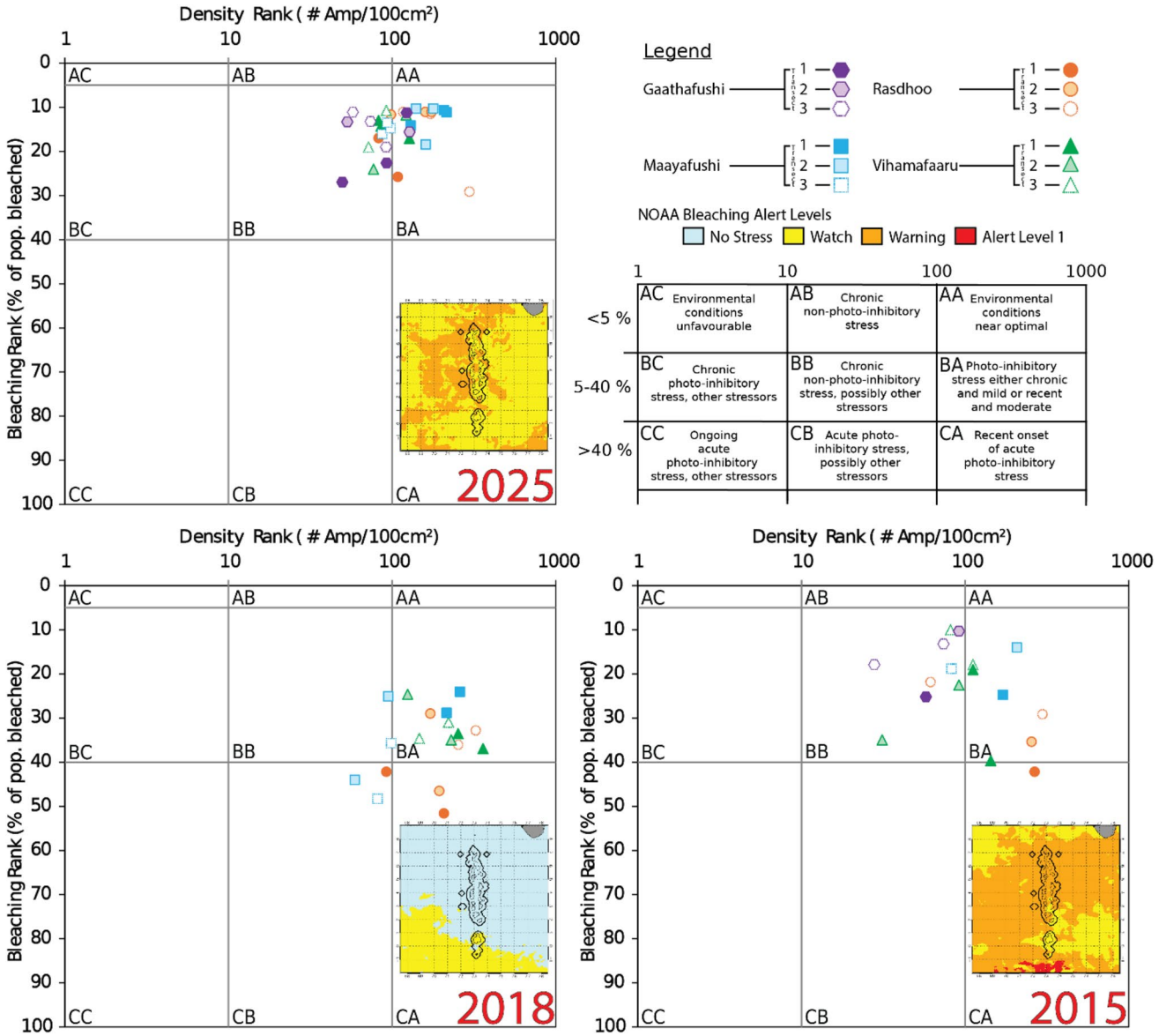


Fig. 9 *Amphistegina* Bleaching Index (ABI) plots for the Maldives showing the density rank relative to the extent of bleaching in each sample from this 2025 study, the 2018 study (Stainbank et al. 2020) and the 2015 study (Spezzaferri et al. 2018). The corresponding bleaching alert map from NOAA is shown in each ABI plot (NOAA 2026). Plots are shown together with the matrix for determining ecological status (Ramirez 2008). Pop. = population. Amp. = *Amphistegina*

Australia-seasonal variability in bleaching and ABI responses

Our results from Lizard Island revealed clear differences in *Amphistegina* population structure and bleaching prevalence between the two sampling intervals. Lower proportions of small individuals and elevated bleaching were observed in austral summer 2024 relative to winter 2022. In contrast to the Maldives comparison, the Australian data captured temporal variability within a single reef system. The two sampling intervals represent contrasting thermal stress contexts on the Great Barrier Reef, with the austral summer 2024 survey coinciding with a regional coral bleaching alert (NOAA 2026), whereas no such alert was in place during winter 2022.

In August 2022 (austral winter), *Amphistegina* assemblages at both North Point and Watson Bay were dominated by larger specimens (> 1 mm in diameter), with smaller individuals comprising <10% of the assemblage at both sites. In February 2024, specimens > 1 mm accounted for roughly half of the assemblages. Although the reproductive cycle of *Amphistegina* in this region has not specifically been documented, the increase in smaller individuals likely reflects the seasonal peak in asexual reproduction during the austral

spring and early summer. Asexual reproduction produces peak juvenile abundances in boreal spring and early summer whenever *Amphistegina* have been sampled over seasonal cycles (Williams et al. 1997; Hallock et al. 2006).

The simultaneous occurrence of elevated proportions of small individuals and of partially bleached adults during spring and summer has been repeatedly observed in *Amphistegina* populations from Florida (Williams et al. 1997; Hallock et al. 2006). Notably, *Amphistegina* and other larger symbiont-bearing foraminifers are remarkably long-lived compared to other protists (e.g. Hohenegger 2018 and references therein). In subtropical populations, seasonal asexual reproduction during spring and early summer produces large numbers of juveniles, which subsequently mature and contribute to the predominance of larger individuals later in the year. This seasonal reproductive cycle can therefore generate strong temporal variation in size structure, with increases in small individuals expected following reproductive events (Harney et al. 1998; Hallock and Reymond 2022).

Even low-latitude environments experience seasonal variability, such as wet–dry monsoonal influences and changes in wave climate and currents. In the Great Barrier Reef, sea surface temperatures typically reach annual minima in August and maxima in February, reflecting seasonal thermal differences between austral winter and summer conditions (e.g. Lough 2007).

Bleaching prevalence increased substantially between sampling intervals (Fig. 7). While minor bleaching was documented at both sites in austral winter of 2022, the proportion of affected specimens was markedly higher in summer of 2024, particularly at Watson Bay, where more than half of the assemblage exhibited some degree of bleaching and bleached individuals comprised a notable proportion of the population. Across both sites and sampling intervals, partial bleaching was more common than full bleaching. However, this pattern is typical in bleaching-stressed *Amphistegina* populations, as extensively bleached individuals experience higher mortality and are therefore less likely to be represented in living assemblages (Hallock et al. 1995). Partially bleached individuals may persist and continue to add chambers, with new chambers able to acquire symbionts despite previous damage to older chambers (Talge and Hallock 2003). These patterns are reflected in the ABI results (Fig. 10). Samples from August 2022 plot predominantly within regions BA and BB of the ABI matrix, consistent with chronic mild or non-photo-oxidative stress. In contrast, February 2024 samples shifted toward regions CB and CA, particularly at Watson Bay, driven by higher bleaching proportions and modestly reduced densities, indicative of the recent onset of acute photo-inhibitory stress, possibly together with other factors. Although some overlap occurred between sampling intervals, the overall displacement of 2024 samples within the ABI matrix indicates a clear stress signal during austral summer conditions. The seasonal changes noted between ABI scores at Lizard Island correspond with changes in NOAA Coral Reef Watch alert status, demonstrating that the ABI provides a biologically based measure of stress responses associated with periods of elevated thermal stress (Fig. 10).

Despite increased bleaching in 2024, *Amphistegina* densities remained above thresholds associated with acute population decline, suggesting that populations were not severely depleted during sampling. This highlights the sensitivity of the ABI to short-term changes in bleaching prevalence, emphasising the importance of considering both bleaching severity and population density when interpreting stress signals.

Overall, the Australian case study indicates that the ABI can capture seasonal-scale variability in *Amphistegina* bleaching and population structure. When combined with environmental data, such assessments can improve the understanding of transient stress dynamics on the Great Barrier Reef and complement longer-term records from other regions.

The ABI as a globally deployable long-term monitoring tool

Our findings build on those of Stainbank et al. (2020) to highlight the potential of the ABI as a simple and relatively low-cost approach (compared to the potential damage linked to reef-wide bleaching) for assessing photo-oxidative stress in shallow reef environments. The continued application of the ABI in the Maldives, following its development in the Florida Keys, highlights its potential for use across a wide range of reef settings and biogeographic regions.

The Australian case study indicates that the ABI can capture variability in bleaching prevalence and population structure over shorter seasonal intervals, as well as the interannual variability previously demonstrated in the Maldives and Florida. As such, the ABI has potential value as both a baseline monitoring tool and a means of detecting transient stress events. When considered together, the Maldives observations and the Australian seasonal dataset demonstrate that the ABI responds consistently to periods of elevated bleaching risk (see Fig. 8, Fig. 9) across contrasting reef settings, seasons, and biogeographic regions. In the Maldives, survey periods characterised by widespread bleaching or heightened thermal stress are associated with increased scatter and elevated bleaching levels. Similarly, at Lizard Island, ABI patterns shift systematically between winter baseline conditions and austral summer conditions, coinciding with coral bleaching alerts identified by NOAA Coral Reef Watch. The agreement with independently derived coral-bleaching alerts

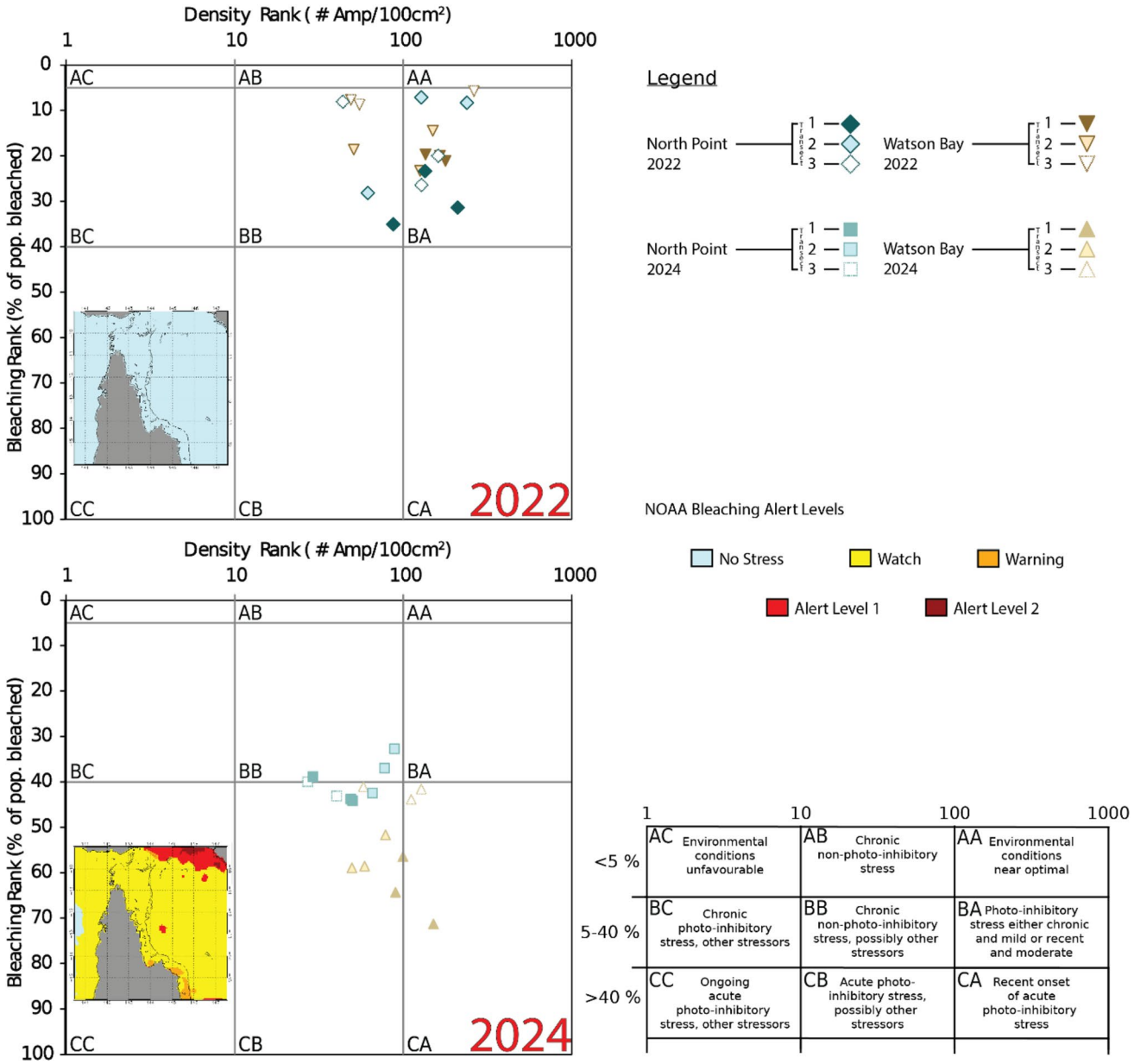


Fig. 10 *Amphistegina* Bleaching Index (ABI) plots showing the density rank relative to the extent of bleaching in each sample, from both 2022 and 2024 sampling at Lizard Island. The corresponding bleaching alert map from NOAA is shown in each ABI plot (NOAA 2026). Plots are shown together with the matrix for determining ecological status (Ramirez 2008). Pop. = population. Amp. = Amphistegina

supports the interpretation of the ABI as a sensitive indicator of elevated bleaching stress on coral reefs. Previous studies have also shown that *Amphistegina* bleaching can precede visible coral bleaching, suggesting that the ABI may provide an early indication of increasing bleaching risk when used alongside other monitoring approaches.

The ABI is most effective when used in combination with complementary approaches, including measurements of physical parameters (e.g. temperature and water transparency) and observations of other reef components (e.g. corals and coralline algae), allowing photo-oxidative stress inferred from *Amphistegina* responses to be placed within a broader ecosystem context.

Future prospectives

Several studies have now shown the applicability of the ABI in the Maldives and Florida Keys, and this study further supports its use as a complementary indicator of photo-oxidative stress on coral reefs (including the Great Barrier Reef). Additional testing across shallow-water reef environments and geographical regions will be valuable to further evaluate the consistency

of ABI responses under different environmental conditions. Continued use of the ABI at sites where it has been used previously (Florida, the Maldives, and Australia) will be important to extend long-term records and strengthen interannual and seasonal comparisons.

As a simple and low-cost method for assessing photo-oxidative stress and potentially forecasting bleaching events, the ABI may complement existing reef monitoring approaches by providing additional biological information on reef condition and stress responses. Although the ABI does not replace large-scale bleaching assessments based on underwater surveys, remote sensing, or aerial observations, it may improve temporal resolution and support monitoring programmes where frequent biological assessments are otherwise difficult to maintain. Training and workshops with reef-dependent stakeholders could help sustain long-term monitoring while integrating local knowledge and practices. Applied alongside existing monitoring tools, bio-indices such as the ABI can improve temporal resolution, spatial coverage, and the diversity of monitoring efforts. This approach also facilitates timely communication of results within communities and may reduce the need for frequent long-distance field visits by external researchers.

Conclusions

- Across both sites and all sampling intervals, ABI results showed patterns consistent with coral bleaching risk identified by NOAA Coral Reef Watch products.
- ABI results indicate that photo-oxidative stress was low in the Maldives during spring 2025 compared to spring 2015, while seasonal variation in Australia revealed higher stress during the austral summer of 2024 compared to winter 2022.
- Lower bleaching levels than both spring 2015 and late summer/early autumn 2018 were recorded in the Maldives in 2025, consistent with reduced photo-oxidative stress and relatively stable *Amphistegina* populations.
- High data scatter and elevated ABI scores observed in the Maldives in 2015, indicative of acute stress prior to extensive bleaching, were not recorded in 2025, despite high SSTs. In Australia, ABI shifts between winter 2022 and summer 2024 captured seasonal changes in bleaching prevalence and *Amphistegina* population structure.
- The ABI is a simple, low-cost, globally deployable method for both short- and long-term reef biomonitoring, capable of detecting interannual and seasonal patterns across geographically distinct reef systems.

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Author contributions T.C. wrote the main manuscript text and prepared the figures. All authors reviewed and edited the manuscript. D.B., C.P., S.St., S.Sp., and E.S. carried out sample collection and analyses at Lizard Island. T.C., D.B., S.F., and B.R. carried out sample collection and analyses in the Maldives.

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Data availability All data used and discussed in this study are provided in the supplementary materials.

Declarations

Conflict of interest The authors declare no conflict of interest.

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