Regional Studies in Marine Science 63 (2023) 103027

Contents lists available at ScienceDirect

Regional Studies in Marine Science

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

Photobiology of Symbiodiniaceae hosted on *Siderastrea stellata* in the southwestern Atlantic

Layla Poubel Tunala [a,b,*], Caroline Rezende Guerra [b], Rafael Gomes de Menezes [b], Celine Philipp Diogo [b], Tailah Bernardo de Almeida [b], Heitor Monteiro Duarte [c], Frederico Tapajós de Souza Tâmega [b], Ricardo Coutinho [a,b]

[a] *Programa de P/'os-Graduação em Dinâmica dos Oceanos e da Terra, Universidade Federal Fluminense, Av. Gen. Milton Tavares de Souza, 24210-346 Niterói, RJ, Brazil*

[b] *Instituto de Estudos do Mar Almirante Paulo Moreira, Departamento de Biotecnologia Marinha, Rua Kioto 253, 28930–000, Arraial do Cabo, RJ, Brazil*

[c] *Laboratório Integrado de Botânica – NUPEM, Universidade Federal do Rio de Janeiro, 27965-045, Macaé, RJ, Brazil*

ARTICLE INFO

Article history:
Received 29 November 2022
Received in revised form 28 March 2023
Accepted 20 May 2023
Available online 26 May 2023

Keywords:
Thermotolerance
Bleaching
Coral reefs
Pigmentation
Photochemistry
Climate changes

ABSTRACT

The health of the coral species *Siderastrea stellata* was investigated as an indicator of climate changes impacts at the Fernando de Noronha Marine National Park, southwestern Atlantic Ocean. Chlorophyll *a* maximum quantum yield and Rapid Light Curves (RLCs) were produced using a red-light pulse amplitude modulated fluorometer, Mini-PAM in *S. stellata* colonies. We collected genetic material from the same colonies in order to identify Symbiodineaceae hosted in each of them, considering that the colonies showed very different pigmentations between them. Our findings showed that colonies with pink pigmentation may be associated with higher temperatures, while indicating a high saturation point (*Ek*) and consequent greater efficiency in the dissipation of radiant energy. Our genetic analysis also demonstrated a high fidelity in association with *Cladocopium* spp. predominantly. Despite this, we hypothesized that this association may be the result of changes in populations of *Breviolum* spp. due to stressful events.

1. Introduction

Global temperatures of oceans' surface were the warmest in 2015 and 2016 since the 19th century. Thus causing, by far, the third longest and most widespread coral bleaching episode in recorded history, estimated to have affected 38% of reefs and extinguished >12,000 km^2 of corals (Swain et al., 2017). Climate change currently affects tropical coral reefs around the world (Anthony et al., 2020; Goreau and Hayes, 2021; Soares et al., 2021). In fact, great mass bleaching events have been occurring with increasing intensity and frequency all around the world and have been considered a major threat to the resilience, productivity and functioning of coral reefs (Hughes et al., 2017, 2018). And this is atypical (Coffroth et al., 1990; Eakin et al., 2019; Wilkinson, 2000). Before 1980's mass death of corals was uncharted and climate change was not on agenda as it is today (Coffroth et al., 1990; Eakin et al., 2019; Suggett and Smith, 2020). However, increases in global temperature, mainly caused by fossil fuel burning, has increased the temperature in the oceans, making them slightly too warmer to be sustainable (Morrison et al., 2020). To support coral reefs in the long term, reduction of greenhouse gas emissions will be required (Van Hooidonk et al., 2016). Notwithstanding, global emissions have been increasing in recent years (Eakin et al., 2019; Friedlingstein et al., 2019). Bleaching events occurs when coral expels the symbiotic microalgae – Symbiodineaceae – or their pigments (Anthony, 2016; Hoegh-Guldberg and Smith, 1989; Howells et al., 2012). This damage is a stress response to several oceanographic parameters, such as high or low temperatures, intense irradiation, changes in salinity, sedimentation or other physical or chemical stresses, even those caused by accelerated industrialization and urbanization (Lapointe et al., 2019; Winter et al., 2016).

Symbiodiniaceae has been performing a powerful role in nutritional support of scleractinian corals over millions of years (Stanley, 2003) and is a cornerstone of the prosperity of reef building corals (Decelle et al., 2018). As a Family, Symbiodiniaceae seems to have high plasticity in photoacclimation and potential

* Corresponding author.
E-mail addresses: laylaptunala@hotmail.com (L.P. Tunala), carolineguerra@gmail.com (C.R. Guerra), rafagmenezes@gmail.com (R.G. Menezes), celinephilipp@gmail.com (C.P. Diogo), tailahbernardo@gmail.com (T.B. Almeida), heitor.m.duarte@gmail.com (H.M. Duarte), fredtamega@gmail.com (F.T.S. Tâmega), rcoutinhosa@yahoo.com (R. Coutinho).

https://doi.org/10.1016/j.rsma.2023.103027
2352-4855/

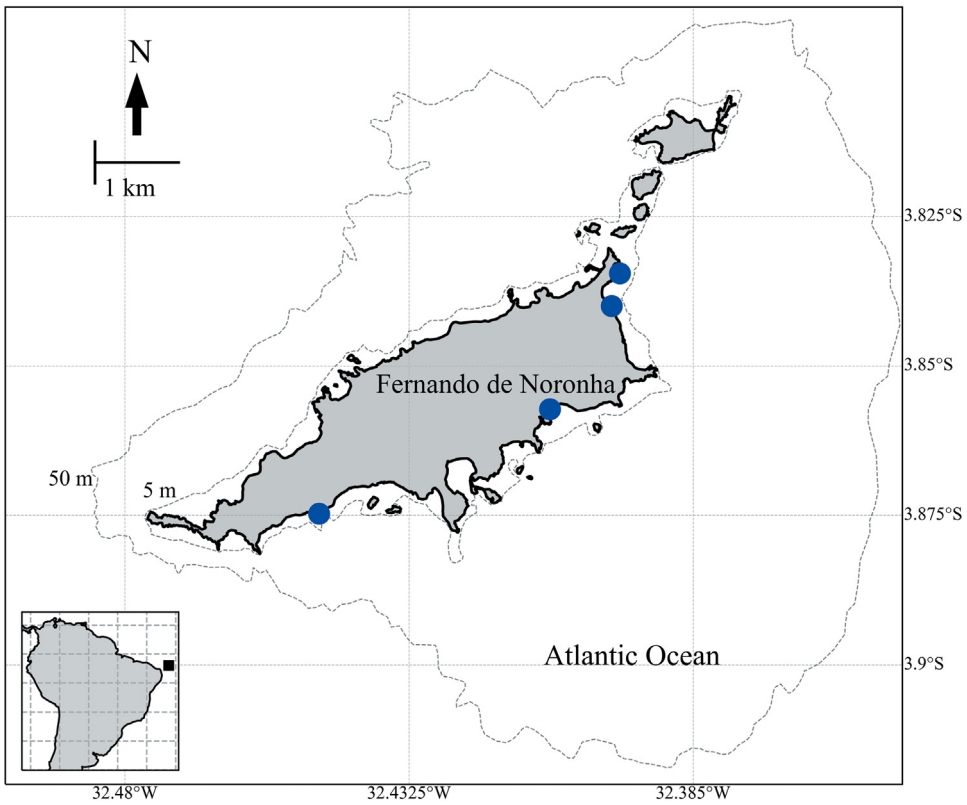

Fig. 1. Fernando de Noronha Archipelago map. Located (3°50′24′S, 32°24′48′W) in Atlantic Ocean, at 345 km far from Brazilian coast with the main island (17 km^2 in area, about 10 km long and 3 km wide). Blue dots refer to sampling sites. From right to left: Raquel, Caieiras, Atalaia and Leão.

photoadaption (Iglesias-Prieto and Trench, 1994). Photoacclimation provide dynamic changes in photosystems according to the light condition in which species better performs (Dubinsky and Stambler, 2009; Suggett et al., 2007). Boundaries of photosynthetic improvement to the variation in light availability, light intensity or spectral quality are defined by photoadaption. Just as well, photoacclimation can be remarkably variable between microalgal species and, indeed, between distinct genetic variation in the same species (Robison and Warner, 2006; Suggett et al., 2007). Besides that, there is a large manifoldness of physiological plasticity as a result of thermal disturbance between several Symbiodiniaceae species (Warner and Suggett, 2016). *Symbiodinium microadriaticum* (Freudenthal, 1962) – until 70's, but now Family Symbiodiniaceae (LaJeunesse et al., 2019) – were considered a single pandemic specie in which all symbiotic dinoflagellates were included Freudenthal (1962) and Taylor (1974). Afterwards, extensive research was able to classify *Symbiodinium* diversity at levels of clades and types (LaJeunesse, 2001; LaJeunesse and Thornhill, 2011; Pochon and Gates, 2010; Rowan and Powers, 1991b; Van Oppen et al., 2001). Rowan and Powers (1991b) assessed DNA sequences diversity of the small ribosomal subunit (SSU rDNA) in *Symbiodinium*. Their phylogeny revealed divergent lineages from the genus.

Consideration of the light harvesting capacity has presented a primary framework for improving our knowledge about how some Symbiodiniaceae genotypes (Iglesias-Prieto and Trench, 1997; Suggett et al., 2015; Warner and Suggett, 2016) have adapted different strategies for alloting resources and light niche improve performance. Active chlorophyll *a* fluorometry defines the balance of absorbed light that is dissipated as photochemistry *versus* heat (Björkman and Demmig-Adams, 1995). Likewise, Symbiodiniaceae genotypes look as if it has similarly expressed differences in their own ratio of heat and photochemistry (Robison and Warner, 2006; Suggett et al., 2007). Although these differences seem to present some relationship with phylogenetic, they also appear to be related to shallow *versus* deeper corals (Iglesias-Prieto et al., 2004; Suggett et al., 2015). However, these interactions are still largely unexplored.

Therefore, we aimed to evaluate the photosynthetic potential of *S. stellata* through chlorophyll *a* fluorescence and to relate them to the Symbiodiniaceae. It is necessary and extremely important to investigate how the ecological value of symbiotic dinoflagellates is threatened by increasing environmental pressures, as they can provide us with an overview of the status of the coral community in reef environments.

2. Material and methods

2.1. Study site

Fernando de Noronha Archipelago (FNA; 3°50′24′S, 32°24′48′W) is located approximately 345 km off north-eastern Brazil. The archipelago is composed by a main volcanic island (17 km^2 in area, about 10 km long and 3 km wide) and 20 small islets (Moreira and Guimarães, 2014) (Fig. 1). The FNA is divided into two protection areas: a Marine National Park (PARNAMAR) fully protected and an Environmental Protection Area (APA) for sustainable use. The Archipelago's reefs are predominantly rocky, wave-exposed, with macroalgae and rhodoliths beds (Amado-Filho et al., 2012; Eston et al., 1986). Krajewski and Floeter (2011) described the presence of *Siderastrea stellata* Verril, 1868, *Montastraea cavernosa* Linnaeus, 1767 and *Mussismillia hispida* Verril, 1902 as the main representatives of the archipelago's coral cover. *S. stellata* occurs on all Brazilian reefs and in coral communities from Maranhão to Rio de Janeiro State (Castro and Pires, 2001; Laborel-Deguen et al., 2019) and is the major reef-building coral in Brazilian reefs (Leão et al., 2016). This species is a colonial, massive and zooxanthellate coral and is considered a

great environmental indicator, due to their ability to resistant to sedimentation, variations in temperature and salinity, as well as strong wave action (Laborel-Deguen et al., 2019; Segal and Castro, 2000).

Four study sites were selected within PARNAMAR:

(a) Atalaia: sandy bottom, low coral diversity, with predominance of *S. stellata*. Some occurrences of *Favia gravida* Verril, 1868 on the edge of the tide pool. This pool undergoes a seasonal natural sedimentation process, where colonies of *S. stellata* are exposed in the months of late summer (February and March, mainly) and autumn. Visiting is allowed under the control and guidance of monitors.

(b) Caieiras: rock beach with tide pool bottom composed of high diversity of macroalgae, mainly turf and calcareous algae. Visiting is allowed under the control and guidance of monitors.

(c) Raquel: tide pool bottom composed mainly by rhodoliths and calcareous algae, an environment with greater complexity and deeper than the previous ones. Strong wave action and high turbidity with a lot of grain particles on water column. Visitation is not permitted, restricted to scientific research.

(d) Leão: a rock beach with high complexity when compared to Atalaia and Caieiras previous mentioned. Zoanthids like *Palythoa caribaeorum* Duchassaing and Michelotti, 1860 are abundant and also fishes. Visitation is not allowed, restricted to scientific research.

2.2. Sampling

Colonies of *S. stellata* ($N = 60$) up to 10 cm in diameter were collected by snorkeling in each sample site (15 colonies/site). Samples were carried to a plastic tray with local sea water. Water temperature in this container was monitored throughout the period of measurements. We also took note of irradiance intensity (i.e. PAR, in μmol m^{-2} s^{-1}) obtained with a Mini Quantum/Temp. Sensor (Mini PAM accessory, Walz) at the time of experimentation and at the depth of the water column in which samples were collected. Colonies were photographed and categorized according to a color gradient (1 to 5 colors), following the standards of Coral Health Chart (Siebeck et al., 2006) (Fig. 2). In addition, we maintained a sensor HOBO Pendant® Temperature/Light 64K Data Logger for 5 days at Atalaia and monitored the other sites with a second similar sensor during the period when we were taking the chlorophyll *a* fluorescence measurement, in order to understand the dynamics during sampling period (i.e. dry tide, peak light in the day and in the summer with clear skies, without cloudiness). This sensor recorded temperature at every second.

For data acquired by HOBO Pendant® Temperature we calculate the "Time Period Mean" (Tp) from the average temperature of the filtered period, that is, temperature between the average (with all data) and the maximum, and time interval that was in the Tp in minutes. These calculations were performed by Python Software.

2.3. Genetic analysis

For zooxanthellae (Symbiodiniaceae) genetic analysis, 10 corals were sampled at each site ($N = 40$) by scraping a part (<1 cm^2) of *S. stellata* tissue using razor blade and gloves. All material was previously sterilized with 70% ethanol between samples. Tissue was transferred to tubes containing 0.25 mL of CHAOS lysis-buffer and stored at room temperature for at least five days (Picciani et al., 2016). Then, total DNA was extracted using a phenol/chloroform protocol according to Picciani et al. (2016). DNA purity and quantity were assessed by Thermo Scientific™ NanoDrop 2000 spectrophotometer. PCR was carried out using specific primers ss3Z and ss5Z which amplified 18S rDNA fragments (~1600 bp) (Rowan and Powers, 1991b). Reaction mixtures contained 1X GoTaq® Green Master Mix (Promega), 0.5 μM of each primer, 4 ng of template DNA and sterile ddH_2O to volume. Cycling conditions were as follows: 5 min at 94 °C (1 cycle); 1 min at 94°, 1 min at 55 °C and 2:30 min at 72 °C (1 cycle); 1 min at 92 °C, 1 min at 55 °C and 2:30 min at 72 °C (29 cycles); final extension at 72 °C for 10 min. PCR products and DNA ladder (100 bp DNA Ladder, Promega) were run on 1% agarose gels in 0.5X TBE buffer stained with Gel Red (Biotium) and visualized under E-Gel™ Imager UV Light Base (ThermoFisher Scientific).

Additionally, PCR products were purified with AxyPrep PCR Cleanup Kit (Axygen Bioscience) and then used for sequencing and Restriction Fragment Length Polymorphism (RFLP) profiling, as previously described in the literature (Karako-Lampert et al., 2004; Rowan and Powers, 1991b). Sequences were manually edited using BioEdit software (7.2 version; Hall, 1999), consensus sequences were generated for each sample and deposited in GenBank (vouchers numbers MT653596, MT653693, MT655952, MT656012, MT657269, MT657270, MT657274, MT657321, MT657960, MT659934, MT657981, MT657982, MT664801, MT661487, MT664801, MT661525, MT664810, MT661604, MT662117, MT662134, MT663216, MT663217, MT663279, MT663344, MT669028, MT668630, MT668704, MT668706, MT668713, MT668714, MT668715 and MT668913). Blast analyses were performed to confirm.

2.4. Chlorophyll a fluorescence

The photosynthetic performance of *S. stellata* was accessed using a portable pulse amplitude modulated fluorometer (Mini-PAM, Walz GmbH, Effeltrich, Germany). Determinations of the maximal quantum yield of PSII (*Fv/Fm*) were made adapting coral colonies for 20 min (Perkins et al., 2001) in a black plastic box. The maximal fluorescence (*Fm*) was measured within a saturating light pulse (SLP) (800 ms, PAR $>$ 4000 μmol m^{-2} s^{-1}) just after acquiring the ground state fluorescence in the dark (F_0). *Fv/Fm* was calculated as (*Fm-Fo*)/*Fm* (Genty et al., 1989). Rapid light response curves (RLCs) were performed to access the photosynthetic potential for photochemistry. The internal program of Mini-PAM was used to apply 9 steps of increasing actinic irradiances of 10 s duration. Within each irradiance step, the Mini-PAM recorded the steady state fluorescence and the maximal fluorescence (within a SLP) of light adapted sample (F and Fm', respectively). The effective quantum yield of PSII ($\Delta F/Fm'$) was calculated as ($Fm'-F)/Fm'$. The relative rate of the photosynthetic electron transport (*rETR*) was calculated as $\Delta F/Fm'$ *x* PAR *x* 0.5, where PAR is the photosynthetically active radiation, and the factor 0.5 assumes that 50% of PAR was absorbed by PSII (Ralph et al., 2002). The regression of rETR by PAR was done fitting the equation $rETR = rETR_m \times \tanh(\alpha \times \text{PAR}/\ \text{rETR}_m)$ (Jassby and Platt, 1976), where the parameter $rETR_m$ is the maximum relative electron transport rate, α corresponds to the rise of the curve in the light-limiting region (Schreiber, 2004), and *Ek* is the saturating irradiance calculated as $rETR_m/\alpha$ (Sakshaug et al., 1997). All regressions and parameter extractions were made in R language and environment for statistical computing (Team, 2015a) under RStudio (Team, 2015b) using the non-linear least square Levenberg–Marquardt minimization algorithm with the package "minpack.lm" (Elzhov et al., 2016).

2.5. Statistical data analysis

For chlorophyll *a* fluorescence data parametric statistical analysis was chosen after performing Shapiro and Wilk's W test for normality and Levene's test for homogeneity of variances (Zar,

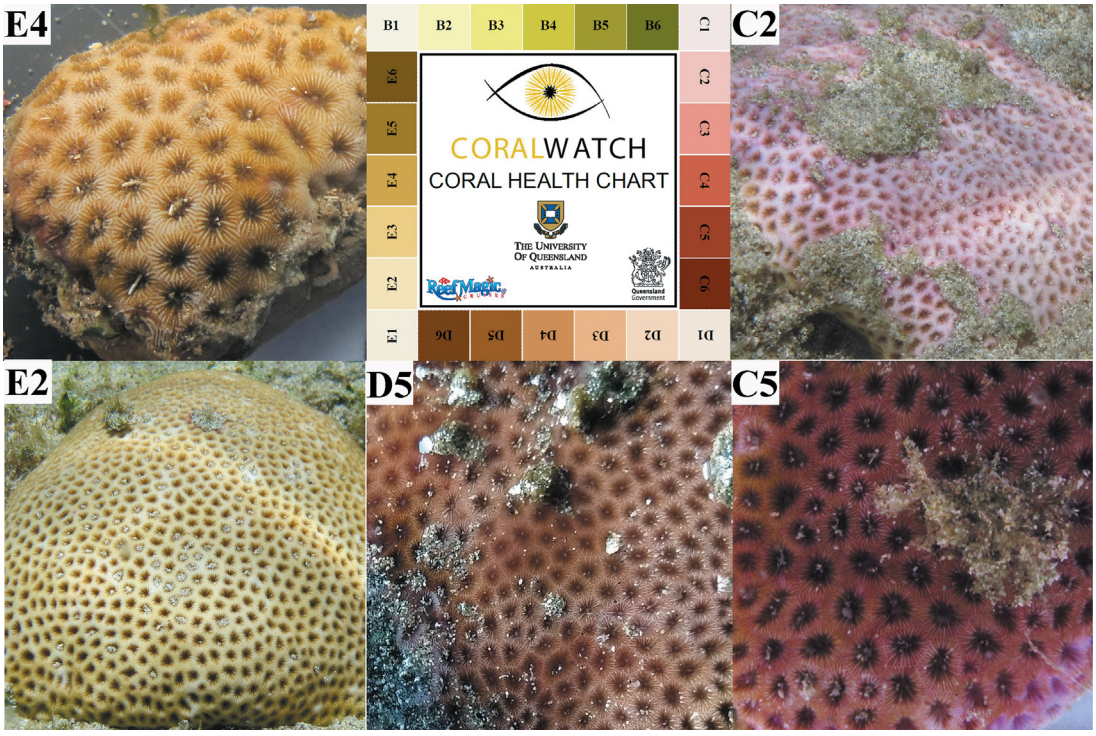

Fig. 2. Color gradient classification with coral colonies specimens conform with the Coral Health Chart at all sample sites. This categorization was defined based on predominant pigmentation in each colony. All fluorescence measurements and collection of genetic material were carried out in the colonies' areas with the definition established for each color category. All samples were classified as E2, E4, C2, C5 and D5. . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2010). The *Fv/Fm* data and the critical points from regression analysis of RLCs were assessed by ANOVA followed by Tukey's HSD. Correspondence analysis (CA) was also performed for *Fv/Fm* data (FactoMineR and FactoExtra packages in R). The contingency table for CA with binary values was built by the categorization of *Fv/Fm* values to each decimal place from 0.3 until 0.7.

3. Results

3.1. Symbiodiniaceae taxon identification

Analysis of ten *S. stellata* individuals of each sampling site ($N = 40$) through RFLP fingerprinting produced SSU rDNA fragments for *Brevolium* spp. and *Cladocopium* spp. (Fig. 3) in accordance with the data published by Karako-Lampert et al. (2004) and Rowan and Powers (1991a). Comparison of the 18S rDNA sequences obtained showed that 38/40 (98%) coral samples hosted *Cladocopium* spp., while 02 samples (5%) hosted *Brevolium* spp., one from the Atalaia and one from the Raquel sites. All sequences showed at least 98% similarity when compared to sequences in GenBank through Blast analysis, confirming the genus identified by RFLP.

3.2. S. stellata photosynthetic performance

3.2.1. Potential quantum yield

The *Fv/Fm* mean value for all samples in all sites together was 0.463 ± 0.098, with maximum of 0.657 and minimum of 0.171. Highest average was observed at Atalaia with mean of 0.509, but the highest overall value of 0.657 was observed at Caieiras. The lower *Fv/Fm* mean value occurred at Raquel (0.371). Tukey's multiple comparisons of means test showed high similarity between Atalaia and Leão ($p = 0.919$). However, Raquel showed a highly significant difference (ANOVA $F = 26.88$, $p = 2.31^{-14}$).

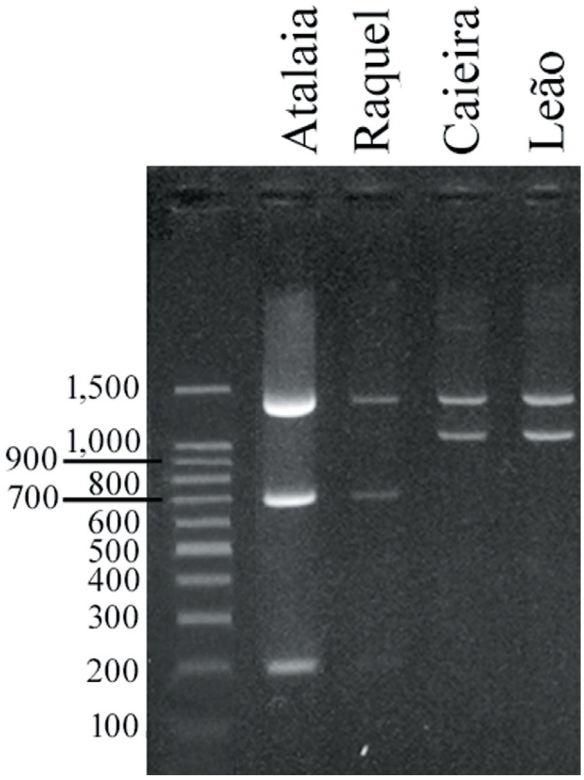

Fig. 3. RFLP patterns of *Taq* I digested 18S rDNA gene fragments amplified from *S. stellata* hosted Symbiodiniaceaea. Lane 1 shows 100bp DNA ladder; Lanes 2 and 3, *Brevolium* spp. samples from Atalaia and Raquel site, respectively; Lanes 4 and 5, represents *Cladocopium* spp. from Caieiras and Leão sites, respectively. Representative gel for all samples, clades were confirmed by sequence analyses.

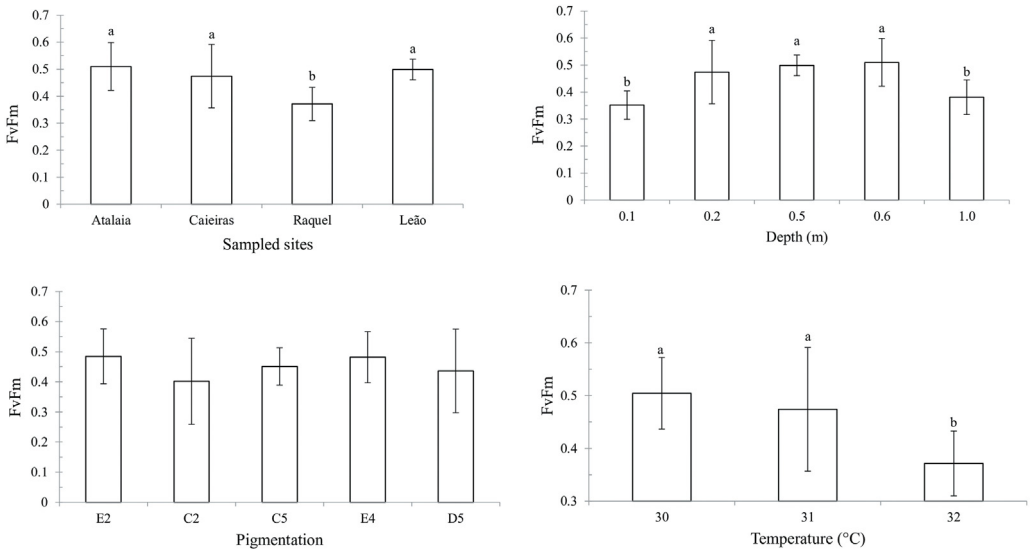

Fig. 4. Chlorophyll *a* maximum quantum yield (dark-adapted samples) in relation to each sampled site, depth (m), pigmentation and temperature (°C). Vertical bars at each point represent standard deviations from the mean. Letters above each bar represent the ANOVA results, where "a" are equal to each other ($p > 0.05$) and different from "b" ($p < 0.05$). Raquel had the lowest overall values, while Caieiras had the lowest raw data. Atalaia and Leão had a very similar distribution. The "b" at the depths of 0.1 m and 1 m, both refer to Raquel. The pigmentation gradient from E2, C2, C5, E4 and D5 showed mean ± sd of 0.484 ± 0.091, 0.402 ± 0.142, 0.451 ± 0.062, 0.481 ± 0.084 and 0.436 ± 0.138, respectively. Temperatures (°C) recorded in containers during the period of fluorescence measurements. We observe that with increasing temperature we have lower *FvFm* values. During measurements we recorded water temperature at that time, which reached the values of 30, 31 and 32 °C. For each of them we observed mean values of 0.504 ± 0.067, 0.474 ± 0.117 and 0.371 ± 0.061, respectively. Highly significant difference was observed between 32 °C and the other temperatures (ANOVA $F = 40.26$, $p = 3.89^{-15}$).

Regarding sampled depths, we detected the same variation found for all sample sites. Significative differences were found for fluorescence yield for 1 m and 0.1 m, which are both referent to Raquel (Fig. 4). The highest averages were for 0.6 m depth (Atalaia) and 0.5 m depth (Leão) with 0.509 ± 0.088 and 0.498 ± 0.037, respectively. No significant differences were found between 0.1 m and 1 m.

The pigmentation gradients from E2, C2, C5, E4 and D5 showed mean ± sd of 0.484 ± 0.091, 0.402 ± 0.142, 0.451 ± 0.062, 0.481 ± 0.084 and 0.436 ± 0.138, respectively. Among them, some significant differences were found (ANOVA $F = 3.754$, $p = 0.0058$). Tukey's multiple comparisons of means test identify high dissimilarity for pallet C2, mainly between E2 ($p = 0.008$) and E4 ($p = 0.01$). Tukey's test also showed a high similarity between pigments E2 and E4 ($p = 0.999$) and D5 and C5 ($p = 0.989$), making the difference of pigment C2 in relation to the others even more evident.

The temperatures recorded in containers during the period of fluorescence measurements had a clear pattern: with higher temperatures we have lower *Fv/Fm* values (Fig. 4). Container water temperature reached the values of 30, 31 and 32 °C. For each of them we observe mean values of 0.504 ± 0.067, 0.474 ± 0.117 and 0.371 ± 0.061, respectively. A high significant difference was observed between 32 °C and the other temperatures (ANOVA $F = 40.26$, $p = 3.89^{-15}$).

Temperature mean and standard deviation for each sampled site were 35.18 ± 1.16, 35.78 ± 1.23, 34.6 ± 1.17 and 32.37 ± 0.7 °C for Atalaia, Caieira, Raquel and Leão, respectively, and their maximum temperatures reached to 36.62, 37.82, 36.4 and 33.64 °C for each one (Table 1). Raw data of the temperatures sampled *in situ* at each of sites are shown in Fig. 5. The black line refers to data from temperature sensor which was used as a form of control to compare the sites amongst themselves and was fixed at Atalaia. Data for February 7 was not included in our analysis, because it was a rainy and cloudy day. The other days of sampling were cloudless days of full sun.

We also build a correspondence map, displaying a two-way table by calculating the coordinates representing its rows and columns, as a primary output to explore relationships among categorical variables (Fig. 6). Fig. 6 allowed the visualization of the relationship between the sets, where the proximity of the points referring to the line and the column indicated association, and the distance a repulsion. The correspondence graph in the two dimensions for the two largest eigenvalues explained about 43% of the total variability. From the decomposition of the total inertia, an estimation of the right number of axis to interpret suggests restricting the analysis to the description of the first 6 axis. These axis present an amount of inertia greater than those obtained by the 0.95-quantile of random distributions (79.57% against 50.83%). This observation suggests that only these axis are carrying a real information. Nevertheless, inertia of the first dimensions shows that there is a strong relationship between variables, and the first two dimensions of analysis express 42.6% of the total dataset inertia (Fig. 6), i.e., total variability is explained by the plane. Thus, we were able to observe 3 very well-defined data sets, in which the numbers represented by the points are each of the samples and the triangles are our categorical variables.

Table 1
Temperature (°C) data registered by HOBO Pendant® Temperature/Light 64K Data Logger at each one of sampling sites. For Atalaia, the sensor monitored for 5 days and a second sensor with the same settings was installed in the other sites with during the period when we were taking the chlorophyll *a* fluorescence measurement, recording temperature at every second. Atalaia, Caieira, Raquel and Leão maximum recorded temperatures reached to 36.62, 37.82, 36.4 and 33.64 °C, respectively.

Site	T °C mean	T °C max	Tp (°C)	Time (min)
Atalaia	35.18 ± 1.16	36.62	35.88	108
Caieira	35.78 ± 1.23	37.82	36.68	81
Raquel	34.6 ± 1.17	36.4	35.51	98
Leão	32.37 ± 0.7	33.64	32.97	134

3.3. Rapid light curves

The results of rETR are presented in Fig. 7. The *rETRm* mean for all samples was 30.87 ±12.51 μmol photons m^{-2} s^{-1}. For

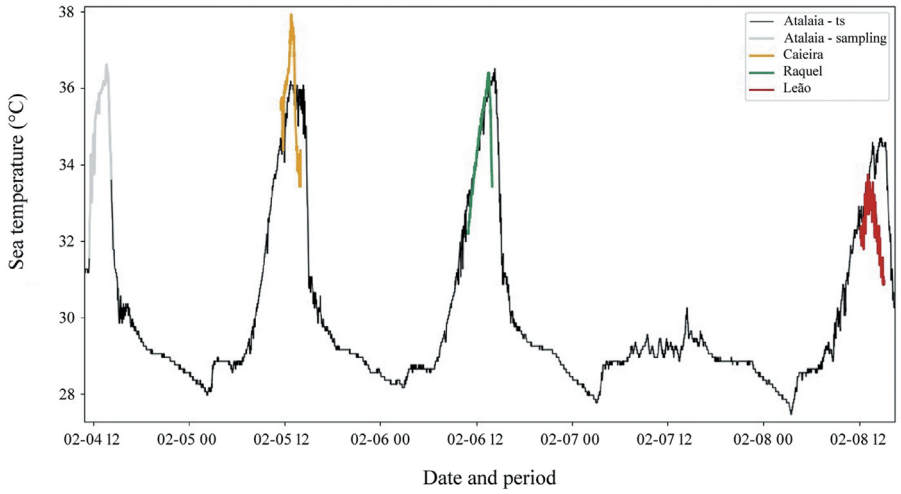

Fig. 5. Raw data of temperatures sampled *in situ* at each site. The black line refers to data from temperature sensor as control to compare the sites with each other and was fixed at Atalaia. The time axis is described as month-day and day period in hours (00 in the night or 12 in the day). Data for February 7 was not included in our analysis because was a rainy and cloudy day. Other days of sampling were cloudless with complete sun exposure.

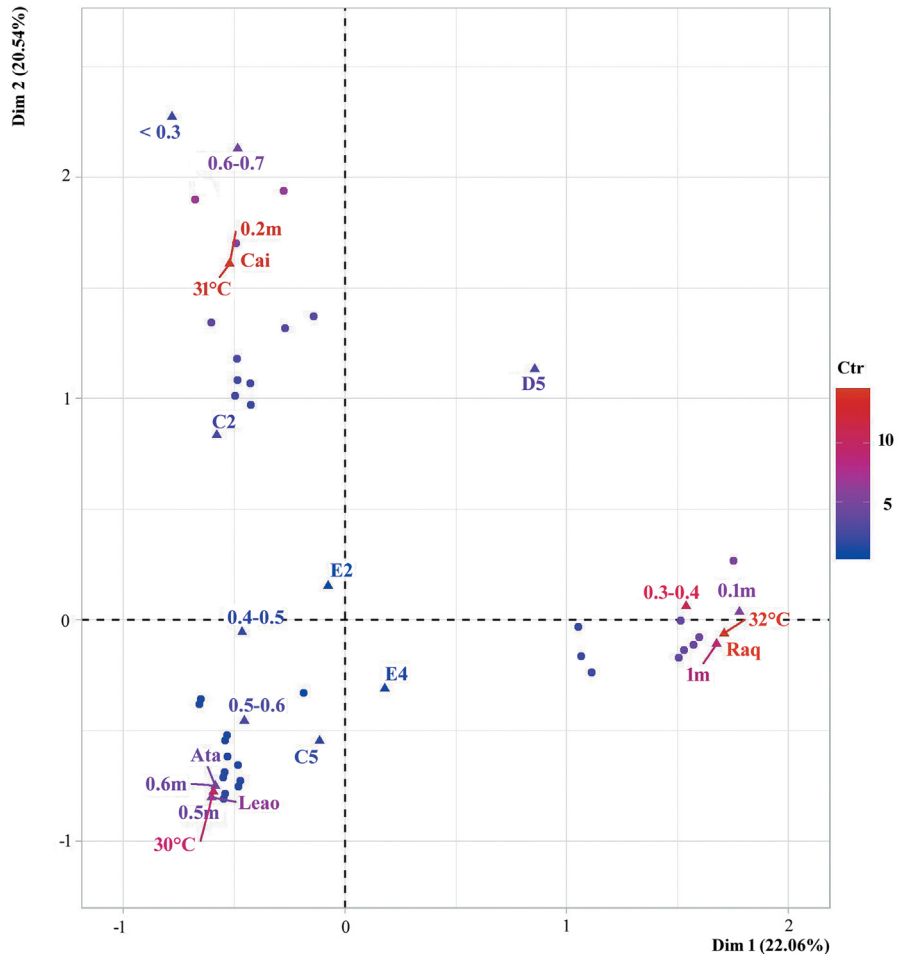

Fig. 6. Correspondence map. The map displays a two-way table by calculating coordinates representing its rows and columns, as a primary output of Correspondence Analysis (CA) to explore relationships among categorical variables. The sidebar "Ctr" refers to the degree of contribution of each of the variables, in which the red represents the largest contribution and blue the lowest contribution. . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

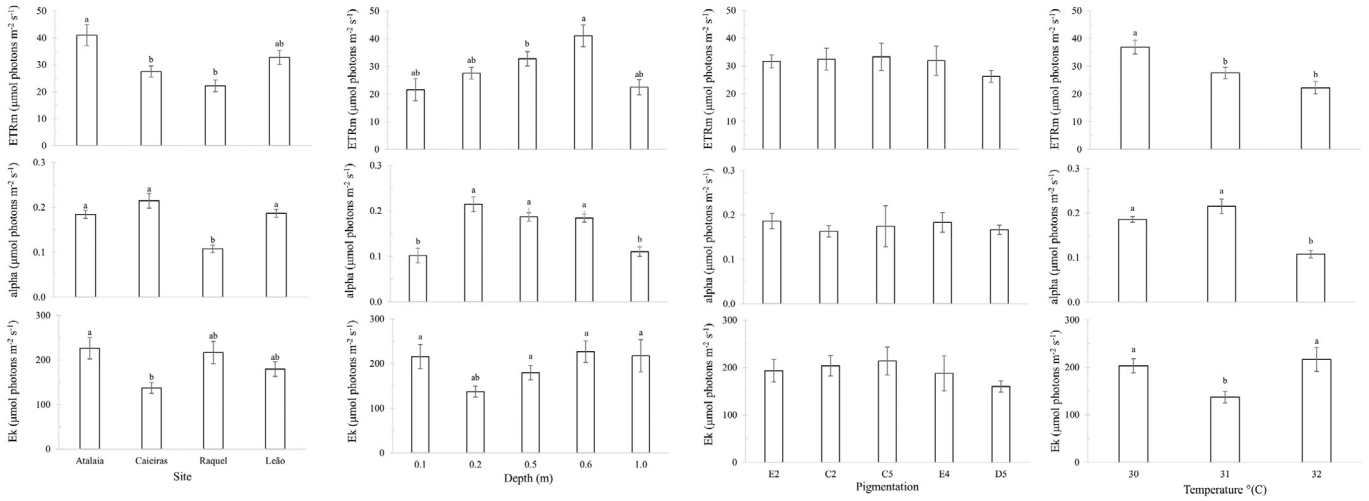

Fig. 7. Rapid Light Curves parameters (rETR, alpha and Ek) for all categories of observations—sampling sites, depth in meters, pigmentation, and temperatures of the containers (°C). Bars represent averages and their standard deviations. For each of intrinsic values calculated from the light curve, there was a correction for the irradiance values. All factors showed a significant difference ($p > 0.05$) represented by the letters above each bar, with exception of pigmentation. All graphs of alpha values showed the same pattern verified for the mean values of *Fv/Fm* and the ANOVA results.

α and *Ek* values were 0.173 ± 0.058 and 190.13 ± 84.19 µmol photons m^{-2} s^{-1}, respectively. *rETRm* exhibited significant differences between locations (ANOVA $F = 8.343$, $p = 0.0001$) and also α_{ETR} (ANOVA $F = 16.48$, $p = 8.54 \times 10^{-8}$) and *Ek* (ANOVA $F = 4.039$, $p = 0.011$). Atalaia was significantly different from Caieiras ($p = 0.006$) and Raquel ($p = 0.00007$), while Leão it intersected with the two groups of well-defined locations, being similar to Atalaia and Caieiras, but different from Raquel ($p = 0.045$). It means that Caieiras and Raquel were remarkably similar. For alpha only Raquel was significantly different from the other locations and *Ek* analysis clustered Raquel and Leão, when Atalaia × Caieiras ($p = 0.014$) and Caieiras × Raquel ($p = 0.360$) were significantly different.

Regarding depths alpha presented two groupings that are closely linked to sampled sites. Depths in 0.1 m and 1.0 m (associated to Raquel) grouped together while 0.2, 0.5 and 0.6 m depth were similar to each other. Significant differences between the depth groups (ANOVA $F = 12.2$, $p = 3.63 \times 10^{-7}$) occurred in 0.1 × 0.2 ($p = 0.00007$), 0.1 × 0.5 ($p = 0.004$), 0.1 × 0.6 ($p = 0.005$), 1.0 × 0.2 ($p = 0.000003$), 1.0 × 0.5 ($p = 0.0008$) and 1.0 × 0.6 ($p = 0.0012$). Ek values also presented differences (ANOVA $F = 2.976$, $p = 0.026$), which was only between 0.6 × 0.2 m depth.

Regarding temperature, we had significant differences for all RLC factors (ETRm ANOVA $F = 9.695$, $p = 0.0002$, alpha ANOVA $F = 25.13$, $p = 1.49 \times 10^{-8}$, Ek ANOVA $F = 4.572$, $p = 0.014$). These differences occurred for ETRm at 30 °C, to alpha at 32 °C and for Ek at 31 °C. Graphs of the RLCs are represented in Fig. 7.

4. Discussion

We used two combined methods to evaluate the physiological characters of zooxanthellae linked to their genetic features. Genetic analysis demonstrated a high fidelity in association with *Cladocopium* spp. predominantly. Despite this, we hypothesized that this association may be the result of changes in populations of *Brevolium* spp. due to stressful events such as the rise in ocean temperatures associated with extreme conditions found in a tidepool. Our findings also showed that colonies with pink pigmentation may be associated with higher temperatures, thus indicating a high saturation point (*Ek*) and consequent greater efficiency in the dissipation of radiant energy. We also considered that pigmentation expression may reflect stress events and potential bleaching events which took place.

Flattened reef tops in the Brazilian coastline are subaerially exposed along low tides and the only corals species that survive in this adverse environment (temperature fluctuation, high irradiance and salinity) are *S. stellata* and *F. gravida* (Leão et al., 2016). Furthermore, Costa et al. (2008) evidenced that the stress-tolerant *S. stellata* is associated with zooxanthellae *Cladocopium* spp., which is considered one of the most bleaching-resistant zooxanthellae groups. Despite these findings, in which they show fidelity in the relationship between *S. stellata* and *Cladocopium* spp., our results suggest that they do not, as well as reported by Toller et al. (2001a,b) and Glynn et al. (2001). Monteiro et al. (2013) also revealed high specificity between *Siderastrea* spp. with *Cladocopium* C46 in East Atlantic, although in the Brazilian coast *Siderastrea* spp. samples were associated with *Cladocopium* spp. and *Breviolum* spp. and some of sampled colonies co-hosted different species of Symbiodineaceae (*Cladocopium* C3 + *Breviolum* B5). *Cladocopium* spp. is widely distributed and shows great tolerance for temperature changes (Karako-Lampert et al., 2004) and based on photochemical efficiency measurements. Abrego et al. (2008) also indicated that *Cladocopium* spp. exhibited much greater thermal tolerance than *Durusdinium* spp., for example. Although *Cladocopium* spp. made up most of our samples, *Brevolium* spp. was also found. Also, some authors have reported the occurrence of *Brevolium* spp. for corals of the genus *Siderastrea* (LaJeunesse, 2002; Santos et al., 2004; Thornhill et al., 2006).

These findings made us consider some works that reported that a marjority of scleractinian corals (about 75%) acquire their dinoflagellates symbionts from the environment each new generation (Baird et al., 2009). The authors confirmed that external environmental conditions, in many cases, promote certain pairings between partners, including combinations that vary with temperature, irradiance or depth gradients, latitude and longitude and host ontogeny (LaJeunesse and Trench, 2000). Thus, several authors have reported changes in the symbiont clades of these corals (Toller et al., 2001a,b; Glynn et al., 2001). Another relevant aspect to consider is the colorful bleaching (Bollati et al., 2020). They consider a mechanism in which loss of symbiont pigments causes internal blue light fluxes to increase in bleached colonies. Then, it induces upregulation of host pigments and, consequently, recovery of symbiont population.

These considerations lead us to hypothesize that zooxanthellae in *Breviolum* spp. may be being replaced by those in *Cladocopium* spp. over generations or from stressful events. Because

Breviolum spp. possess the greatest ability to photo-acclimate to high and low irradiances (Iglesias-Prieto and Trench, 1997), it may be an advantage for *S. stellata* to host *Cladocopium* spp. which is the ability to be more thermotolerant than *Breviolum* spp. LaJeunesse et al. (2010) verified that *Breviolum* spp. under temperature changes did not persist and was displaced by *Cladocopium* spp. If we see a scenario where the temperature factor promotes over time, a higher determining influence on performance coral-zooxanthella association, then this may be a viable strategy to ensure the prevalence of coral. This relationship can be explained by the "adaptative bleaching hypothesis" from Buddemeier and Fautin (1993), which postulated that shifts on Symbiodiniaceae communities occur in response to environmental perturbations (Baker, 2001; Howells et al., 2013; LaJeunesse et al., 2009; Hoadley et al., 2021). Moreover, harboring a diverse symbiont community potentially provides physiological versatility, offering hosts a buffer when facing a changing environment (Silverstein et al., 2012; Howells et al., 2013). It is necessary to consider that although our analysis of zooxanthellae genetic material was based on the classification proposed by Pochon and Gates (2010). Despite this, a review for a new classification has been proposed, in which the A-G clades have been reorganized as species, considering the divergent *Symbiodinium* clades equivalent to genera in the Family Symbiodiniaceae, using the ITS-2 marker (LaJeunesse et al., 2018).

The Coral Health Chart brought us precious information regarding coral pigmentation. According to Siebeck et al. (2006), it can point out symptoms of stress in reef-building corals: changes on scale reflect shift in symbiont density and chlorophyll a content, and therefore the bleaching state of the coral. Thus, in addition to the findings in genetic aspects, our general results revealed that colonies with pink pigmentation may be associated with higher temperatures, however indicating a high saturation point (*Ek*) and consequent greater efficiency in the dissipation of radiant energy. Furthermore, variables such as turbidity seem to interfere with photosynthetic efficiency.

When we grouped samples for each of sampled sites, we observed highly significant differences between all sites in relation to Raquel (Fig. 4). Although Caieiras had the highest number of fluorescence measurements below 0.3, averages and medians of measurements obtained in Raquel were lower. That is, the measurements were grouped significantly below the other locations. If we consider environmental characteristics that distinguish these four locations, we observe that Raquel was a deeper environment with the greatest turbidity, i.e., with particles in suspension visibly at rates higher than the other sampled sites, for this time of year, although the southeastern side of the island is calmer from January to May (Maida and Ferreira, 1997). Also, visible forms of marine erosion are present and can be observed at Raquel (Moreira and Guimarães, 2014). Tunala et al. (2019) found lower *Fv/Fm* values for scleractinian coral colonies under different levels of sedimentation and observed that higher sediment levels decrease their photosynthetic efficiency. *S. stellata* exposed to total burial likewise exhibited a tissue discoloration (Tunala et al., 2019), beyond which irreversible bleaching and tissue damage occurred (Philipp and Fabricius, 2003; Erftemeijer et al., 2012). Furthermore, in the field we observed that colonies sampled at Raquel seemed to produce more mucus than those at other locations when we manipulated them. Sediment severely interferes with coral energetics (Abdel-Salam et al., 1988) and directly disturbs the coral's energy budget through the increasing energy demand for active rejection, in other words, mucus production (Aller and Dodge, 1974; Erftemeijer et al., 2012; Stafford-Smith and Ormond, 1992; Wild et al., 2004).

Moreover, RLC parameters for Raquel were also distinct from the others sampled sites. A lowest alpha (α) values were detected – except for one of temperatures (32 °C) that was even lower, but we will see later – at Raquel. Alpha is the coefficient of maximum use of light by PSII, i.e., the initial rate at which increased light induces the transport of electrons. Also, Cruz and Serôdio (2008) confirmed the very strong association between the light responses of Non-Photochemical Quenching (NPQ) and alpha. Decrease in α follows proportionally the build-up of NPQ and a clear inverse relationship was consistently found. Higher NPQ values may also be caused by an increase of photoinhibitory damages to the photosynthetic apparatus (Cruz and Serôdio, 2008).

RLC patterns found for depth said little about this variable because ETRm, α and Ek did not explain the significant differences observed, but repeated patterns very similar to those presented by location. Values of ETRm and Ek showed a proportional increase, although not statistically significant (the depths of 0.2 m and 0.6 m showed differences between them in relation to Ek, though), with the increase in depth, except for the depths of 0.1 m and 1.0 m, referring to Raquel. ETRm and Ek values are expressions of actual photochemical capacity. Measurements from corals over a continuum of light environments have described that coral photobiological patterns seems to be highly conserved (Suggett et al., 2012; Warner and Suggett, 2016). Specifically, key parameters describing photoacclimation, such as intensity of light-saturated photosynthesis (Ek) and the maximum rate of photochemistry (the electron transport rate, ETR), follow a simple linear relation with irradiance levels (Nitschke et al., 2018; Suggett et al., 2012). Thus, in the case of our current research, values obtained for ETR and Ek from the samples grew linearly, as expected from their intrinsic relationships to the RLCs. Despite the pattern, we found a decrease in electron transport rate according to the increase in temperatures. Thus, according to Hoadley et al. (2021), the opposite would indicate acclimation to warming for *Cladocopium* spp. However, different functional traits among closely related symbionts have already been evidenced (Hoadley et al., 2021). This may indicate that, despite resilience, mainly C2, C5 and E4 colonies are not fully acclimatized to temperature stress.

Therefore, Symbiodiniaceae in high depths, i.e., low light regimes, maximizes light absorption and utilization by increasing photosynthetic pigments and photosynthetic efficiency (Anthony and Hoegh-Guldberg, 2003; Falkowski and Dubinsky, 1981; Iglesias-Prieto et al., 2004; López-Londoño et al., 2021), as observed in our results. However, it would be untrustworthy to say that a depth less than 1 m is high, so we do not attribute these differences found only to the depth. When we observed values found for the maximum quantum efficiency (*Fv/Fm*), there was no significant difference for each of these three depths (0.2, 0.5 and 0.6 m), which reiterates the hypothesis that more than one factor may be influencing the response of measurements of the light curve for the groups of colonies evaluated, such as temperature, for instance.

When ocean water becomes too warm for corals, some individuals produce a brightly colored "chemical sunscreen" to try to protect themselves against fatally high-water temperatures and sun exposure (Bollati et al., 2020; Gittins et al., 2015; Ramesh et al., 2020; Salih et al., 2000; Smith et al., 2013). Some research has verified that this phenomenon is a final line of defense before the coral bleaches to white and dies (Bollati et al., 2020; Roth and Deheyn, 2013). Our results showed that C2 presented a behavior pattern different from other color palettes, mainly about *Fv/Fm*. C2 presented the lowest raw data, reaching <0.2 *Fv/Fm* values. According to Tunala et al. (2019), values found below 0.2 can be considered highly harmful and – depending on the intensity and duration of the stress – can be a point of no return for the recovery of its photosynthetic efficiency, which can induce coral to die. In a dark-adapted sample, *Fv/Fm* values correspond

to the fraction of reaction centers which are able to convert absorbed light to photochemical energy, thus it has been used as an indicator for extensive environmental stresses (Krause and Weis, 1991). In addition, C2 also showed the lowest α values, that may be representing a photoinhibition due to damage to the photosynthetic apparatus (Cruz and Serôdio, 2008). However, despite the α values being the lowest for C2, Ek did not show this same course for the pigmentation parameter. This means that its saturation point has also remained high as well as its electron transport rate (ETRm), maintaining its relative quantum efficiency even at high levels of irradiance exposure. Irradiance values measured in the field – at midday in a clear summer sky, at 0 m in the dry tide, leaving C2 pigmentation colonies exposed, mainly – reached a maximum of 1548 μmol photons m^{-2} s^{-1}. Corals and their symbionts require mechanisms for acclimation and adaptation to diverse irradiances and temporal fluctuation in light field. Even at the scale of a single colony, there are extensive variations in light exposure of coral tissues (Falkowski et al., 1993; Smith et al., 2013). These mechanisms can be expressed through pigmentation (Smith et al., 2013). These pigments apply a photoprotective function in corals by absorbing photons or delivering them away from the main absorption bands of symbionts photosynthetic pigments, converting light's wavelength (Ben-Zvi et al., 2022). A photoprotective function of green fluorescent protein (GFP)-like pigments has been considered and are divided into two major groups: the fluorescent proteins (FPs), in charge for cyan to red hues and the non-fluorescent chromoproteins (CPs), which produce pink, purple and blue pigmentation (Dove et al., 2001; Roth et al., 2010). It is proposed that these pigments act through screening (Bollati et al., 2020; Salih et al., 2000), a process whereby the light received by the photosynthetic pigments has passed through a layer containing the photoprotective pigments, i.e. convert short energetic wavelengths into longer, less harmful wavelengths (Ben-Zvi et al., 2022; Roth et al., 2010; Salih et al., 2000). There is evidence that under high irradiance and temperature stress, symbiont capacity for photoprotection can be exceeded and photodamage can occur (Iglesias-Prieto et al., 1992; Warner et al., 1999). Furthermore, CPs could additionally act to promote survival during occasional periods of extraordinary stress (Dove et al., 2001; Smith et al., 2013). In this way, we believe that it is possible that colonies classified as C2 may be expressing these proteins, suggested by the photobiology presented together with the color character expressed by them and the extreme environmental conditions observed in the field, requiring studies with appropriate techniques to test this hypothesis. Intraspecific variability in expression of coral pigments from GFP-family elucidates the genomic basis for the plasticity of stress responses among reef corals (Gittins et al., 2015). In addition, maximum *Fv/Fm* values followed the order where E2 > D5 > E4 > C2 = C5. In this way, we can suggest that the expression of GFP proteins in C5 can also be considered. Ek values were even higher than C2, indicating a high saturation point and, consequently, greater efficiency in the dissipation of radiant energy. Also, Sassi et al. (2015) monitored colonies of *Siderastrea* spp in seasonality patterns and found that pink colonies are associated with bleaching events. Pink colonies persistence for long periods can increase both the host and zooxanthellae mortalities. This host pigmentation response phenomenon to a variety of stressors is possibly an immune response and the presence of purple pigment occurs due the pocilloporin fluorescent pigments (GFPs)in tissue after the loss of zooxanthellae (Bongiorni and Rinkevich, 2005).

Analyzing our temperature measurements made during the chlorophyll *a* fluorescence measurement, we noticed a very clear pattern: the increase in temperature leads a gradual drop in the maximum photosynthetic efficiency sampled. When photosynthesis is working at peak efficiency, *Fv/Fm* values, as measured by PAM fluorometry, are usually in the range of 0.50–0.70, according to the species of coral and its depth location (Warner et al., 1996; Tunala et al., 2019). In this study we obtained about 0.4 for *Fv/Fm* at higher temperatures. Bleaching events have been observed in coral reefs around the world, and most of them have been associated with changes in water temperature (Glynn, 1993; Nielsen et al., 2020). Studies have demonstrated a disruption of photosynthesis in zooxanthellae during exposure to temperatures above 32 °C (Coles and Jokiel, 1978; Iglesias-Prieto et al., 1992). High temperatures can lead to a decrease in *Fv/Fm* in zooxanthellae (Hoegh-Guldberg and Smith, 1989; Iglesias-Prieto et al., 1992; Warner and Suggett, 2016) and significant photoinactivation can be noted (Hoegh-Guldberg and Smith, 1989; Warner et al., 1996), which was also observed in this study. In zooxanthellae, photodamage to PSII is a fundamental reaction to prevent rising of photoinhibition of PSII (Takahashi and Murata, 2008; Warner and Suggett, 2016). A repair process which consists of several steps – degradation of the D1 protein; synthesis of the precursor to the D1 protein; inclusion of the synthesized precursor into the thylakoid membrane; maturation of the D1 protein and assembly of the oxygen-evolving machinery (Aro et al., 1993, 2005) – it is the balance between the rate of photodamage to PSII and the rate of repair. Thus, excess of light energy absorbed in elevated temperatures by photosynthetic pigments accelerates photoinhibition through suppressing the repair of photodamaged PSII (Takahashi and Murata, 2008). Reduced *Fv/Fm* was accompanied by lower ETRm and increased NPQ similarly to Hoadley et al. (2019). Instead, Ek had the highest rates found in this study among all the factors analyzed, when under 32 °C. On the other hand, α represents the lowest values for 32 °C, performing values for the light-limited coefficient for PSII photochemistry. As previously mentioned, α has an intrinsic and inversely proportional relationship with NPQ and some studies have documented a significant rise in NPQ shortly after exposing corals to elevated temperature (Warner et al., 1996; Hill et al., 2004).

Regarding the temperatures experienced in the tidepools, corals in PARNAMAR Fernando de Noronha, endure summer temperatures of up to 37 °C, making them ideal subjects to study the mechanisms underlying thermal tolerance. Caieiras had the highest temperatures in the field. However, the persistence of high temperatures above the average lasted less time than in the other places (81 min). When comparing data on Fig. 4, we observed a clear pattern of occurrence of the lowest values of *Fv/Fm* in colonies with C2 pigmentation occurring in Caieiras. This comparison allows us to reaffirm that this pigmentation can be an indication of high photoinhibition and, consequently, a pathway to bleaching events.

In correspondence analysis, three very well-defined groupings can be identified, at first. These groups are strongly connected to sampled sites, where Raquel and Caieiras are grouped separately, and Atalaia and Leão form a large group, showing high similarity between samples, as well as that previously detected by ANOVA. Dimension 1 opposes the samples in the right side of the graph characterized by a strongly positive coordinate on the axis. There, a highly connected group is formed. This cluster refers to Raquel's samples, proving to be very well defined by their local characteristics and quite distinct from the other groups, where samples with a tendency to values in the range 0.3–0.4 of *Fv/Fm* prevailed. Inside this group, where samples characterized by a positive coordinate on the axis is, sharing high frequency for the factors *Fv/Fm* on interval of 0.3–0.4, at 32 °C at Raquel, color gradient E4 and 1 m depth. Note that the Raquel site and temperature 32 °C are highly correlated with the dimension (respective correlation of 0.97 and 0.97). We also see a relatively high frequency for the factors D5 and 0.1 m. Furthermore, we were able to detect high frequency for the pigment factor C5 with

Atalaia and 0.4–0.5 *Fv/Fm* values. When we look at the CA factor map, we see that the temperature factor contributes strongly to the map distribution, according to the scale bar that concerns the contribution of the factors, where the red represents greater and the blue the lesser contribution of factors (triangles) in relation to the samples (circles). That is, it reaffirms temperature as an important factor for the maximum quantum efficiency of the samples of *S. stellata* in the four sampled places.

5. Conclusions

Our results showed that colonies with different pigmentations do not necessarily imply a different quantum yield. Photoinhibition mechanisms and other strategies such as the production of proteins such as those of GFP-family can play a fundamental role in resilience of coral species. Thus, we strongly recommend that research around this approach be applied to these corals that live in extreme conditions like those of tidepools at PARNAMAR Fernando de Noronha. Furthermore, we were able to observe that the duration of a heat event can be more aggravating than the temperature increase itself, to some extent. Colonies exposed to heat waves for a longer period have a lesser capacity to maintain themselves with high yield. This can directly reflect on the organism's resilience in face of a bleaching event. Our genetic analysis also indicated a strong association between *S. stellata* and *Cladocopium* spp. However, we suggest that monitoring studies be implemented to assess whether this association is of fidelity or if there may be fluctuations in zooxanthella hosting according to climatic events. Finally, we suggest that visitation activities in the Caieiras Pools be closely monitored and that a new proposal for carrying capacity for visitation be carried out, especially on days of greater tide variation and intense heat and irradiance, so that other factors do not act in synergy with climatic factors. Especially, considering that the temperatures observed on this site were the highest observed and, consequently, may be the most worrying.

CRediT authorship contribution statement

Layla Poubel Tunala: Conceptualization, Investigation, Formal analysis, Writing, editing and reviewing – original draft. **Caroline Rezende Guerra:** Investigation, Formal analysis, Writing – editing and reviewing. **Rafael Gomes de Menezes:** Investigation, Writing and editing. **Celine Philipp Diogo:** Investigation, Writing and editing. **Tailah Bernardo de Almeida:** Investigation, Formal analysis, Writing. **Heitor Monteiro Duarte:** Conceptualization, Investigation, Formal analysis, Writing, editing and reviewing – original draft, Supervision. **Frederico Tapajós de Souza Tâmega:** Writing, editing and reviewing – original draft, Supervision. **Ricardo Coutinho:** Conceptualization, Investigation, Writing, editing and reviewing – original draft, Supervision, Funding acquisition.

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.

Data availability

Data will be made available on request

Acknowledgments

We are grateful to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brazil for providing the Doctoral fellowship (LPT) and Productivity fellowship (RC); Administration of State District of Fernando de Noronha (Pernambuco State) by exemption from Environmental Preservation Fee and support for staying and transporting on the island; Instituto Chico Mendes de Conservação da Biodiversidade (ICMBIO), Brazil for research license SISBIO number 67290-1. The authors thank the LABCEN/CCB Sequencing Platform at Universidade Federal de Pernambuco (UFPE) for use of its facilities and Instituto de Estudos do Mar Almirante Paulo Moreira (IEAPM) for laboratory and equipment support.

References

Abdel-Salam, H.A., Porter, J.W., Hatcher, B.G., 1988. Physiological effects of sediment rejection on photosynthesis and respiration in three Caribbean reef corals. In: Proc. 6th Int. Coral Reef Symp., Vol. 2. pp. 285–292.

Abrego, D., Ulstrup, K.E., Willis, B.L., van Oppen, M.J., 2008. Species–specific interactions between algal endosymbionts and coral hosts define their bleaching response to heat and light stress. Proc. R. Soc. B 275 (1648), 2273–2282. http://dx.doi.org/10.1098/rspb.2008.0180.

Aller, R.C., Dodge, R.E., 1974. Animal-sediment relations in a tropical lagoon: discovery bay. Jam. J. Mar. Res. 32, 209–232.

Amado-Filho, G.M., Pereira-Filho, G.H., Bahia, R.G., Abrantes, D.P., Veras, P.C., Matheus, Z., 2012. Occurrence and distribution of rhodolith beds on the Fernando de Noronha Archipelago of Brazil. Aquat. Bot. 101, 41–45. http://dx.doi.org/10.1016/j.aquabot.2012.03.016.

Anthony, K.R.N., 2016. Coral reefs under climate change and ocean acidification: challenges and opportunities for management and policy. Annu. Rev. Environ. Resour. 41, 59–81. http://dx.doi.org/10.1146/annurev-environ-110615-085610.

Anthony, K.R., Helmstedt, K.J., Bay, L.K., Fidelman, P., Hussey, K.E., Lundgren, P., Mead, D., McLeod, I.M., Mumby, P.J., Newlands, M., Schaffelke, B., Wilson, K.A., Hardisty, P.E., 2020. Interventions to help coral reefs under global change – A complex decision challenge. PLoS One 15 (8), e0236399. http://dx.doi.org/10.1371/journal.pone.0236399.

Anthony, K.R.N., Hoegh-Guldberg, O., 2003. Variation in coral photosynthesis, respiration and growth characteristics in contrasting light microhabitats: an analogue to plants in forest gaps and understoreys? Funct. Ecol. 17, 246–259.

Aro, E.M., Suorsa, M., Rokka, A., Allahverdiyeva, Y., Paakkarinen, V., Saleem, A., Battchikova, N., Rintamäki, E., 2005. Dynamics of photosystem II: a proteomic approach to thylakoid protein complexes. J. Exp. Bot. 56 (411), 347–356. http://dx.doi.org/10.1093/jxb/eri041.

Aro, E.M., Virgin, I., Andersson, B., 1993. Photoinhibition of photosystem II. Inactivation, protein damage and turnover. Biochim. Biophys. Acta - Bioenergy 1143 (2), 113–134.

Baird, A.H., Guest, J.R., Willis, B.L., 2009. Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. Annu. Rev. Ecol. Evol. Syst. 40, 551–571. http://dx.doi.org/10.1146/annurev.ecolsys.110308.120220.

Baker, A.C., 2001. Reef corals bleach to survive change. Nature 411 (6839), 765–766.

Ben-Zvi, O., Lindemann, Y., Eyal, G., Loya, Y., 2022. Coral fluorescence: a prey-lure in deep habitats. Commun. Biol. 5 (1), 537. http://dx.doi.org/10.1038/s42003-022-03460-3.

Björkman, O., Demmig-Adams, B., 1995. Regulation of photosynthetic light energy capture, conversion, and dissipation in leaves of higher plants. In: Ecophysiology of Photosynthesis. Springer, Berlin, Heidelberg, pp. 17–47. http://dx.doi.org/10.1007/978-3-642-79354-7_2.

Bollati, E., D'Angelo, C., Alderdice, R., Pratchett, M., Ziegler, M., Wiedenmann, J., 2020. Optical feedback loop involving dinoflagellate symbiont and scleractinian host drives colorful coral bleaching. Curr. Biol. 30 (13), 2433–2445. http://dx.doi.org/10.1016/j.cub.2020.04.055.

Bongiorni, L., Rinkevich, B., 2005. The pink-blue spot syndrome in *Acropora eurystoma* (Eilat, Red sea): A possible marker of stress? Zoology 108 (3), 247–256. http://dx.doi.org/10.1016/j.zool.2005.05.002.

Buddemeier, R.W., Fautin, D.G., 1993. Coral bleaching as an adaptive mechanism. Bioscience 43 (5), 320–326. http://dx.doi.org/10.2307/1312064.

Castro, C.B., Pires, D.O., 2001. Brazilian coral reefs: what we already know and what is still missing. Bull. Mar. Sci. 69, 357–371.

Coffroth, M.A., Lasker, H.R., Oliver, J.K., 1990. Coral Mortality Outside of the Eastern Pacific During 1982-1983: Relationship to El Nino. In: Elsevier Oceanography Series, vol. 52, pp. 141–182.

Coles, S.L., Jokiel, P.L., 1978. Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. Mar. Biol. 49, 187–195.

Costa, C.F., Sassi, R., Gorlach-Lira, K., 2008. Zooxanthellae genotypes in the coral *Siderastrea stellata* from coastal reefs in northeastern Brazil. J. Exp. Mar. Biol. Ecol. 367 (2), 149–152. http://dx.doi.org/10.1016/j.jembe.2008.09.012.

Cruz, S., Serôdio, J., 2008. Relationship of rapid light curves of variable fluorescence to photoacclimation and non-photochemical quenching in a benthic diatom. Aquat. Bot. 88 (3), 256–264. http://dx.doi.org/10.1016/j.aquabot.2007.11.001.

Decelle, J., Carradec, Q., Pochon, X., Henry, N., Romac, S., Mahé, F., Dunthorn, M., Kourlaiev, A., Voolstra, C.R., Wincker, P., de Vargas, C., 2018. Worldwide occurrence and activity of the reef-building coral symbiont *Symbiodinium* in the open ocean. Curr. Biol. 28 (22), 3625–3633. http://dx.doi.org/10.1016/j.cub.2018.09.024.

Dove, S.G., Hoegh-Guldberg, O., Ranganathan, S., 2001. Major colour patterns of reef-building corals are due to a family of GFP-like proteins. Coral Reefs 19 (3), 197–204. http://dx.doi.org/10.1007/PL00006956.

Dubinsky, Z., Stambler, N., 2009. Photoacclimation processes in phytoplankton: mechanisms, consequences, and applications. Aquat. Microb. Ecol. 56 (2–3), 163–176. http://dx.doi.org/10.3354/ame01345.

Eakin, C.M., Sweatman, H.P., Brainard, R.E., 2019. The 2014–2017 global-scale coral bleaching event: insights and impacts. Coral Reefs 38 (4), 539–545. http://dx.doi.org/10.1007/s00338-019-01844-2.

Elzhov, T.V., Mullen, K.M., Spiess, A.N., Bolker, B., Mullen, M.K.M., Suggests, M.A.S.S., 2016. Package 'minpack.lm': R interface to the levenberg–marquardt nonlinear least-squares algorithm found in minpack, plus support for bounds. pp. 1–2, R package version. 1.

Erftemeijer, P.L., Riegl, B., Hoeksema, B.W., Todd, P.A., 2012. Environmental impacts of dredging and other sediment disturbances on corals: a review. Mar. Pollut. Bull. 64 (9), 1737–1765. http://dx.doi.org/10.1016/j.marpolbul.2012.05.008.

Eston, V.R.D., Migotto, A.E., Oliveira Filho, E.C.D., Rodrigues, S.D.A., Freitas, J.C.D., 1986. Vertical distribution of benthic marine organisms on rocky coasts of the Fernando de Noronha Archipelago (Brazil). Bol. Inst. Oceanogr. 34, 37–53.

Falkowski, P.G., Dubinsky, Z., 1981. Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. Nature 289 (5794), 172–174.

Falkowski, P.G., Dubinsky, Z., Muscatine, L., McCloskey, L., 1993. Population control in symbiotic corals. Bioscience 43 (9), 606–611.

Freudenthal, H.D., 1962. Symbiodinium gen. nov. and *Symbiodinium microadriaticum* sp. nov. a zooxanthella: taxonomy, life cycle, and morphology. J. Protozool. 9 (1), 45–52.

Friedlingstein, P., Jones, M.W., O'sullivan, M., Andrew, R.M., Hauck, J., Peters …, G.P., Zaehle, S., 2019. Global carbon budget 2019. Earth Syst. Sci. Data 11 (4), 1783–1838. http://dx.doi.org/10.5194/essd-11-1783-2019.

Genty, B., Briantais, J.M., Baker, N.R., 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. BBA Gen. Subj. 990, 87–92.

Gittins, J.R., D'Angelo, C., Oswald, F., Edwards, R.J., Wiedenmann, J., 2015. Fluorescent protein-mediated colour polymorphism in reef corals: multicopy genes extend the adaptation/acclimatization potential to variable light environments. Mol. Ecol. 24 (2), 453–465. http://dx.doi.org/10.1111/mec.13041.

Glynn, P.W., 1993. Coral reef bleaching: ecological perspectives. Coral Reefs 12 (1), 1–17.

Glynn, P.W., Maté, J.L., Baker, A.C., Calderón, M.O., 2001. Coral bleaching and mortality in Panama and Ecuador during the 1997–1998 El Niño–southern oscillation event: spatial/temporal patterns and comparisons with the 1982–1983 event. Bull. Mar. Sci. 69 (1), 79–109.

Goreau, T.J., Hayes, R.L., 2021. Global warming triggers coral reef bleaching tipping point. Ambio 50 (6), 1137–1140. http://dx.doi.org/10.1007/s13280-021-01512-2.

Hall, T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for windows 95/98/NT. Nucl. Acids. Symp. Ser. 41, 95–98.

Hill, R., Schreiber, U., Gademann, R., Larkum, A.W.D., Kühl, M., Ralph, P.J., 2004. Spatial heterogeneity of photosynthesis and the effect of temperature-induced bleaching conditions in three species of corals. Mar. Biol. 144 (4), 633–640. http://dx.doi.org/10.1007/s00227-003-1226-1.

Hoadley, K.D., Lewis, A.M., Wham, D.C., Pettay, D.T., Grasso, C., Smith ., R., Warner, M.E., 2019. Host–symbiont combinations dictate the photo-physiological response of reef-building corals to thermal stress. Sci. Rep. 9 (1), 1–15. http://dx.doi.org/10.1038/s41598-019-46412-4.

Hoadley, K.D., Pettay, Daniel T., Lewis, A., Wham, D., Grasso, C., Smith, R., Kemp, D.W., LaJeunesse, T., Warner, M.E., 2021. Different functional traits among closely related algal symbionts dictate stress endurance for vital Indo-Pacific reef-building corals. Glob. Change Biol. 27, 5295–5309. http://dx.doi.org/10.1111/gcb.15799.

Hoegh-Guldberg, O., Smith, G.J., 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 *Seriatopo rahystrix dana*. J. Exp. Mar. Biol. Ecol. 129, 279–303. http://dx.doi.org/10.1111/mec.12342.

Howells, E.J., Beltran, V.H., Larsen, N.W., Bay, L.K., Willis, B.L., Van Oppen, M.J.H., 2012. Coral thermal tolerance shaped by local adaptation of photosymbionts. Nat. Clim. Change. 2, 116–120. http://dx.doi.org/10.1038/NCLIMATE1330.

Howells, E.J., Willis, B.L., Bay, L.K., van Oppen, M.J., 2013. Spatial and temporal genetic structure of *Symbiodinium* populations within a common reef-building coral on the great barrier reef. Mol. Ecol. 22 (14), 3693–3708. http://dx.doi.org/10.1111/mec.12342.

Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough ., J.M., Wilson, S.K., 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359 (6371), 80–83. http://dx.doi.org/10.1126/science.aan8048.

Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird ., A.H., Wilson, S.K., 2017. Global warming and recurrent mass bleaching of corals. Nature 543 (7645), 373–377. http://dx.doi.org/10.1038/nature21707.

Iglesias-Prieto, R., Beltran, V.H., LaJeunesse, T.C., Reyes-Bonilla, H., Thome, P.E., 2004. Different algal symbionts explain the vertical distribution of dominant reef corals in the eastern Pacific. Proc. R. Soc. B 271 (1549), 1757–1763. http://dx.doi.org/10.1098/rspb.2004.2757.

Iglesias-Prieto, R., Matta, J.L., Robins, W.A., Trench, R.K., 1992. Photosynthetic response to elevated temperature in the symbiotic dinoflagellate *Symbiodinium microadriaticum* in culture. Proc. Natl. Acad. Sci. 89, 10302–10305. http://dx.doi.org/10.1073/pnas.89.21.10302.

Iglesias-Prieto, R., Trench, R.K., 1994. Acclimation and adaptation to irradiance in symbiotic dinoflagellates. I. Responses of the photosynthetic unit to changes in photon flux density. Mar. Ecol. Prog. Ser. 113 (1), 163–175.

Iglesias-Prieto, R., Trench, R.K., 1997. Acclimation and adaptation to irradiance in symbiotic dinoflagellates. II. Response of chlorophyll–protein complexes to different photon-flux densities. Mar. Biol. 130 (1), 23–33. http://dx.doi.org/10.1007/s002270050221.

Jassby, A.D., Platt, T., 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. 21 (4), 540–547. http://dx.doi.org/10.4319/lo.1976.21.4.0540.

Karako-Lampert, S., Katcoff, D.J., Achituv, Y., Dubinsky, Z., Stambler, N., 2004. Do clades of symbiotic dinoflagellates in scleractinian corals of the gulf of Eilat (Red sea) differ from those of other coral reefs? J. Exp. Mar. Biol. Ecol. 311 (2), 301–314. http://dx.doi.org/10.1016/j.jembe.2004.05.015.

Krajewski, J.P., Floeter, S.R., 2011. Reef fish community structure of the Fernando de Noronha Archipelago (equatorial western Atlantic): the influence of exposure and benthic composition. Environ. Biol. Fish. 92 (1), 25–40. http://dx.doi.org/10.1007/s10641-011-9813-3.

Krause, G.H., Weis, E., 1991. Chlorophyll fluorescence and photosynthesis: the basics. Annu. Rev. Plant. Biol. 42, 313–349.

Laborel-Deguen, F., Castro, C.B., Nunes, F., Pires, D.O., 2019. Recifes Brasileiros: O Legado de Laborel. Museu Nacional, Rio de Janeiro, p. 376.

LaJeunesse, T.C., 2001. Investigating the biodiversity, ecology, and phylogeny of endosymbiotic dinoflagellates in the genus *Symbiodinium* using the ITS region: in search of a species level marker. J. Phycol. 37 (5), 866–880. http://dx.doi.org/10.1046/j.1529-8817.2001.01031.x.

LaJeunesse, T.J.M.B., 2002. Diversity and community structure of symbiotic dinoflagellates from Caribbean coral reefs. Mar. Biol. 141 (2), 387–400. http://dx.doi.org/10.1007/s00227-002-0829-2.

LaJeunesse, T.C., Parkinson, J.E., Gabrielson, P.W., Jeong, H.J., Reimer, J.D., Voolstra, C.R., Santos, S.R., 2018. Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Curr. Biol. 28 (16), 2570–2580. http://dx.doi.org/10.1016/j.cub.2018.07.008.

LaJeunesse, T.C., Parkinson, J.E., Gabrielson, P.W., Jeong, H.J., Reimer, J.D., Voolstra, C.R., Santos, S.R., 2019. Systematic revision of symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Curr. Biol. 28, 2570–2580.e6. http://dx.doi.org/10.1016/j.cub.2018.07.008.

LaJeunesse, T.C., Smith, R.T., Finney, J., Oxenford, H., 2009. Outbreak and persistence of opportunistic symbiotic dinoflagellates during the 2005 Caribbean mass coral 'bleaching' event. Proc. R. Soc. B 276 (1676), 4139–4148. http://dx.doi.org/10.1098/rspb.2009.1405.

LaJeunesse, T.C., Smith, R., Walther, M., Pinzón, J., Pettay, D.T., McGinley ., M., Warner, M.E., 2010. Host-symbiont recombination versus natural selection in the response of coral-dinoflagellate symbioses to environmental disturbance. Proc. R. Soc. B 277 (1696), 2925–2934. http://dx.doi.org/10.1098/rspb.2010.0385.

LaJeunesse, T.C., Thornhill, D.J., 2011. Improved resolution of reef-coral endosymbiont (*Symbiodinium*) species diversity, ecology, and evolution through *psb*a non-coding region genotyping. PLoS One 6 (12), e29013. http://dx.doi.org/10.1371/journal.pone.0029013.

LaJeunesse, T.C., Trench, R.K., 2000. Biogeography of two species of *Symbiodinium* (Freudenthal) inhabiting the intertidal sea anemone *Anthopleura elegantissima* (Brandt). Biol. Bull. 199 (2), 126–134. http://dx.doi.org/10.2307/1542872.

Lapointe, B.E., Brewton, R.A., Herren, L.W., Porter, J.W., Hu, C., 2019. Nitrogen enrichment, altered stoichiometry, and coral reef decline at Looe key, Florida keys, USA: a 3-decade study. Mar. Biol. 166 (8), 1–31. http://dx.doi.org/10.1007/s00227-019-3538-9.

Leão, Z.M., Kikuchi, R.K., Ferreira, B.P., Neves, E.G., Sovierzoski, H.H., Oliveira, M.D., Maida, M., Correia, M.D., Johnsson, R., 2016. Brazilian coral reefs in a period of global change: A synthesis. Braz. J. Oceanogr. 64, 97–116. http://dx.doi.org/10.1590/S1679-875920160916064sp2.

Leão, Z.M., Kikuchi, R.K., Ferreira, B.P., Neves, E.G., Sovierzoski, H.H., Oliveira ., M.D., Johnsson, R., 2016. Brazilian coral reefs in a period of global change: A synthesis. Braz. J. Oceanogr. 64, 97–116. http://dx.doi.org/10.1590/S1679-875920160916064sp2.

López-Londoño, T., Galindo-Martínez, C.T., Gómez-Campo, K., González-Guerrero, L.A., Roitman, S., Pollock, F.J., Pizarro, V., López-Victoria, M., Medina, M., Iglesias-Prieto, R., 2021. Physiological and ecological consequences of the water optical properties degradation on reef corals. Coral Reefs 1–14. http://dx.doi.org/10.1007/s00338-021-02133-7.

Maida, M., Ferreira, B.P., 1997. Coral reefs of Brazil: Overview and field guide. In: Proc. 8th Int. Coral Reef Sym., Vol. 1. pp. 263–274.

Monteiro, J.G., Costa, C.F., Gorlach-Lira, K., Fitt, W.K., Stefanni, S.S., Sassi, R., Santos, R.S., LaJeunesse, T.C., 2013. Ecological and biogeographic implications of siderastrea symbiotic relationship with Symbiodinium sp. C46 in Sal island (Cape Verde, east Atlantic ocean). Mar. Biodivers. 43, 261–272. http://dx.doi.org/10.1007/s12526-013-0153-8.

Moreira, J.C., Guimarães, G.B., 2014. Fernando de noronha archipelago: a paradise formed by volcanism in Brazil. In: Volcanic Tourist Destinations. Springer, Berlin, Heidelberg, pp. 315–323.

Morrison, T.H., Adger, N., Barnett, J., Brown, K., Possingham, H., Hughes, T., 2020. Advancing coral reef governance into the Anthropocene. One Earth 2 (1), 64–74. http://dx.doi.org/10.1016/j.oneear.2019.12.014.

Nielsen, J.J.V., Kenkel, C.D., Bourne, D.G., Despringhere, L., Mocellin, V.J.L., Bay, L.K., 2020. Physiological effects of heat and cold exposure in the common reef coral *Acropora millepora*. Coral Reefs 1–11. http://dx.doi.org/10.1007/s00338-019-01881-x.

Nitschke, M.R., Gardner, S.G., Goyen, S., Fujise, L., Camp, E.F., Ralph, P.J., Suggett, D.J., 2018. Utility of photochemical traits as diagnostics of thermal tolerance amongst great barrier reef corals. Front. Mar. Sci. 5 (45), http://dx.doi.org/10.3389/fmars.2018.00045.

Perkins, G.R., Underwood, J.C.G., Brotas, V., Snow, G.C., et al., 2001. Responses of microphytobenthos to light: primary production and carbohydrate allocation over an emersion period. Mar. Ecol. Prog. Ser. 223, 101–112. http://dx.doi.org/10.3354/meps223101.

Philipp, E., Fabricius, K., 2003. Photophysiological stress in scleractinian corals in response to short-term sedimentation. J. Exp. Mar. Biol. Ecol. 287, 57–78. http://dx.doi.org/10.1016/S0022-0981(02)00495-1.

Picciani, N., Seiblitz, I.G.D.L., de Paiva, P.C., Castro, C.B., Zilberberg, C., 2016. Geographic patterns of *Symbiodinium* diversity associated with the coral *Mussismilia hispida* (Cnidaria, Scleractinia) correlate with major reef regions in the southwestern Atlantic ocean. Mar. Biol. 163 (11), 1–11. http://dx.doi.org/10.1007/s00227-016-3010-z.

Pochon, X., Gates, R.D., 2010. A new *Symbiodinium* clade (Dinophyceae) from soritid foraminifera in Hawai'i. Mol. Phyl. Evol. 56 (1), 492–497. http://dx.doi.org/10.1016/j.ympev.2010.03.040.

Ralph, P., Gademann, R., Larkum, A., Kühl, M., 2002. Spatial heterogeneity in active chlorophyll fluorescence and PSII activity of coral tissues. Mar. Biol. 141 (4), 639–646. http://dx.doi.org/10.1007/s00227-002-0866-x.

Ramesh, C.H., Koushik, S., Shunmugaraj, T., Murthy, M.R., 2020. Coral colors as a heat stress indicator during bleaching events. J. Wildl. Res. 8 (03), 68–70.

Robison, J.D., Warner, M.E., 2006. Differential impacts of photoacclimation and thermal stress on the photobiology of four different phylotypes of *Symbiodinium* (pyrrhophyta) 1. J. Phycol. 42 (3), 568–579. http://dx.doi.org/10.1111/j.1529-8817.2006.00232.x.

Roth, M.S., Deheyn, D.D., 2013. Effects of cold stress and heat stress on coral fluorescence in reef-building corals. Sci. Rep. 3 (1), 1–8. http://dx.doi.org/10.1038/srep01421.

Roth, M.S., Latz, M.I., Goericke, R., Deheyn, D.D., 2010. Green fluorescent protein regulation in the coral *Acropora yongei* during photoacclimation. J. Exp. Biol. 213 (21), 3644–3655. http://dx.doi.org/10.1242/jeb.040881.

Rowan, R.O.B., Powers, D.A., 1991a. A molecular genetic classification of zooxanthellae and the evolution of animal-algal symbioses. Science 251 (4999), 1348–1351. http://dx.doi.org/10.1126/science.251.4999.1348.

Rowan, R., Powers, D.A., 1991b. Molecular genetic identification of symbiotic dinoflagellates (zooxanthellae). Mar. Ecol. Prog. Ser. 71 (1), 65–73.

Sakshaug, E., Bricaud, A., Dandonneau, Y., Falkowski, P.G., Kiefer, D.A., Legendre ., L., Takahashi, M., 1997. Parameters of photosynthesis: definitions, theory and interpretation of results. J. Plankton Res. 19 (11), 1637–1670. http://dx.doi.org/10.1093/plankt/19.11.1637.

Salih, A., Larkum, A., Cox, G., Kühl, M., Hoegh-Guldberg, O., 2000. Fluorescent pigments in corals are photoprotective. Nature 408 (6814), 850–853. http://dx.doi.org/10.1038/35048564.

Santos, S.R., Shearer, T.L., Hannes, A.R., Coffroth, M.A., 2004. Fine-scale diversity and specificity in the most prevalent lineage of symbiotic dinoflagellates (*Symbiodinium*, Dinophyceae) of the Caribbean. Mol. Ecol. 13 (2), 459–469. http://dx.doi.org/10.1046/j.1365-294X.2003.02058.x.

Sassi, R., Sassi, C.F.C., Gorlach-Lira, K., Fitt, W.K., 2015. Pigmentation changes in *Siderastrea* spp. during bleaching events in the costal reefs of northeastern Brazil. Lat. Am. J. Aquat. Res. 43 (1), 176–185.

Schreiber, U., 2004. Pulse-amplitude-modulation (PAM) fluorometry and saturation pulse method: an overview. In: Chlorophyll a Fluorescence, Vol. 19. Springer, Dordrecht, pp. 279–319. http://dx.doi.org/10.1007/978-1-4020-3218-9_11.

Segal, B., Castro, C.B., 2000. Slope preferences of reef corals (Cnidaria, Scleractinia) in the Abrolhos Archipelago. Braz. Bol. Mus. Nac. 418, 1–10.

Siebeck, U.E., Marshall, N.J., Klüter, A., Hoegh-Guldberg, O., 2006. Monitoring coral bleaching using a colour reference card. Coral Reefs 25 (3), 453–460. http://dx.doi.org/10.1007/s00338-006-0123-8.

Silverstein, R.N., Correa, A.M., Baker, A.C., 2012. Specificity is rarely absolute in coral-algal symbiosis: implications for coral response to climate change. Proc. R. Soc. B 279 (1738), 2609–2618. http://dx.doi.org/10.1098/rspb.2012.0055.

Smith, E.G., D'Angelo, C., Salih, A., Wiedenmann, J., 2013. Screening by coral green fluorescent protein (GFP)-like chromoproteins supports a role in photoprotection of zooxanthellae. Coral Reefs 32 (2), 463–474. http://dx.doi.org/10.1007/s00338-012-0994-9.

Soares, M.O., Rossi, S., Gurgel, A.R., Lucas, C.C., Tavares, T.C.L., Diniz, B., Feitosa, C.V., Rabelo, E.F., Pereira, P.H.C., Kikuchi, R.K.P., Leão, Z.M.A.N., Cruz, I.C.S., Carneiro, P.B.M., Alvarez-Filip, L., 2021. Impacts of a changing environment on marginal coral reefs in the tropical southwestern Atlantic. Ocean Coast. Manage. 210, 105692. http://dx.doi.org/10.1016/j.ocecoaman.2021.105692.

Stafford-Smith, M.G., Ormond, R.F.G., 1992. Sediment-rejection mechanisms of 42 species of Australian scleractinian corals. Mar. Freshw. Res. 43, 683–705. http://dx.doi.org/10.1071/MF9920683.

Stanley, Jr., G.D., 2003. The evolution of modern corals and their early history. Earth-Sci. Rev. 60 (3–4), 195–225. http://dx.doi.org/10.1016/S0012-8252(02)00104-6.

Suggett, D.J., Goyen, S., Evenhuis, C., Szabó, M., Pettay, D.T., Warner, M.E., Ralph, P.J., 2015. Functional diversity of photobiological traits within the genus *S ymbiodinium* appears to be governed by the interaction of cell size with cladal designation. New Phytol. 208 (2), 370–381. http://dx.doi.org/10.1111/nph.13483.

Suggett, D.J., Kikuchi, R.K., Oliveira, M.D., Spanó, S., Carvalho, R., Smith, D.J., 2012. Photobiology of corals from Brazil's near-shore marginal reefs of Abrolhos. Mar. Biol. 159, 1461–1473. http://dx.doi.org/10.1007/s00227-012-1925-6.

Suggett, D.J., Le Floc', H.E., Harris, G.N., Leonardos, N., Geider, R.J., 2007. Different strategies of photoacclimation by two strains of *Emiliania huxleyi* (Haptophyta) 1. J. Phycol. 43 (6), 1209–1222. http://dx.doi.org/10.1111/j.1529-8817.2007.00406.x.

Suggett, D.J., Smith, D.J., 2020. Coral bleaching patterns are the outcome of complex biological and environmental networking. Glob. Change Biol. 26 (1), 68–79. http://dx.doi.org/10.1111/gcb.14871.

Swain, T.D., Chandler, J., Backman, V., Marcelino, L., 2017. Consensus thermo tolerance ranking for 110 Symbiodinium phylotypes: an exemplar utilization of a novel iterative partial rank aggregation tool with broad application potential. Funct. Ecol. 31, 172–183. http://dx.doi.org/10.1111/1365-2435.12694.

Takahashi, S., Murata, N., 2008. How do environmental stresses accelerate photoinhibition? Trends Plant Sci. 13 (4), 178–182. http://dx.doi.org/10.1016/j.tplants.2008.01.005.

Taylor, D.L., 1974. Symbiotic marine algae; taxonomy and biological fitness. In: Symbiosis in the Sea. University of South Carolina Press, Columbia pp. 245–262.

Team, R.C., 2015a. R: A language and environment for statistical computing. In: R Foundation for Statistical Computing; 2014. R Foundation for Statistical Computing, Vienna, Austria.

Team, R.S., 2015b. R-Studio: Integrated Development for R. R-Studio, Inc, Boston, MA, USA.

Thornhill, D.J., Fitt, W.K., Schmidt, G.W., 2006. Highly stable symbioses among western Atlantic brooding corals. Coral Reefs 25 (4), 515–519. http://dx.doi.org/10.1007/s00338-006-0157-y.

Toller, W.W., Rowan, R., Knowlton, N., 2001a. Repopulation of zooxanthellae in the Caribbean corals *Montastraea annularis* and *M. faveolata* following experimental and disease-associated bleaching. Biol. Bull. 201, 360–373. http://dx.doi.org/10.2307/1543614.

Toller, W.W., Rowan, R., Knowlton, N., 2001b. Zooxanthellae of the *Montastraea annularis* species complex: patterns of distribution of four taxa of *Symbiodinium* on different reefs and across depths. Biol. Bull. 201, 348–359. http://dx.doi.org/10.2307/1543613.

Tunala, L.P., Tâmega, F.T., Duarte, H.M., Coutinho, R., 2019. Stress factors in the photobiology of the reef coral *Siderastrea stellata*. J. Exp. Mar. Biol. Ecol. 519, 151188. http://dx.doi.org/10.1016/j.jembe.2019.151188.

Van Hooidonk, R., Maynard, J., Tamelander, J., Gove, J., Ahmadia, G., Raymundo, L., Heron, S.F., Planes, S., 2016. Local-scale projections of coral reef futures and implications of the Paris agreement. Sci. Rep. 6 (1), 1–8. http://dx.doi.org/10.1038/srep39666.

Van Oppen, M.J., Palstra, F.P., Piquet, A.M.T., Miller, D.J., 2001. Patterns of coral-dinoflagellate associations in *Acropora*: significance of local availability and physiology of *Symbiodinium* strains and host-symbiont selectivity. Proc. R. Soc. B 268 (1478), 1759–1767. http://dx.doi.org/10.1098/rspb.2001.1733.

Warner, M.E., Fitt, W.K., Schmidt, G.W., 1996. The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae in hospite from four different species of reef coral: a novel approach. Plant Cell Environ. 19, 291–299. http://dx.doi.org/10.1111/j.1365-3040.1996.tb00251.x.

Warner, M.E., Fitt, W.K., Schmidt, G.W., 1999. Damage to photosystem II in symbiotic dinoflagellates: a determinant of coral bleaching. Proc. Natl. Acad. Sci. USA 96, 8007–8012. http://dx.doi.org/10.1073/pnas.96.14.8007.

Warner, M.E., Suggett, D.J., 2016. The photobiology of *Symbiodinium* spp.: linking physiological diversity to the implications of stress and resilience. In: The Cnidaria, Past, Present and Future. Springer, Cham, pp. 489–509. http://dx.doi.org/10.1007/978-3-319-31305-4_30.

Wild, C., Huettel, M., Klueter, A., Kremb, S.G., Rasheed, M., 2004. Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. Nature 428, 66–70. http://dx.doi.org/10.1038/NATURE02344.

Wilkinson, C., 2000. Status of Coral Reefs of the World: 2000. Australian Institute for Marine Science, Townsville.

Winter, A.P.M., Chaloub, R.M., Duarte, G.A.S., Castro, C.B., 2016. Photosynthetic responses of corals *Mussismilia harttii* (Verrill, 1867) from turbid waters to changes in temperature and presence/absence of light. Braz. J. Oceanogr. 64, 203–216. http://dx.doi.org/10.1590/S1679-87592016080806403.

Zar, J.H., 2010. Biostatistical Analysis, fifth ed. Prentice-Hall/Pearson.