REPORT

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 compromises 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. Low-light phenotypes close to theoretical limits of photoacclimation were found at shallow depths as a result of reduced light penetration. The estimated photosynthetically fixed energy depletion with increasing depth was associated with patterns of colony mortality and vertical habitat compression. A numerical model illustrates

the potential effect of the progressive water quality degradation on coral mortality and population decline along the depth gradient. Collectively, our findings suggest that preserving the water properties seeking to maximize light penetration through the water column is essential for maintaining the coral reef structure and associated ecosystem services.

Keywords Varadero reef · Corals · Photobiology · Ecology · 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. We have already lost nearly a quarter of the world's coral reefs, with the largest cause being the increasing frequency and magnitude of massive climate-related bleaching events (Wilkinson 2008; Lough et al. 2018). 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 et al. 2014). Approximately 75% of remaining reef areas are rated as threatened due to the synergistic effects of large-scale stressors and regional and local factors such as water pollution and overfishing (Hoegh-Guldberg et al. 2007; Burke et al. 2011; Zaneveld et al. 2016; Hughes et al. 2018).

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

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algal symbionts and opportunistic microorganisms (e.g., Symbiodiniaceae and bacteria) (Shantz and Burkepile 2014; Morris et al. 2019) and (b) disease prevalence and energetic losses resulting from the physical disturbance of particle abrasion and deposition on the coral tissue (Junjie et al. 2014; Pollock et al. 2014). In areas exposed to terrestrial runoff or dredging-related activities, recent evidence suggests that the energetic imbalance produced by the reduction in light availability and symbiotic algae photosynthesis, as well as the process of particle clearance, compromises reef-building capacity, coral survivorship and coral reef structure (Junjie et al. 2014; Bessell-Browne et al. 2017; Fisher et al. 2019; Omachi et al. 2019; Morgan et al. 2020). Moreover, that these responses to water turbidity alone or in combination with other type of stressors may be species-specific and mediated by the duration and intensity of the exposure. Despite the recent advances in knowledge, a holistic approach is still needed to gain a broader understanding of the effects of pollution on the water optical properties, the underwater light climate, and the physiology and ecology of reef corals.

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). As a result of major rectification works between the 1920's and 1980's (Mogollón 2013), the Dique channel delivers large freshwater discharges ($8833 \text{ m}^{-3} \text{ s}^{-1}$) with high sediment load ($23,906 \text{ t d}^{-1}$) into the Cartagena Bay (Restrepo et al. 2018). The permanence of this reef under suboptimal environmental conditions provides a unique opportunity to explore the physiological and ecological consequences on reef corals produced by the progressive degradation of the water optical properties. Taking a holistic approach, we investigated these effects using as a proxy the coral species *Orbicella faveolata*, an ecologically dominant and major reef-builder in the Caribbean. We hypothesize that the reduction in light penetration as a result of water pollution has important effects on the physiology and energy balance of *O. faveolata* colonies, which in turn affect the vertical distribution and population structure of this and potentially other symbiotic coral species. 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 but similar total light exposure were considered: a turbid-water reef “Varadero”, close to the Dique channel outlet ($10^{\circ} 18' 23.3'' \text{ N}$, $75^{\circ} 35' 08.0'' \text{ W}$), 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” ($10^{\circ} 11' 12.1'' \text{ N}$, $75^{\circ} 44' 43.0'' \text{ W}$) (Fig. 1). The Dique is a man-made distributary channel that diverges 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. A detailed description of the study sites is provided in the Supplementary Material.

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 pendant dataloggers (UA-002–64, Onset Computer Corporation, USA). A small (0.27° C) but significant difference in temperature was detected between sites (29.15 ± 1.22 (daily mean $\pm$ SD) in Varadero and $28.88 \pm 0.89^{\circ} \text{ C}$ 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, small coral fragments ($\sim 10 \text{ cm}^2$) were collected from the edge of 15 apparently healthy *Orbicella faveolata* colonies at each site minimizing sampling impacts. Source colonies were chosen randomly at a constant depth of $\sim 3.5 \text{ m}$ in Varadero and $\sim 12 \text{ m}$ in Rosario, where total light exposure was similar. Coral colonies can produce internal light gradients depending on colony geometry which affect the photoacclimation status (Vermeij and Bak 2002; Kaniewska et al. 2014). In order to eliminate this effect and obtain a constant photoacclimation mediated by depth and downwelling irradiance, coral fragments were fixed in horizontal position to PVC panels

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 (gray 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

with non-toxic epoxy (Z-Spar A-788 epoxy). Corals were allowed to heal and fully recover for seven months at the same depth of collection, after which a subsample from the survivors (12 in Rosario and 15 in Varadero) was used for physiological analysis and genetic identification of algal symbionts.

Irradiance measurements

Irradiance was monitored every ten minutes for one year (November 2016–November 2017) at each site with cosine-corrected light sensors (Odyssey PAR, 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 was 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 synchronously recorded onshore, and underwater was used to estimate instantaneous values of K_d with the equation:

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

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 used. 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 irradiance at ocean surface and at several depths at each site. A bubble level was used to keep the light sensor horizontal, avoiding 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 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). Sequence 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.

Photophysiological responses

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):

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

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* ($a_{\text{Chl } a}^*$) was calculated according to Enríquez et al. (2005):

$$a_{\text{Chla}}^* = (D_{675}/\rho) * \ln(10) \quad (3)$$

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 ($\text{mg Chl } a \text{ m}^{-2}$). Coral reflectance was measured using a similar optical set-up as Vásquez-Elizondo et al. (2017). Coral surface area for these and other metrics was determined with the aluminum foil technique (Marsh 1970). Cell counts to estimate algal density and cell pigmentation were not reliable due to improper sample preservation and not included in any 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 ($0.45 \mu\text{m}$) 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 16 W LED warm white 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 $\sim 1400 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$. 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 10×1 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.*, coral 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 species identification uncertainty.

Autotrophic capacity

Variation of the phototropic contribution of algal symbionts to the energy requirements of *O. faveolata* colonies across depths was estimated using as a proxy the daily integrated photosynthesis-to-respiration [P/R] ratios. This index of autotrophic capacity was estimated using the PE curve parameters (mean values) and light availability across depths, calculated based on the oscillation of estimated K_d 's (derived from Eq. 1). Daily integrated photosynthesis (P_{day}^g) was calculated with a hyperbolic tangent function (Jassby and Platt 1976):

$$P_{\text{day}}^g = \int_0^{24} [P_{\text{max}}^g \tanh(E_z/P_{\text{max}}^g)] dE_z \quad (4)$$

where P_{max}^g 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 an equation modified from Chalker (1981):

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

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 indicates 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 ($1.93 \pm 0.26 \text{ m}^{-1}$, mean $\pm$ SD), and a clear subsurface layer with significantly lower K_d ($0.31 \pm 0.11 \text{ m}^{-1}$) ($t_{(7)} = 15.31$, $p < 0.01$). No noticeable stratification was detected in Rosario, which revealed a monotonic K_d ($0.16 \pm 0.01 \text{ m}^{-2}$) (Fig. 2a). The estimated K_d 's based on the synchronous oscillation of onshore and underwater irradiance were $0.92 \pm 0.26 \text{ m}^{-1}$ and ranged between 0.38 and 1.95 m^{-1} (Fig. 2b).

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 ($1.93 \pm 0.26 \text{ m}^{-1}$, dark-brown) and a clearer subsurface layer with low K_d ($0.31 \pm 0.11 \text{ m}^{-1}$, light-brown), compared with Rosario monotonic K_d ($0.16 \pm 0.01 \text{ m}^{-1}$, blue). The inset shows light data distribution with depth in log-scale. **b** Temporal variation of mean daily K_d in

Varadero estimated from onshore and underwater irradiance (shaded area represents SD). **c** $K_d \lambda$ in Varadero (brown) and Rosario (blue) (shaded areas represent 95% confidence intervals). **d** Estimated light attenuation due to absorbance of dissolved organic matter associated to Dique discharges based on a differential normalized spectrum in Varadero. Vertical line in **c** and **d** separates the two contrasting spectral regions

Analyses of $K_d \lambda$ indicated distinctive light scattering and absorbing characteristics of dissolved and particulate matter in the water at each site (Fig. 2c). Varadero's high variability of $K_d \lambda$ (*i.e.*, wide confidence intervals) (Fig. 2c) was consistent with the strong stratification (Fig. 1a) and the temporal variation of K_d (Fig. 2b). $K_d \lambda$ evidenced two spectral regions with contrasting characteristics. One below $\sim 600 \text{ nm}$ with increasing attenuation toward shorter wavelengths in Varadero and low attenuation in

Rosario attributed to light absorption of dissolved organic material of continental origin (Maritorena and Guillocheau 1996). And a spectral region above 600 nm with nearly constant properties despite differences in attenuation magnitude among sites attributed to light attenuation due to scattering by particulate matter with small effect on spectral quality (Fig. 2c). The estimated attenuation due to absorbance of dissolved organic matter obtained from a differential normalized spectrum (Fig. 2d) demonstrated

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) irradiance on six random days. **c** K_d variation estimated from onshore and underwater irradiance

the high concentration of dissolved organic matter in Varadero associated with the Dique plume and its critical role in modifying the underwater light quality.

Dramatic changes of K_d were detected within and between days (Fig. 3), highlighting the variable nature of the water optical properties and underwater light climate associated with the Dique plume dynamics in Varadero. On average, the daily integrated irradiance was 7% lower in

Varadero than in Rosario (2.03 ± 1.32 and $2.17 \pm 0.91 \text{ mol quanta m}^{-2} \text{d}^{-1}$, respectively) ($H_{(1)} = 7.92$, $p < 0.05$). Prevalent irradiance at both sites was consistent with low-light reef environments (Anthony and Hoegh-Guldberg 2003; DiPerna et al. 2018).

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

Symbiont identity

Analyses of Internal Transcribed Spacer 2 (ITS2) rRNA sequences identified distinctive ITS2 profile combinations diagnostic of five separate Symbiodiniaceae genotypes. One belonged to the genus *Symbiodinium* (ITS2 type A3), one to *Breviolum* (ITS2 type B1) and three to *Cladocopium* (ITS2 types C7, C7/C12c, C3ee/C21/C3an) (Fig. 4, Fig. S3). The community structure of algal symbionts in terms of ITS2 profiles composition was different between sites ($p = 0.001$, PERMANOVA on Bray–Curtis matrix). In Varadero, a single *Cladocopium* genotype (ITS2 type C3ee/C21/C3an) was present in all colonies sampled and in nearly half of them it was the only dominant symbiont (abundance of $> 80\%$). A *Symbiodinium* genotype (ITS2 type A3) was also present in 67% of colonies. The symbiont diversity in coral samples from Rosario was more diverse and included representatives of the five different genotypes. *Cladocopium* ITS2 type C7/C12c and *Symbiodinium* ITS2 type A3 were the most abundant symbionts in corals from Rosario, detected, respectively, in 50% and 42% of the colonies. A *Breviolum* genotype (ITS2 type B1) was detected in half of the samples but in low background levels (abundance of $< 13\%$). *Cladocopium* ITS2 type C3ee/C21/C3an, also detected in Varadero, and *Cladocopium* ITS2 type C7 was present in a few corals from Rosario (17% and 25%, respectively) being the only dominant symbiont. Interestingly, the three *Cladocopium* genotypes detected in Rosario never occurred together on the same colony.

Photophysiological responses

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 $a^*_{\text{Chl } a}$) were significantly different between sites. Parameters derived from the photosynthetic potential (α , E_c , E_k , R_d , P_{max} and $1/\Phi_{\text{max}}$) and corals capacity to absorb light (A_{PAR}) were non-significantly different (Table 1). F_v/F_m values (0.669 ± 0.019 and 0.676 ± 0.012 in Varadero and Rosario, respectively) differed by 1% ($t_{(74)} = 2.26$, $p = 0.027$). Values of $\Delta F/F_m'$ and Q_m (0.579 ± 0.052 and 0.610 ± 0.033 , and 0.135 ± 0.062 and 0.097 ± 0.051 in Varadero and Rosario, respectively) varied by 5% ($t_{(75)} = 3.38$, $p = 0.001$) and 28% ($t_{(84)} = -3.09$, $p = 0.003$), respectively. Estimated values of $1/\Phi_{\text{max}}$ (11.24 ± 1.87 and 11.62 ± 3.16 quanta O_2^{-1} in Varadero and Rosario, respectively) were lower than previous reports (Wyman et al. 1987; Rodriguez-Roman et al. 2006) and close to minimum practical limits of ~ 10 – 12 quanta O_2^{-1} (Hill and Govindjee 2014).

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 $a \text{ m}^{-2}$, respectively). Changes in Chl a density resulted in significant variations of $a^*_{\text{Chl } a}$ (0.013 ± 0.002 and $0.031 \pm 0.012 \text{ m}^2 \text{ mg Chl } a^{-1}$ in Varadero and Rosario, respectively, $H_{(1)} = 10.5$, $p = 0.001$). Comparative analyses of changes in $a^*_{\text{Chl } a}$ 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

Table 1 Photoacclimation parameters of *O. faveolata* in Varadero at 3.5 m and Rosario at 12 m

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 <i>a</i> (mg Chl <i>a</i> m ⁻²)	Chlorophyll <i>a</i> 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 <i>a</i> ⁻¹)	Chlorophyll <i>a</i> 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)	$t_{(7)} = 0.27, p = 0.798$

Values correspond to the mean $\pm$ SD (sample size *n*). *t* tests (*t*) and Kruskal–Wallis tests (*H*) were conducted after testing of assumptions (normality with the use of K-S test) to determine whether differences between sites were statistically significant. Values of photosynthetic parameters used to estimate the productivity of colonies (integrated daily P/R ratios) are highlighted in bold

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 $\pm$ 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

normalized per unit area (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 colony density (3.20 ± 2.85 colonies transect⁻¹) and coral cover (4.46 ± 4.57 m² transect⁻¹) than Rosario

(1.70 ± 1.18 colonies transect⁻¹ and 4.20 ± 5.48 m² 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 ($7.5 \pm 3.5\%$) and the highest at 9 m ($73.3 \pm 26.4\%$). In Rosario, the lowest mortality occurred at the maximum depth ($5.0 \pm 12.2\%$ at 17 m) and the highest at an intermediate depth ($73.3 \pm 20.8\%$ 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.

Autotrophic capacity

The index of autotrophic capacity of *O. faveolata* colonies from Varadero suggested 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, the index had a mean of 0.64 ± 0.18 (SD). On days with increased light penetration in the water column (i.e., low K_d), the index increased up to 0.99 while on days with reduced light penetration it dropped to 0.20. At 9 m, the maximum depth where living *O. faveolata* colonies were found in Varadero, the index had a mean of 0.01 ± 0.01 and oscillated between 4.49×10^{-6} and 0.07 (Fig. 5). A strong, negative correlation was found between colonies partial mortality and the index of autotrophic capacity (Spearman $r_s = -0.94$, $p = 0.005$). The coefficient of determination of an exponential regression indicated that the autotrophic capacity explains 78% of the mortality variation across depths in *O. faveolata* (Fig. S7).

In Rosario at 3 m and 17 m, the local vertical limits of *O. faveolata*, the index of autotrophic capacity had a mean of 0.84 ± 0.14 and 0.19 ± 0.07 , respectively. The index' range of variation was 0.20–0.98 and 0.02–0.27 in the upper and lower depth limits, respectively, depending on changes in light availability (Fig. 5). Corals from Rosario had significantly higher autotrophic capacity than corals from Varadero both at the upper ($H_{(1)} = 73.29$, $p < 0.001$) and lower ($H_{(1)} = 189.25$, $p < 0.001$) local depth limits. There was no significant correlation between colony partial mortality and the autotrophic capacity of corals from Rosario (Spearman $r_s = 0.60$, $p = 0.208$).

Discussion

We identified three main features of the underwater light climate in the turbid-water Varadero reef: (1) light-limiting conditions due to the strong attenuation generated by

particulate matter and dissolved substances concentrated in a superficial layer of water, (2) substantial variation of the underwater light climate in response to fluctuations of 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 of a superficial layer directly affected by the Dique channel discharges and a subsurface clear layer of oceanic waters (Lonin et al. 2004). This stratification seems to isolate Varadero from the direct influence of the Dique freshwater discharges, but have a critical impact on the underwater light availability.

The variation of the water optical properties in Varadero inferred from the synchronous oscillation of onshore and underwater irradiance explains 81% of the overall temporal variation of underwater light availability. This estimation is in close proximity to irradiance variation in other turbid-water reefs due to suspended solids (Anthony et al. 2004). Maximum K_d 's were higher compared to previous reports at this site (Pizarro et al. 2017; Roitman et al. 2020) and other turbid-water reefs (Hennige et al. 2010; Omachi et al. 2019). The extremes within the K_d range of variation indicate that irradiance can vary by up to two orders of magnitude only due to changes in water optical properties attributed to meteorological conditions affecting the Dique plume dynamics (Lonin et al. 2004; Tosic et al. 2019). At Rosario, the clear-water site, although the water column was significantly clearer than Varadero, the K_d 's for the whole PAR range (0.158 m⁻¹) and toward 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 that their influence extend far beyond the channel mouth to this natural protected area.

Our results suggest that *O. faveolata* colonies host distinctive Symbiodiniaceae communities in Varadero and Rosario. Symbiodiniaceae communities were more diverse in corals from Rosario than in Varadero mainly due to an increased richness of *Cladocopium* genotypes. It is known that *O. faveolata* associates with genetically distinct symbionts from four genera following gradients of irradiance, with combinations of *Symbiodinium*, *Breviolum* and *Durisdinium* genotypes typically found in high-light environments and *Cladocopium* genotypes in low-light environments (Rowan et al. 1997; LaJeunesse 2002; Kemp et al. 2015). The greater diversity and abundance of *Cladocopium*, a highly diverse taxa throughout the

Caribbean (Thornhill et al. 2014), as well as the absence of *Symbiodinium* genotypes in Rosario may indicate the occurrence of coral–algae associations favored by a more predictable low-light environment. In Varadero, the presence of *Symbiodinium* genotypes in some samples and the reduced diversity of Symbiodiniaceae may be indicators of the strong selective pressure exerted by the turbid plume dynamics on the symbiont communities, similar to previous reports in other turbid marginal reef environments (Smith et al. 2020).

Low-light phenotypes of *O. faveolata* were found both in Varadero at 3.5 m and in Rosario at 12 m, which highlights the essential role of the water optical properties on the photoacclimation status and illustrates the constraint of using depth as main proxy. Estimated minimum quantum requirements ($1/\Phi_{\max}$) of corals growing at both sites indicate similar light utilization efficiency close to theoretical operational limits of ~ 10 – 12 quanta O_2^{-1} (Hill and Govindjee 2014). Q_m values close to 0 indicate that even at noon when corals are exposed to maximal irradiance, most PSII reaction centers of symbiotic algae remained open suggesting light-limited photosynthetic rates (Iglesias-Prieto et al. 2004). Both Q_m and $1/\Phi_{\max}$ normally decrease with increasing depth until reaching the minimal practical values, which corresponds to the limits of potential photoacclimation capacity and tolerance range for the symbiosis (Wyman et al. 1987; Iglesias-Prieto et al. 2004). The values of Q_m and $1/\Phi_{\max}$ close to theoretical minimums suggest that the photoacclimation of *O. faveolata* symbionts is close to the limit for maximum efficiency of solar energy utilization and, therefore, the lower vertical distribution limit of the species at each site despite the differences in depth.

Comparative analyses of the parameters derived from the P-E curves indicate that corals at both locations have very similar photosynthetic potential, even when corals from Varadero are occasionally exposed ($\sim 10\%$ of days) to supersaturating irradiance. During these periods, irradiance can be almost twice the light saturation point (E_k), representing a potential source of over-excitation of the photosynthetic apparatus that must be dissipated by photoprotective mechanisms. A greater reduction of the quantum yield of photosystem II (PSII) measured at noon ($\Delta F/F_m'$) relative to its maximum value at dusk (F_v/F_m) indicates that corals from Varadero were indeed exposed to a higher irradiance during measurements, compared to Rosario. It must be stressed, however, that the almost identical values of F_v/F_m between sites indicate similar photochemical energy conversion efficiency of coral symbionts. This suggests that the occasional exposure to higher irradiance in Varadero is not intense enough as to induce a chronic photoinactivation of a population of PSII reaction centers in order to increase the capacity to dissipate excess

excitation via non-photochemical quenching (Hoegh-Guldberg and Jones 1999).

Corals in Varadero had greater Chl *a* content and lower light absorption efficiency of algal pigments than corals from Rosario, potentially associated with other runoff impacts in the water column besides a reduction in light penetration. It is known that the presence of particulate matter and dissolved compounds in the water column can interfere in the coral holobiont metabolism (Anthony and Fabricius 2000; Houlbrèque and Ferrier-Pagès 2009; Morris et al. 2019), which may be reflected in the pigment content and/or algal cell density. The potential metabolic interference of nutrient enrichment results in a reduction of $a^*_{\text{Chl } a}$, indicating that the highly pigmented corals from Varadero are less efficient at collecting light per unit of pigment than corals from Rosario as a result of the “pigment packaging” effect (Scheufen et al. 2017a). The nearly constant capacity of corals to absorb $\sim 90\%$ of incident light at both sites indicates that the increased pigmentation in corals from Varadero does not confer them with any additional advantage in terms of light harvesting. Furthermore, the lack of differences among photosynthetic parameters indicates that the light absorbed is also utilized with similar efficiency (per unit area) by corals at both sites. These results suggest that a potential nutrient enrichment linked to Dique discharges does not significantly affect the photosynthetic potential of *O. faveolata*.

The estimated index of photosynthetic potential revealed that the daily phototrophic contribution of algal symbionts to the coral host metabolism is low and highly variable due to the temporal dynamics of water turbidity. The reduction of carbon acquisition through photosynthesis with increasing depth and during exposure to elevated turbidity could potentially be counterbalanced by increasing the heterotrophic energy acquisition, as has been observed in some coral species (Anthony and Fabricius 2000; Hoogenboom et al. 2010). It should be noted, however, that the Dique plume particles can also represent a stress factor for coral colonies even with lethal effects, particularly if the sediments infer low nutritional value and there is low-light availability (Junjie et al. 2014; Bessell-Browne et al. 2017; Fisher et al. 2019). 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. The energetically costly process of coral clearance is expected to be strongly limited below this depth due to the negligible phototrophic contribution of algal symbionts and the metabolic depression of the holobiont. Thus, a potential nutritional benefit obtained by particle feeding may be insufficient to maintain a positive energy balance due to the costs of particle clearance and acute light energy limitation, mostly below certain depths.

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 modeled 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)

The size of *O. faveolata* colonies in Varadero with diameters exceeding 5 m (Pizarro et al. 2017) indicates that these colonies are probably hundreds of years old and that the population was established in Varadero long before the Dique major rectification works between the 1920's and 1980's (Mogollón 2013). The current vertical distribution of this species is restricted to shallower depths (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 the autotrophic capacity of corals from Varadero, suggests the occurrence of a progressive decline of *O. faveolata* population from the bottom to the top of the reef (Fig. 6). This vertical “compression” effect has also

been reported for the whole coral community in other turbid reefs (Morgan et al. 2020). The gradual but sustained degradation of the water optical properties in Varadero, firstly due to the Dique channeling works and secondly due to the sustained acceleration of soil erosion along the Magdalena River basin (Restrepo et al. 2018), seems to be key factors in the population decline and vertical range contraction of *O. faveolata*.

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 keep rising and driving reefs toward the breaking point of collapse (Hughes et al. 2018). Our findings demonstrate the substantial implications that the progressive degradation of the optical properties of coastal waters globally can have on the physiology and vertical distribution of reef-building corals, which in turn inevitable affect the structure of reef coral communities. Future studies should explore with a holistic approach the gradual changes, both at temporal and spatial scales, in photoacclimation and metabolic responses linked to the disruption of corals energy balance in the increasingly abundant marginal environments. 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.

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Author contributions MM, VP, MLV and RIP conceived the study. CTGM, KGC, LAGG, SR, FJP, VP, MLV and TLL participated in field work and data collection. SR performed Symbiodiniaceae analysis. CTGM and TLL performed water properties analysis. TLL, CTGM, KGC and LAGG conducted physiological analyses. TLL and RIP wrote the manuscript. MM, SR, CTGM, KGC and LAGG supported writing and editing the manuscript.

Data availability Figures and data generated and analyzed in this manuscript are openly available in the digital repository <https://>

figshare.com/s/e5e49575f67b90202579 (<https://doi.org/10.6084/m9.figshare.12156168>).

Declarations

Conflict of interest The authors declare no conflicting interests.

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