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Physiological and ecological consequences of the water optical properties degradation on reef corals

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Abstract

Degradation of water optical properties due to anthropogenic disturbances is a common phenomenon in coastal waters globally. Although this condition is associated with multiple drivers that affect corals health in multiple ways, its effect on light availability and photosynthetic energy acquisition has been largely neglected. Here, we describe how declining the water optical quality in a coastal reef exposed to a turbid plume of water originating from a man-made channel compromise the functionality of the keystone coral species *Orbicella faveolata*. We found highly variable water optical conditions with significant effects on the light quantity and quality available for corals. Reduction of light penetration into the water column elicits the development of low-light phenotypes close to theoretical limits of photoacclimation despite their occurrence at shallow depths. Predicted photosynthetic energy depletion with increasing depth is associated with patterns of colony mortality and contraction of the habitable space for the population. A numerical model illustrates the potential effect the progressive degradation of water optical properties on the gradual mortality and population decline of *O. faveolata*. Our findings suggest that preserving the water optical properties seeking to maximize light penetration into the water

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column may have an extraordinary impact on coral reefs conservation, mostly toward the deeper portions of reefs.

Keywords: Varadero reef, corals, photobiology, ecophysiology, water optical properties, turbidity

Introduction

Coral reefs are recognized not only as one of the most complex, productive and biologically diverse ecosystems (Odum and Odum 1955), but also as icons of the devastating effects of anthropogenic stressors to the natural environment. At a planetary scale, we have already lost one fifth of total coral reefs (Wilkinson 2008) as a result of the synergistic effects of large-scale stressors (Ainsworth et al. 2016) and regional and local factors (Carlson et al. 2019). Reefs in the Indo-Pacific and the Caribbean, in particular, have lost nearly half of their coral cover due to human impacts (Bruno and Selig 2007; Jackson 2014). Approximately 60% of remaining coral reef areas are threatened by the continuous increase of sediments, nutrients, and pollutants in the water associated with coastal development and terrestrial runoff (Burke et al. 2011; Carlson et al. 2019).

Ample evidence demonstrates that water-quality deterioration affects reef corals in different ways. Two main stress-related factors are: a) interference of nutrient enrichment in the host's capacity to control populations of algal symbionts and opportunistic microorganisms (*e.g.,* Symbiodiniaceae and bacteria) (Shantz and Burkepile 2014); and b) disease prevalence and energetic losses resulting from the physical disturbance of particle abrasion and deposition on coral tissue (Junjie et al. 2014; Pollock et al. 2014). The effects of altered water optical properties and light climate derived from pollution on the physiology and ecology of reef corals has been largely neglected (Yentsch et al. 2002), although this condition has drawn increasing attention (Anthony et al. 2004; Bessell-Browne et al. 2017; Omachi et al. 2019). Current evidence suggests that the energetic imbalance derived from reduced light penetration in the water column compromises the reef-building capacity and coral survivorship, mainly in areas increasingly exposed to terrestrial runoff and dredging-related activities (Junjie et al. 2014; Bessell-Browne et al. 2017; Fisher et al. 2019).

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Varadero reef in the southern end of the Caribbean, at the mouth of the Cartagena Bay, Colombia, is exposed to a turbid plume of water originating from a man-made channel (Pizarro et al. 2017). The Dique channel currently delivers large freshwater discharges (currently 8,833 m^{-3} s^{-1}) with high sediment load (23,906 t d^{-1}) into the Cartagena Bay (Restrepo et al. 2018) as a result of the major rectification works that took place during the 1920's - 1980's period (Mogollón 2013). The permanence of this reef under suboptimal environmental conditions provides a unique opportunity to explore the effects of the progressive degradation of the water column optical properties on reef corals. Here, we investigated the effects of these disturbances on the physiology and ecology of the keystone coral species *Orbicella faveolata*, a major reef-builder in the Caribbean. A better understanding of these effects is essential for predicting future impacts associated with coastal development and terrestrial runoff and for the implementation of more effective management efforts seeking to control local key stressors on coral reef ecosystems.

Material and Methods

Site selection criteria

Two sites within the Cartagena Reef System with contrasting water optical properties were considered: a turbid-water reef "Varadero", close to the Dique channel outlet (10° 18' 23.3'' N, 75° 35' 08.0'' W), and a clear-water reef located 21 km southwest of Varadero within the marine protected area Parque Nacional Natural Corales del Rosario y San Bernardo, hereafter referred as "Rosario" (10° 11' 12.1'' N, 75° 44' 43.0'' W) (Fig. 1). The Dique channel is a man-made distributary from the Magdalena River, the largest river system of Colombia and major contributor of continental fluxes into the Caribbean (Restrepo et al. 2018). The shallow portion of Varadero reef is in good condition in terms of coral cover (up to 50-60%) (Pizarro et al. 2017), despite its proximity to the Dique outlet and Cartagena city. A detailed description of the study sites is provided in the Supplementary Material.

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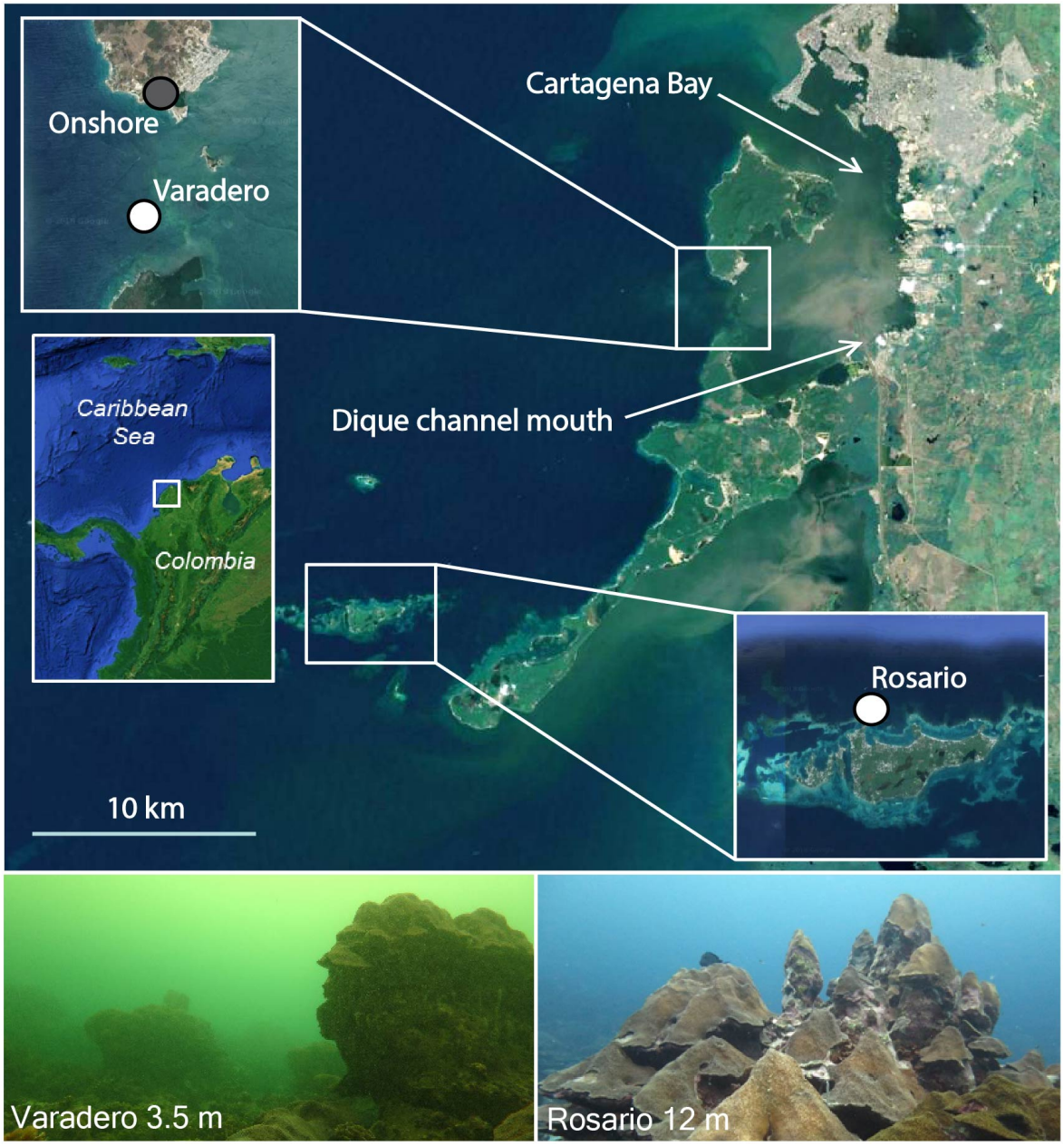

Fig. 1. Study sites with contrasting exposure to the Dique plume. Varadero is located ~6 km west of Dique mouth, and Rosario 21 km southwest of Cartagena Bay (white circles). Surface irradiance was measured onshore close to Varadero (grey circle) to estimate K_d variation. Arrows indicate the location of Cartagena Bay and Dique channel mouth. Lower panels illustrate a general view of the study sites. Map data: Google, Maxar Technologies.

Preliminary analyses of the vertical diffuse attenuation coefficient for downwelling irradiance (K_d) obtained by measuring light intensities across depths using the cosine-corrected PAR sensor of a Diving PAM (Walz, Germany), indicated that the total light exposure at 3.5 m in Varadero and at 12 m in Rosario was similar. Temperature at these depths was recorded every 30 min between November 2016 and July 2017 with HOBO

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pendant dataloggers (UA-002-64, Onset Computer Corporation, USA). A small (0.27 ºC) but significant difference in temperature was detected between sites (29.15 ± 1.22 (daily mean ± SD) in Varadero and 28.88 ± 0.89 °C in Rosario; $H_{(1)} = 5.58$, $p = 0.018$). However, the resulting variation in *O. faveolata* metabolic rates based on the scaling quotient of temperature (Q_{10}) (Scheufen et al. 2017b) is estimated to be negligible (<4%).

Coral Sampling

On October of 2016, coral fragments (10 cm^2) were collected from the edge of 15 apparently healthy *Orbicella faveolata* colonies at each site. Source colonies were chosen randomly at a constant depth of ~3.5 m in Varadero and ~12 m in Rosario, where total light exposure was similar. Fragments were fixed to PVC panels with non-toxic epoxy (Z-Spar A-788 epoxy) placed at the depths of collection. Corals were allowed to recover and fully acclimate for seven months at each site. On May 2017, a subsample from the survivors (12 in Rosario and 15 in Varadero) was used for symbiont genotypification and physiological analysis.

Irradiance measurements

Irradiance was monitored every ten minutes for one year (November 2016 - November 2017) at each site with cosine-corrected light sensors (Odyssey submersible PAR logger, Dataflow systems, New Zealand), previously cross-calibrated against a manufacturer-calibrated quantum sensor (LI-1400, LI-COR, USA). The light sensors were cleaned and downloaded periodically (every two months or less). Visual inspections at each visit showed that sediments and biofouling were not covering the sensors, potentially related to the type of sediments of the Dique plume (mainly fine silts and clays) which tend to remain suspended in the water column (Lonin et al. 2004). Even if the potential interference of sediments in the sensor's signal is low, a linear regression on the data was used for correcting cumulative signal attenuation (Fig. S1).

Spatiotemporal variation of water optical properties

To estimate the variation of the water optical properties resulting from the Dique plume dynamics, light data recorded underwater were compared with data simultaneously recorded onshore close to Varadero (Fig. 1). With this array, we isolated the variations of irradiance associated with the plume from variations due to cloud coverage. The irradiance

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synchronously recorded onshore and underwater was used to estimate instantaneous values of K_d based on the Lambert-Beer's law:

$$K_d = \ln(E_z/E_0) / -z \quad (1)$$

where E_z is underwater irradiance, E_0 is onshore irradiance, and z is the depth of the underwater sensor (3.5 m). Only data recorded between 7:00 and 17:00 were employed. The analysis was performed over one-hour averages, smoothing out anomalies due to differences in cloud coverage between sites at short time intervals. Occasional failures of either sensor reduced the amount of time intervals that could be used to estimate K_d's, leaving a total of 86 days of usable data.

The vertical spectral diffuse attenuation coefficient for downwelling irradiance ($K_d\,\lambda$) was estimated by modifying the methodology of Maritorena and Guillocheau (1996). A mini-spectrophotometer (Flame T-UV-VIS-ES, Ocean Optics, USA) connected to a cosine-corrected sensor through a 30 m fiber optic cable (Avantes, Apeldoorn, The Netherlands) was used to measure in triplicate the irradiance at ocean surface and at several depths at each site. A bubble level was used to keep the light sensor horizontal, avoiding interference of divers or boat shading. $K_d\,\lambda$ was calculated based on the change of underwater light spectra relative to surface. The spectral sensitivity of the instrument and the attenuation of the fiber optic were accounted for by normalizing the surface spectra against a traceable solar spectra reference (SORCE/SIM 2020).

Symbiont identity

Coral samples were stored at -80 °C prior to processing. 50 µl of DNA was extracted from each sample (n = 15 in Varadero; n = 12 in Rosario) using the MoBio Powersoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, California). Two-stage amplicon PCR was performed on the Internal Transcribed Spacer 2 (ITS2) rRNA marker gene. We used modified versions of the itsD and its2rev2 (Stat et al. 2009), including universal primer sequences that are required for Illumina MiSeq amplicon tagging and indexing. The PCR amplification was structured as follows: 2 min of denaturation at 94 °C; 35 cycles of 45 s at 94 °C, 60 s at 55 °C, and 90 s at 68 °C; then finally 7 min at 68 °C. Samples were sequenced using the Illumina MiSeq platform at the DNA Services Facility at the University of Chicago, Illinois. Resulting sequences were submitted to SymPortal for further processing and downstream analyses (Hume et al. 2019). Sequences within the Symbiodiniaceae family

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were identified and separated into genera, formerly "clades" (LaJeunesse et al. 2018), which were further separated into ITS2 type profiles representative of putative Symbiodiniaceae taxa (Hume et al. 2019). Sequences variants occurring in less than 1% of the sample were omitted in order to remove rare intragenomic variants and sequence artifacts generated by MiSeq sequencing.

Photophysiology

Chlorophyll *a* (Chl *a*) fluorescence data were collected *in situ* with a submersible pulse amplitude modulated fluorometer (Diving-PAM, Walz, Germany). Details of PAM settings and environmental conditions during measurements are provided in the Supplementary Material. On cloudless days (n = 3 at each site), we quantified PSII photochemical yields in algal symbionts of 15 colonies randomly distributed near the experimental sites at constant depths (~3.5 m Varadero and ~12 m Rosario). Measurements were taken in the horizontal-uppermost part of colonies to avoid interference of intra-colony light gradients. The effective quantum yield ($\Delta F/F_m'$) of photosystem II (PSII) was recorded at local noon and the maximum quantum yield (F_v/F_m) of PSII at dusk or dawn. The maximum excitation pressure over PSII (Q_m) was calculated following Iglesias-Prieto et al. (2004):

$$Q_m = 1 - \left[\left(\Delta F/F_m' \text{ at noon}\right) / \left(F_v/F_m \text{ at dusk}\right)\right] \quad (2)$$

Chl *a* was extracted from tissue slurries (n = 7 Varadero; n = 8 Rosario) obtained with an air gun connected to a scuba tank and subsequently homogenized with a Tissue-Tearor Homogenizer (BioSpec Inc, USA). Pigment extraction was performed in acetone/dimethyl sulfoxide (95:5 vol/vol). Chl *a* density was estimated spectrophotometrically (n = 3 per sample) with a modular spectrometer (Flame-T-UV-VIS, Ocean Optics Inc., USA) using the equations of Jeffrey and Humphrey (1975). The specific absorption coefficient of Chl *a* ($a^*_{\text{Chl } a}$), descriptor of pigment light absorption efficiency of intact corals, was calculated according to Enríquez et al. (2005):

$$a^*_{\text{Chl } a} = (D_{675}/\rho) * \ln(10) \quad (3)$$

where D_{675} is the estimated absorbance value of corals at 675 nm, calculated from reflectance (R) measurements as [$D_{675} = \log(1/R_{675})$], and ρ is the pigment content per projected area (mg Chl *a* m^{-2}). Corals reflectance spectra was measured using a similar optical set-up as Vásquez-Elizondo et al. (2017). Coral surface area for these and other

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metrics was determined with the aluminum foil technique (Marsh 1970). Cell counts to estimate algal density and cell pigmentation were not reliable due improper sample preservation and not included in analysis.

Photosynthetic parameters were obtained from PE (photosynthesis vs irradiance) curves performed under laboratory conditions in a gradient of artificial light. Incubations (n = 8 in Varadero; n = 6 in Rosario) were performed in a custom-made acrylic chamber with four hermetic compartments (~650 ml each) filled with filtered seawater (0.45 µm) under constant agitation. Temperature was maintained at 28 °C with an external circulating water bath (Isotemp, Fisher Scientific). Ten levels of irradiance previously measured with a Diving-PAM light sensor were supplied at 10-min intervals with four 26 W LED bulbs (UL PAR38, LED Wholesalers Inc, USA) controlled with a custom-made software in continuous-mode. The range of light intensity covered was 0 to ~1400 µmol quanta m^{-2} s^{-1}. Oxygen concentrations were measured with a 4-channel fiber-optic oxygen meter system (FireSting, Pyroscience). Parameters were calculated following Iglesias-Prieto and Trench (1994). Additional information on the light system and photosynthetic parameters is provided in the Supplementary Material.

Ecological survey

We performed ecological surveys to estimate the condition of *O. faveolata* populations. Random dives near each site allowed us to define the vertical distribution ranges of the species. Colony abundance and percentage of old mortality were recorded across five sequential 10x1 m belt transects deployed perpendicular to the reef slope at six depths in Varadero (2, 3, 4.5, 6, 7.5 and 9 m) and Rosario (3, 5, 7, 9, 13 and 17 m). The percentage of old mortality was estimated following the AGRAA protocol (*i.e.*, the skeleton is no longer white and has been lost or covered by epibenthic organisms) (Lang 2003). Completely dead colonies were excluded from surveys due to the typical loss of corallite skeletal structures that allow to differentiate species.

Integrated productivity

Variation of the phototropic contribution of algal symbionts to the energy requirements of *O. faveolata* colonies across depths was estimated based on daily integrated photosynthesis to respiration [P:R] ratios. P:R ratios were estimated using the PE curve

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parameters (mean values) and light availability across depths, calculated from the estimated K_d's (derived from equation 1). Daily integrated photosynthesis (P^{g}_{day}) was calculated with a hyperbolic tangent function (Jassby and Platt 1976):

$$P^{g}_{day} = \int_0^{24} \left[P^{g}_{max} \tanh\left(\alpha E_z / P^{g}_{max}\right) \right] dE_z \quad (4)$$

where P^{g}_{max} is maximum gross photosynthesis, α is photosynthetic efficiency, and E_z is the estimated irradiance at depth z. The daily integrated respiration (R_{day}) was calculated with a hyperbolic tangent function modified from Chalker (1981):

$$R_{day} = \int_0^{24} \left[[\Delta R_d \tanh(E_z/E_k)] + R_{d-pre} \right] dE \quad (5)$$

where ΔR_d represents the difference between the post- and pre-illumination respiration rates, E_k is saturating irradiance, and $R_{d\text{-}pre}$ is pre-illumination respiration rate. We assumed a light-associated asymptotic increase of the respiratory activity until reaching a maximum determined by E_k. This assumption is based on evidence that indicate that respiration rates in corals are light-driven and closely coupled with the internal oxygen concentration (Colombo-Pallotta et al. 2010; Holcomb et al. 2014) (Fig. S2).

Results

Spatiotemporal variation of water optical properties

Analysis of K_d's obtained at the beginning of the study with a Diving-PAM light sensor indicated a strong stratification of the water column in Varadero (Fig. 2a). The stratification was characterized by a superficial layer of ~1 m with an extremely high K_d (1.93 ± 0.26 m^{-1}, mean ± SD), and a clear subsurface layer with significantly lower K_d (0.31 ± 0.11 m^{-1}) ($t_{(7)} = 15.31$, $p < 0.01$). No noticeable stratification was detected in Rosario, which revealed a monotonic K_d (0.16 ± 0.01 m^{-2}) (Fig. 2a).

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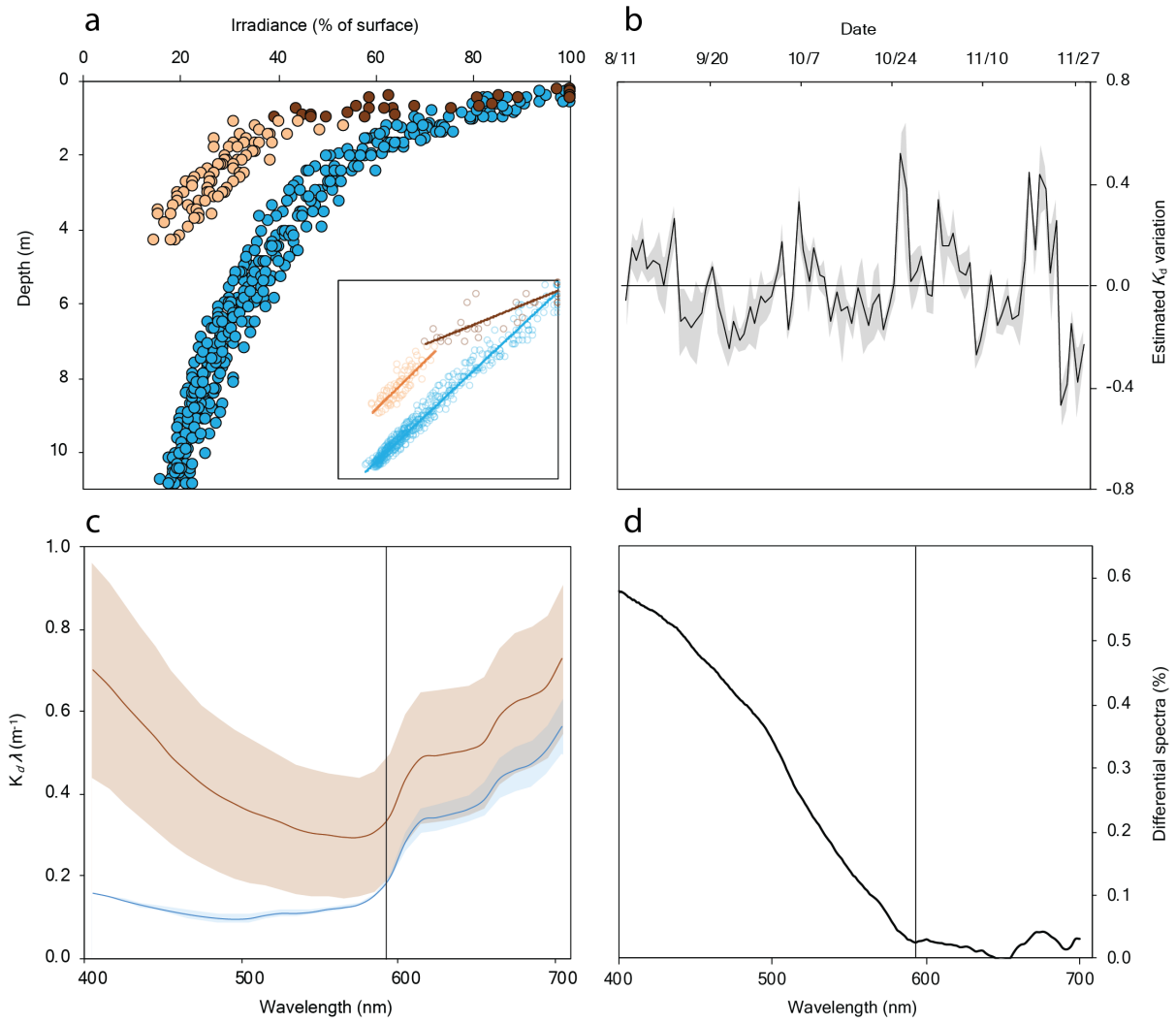

Fig. 2. Variation of underwater light climate and water optical properties. **a** Strong stratification of the water column in Varadero characterized by a superficial layer with high K_d (1.93 ± 0.26 m^{-1}, dark brown) and a clearer subsurface layer with low K_d (0.31 ± 0.11 m^{-1}, light brown), compared with Rosario monotonic K_d (0.16 ± 0.01 m^{-1}, blue). The insert shows light data distribution with depth in log-scale. **b** Temporal variation of mean daily K_d in Varadero estimated from onshore and underwater irradiances (shaded area represents SD). **c** K_d λ in Varadero (brown) and Rosario (blue) (shaded areas represent 95% confidence intervals). **d** Estimated light attenuation due to absorptance of dissolved organic matter associated to Dique discharges based on a differential normalized spectrum in Varadero. Vertical line in **c** and **d** separate the two contrasting spectral regions.

Estimated K_d's from the synchronous oscillation of onshore and underwater irradiances evidenced a strong oscillation of water optical properties in Varadero (Fig. 2b). Estimated K_d's were 0.92 ± 0.26 m^{-1} and ranged between 0.38 and 1.95 m^{-1}. Extremes within this range indicate that underwater irradiance can vary by up to two orders of magnitude only due to changes in water optical properties. Maximum K_d's were higher compared to previous

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256 reports at this site (Pizarro et al. 2017; Roitman et al. 2020) and other turbid-water reefs
257 (Hennige et al. 2010; Omachi et al. 2019).

258 Analyses of $K_d\ \lambda$ indicate distinctive light scattering and absorbing characteristics of
259 dissolved and particulate matter in the water at each site (Fig. 2c). Varadero's high
260 variability of $K_d\ \lambda$ (*i.e.*, wide confidence intervals) (Fig. 2c) is consistent with the strong
261 stratification (Fig. 1a) and the temporal variation of K_d (Fig. 2b). $K_d\ \lambda$ evidenced two spectral
262 regions with contrasting characteristics. One below ~600 nm with increasing attenuation
263 toward shorter wavelengths in Varadero and low attenuation in Rosario, attributed to light
264 absorption of dissolved organic material of continental origin (Maritorena and Guillocheau
265 1996). And a spectral region above 600 nm with nearly constant properties despite
266 differences in attenuation magnitude among sites, attributed to light attenuation due to
267 scattering by particulate matter with small effect on spectral quality (Fig. 2c). The estimated
268 attenuation due to absorptance of dissolved organic matter obtained from a differential
269 normalized spectrum (Fig. 2d), demonstrates the high concentration of dissolved organic
270 matter in Varadero associated with the Dique plume and its critical role in modifying the
271 light quality.

272 Dramatic changes of K_d were detected within and between days (Fig 3), highlighting
273 the variable nature of the water optical properties and underwater light climate associated
274 with the Dique plume dynamics in Varadero. On average, the daily integrated irradiance was
275 7% lower in Varadero than in Rosario (2.03 ± 1.32 and 2.17 ± 0.91 mol quanta $m^{-2}\ d^{-1}$,
276 respectively) ($H_{(1)} = 7.92$, $p < 0.05$). Prevalent irradiance at both sites was consistent with
277 low-light reef environments (Anthony and Hoegh-Guldberg 2003; DiPerna et al. 2018).

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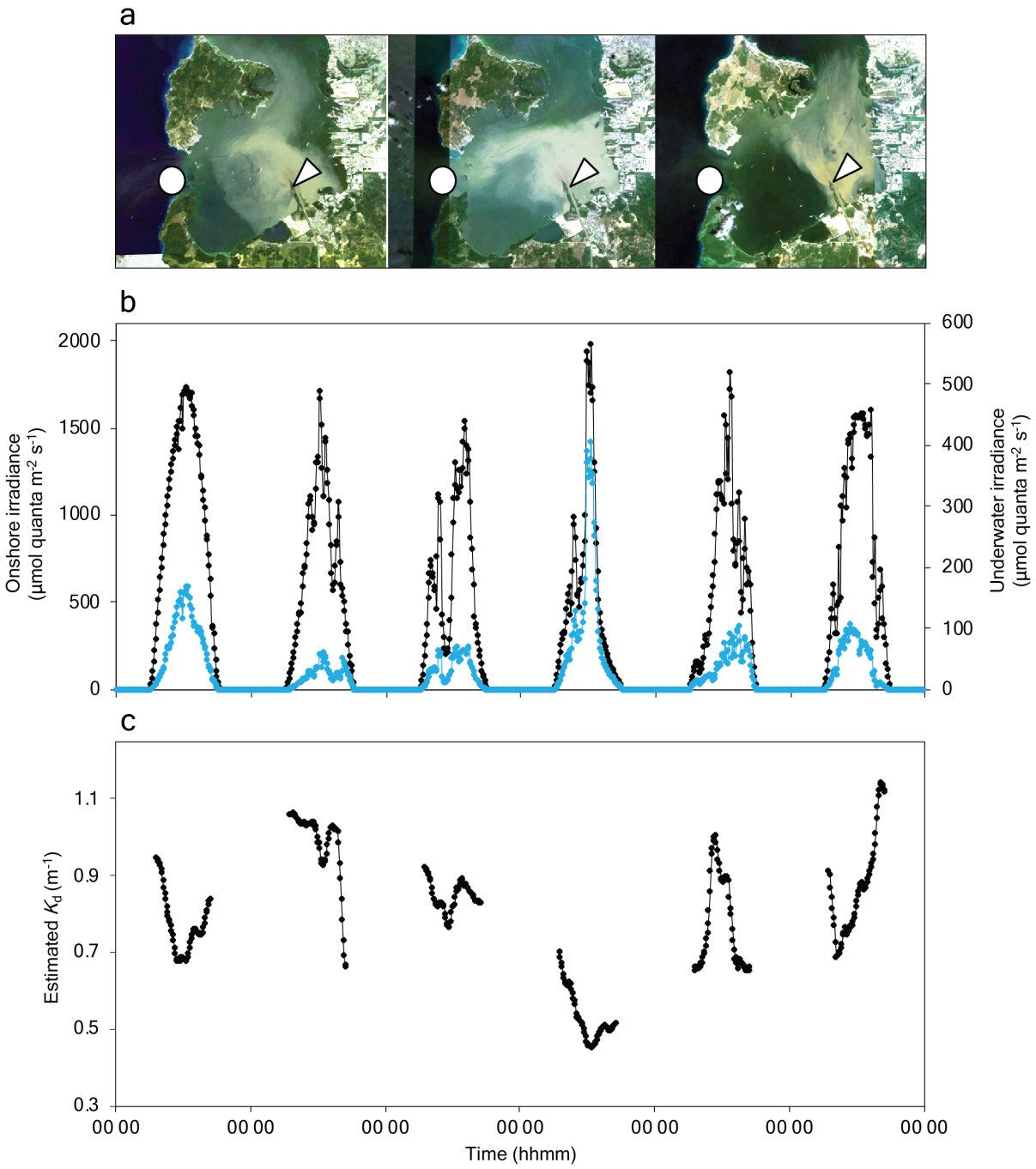

Fig. 3. Effect of Dique plume dynamics on K_d. **a** Satellite images illustrating contrasting spatial patterns of the plume, signaling the location of Varadero (circle) and the Dique mouth (arrow). **b** Oscillation patterns of onshore (black line) and underwater (blue line) irradiances on six random days. **c** K_d variation estimated from onshore and underwater irradiances.

Symbiont identity

Analyses of Internal Transcribed Spacer 2 (ITS2) rRNA sequences identified distinctive ITS2 profiles combinations diagnostic of five separate genotypes. One belonged

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to the genus *Symbiodinium* (ITS2 type A3), and three to *Cladocopium* (ITS2 types C7, C7/C12c, C3ee/C21/C3an) (Fig. 4, Fig. S3). A *Breviolum* genotype (ITS2 type B1) was only detected in some corals from Rosario but in low background levels. *Symbiodinium* ITS2 type A3 occurred in colonies from both locations and in some samples, it was the only dominant symbiont. Many colonies from Varadero contained a *Cladocopium* genotype (ITS2 type C3ee/C21/C3an), which occurred alone or in combination with *Symbiodinium* ITS2 type A3. This *Cladocopium* genotype was also found in a few corals from Rosario as the dominant symbiont. Two additional albeit related *Cladocopium* genotypes (ITS2 types C7 and C7/C12c) were also present in certain colonies from Rosario, but never together. Statistical tests confirmed that the Symbiodiniaceae communities in terms of ITS2 profiles composition were different between sites ($p = 0.001$, PERMANOVA on Bray-Curtis matrix).

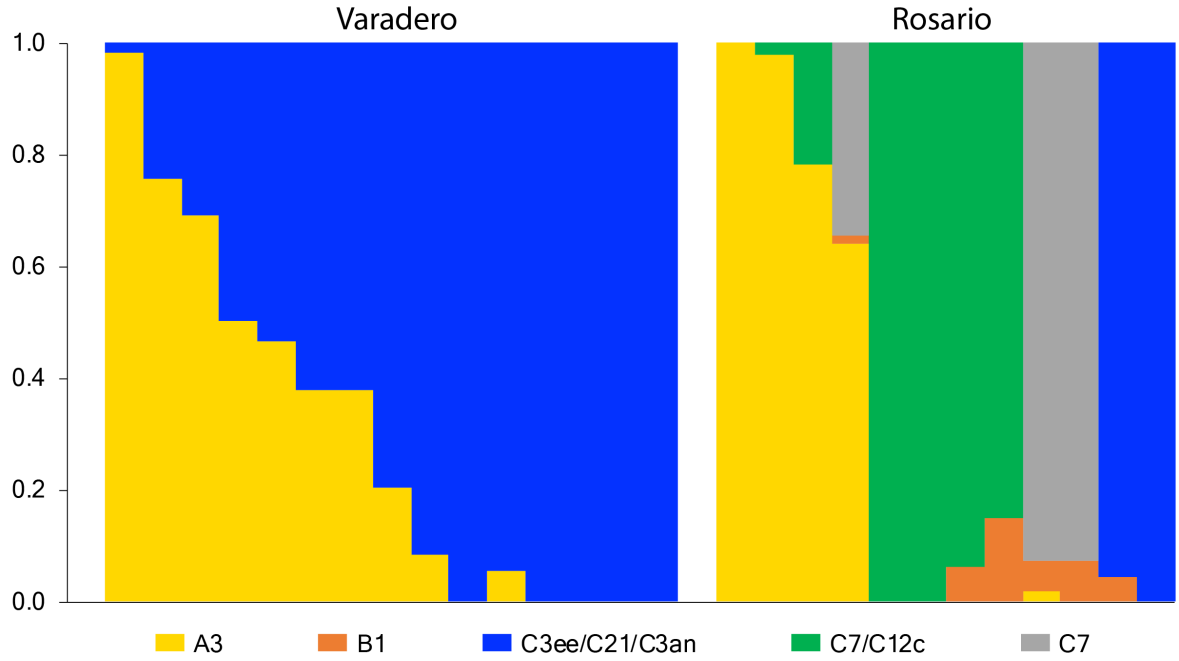

Fig. 4. Predominant Symbiodiniaceae ITS2 profiles associated to corals from Varadero and Rosario. Each column of stacked bars represents one sample, with bar heights within each column representing the relative abundance of sequences. Raw diversity of ITS2 type profiles is provided in Fig. S3.

Photophysiology

Photosynthetic parameters derived from the PSII photochemical yield of symbionts (F_v/F_m, $\Delta F/F_m'$ and Q_m) and host pigmentation (Chl *a* content and $a^*_{Chl\ a}$) were significantly different between sites. Parameters derived from the photosynthetic potential (α, E_c, E_k, R_d,

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306 P_{max} and $1/\Phi_{max}$) and corals capacity to absorb light (A_{PAR}) were non-significantly different
307 (Table 1). F_v/F_m values (0.669 ± 0.019 and 0.676 ± 0.012 in Varadero and Rosario,
308 respectively) differed by 1% ($t_{(74)} = 2.26$, $p = 0.027$). Values of $\Delta F/F_m$' and Q_m (0.579 ±
309 0.052 and 0.610 ± 0.033, and 0.135 ± 0.062 and 0.097 ± 0.051 in Varadero and Rosario,
310 respectively), varied by 5% ($t_{(75)} = 3.38$, $p = 0.001$) and 28% ($t_{(84)} = -3.09$, $p = 0.003$),
311 respectively. Estimated values of $1/\Phi_{max}$ (11.24 ± 1.87 and 11.62 ± 3.16 quanta O_2^{-1} in
312 Varadero and Rosario, respectively) were lower than previous reports (Wyman et al. 1987;
313 Rodriguez-Roman et al. 2006) and close to minimum practical limits of ~10-12 quanta O_2^{-1}
314 (Hill and Govindjee 2014).
315
316 **Table 1.** Photoacclimation parameters of *O. faveolata* in Varadero at 3.5 m and Rosario at 12 m. Values
317 correspond to the mean ± SD (sample size *n*). *t*-tests (*t*) and Kruskal-Wallis tests (*H*) were conducted after testing
318 of assumptions (normality with the use of K-S test) to determine if differences between sites were statistically
319 significant. Values of photosynthetic parameters used to estimate the productivity of colonies (integrated daily
320 P:R ratios) are highlighted in bold.

Parameter (units)	Definition	Varadero	Rosario	Statistic
F_v/F_m (Dimensionless)	Maximum quantum yield of PSII at dusk	0.669 ± 0.019 (45)	0.676 ± 0.012 (44)	$t_{(74)} = 2.26$, $p = 0.027$
$\Delta F/F_m'$ (Dimensionless)	Effective quantum yield of PSII at noon	0.579 ± 0.052 (45)	0.610 ± 0.033 (44)	$t_{(75)} = 3.38$, $p < 0.001$
Q_m (Dimensionless)	Maximum excitation pressure over PSII	0.135 ± 0.062 (45)	0.097 ± 0.051 (44)	$t_{(84)} = -3.09$, $p < 0.001$
A_{PAR} (Dimensionless)	Light absorptance	0.87 ± 0.02 (8)	0.88 ± 0.04 (8)	$t_{(11)} = 0.49$, $p = 0.632$
Chl *a* (mg Chl *a* m^{-2})	Chlorophyll *a* content per area	195.27 ± 37.61 (7)	95.07 ± 25.54 (8)	$t_{(10)} = -5.95$, $p < 0.001$
$a^*_{Chl\ a}$ (m^2 mg Chl a^{-1})	Chlorophyll *a* specific absorption coefficient	0.013 ± 0.002 (7)	0.031 ± 0.012 (8)	$H_{(1)} = 10.5$, $p = 0.001$
E_c (µmol quanta m^{-2} s^{-1})	Compensating irradiance	88.84 ± 17.60 (8)	88.11 ± 15.20 (6)	$t_{(11)} = -0.08$, $p = 0.935$
E_k (µmol quanta m^{-2} s^{-1})	Saturating irradiance	**217.88 ± 26.60 (8)**	210.18 ± 41.28 (6)	$t_{(8)} = -0.4$, $p = 0.7$
R_d (µmol O_2 m^{-2} s^{-1})	Dark respiration rate	**3.40 ± 0.30 (8)**	3.43 ± 0.62 (6)	$t_{(6)} = -0.1$, $p = 0.92$
P_{max} (µmol O_2 m^{-2} s^{-1})	Maximum gross photosynthetic rate	**5.04 ± 1.16 (8)**	4.76 ± 1.31 (6)	$H_{(1)} = 0.27$, $p = 0.606$
α (quanta O_2^{-1})	Photosynthetic efficiency	**0.039 ± 0.006 (8)**	0.041 ± 0.014 (6)	$H_{(1)} = 0.15$, $p = 0.698$
$1/\phi_{max}$ (quanta O_2^{-1})	Minimum quantum requirement	11.24 ± 1.87 (8)	11.62 ± 3.16 (6)	$t_{(7)} = 0.27$, $p = 0.798$

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Chl *a* density was significantly higher ($t_{(10)} = -5.95$, $p < 0.001$) in corals from Varadero compared to Rosario (195.27 ± 37.61 and 95.07 ± 25.54 mg Chl *a* m^{-2}, respectively). Changes in Chl *a* density resulted in significant variations of $a^*_{Chl\ a}$ (0.013 ± 0.002 and 0.031 ± 0.012 m^2 mg Chl a^{-1} in Varadero and Rosario respectively, $H_{(1)} = 10.5$, $p = 0.001$). Comparative analyses of changes in $a^*_{Chl\ a}$ as a function of Chl *a* content indicate a relatively steady light harvesting efficiency despite larger differences in pigment content in corals from Varadero. In contrast, reduced Chl *a* content variation in Rosario resulted in more dramatic changes of the effective absorption cross section of algal pigments (Fig. S4). Our data provide no clear evidence that these differences were associated with distinctive Symbiodiniaceae composition (Fig. S5). No significant differences were found in light absorption capacity (A_{PAR}) and photosynthetic descriptors (α, E_c, E_k, R_d and P_{max}) between sites (Table 1).

Ecological survey

O. faveolata vertical distribution ranged between 2 and 9 m in Varadero, and 3 and 17 m in Rosario. Varadero had both higher density of colonies (3.20 ± 2.85 colonies $transect^{-1}$) and coral cover (4.46 ± 4.57 m^2 $transect^{-1}$) than Rosario (1.70 ± 1.18 colonies $transect^{-1}$ and 4.20 ± 5.48 m^2 $transect^{-1}$, respectively). The highest abundance (38% of total colonies) occurred at 4.5 m in Varadero and at 9 m (33%) in Rosario (Fig. S6). In Varadero, the lowest partial colony mortality occurred at 2 m (7.5 ± 3.5%) and the highest at 9 m (73.3 ± 26.4%). In Rosario, the lowest mortality occurred at the maximum depth (5.0 ± 12.2% at 17 m) and the highest at an intermediate depth (73.3 ± 20.8% at 5 m) (Fig. 5). Depth and mortality had a strong exponential relationship in Varadero ($R^2 = 0.77$, $p<0.01$) and a non-significant linear ($R^2 = 0.43$, $p = 0.16$) or exponential ($R^2 = 0.33$, $p = 0.23$) relationship in Rosario.

Integrated productivity

Integrated daily P:R ratios of *O. faveolata* colonies in Varadero suggest a variable phototrophic contribution of algal symbionts to the metabolic demand of coral holobionts, both spatially (across depths) and temporally, as a consequence of changes in light availability. At 2 m depth, it is estimated that symbionts can supply, on average, 64% of daily holobiont's energy requirements (P:R = 0.64 ± 0.18). On days with increased light penetration the symbionts supply 99% of holobiont's requirements while on days with

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highest K_d's the supply drops to ~20%. At 9 m, the maximum depth where living *O. faveolata* colonies are currently found in Varadero, the contribution of symbionts is, on average, 1% of holobiont's energy requirements, although it drops to practically zero during days with highest K_d's (P:R = 4.49 x 10^{-6}) (Fig. 5). A strong, negative correlation was found between colonies partial mortality and daily P:R ratios (Spearman r_s = -0.94, p = 0.005). The coefficient of determination of an exponential regression indicates that the phototrophic contribution explains 78% of the mortality variation across depths in *O. faveolata* (Fig. S7).

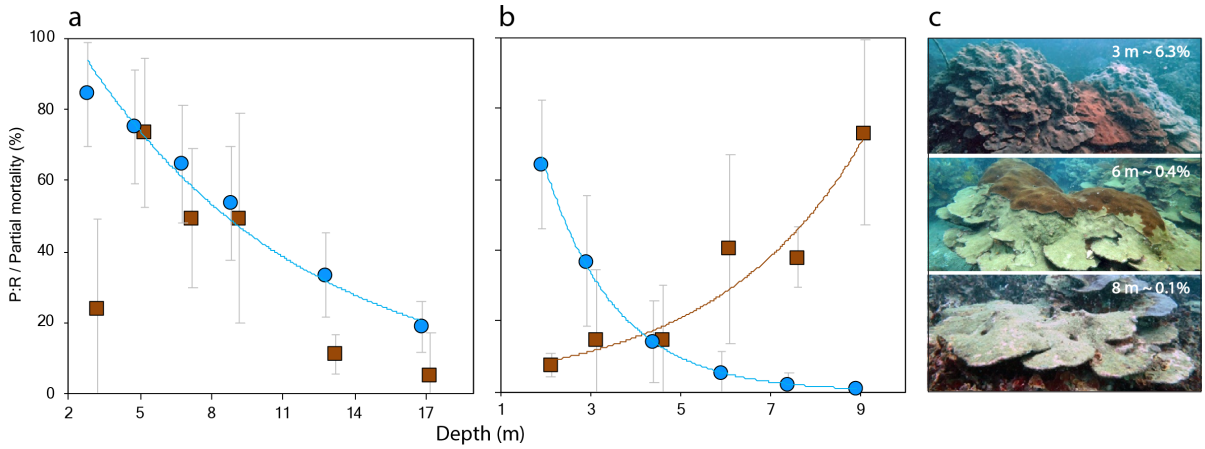

Fig. 5. Productivity and mortality of *O. faveolata* across depths. Partial mortality (brown squares) and daily integrated P:R ratios (%, blue circles) in Rosario (**a**) and Varadero (**b**). Values correspond to mean ± SD. Exponential regressions were used to fit the data (only significant relationships are depicted). **c** Mortality patterns across depths in Varadero, indicating the % surface light at each depth based on the mean estimated K_d.

In Rosario at 3 m, the shallowest depth of *O. faveolata*, it is estimated that the symbionts supply, on average, 84% of the holobiont's energy requirements (P:R = 0.84 ± 0.14). At 17 m, the maximum depth of *O. faveolata*, the symbionts supply is of 19% (P:R = 0.19 ± 0.07), whit minimum and maximum values of 2% and 27% depending on changes in light availability (Fig. 5). Rosario had significantly higher estimated P:R ratios than Varadero both at the upper ($H_{(1)}$ = 73.29, p < 0.001) and lower ($H_{(1)}$ = 189.25, p < 0.001) local depth limits of *O. faveolata*. A non-significant correlation was found between colonies partial mortality and estimated P:R ratios in Rosario (Spearman r_s = 0.60, p = 0.208).

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Discussion

We identified three main features of the underwater light climate in Varadero, a coastal reef exposed to a turbid plume of water originating from a man-made channel: 1) light-limiting conditions due to the strong attenuation generated by particulate matter and dissolved substances concentrated in a superficial layer, 2) substantial variation of the underwater light climate in response to fluctuations on water optical properties, and 3) altered spectral composition of light due to the wavelength-selective absorption by organic matter of continental origin (Maritorena and Guillocheau 1996; Hennige et al. 2010). These patterns are produced by the freshwater discharges with high sediment load from the Dique channel in the vicinity of the reef. The strong stratification, also reported in previous studies (Pizarro et al. 2017; Tosic et al. 2019), results from the different properties (*e.g.*, salinity and temperature) of a superficial layer directly affected by the Dique channel discharges and a subsurface clear layer of oceanic waters (Lonin et al. 2004). The strong stratification of the water column seems to isolate the Varadero reef from the Dique freshwater discharges but have a critical impact on the underwater light availability and photosynthetic energy acquisition in corals.

The variation of water optical properties in Varadero explains 81% of the overall temporal variation of underwater irradiance. This estimation is in close proximity to irradiance variation in other turbid-water reefs due to suspended solids (Anthony et al. 2004). The observed variability is attributed to meteorological conditions affecting the Dique plume dynamics (Lonin et al. 2004; Tosic et al. 2019). At Rosario, although the water column is significantly clearer than Varadero, the K_d's for the whole PAR range (0.158 m^{-1}) and towards the blue part of the spectrum (0.160 m^{-1} at 400 nm) were still notably higher compared to other reports in clear waters (Maritorena and Guillocheau 1996). This suggests an increased attenuation likely associated with the Dique discharges, highlighting the strong influence of continental runoff on the underwater light climate far beyond the channel mouth.

Our results suggest that *O. faveolata*, a major reef-building coral in the Caribbean, hosts distinctive Symbiodiniaceae communities in Varadero and Rosario. Two features of the Symbiodiniaceae communities are highlighted: 1) Despite the extreme fluctuations of the water optical conditions in Varadero, *Durusdinium trenchii* (ITS2 type D1a) was not

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405 detected in coral samples at this site. This known stress-tolerant species is adapted to survive
406 in regions exposed to high temperature and irradiance (LaJeunesse et al. 2009). Given the
407 distinctive features of Varadero reef environment, *D. trenchii* would be expected to thrive in
408 *O. faveolata* colonies, but instead *Cladocopium* ITS2 type C3 and *Symbiodinium* ITS2 type
409 A3 were dominant. And 2) corals from Rosario showed a greater diversity of
410 Symbiodiniaceae communities, mainly due to an increased richness of *Cladocopium*
411 genotypes. The reduced diversity of the symbiont community in corals from Varadero,
412 similar to other turbid marginal reef environments (Smith et al. 2020), may be an indicator of
413 the strong selective pressure exerted by the turbid plume dynamics on the symbiont
414 communities.
415 *O. faveolata* corals display similar phenotypes in Varadero at 3.5m and Rosario at
416 12m. This highlights the essential role of the water optical properties on the underwater light
417 climate and illustrates the constraint of using depth as main proxy for corals
418 photoacclimation status. Estimated minimum quantum requirements ($1/\Phi_{max}$) of corals
419 growing at both sites indicate similar light utilization efficiency close to theoretical
420 operational limits of ~10-12 quanta O_2^{-1} (Hill and Govindjee 2014). Q_m values close to 0
421 indicate that even at noon when corals are exposed to maximal irradiances, most PSII
422 reaction centers of symbiotic algae remained open suggesting light-limited photosynthetic
423 rates (Iglesias-Prieto et al. 2004). Both Q_m and $1/\Phi_{max}$ normally decrease with increasing
424 depth until reaching the minimal practical values, which corresponds to the limits of
425 potential photoacclimation capacity and tolerance range for the symbiosis (Wyman et al.
426 1987; Iglesias-Prieto et al. 2004). The values of Q_m and $1/\Phi_{max}$ close to theoretical
427 minimums suggest that the photoacclimation of *O. faveolata* symbionts is close to the limit
428 for maximum efficiency of solar energy utilization and, therefore, the lower vertical
429 distribution limit of the species at each site despite the contrasting depth differences.
430 Although the average daily irradiance at both sites is consistent with low-light
431 environments (Anthony and Hoegh-Guldberg 2003; DiPerna et al. 2018), corals from
432 Varadero are occasionally exposed (~10% of days) to supersaturating irradiances that exceed
433 the saturation point, E_k, of algal symbionts. Irradiances at local noon during these days can
434 be almost twice the estimated E_k, representing a potential source of over-excitation of the
435 photosynthetic apparatus that must be dissipated by photoprotective mechanisms. A greater

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436 reduction of the quantum yield of photosystem II (PSII) measured at noon ($\Delta F/F_m'$) relative
437 to its maximum value at dusk (F_v/F_m), indicate that corals at Varadero were indeed exposed
438 to higher peaks of irradiance during these measurements, compared to Rosario. It must be
439 stressed, however, that the almost identical values of F_v/F_m between sites indicate similar
440 photochemical energy conversion efficiency of the PSII of coral symbionts. This suggests
441 that the occasional exposure to higher irradiances in Varadero are not intense enough as to
442 induce a chronic photoinactivation of a population of PSII reaction centers in order to
443 increase the capacity to dissipate excess excitation via non-photochemical quenching
444 (Hoegh-Guldberg and Jones 1999). Consistently, comparative analyses of the parameters
445 derived from the P-E curves indicate that corals at both locations have very similar
446 photosynthetic potential. Collectively, these results indicate that the occasional exposure to
447 supersaturating irradiances in Varadero does not compromise the photosynthetic
448 performance of symbionts.
449 Interestingly, corals in Varadero had greater Chl *a* content than in Rosario, which
450 resulted in a significant reduction of the light absorption efficiency of algal pigments, $a^*_{Chl\ a}$,
451 due to pigment self-shading (Scheufen et al. 2017a). Differences in $a^*_{Chl\ a}$ indicate that
452 Varadero highly pigmented corals are less efficient at collecting light per unit of pigment.
453 Although a detailed analysis of the water quality in Varadero is beyond the scope of this
454 study, we speculate that the nutrient enrichment that exists within Cartagena Bay due to the
455 Dique discharges (Tosic et al. 2019) may also extend to Varadero. It is known that nutrient
456 enrichment interference on coral's metabolism can result in increased algal densities and/or
457 Chl *a* content within cells (Shantz and Burkepile 2014), which in turn can affect the
458 photosynthetic potential of the coral. The nearly constant capacity of corals to absorb ~90%
459 of incident light at both sites, despite differences in Chl *a* content and $a^*_{Chl\ a}$, indicate that the
460 increased pigmentation in corals from Varadero does not confer them with any additional
461 advantage in terms of light harvesting. This condition may be related with the particular
462 capacity of *O. faveolata* to maximize light absorption at low pigmentation (Scheufen et al.
463 2017a). The lack of differences among photosynthetic parameters indicates that the light
464 absorbed is also utilized with similar efficiency in photosynthesis by corals at both sites, and
465 that a potential nutrient enrichment linked to Dique discharges is not affecting the
466 photosynthetic potential of *O. faveolata*. Although it is known that the symbiont genotype

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can influence the coral host physiology (Kemp et al. 2014), we found no evidence that the differences in pigmentation and efficiency to collect light were connected with distinctive symbiont genotypes.

The productivity model based on P:R ratios reveals that the daily phototrophic contribution of algal symbionts is highly variable. The reduction of primary production with increasing depth and during exposure to periods of high light extinction could be counterbalanced by photoacclimation and heterotrophic plasticity (Anthony and Fabricius 2000). The low-light phenotypes with physiological metrics signaling maximal theoretical limits of photoacclimation in Varadero suggests that enhance feeding on suspended particles originating from the plume may be the more relevant alternative to compensate for reduced photosynthesis. However, the Dique plume particles not only represent a potential source of nutrition but also a stress factor for coral colonies with even lethal effects due to the energetically costly process of particle clearance and microbe-mediated infections favored by sedimentation (Junjie et al. 2014; Pollock et al. 2014). The minimum irradiance at which photosynthesis outweighs respiration (E_c) is estimated to be exceeded only above 6 m, at least for short periods of time. Corals clearance capacity below this depth is expected to be strongly limited by the negligible phototrophic contribution of algal symbionts and the metabolic depression of the holobiont. Due to photosynthetic energy deprivation and physical disturbance of particulate matter, coral colonies would not be expected to survive at much greater depths.

Colonies censused in this study were sexually mature (> 100 cm^2) and some were probably hundreds of years old based on their height (>2 m), which suggests that the local population of *O. faveolata* was established in Varadero before the Dique major rectification works (Mogollón 2013). Current vertical distribution is restricted to a much narrower and shallower depth range (2-9 m) compared not only with Rosario (3-17 m) but also with other clear-water sites in the Caribbean (*e.g.*, 2-20 m in Belize (Pandolfi and Budd 2008) and 3-25 m in Curacao (Van Veghel 1994)). The compressed vertical distribution, together with the strong correlation between partial colony mortality and depth, suggest the occurrence of a progressive decline of the coral population from the bottom to the top of the reef. Although other environmental impacts linked to the plume that were not accounted for in this study may also lead to corals mortality, the physiological evidence suggest that the current

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condition of *O. faveolata* population in Varadero is associated with light-limiting conditions and photosynthetic energy deprivation as a result of the progressive degradation of water optical properties (Fig. 6).

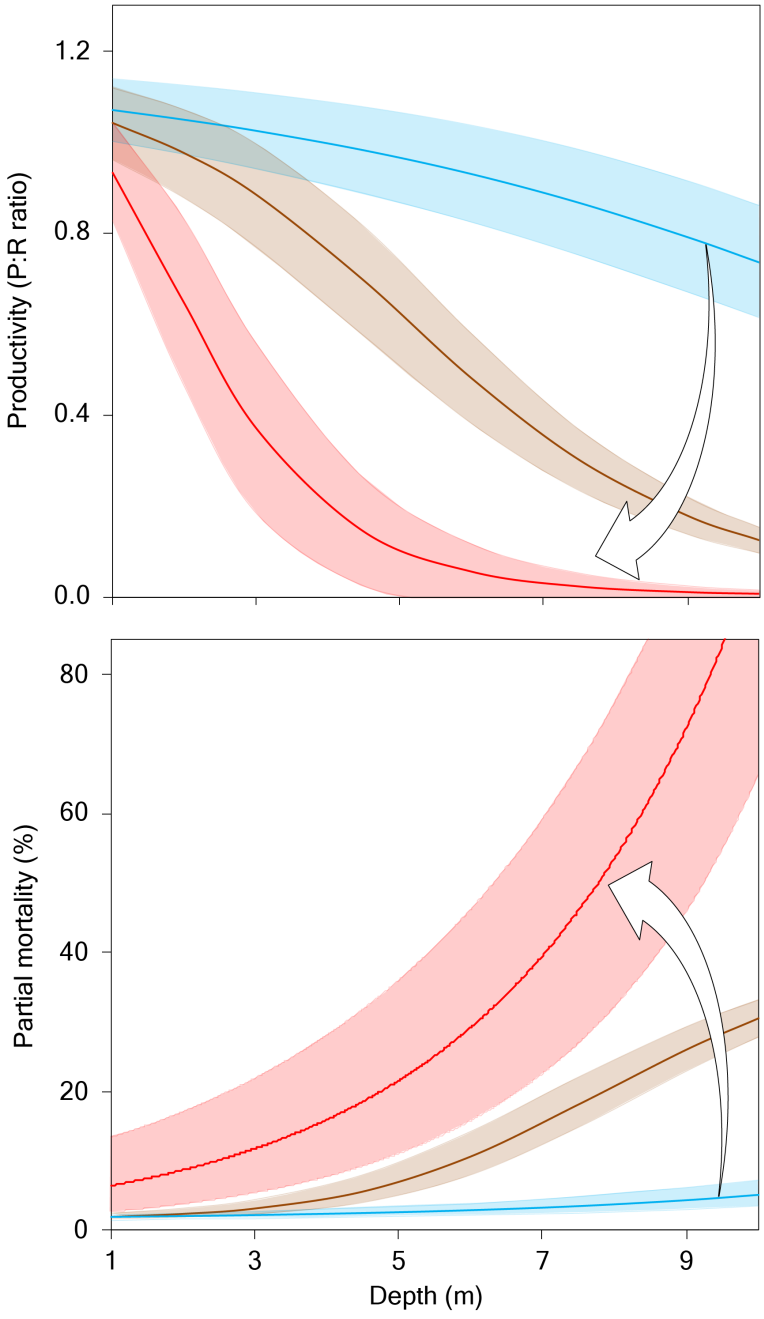

Fig. 6. Predicted effect of the progressive degradation of water optical properties on colonies productivity and partial mortality across depths. Top panel: Estimated productivity (daily P:R ratios) with water of different K_d's. Lower panel: Predicted partial colony mortality based on the exponential regression describing the relation between P:R ratios and mortality. Responses were modelled under current K_d variation (red); under persistent low-intensity effect of the Dique plume (lowest estimated K_d, 0.34 m^{-1}) (brown), and under minimal influence of the plume (K_d of Rosario, 0.16 m^{-1}) (blue).

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Recent studies have documented higher coral cover and/or lower incidence of coral bleaching in turbid reefs potentially connected with an alleviating effect of reduced light levels in the water column (van Woesik et al. 2012; Morgan et al. 2017). This evidence has supported the idea that marginal coral reefs may act as refuges during the current coral reef crises. Our results partially support this hypothesis in the sense that a potential stress-relieving effect linked to turbidity could help explain the reduced partial mortality of *O. faveolata* colonies only in the shallowest portion of Varadero (< 4.5 m). However, with increasing depth, the elevated mortality and total absence of living colonies of *O. faveolata* below 9 m indicate that the gains from a potential alleviating effect are exceeded by the losses associated with the photosynthetic energy depletion resulting from light limitation.

Most coral reefs will be lost in a few decades unless there is a major scaling-up of management efforts and commitment based on an improved understanding of current ecological processes (Kennedy et al. 2013). Despite the significant steps taken to conserve coral reefs and their ecosystem services, the success of management efforts at large scales is low. In addition, major threats, such as global warming and ocean acidification, keep rising and driving reefs toward the breaking point of collapse (Ainsworth et al. 2016). Our findings suggest that effective policies seeking to improve water optical properties at local and regional scales should be considered a priority goal for coral reef conservation, a challenge that extends far beyond the limits of the coastal zone environment. If no action is taken to control the water optical quality and the current trajectory of increasing the flux of sediments into the coastal zone persists (Burke et al. 2011; Carlson et al. 2019), populations of reef-building corals like *O. faveolata* will be increasingly restricted to shallower depths, thereby eroding the ecosystemic benefits that these species provide.

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539 extensive logistical support during field activities. The light system for PE curves was
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543 permit No. 0546 from 2014 issued by "Autoridad Nacional de Licencias Ambientales
544 ANLA".

545

546 Author contributions

547 MM and RIP conceived and, along with FJP and TLL, designed the study. CTGM, KGC,
548 LAGG, SR, FJP, VP, MLV and TLL participated in field work and data collection. SR
549 performed Symbiodiniaceae analysis. CTGM and TLL performed water optical properties
550 analysis. TLL, CTGM, KGC and LAGG performed physiological analysis. TLL and RIP
551 wrote the manuscript. MM, SR, CTGM, KGC and LAGG supported writing and editing the
552 manuscript.

553

554 References

555 Ainsworth TD, Heron SF, Ortiz JC, Mumby PJ, Grech A, Ogawa D, Eakin CM, Leggat W (2016) Climate
556 change disables coral bleaching protection on the Great Barrier Reef. Science 352:338-342
557 Anthony KRN, Fabricius KE (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under
558 varying turbidity. J Exp Mar Biol Ecol 252:221-253
559 Anthony KRN, Hoegh-Guldberg O (2003) Variation in coral photosynthesis, respiration and growth
560 characteristics in contrasting light microhabitats: an analogue to plants in forest gaps and
561 understoreys? Funct Ecol 17:246-259
562 Anthony KRN, Ridd PV, Orpin AR, Larcombe P, Lough J (2004) Temporal variation of light availability in
563 coastal benthic habitats: Effects of clouds, turbidity, and tides. Limnol Oceanogr 49:2201-2211
564 Bessell-Browne P, Negri AP, Fisher R, Clode PL, Jones R (2017) Impacts of light limitation on corals and
565 crustose coralline algae. Sci Rep-Uk 7:11553
566 Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional
567 comparisons. PLoS One 2:e711
568 Burke L, Reytar K, Spalding M, Perry A (2011) Reefs at risk revisited. World Resources Institute, Washington,
569 DC
570 Carlson RR, Foo SA, Asner GP (2019) Land Use Impacts on Coral Reef Health: A Ridge-to-Reef Perspective.
571 Frontiers in Marine Science 6:562
572 Chalker BE (1981) Simulating light-saturation curves for photosynthesis and calcification by reef-building
573 corals. Mar Biol 63:135-141
574 Colombo-Pallotta MF, Rodriguez-Roman A, Iglesias-Prieto R (2010) Calcification in bleached and unbleached
575 Montastraea faveolata: evaluating the role of oxygen and glycerol. Coral Reefs 29:899-907
576 DiPerna S, Hoogenboom M, Noonan S, Fabricius K (2018) Effects of variability in daily light integrals on the
577 photophysiology of the corals Pachyseris speciosa and Acropora millepora. PLoS One 13:e0203882
578 Enríquez S, Méndez ER, Iglesias-Prieto R (2005) Multiple scattering on coral skeletons enhances light
579 absorption by symbiotic algae. Limnol Oceanogr 50:1025-1032

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580 Fisher R, Bessell-Browne P, Jones R (2019) Synergistic and antagonistic impacts of suspended sediments and
581 thermal stress on corals. Nat Commun 10:2346
582 Hennige SJ, Smith DJ, Walsh S-J, McGinley MP, Warner ME, Suggett DJ (2010) Acclimation and adaptation
583 of scleractinian coral communities along environmental gradients within an Indonesian reef system. J
584 Exp Mar Biol Ecol 391:143-152
585 Hill JF, Govindjee (2014) The controversy over the minimum quantum requirement for oxygen evolution.
586 Photosynth Res 122:97-112
587 Hoegh-Guldberg O, Jones RJ (1999) Photoinhibition and photoprotection in symbiotic dinoflagellates from
588 reef-building corals. Mar Ecol Prog Ser 183:73-86
589 Holcomb M, Tambutte E, Allemand D, Tambutte S (2014) Light enhanced calcification in Stylophora pistillata:
590 effects of glucose, glycerol and oxygen. Peerj 2:e375
591 Hume BCC, Smith EG, Ziegler M, Warrington HJM, Burt JA, LaJeunesse TC, Wiedenmann J, Voolstra CR
592 (2019) SymPortal: A novel analytical framework and platform for coral algal symbiont next-
593 generation sequencing ITS2 profiling. Mol Ecol Resour 19:1063-1080
594 Iglesias-Prieto R, Trench RK (1994) Acclimation and Adaptation to Irradiance in Symbiotic Dinoflagellates .1.
595 Responses of the Photosynthetic Unit to Changes in Photon Flux-Density. Mar Ecol Prog Ser 113:163-
596 175
597 Iglesias-Prieto R, Beltran VH, LaJeunesse TC, Reyes-Bonilla H, Thome PE (2004) Different algal symbionts
598 explain the vertical distribution of dominant reef corals in the eastern Pacific. Proc Biol Sci 271:1757-
599 1763
600 Jackson J, M. Donovan, K. Cramer and V. Lam (2014) Status and trends of Caribbean coral reefs: 1970-2012.
601 Global Coral Reef Monitoring Network, IUCN
602 Jassby AD, Platt T (1976) Mathematical formulation of the relationship between photosynthesis and light for
603 phytoplankton. Limnol Oceanogr 21:540-547
604 Jeffrey SW, Humphrey GF (1975) New Spectrophotometric Equations for Determining Chlorophylls a, B, C1
605 and C2 in Higher-Plants, Algae and Natural Phytoplankton. Biochem Physiol Pfl 167:191-194
606 Junjie RK, Browne NK, Erftemeijer PLA, Todd PA (2014) Impacts of Sediments on Coral Energetics:
607 Partitioning the Effects of Turbidity and Settling Particles. Plos One 9:e107195
608 Kemp DW, Hernandez-Pech X, Iglesias-Prieto R, Fitt WK, Schmidt GW (2014) Community dynamics and
609 physiology of Symbiodinium spp. before, during, and after a coral bleaching event. Limnol Oceanogr
610 59:788-797
611 Kennedy EV, Perry CT, Halloran PR, Iglesias-Prieto R, Schonberg CHL, Wisshak M, Form AU, Carricart-
612 Ganivet JP, Fine M, Eakin CM, Mumby PJ (2013) Avoiding Coral Reef Functional Collapse Requires
613 Local and Global Action. Curr Biol 23:912-918
614 LaJeunesse TC, Smith RT, Finney J, Oxenford H (2009) Outbreak and persistence of opportunistic symbiotic
615 dinoflagellates during the 2005 Caribbean mass coral bleaching event. Proceedings of the Royal
616 Society B: Biological Sciences 276:4139-4148
617 LaJeunesse TC, Parkinson JE, Gabrielson PW, Jeong HJ, Reimer JD, Voolstra CR, Santos SR (2018)
618 Systematic Revision of Symbiodiniaceae Highlights the Antiquity and Diversity of Coral
619 Endosymbionts. Curr Biol 28:2570-2580.e2576
620 Lang JC (2003) Status of Coral Reefs in the Western Atlantic: Results of Initial Surveys, Atlantic and Gulf
621 Rapid Reef Assessment (AGRAA) Program. Atoll Research Bulletin 496:625
622 Lonin S, Parra C, Andrade C, Thomas Y (2004) Patrones de la pluma turbia del canal del Dique en la bahía de
623 Cartagena. Boletín Científico CIOH 22:77-89
624 Maritorena S, Guillocheau N (1996) Optical properties of water and spectral light absorption by living and non-
625 living particles and by yellow substances in coral reef waters of French Polynesia. Mar Ecol Prog Ser
626 131:245-255
627 Marsh JA (1970) Primary Productivity of Reef-Building Calcareous Red Algae. Ecology 51:255-263
628 Mogollón JV (2013) El Canal del Dique. Historia de un desastre ambiental. El Ancora Editores, Bogotá
629 Morgan KM, Perry CT, Johnson JA, Smithers SG (2017) Nearshore Turbid-Zone Corals Exhibit High
630 Bleaching Tolerance on the Great Barrier Reef Following the 2016 Ocean Warming Event. Frontiers
631 in Marine Science 4:224
632 Odum HT, Odum EP (1955) Trophic Structure and Productivity of a Windward Coral Reef Community on
633 Eniwetok Atoll. Ecol Monogr 25:291-320
634 Omachi CY, Asp NE, Siegle E, Couceiro MAA, Francini-Filho RB, Thompson FL (2019) Light availability for
635 reef-building organisms in a plume-influenced shelf. Continental Shelf Research 181:25-33

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636 Pandolfi JM, Budd AF (2008) Morphology and ecological zonation of Caribbean reef corals: the Montastraea
637 'annularis' species complex. Mar Ecol Prog Ser 369:89-102
638 Pizarro V, Rodriguez SC, Lopez-Victoria M, Zapata FA, Zea S, Galindo-Martinez CT, Iglesias-Prieto R,
639 Pollock J, Medina M (2017) Unraveling the structure and composition of Varadero Reef, an
640 improbable and imperiled coral reef in the Colombian Caribbean. Peerj 5:e4119
641 Pollock FJ, Lamb JB, Field SN, Heron SF, Schaffelke B, Shedrawi G, Bourne DG, Willis BL (2014) Sediment
642 and Turbidity Associated with Offshore Dredging Increase Coral Disease Prevalence on Nearby Reefs.
643 Plos One 9:e102498
644 Restrepo JD, Escobar R, Tosic M (2018) Fluvial fluxes from the Magdalena River into Cartagena Bay,
645 Caribbean Colombia: Trends, future scenarios, and connections with upstream human impacts.
646 Geomorphology 302:92-105
647 Rodriguez-Roman A, Hernandez-Pech X, Thome PE, Enriquez S, Iglesias-Prieto R (2006) Photosynthesis and
648 light utilization in the Caribbean coral Montastraea faveolata recovering from a bleaching event.
649 Limnol Oceanogr 51:2702-2710
650 Roitman S, López-Londoño T, Joseph Pollock F, Ritchie KB, Galindo-Martínez CT, Gómez-Campo K,
651 González-Guerrero LA, Pizarro V, López-Victoria M, Iglesias-Prieto R, Medina M (2020) Surviving
652 marginalized reefs: assessing the implications of the microbiome on coral physiology and
653 survivorship. Coral Reefs 39:795-807
654 Scheufen T, Iglesias-Prieto R, Enríquez S (2017a) Changes in the Number of Symbionts and Symbiodinium
655 Cell Pigmentation Modulate Differentially Coral Light Absorption and Photosynthetic Performance.
656 Frontiers in Marine Science 4:309
657 Scheufen T, Kramer WE, Iglesias-Prieto R, Enriquez S (2017b) Seasonal variation modulates coral sensibility
658 to heat-stress and explains annual changes in coral productivity. Sci Rep 7:4937
659 Shantz AA, Burkepile DE (2014) Context-dependent effects of nutrient loading on the coral-algal mutualism.
660 Ecology 95:1995-2005
661 Smith EG, Gurskaya A, Hume BCC, Voolstra CR, Todd PA, Bauman AG, Burt JA (2020) Low
662 Symbiodiniaceae diversity in a turbid marginal reef environment. Coral Reefs 39:545-553
663 SORCE/SIM (2020) SOlar Radiation and Climate Experiment, Spectral Irradiance Monitor SIM. University of
664 Colorado, Laboratory for Atmospheric and Space Physics. https://lasp.colorado.edu/home/sorce/data/
665 Stat M, Pochon X, Cowie ROM, Gates RD (2009) Specificity in communities of Symbiodinium in corals from
666 Johnston Atoll. Mar Ecol Prog Ser 386:83-96
667 Tosic M, Restrepo JD, Lonin S, Izquierdo A, Martins F (2019) Water and sediment quality in Cartagena Bay,
668 Colombia: Seasonal variability and potential impacts of pollution. Estuar Coast Shelf S 216:187-203
669 Van Veghel MLJ (1994) Polymorphism in the Caribbean reef building coral Montastrea annularis. Ph.D. thesis.
670 University of Amsterdam, p128
671 van Woesik R, Houk P, Isechal AL, Idechong JW, Victor S, Golbuu Y (2012) Climate-change refugia in the
672 sheltered bays of Palau: analogs of future reefs. Ecol Evol 2:2474-2484
673 Vásquez-Elizondo RM, Legaria-Moreno L, Pérez-Castro MA, Kramer WE, Scheufen T, Iglesias-Prieto R,
674 Enríquez S (2017) Absorptance determinations on multicellular tissues. Photosynth Res 132:311-324
675 Wilkinson C (2008) Status of coral reefs of the world: 2008. Global Coral Reef Monitoring Network and Reef
676 and Rainforest Research Centre, Townsville
677 Wyman KD, Dubinsky Z, Porter JW, Falkowski PG (1987) Light-Absorption and Utilization among
678 Hermatypic Corals - a Study in Jamaica, West-Indies. Mar Biol 96:283-292
679 Yentsch CS, Yentsch CM, Cullen JJ, Lapointe B, Phinney DA, Yentsch SW (2002) Sunlight and water
680 transparency: cornerstones in coral research. J Exp Mar Biol Ecol 268:171-183

681