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RESEARCH ARTICLE

Nocturnal dissolved organic matter release by turf algae and its role in the microbialization of reefs

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Abstract

1. The increased release of dissolved organic matter (DOM) by algae has been associated with the fast but inefficient growth of opportunistic microbial pathogens and the ongoing degradation of coral reefs. Turf algae (consortia of microalgae and macroalgae commonly including cyanobacteria) dominate benthic communities on many reefs worldwide. Opposite to other reef algae that predominantly release DOM during the day, turf algae containing cyanobacteria may additionally release large amounts of DOM at night. However, this night-DOM release and its potential contribution to the microbialization of reefs remains to be investigated.
2. We first tested the occurrence of hypoxic conditions at the turf algae–water interface, as a lack of oxygen will facilitate the production and release of fermentation intermediates as night-time DOM. Second, the dissolved organic carbon (DOC) release by turf algae was quantified during day time and nighttime, and the quality of day and night exudates as food for bacterioplankton was tested. Finally, DOC release rates of turf algae were combined with estimates of DOC release based on benthic community composition in 1973 and 2013 to explore how changes in benthic community composition affected the contribution of night-DOC to the reef-wide DOC production.
3. A rapid shift from supersaturated to hypoxic conditions at the turf algae–water interface occurred immediately after the onset of darkness, resulting in night-DOC release rates similar to those during daytime. Bioassays revealed major differences in the quality between day and night exudates: Night-DOC was utilized by bacterioplankton two times faster than day-DOC, but yielded a four times lower growth efficiency. Changes in benthic community composition were estimated to have resulted in a doubling of DOC release since 1973, due to an

increasing abundance of benthic cyanobacterial mats (BCMs), with night-DOC release by BCMs and turf algae accounting for >50% of the total release over a diurnal cycle.

4. Night-DOC released by BCMs and turf algae is likely an important driver in the microbialization of reefs by stimulating microbial respiration at the expense of energy and nutrient transfer to higher trophic levels via the microbial loop, thereby threatening the productivity and biodiversity of these unique ecosystems.

KEYWORDS
Caribbean coral reef, cyanobacteria, dissolved organic carbon, dissolved organic nitrogen, fermentation, hypoxia, microbialization, night-DOM release, turf algae

1 | INTRODUCTION

Dissolved organic matter (DOM) is a key component in the biogeochemistry and overall functioning of terrestrial, freshwater and marine ecosystems (e.g. Baines & Pace, 1991; Friedlingstein et al., 2020; Hansell & Carlson, 2001; Kalbitz et al., 2000; Thomas, 1997). Fixation of atmospheric CO_2 and subsequent release of DOM by photosynthetic organisms provide a major source of organic carbon into lakes, oceans and soils (Hansell & Carlson, 2001; Thornton, 2014). Rapid consumption and modification of photosynthetically derived DOM by heterotrophic microbial communities decomposes DOM to CO_2 that can be released back into the atmosphere, converts DOM into biomass (Ducklow & Carlson, 1992; Hansell et al., 2009) or sequesters it as recalcitrant DOM in the deep ocean (Hansell, 2013; Jiao et al., 2010). Shifts in the community composition of primary producers or decomposers that modify DOM production, alter DOM transformations, or affect DOM consumption may have major implications for the local, regional or even global carbon cycle.

In coastal ecosystems, the DOM pool is often primarily fuelled by abundant benthic primary producers (Ziegler & Benner, 1999; Wada & Hama, 2013; Barrón et al., 2014; Reed et al., 2015). An example is provided by tropical coral reefs, which represent some of the most productive and diverse ecosystems in the world's oceans (Hatcher, 1988; Odum & Odum, 1955). Up to 50% of the photosynthates produced on coral reefs is released as DOM into the surrounding water (Davies, 1984; Haas et al., 2011). This complex mixture of organic molecules, including polysaccharides, proteins and lipids, is not directly available to most heterotrophic organisms as food source (Carlson, 2002; Dittmar & Stubbins, 2014; Hansell & Carlson, 2001). Processing of the DOM released by corals and algae into organic particles and the subsequent transfer to higher trophic levels via the microbial loop (Azam et al., 1983) and the sponge loop (de Goeij et al., 2013) can reduce the loss of energy and nutrients stored in this locally produced DOM to the open ocean, and is therefore considered pivotal to sustain the high productivity of coral reefs under oligotrophic conditions.

A combination of anthropogenic disturbances (e.g. eutrophication, overfishing, ocean acidification, global warming) has led to a devastating decline in the abundance of scleractinian corals, and a concomitant increase in fleshy macroalgae, benthic cyanobacterial mats (BCMs) and turf algae on many reefs around the world (Gardner et al., 2003; Hoegh-Guldberg, 1999; Hughes et al., 2017; McCook et al., 2001). Since these non-calcifying taxa release more DOM per surface area than scleractinian corals (Haas et al., 2011; Mueller et al., 2014), this shift in benthic community composition results in an increase in benthic DOM production with potentially major implications for coral reef functioning (de Goeij et al., 2017; Haas et al., 2016; Pawlik et al., 2016). The relative abundance of turf algae has increased dramatically on many reefs, making them often the most abundant functional group within exposed benthic reef communities (Barott et al., 2012; Kramer, 2003; Vermeij et al., 2010). Turf algae are heterogeneous consortia of Chlorophyta, Phaeophyta and Rhodophyta commonly including filamentous cyanobacteria and a distinct community of other associated microbes (Barott et al., 2011; Connell et al., 2014; Fricke et al., 2011; Steneck & Dethier, 1994). Fast growth (Littler et al., 2006), rapid nutrient uptake (den Haan et al., 2016) and the ability to fix dinitrogen (Charpy et al., 2010; den Haan et al., 2014) allow turf algae to outcompete other reef organisms by rapidly occupying new space. Furthermore, their net areal primary production rates and dissolved organic carbon (DOC) release rates (i.e. during daylight) are among the highest reported for benthic primary producers on coral reefs (Adey & Goertemiller, 1987; Haas et al., 2010).

In general, the release of photosynthetically fixed carbon as DOC is directly linked to primary production with a positive relationship between DOC release and light availability (e.g. Baines & Pace, 1991; Cherrier et al., 2014; Zlotnik & Dubinsky, 1989). Reported DOC release rates in the dark are therefore typically much lower than DOC release rates in the light (Barrón et al., 2014; Haas et al., 2010; Mueller et al., 2014; Zlotnik & Dubinsky, 1989). In contrast, BCMs dominated by the cyanobacterium *Oscillatoria bonnemaisonii* not only release large quantities of DOC during the day, but also release two times more DOC at night (Brocke, Wenzhoefer, et al., 2015). Due to the absence of light, nightime DOC release is likely caused by incomplete degradation and anaerobic fermentation of carbohydrates that have accumulated in cyanobacterial cells by their photosynthetic activity during daytime, as has previously been reported for several *Oscillatoria* species (Heyer et al., 1989;

Heyer & Krumbein, 1991; Stal & Moezelaar, 1997). Cyanobacteria typically contribute 20%–50% of the total biomass of turf algae in the Southern Caribbean and are often dominated by *Oscillatoria* spp. (Fricke et al., 2011). Consequently, these turf algae may also release large amounts of DOC at night (Müller, 2015), but these rates as well as their contribution to carbon cycling within reef communities have not been studied.

It is becoming increasingly evident that not only the quantity, but also the quality (i.e. bio-availability and utilization) of DOM for key DOM consumers (i.e. microbes and sponges) differs considerably among primary producers. Microbes and sponges metabolize algal-DOM faster than coral-DOM (Campana et al., 2021; Nelson et al., 2013; Rix et al., 2017; Silva et al., 2021). Algal-DOM further increases microbial respiration and fuels the fast but inefficient growth of opportunistic microbes (i.e. large amounts of DOM required to support growth; Nelson et al., 2013). This shifts the microbial community metabolism from net autotrophy to net heterotrophy (Haas et al., 2013) and depletes the local DOM pool to sustain a greater microbial biomass, instead of transferring energy and nutrients stored in DOM to higher trophic levels. This process is commonly referred to as the 'microbialization of reefs' (Haas et al., 2016; McDole et al., 2012).

To date, the contribution of fermentation-derived DOM released at night to the total reef-wide DOM production, its bio-availability to and utilization by microbial communities, and its potential role in the microbialization of reefs remains virtually unknown. This study therefore aims to quantify DOC released by turf algae during the day and at night (from here on referred to as 'day-DOC' and 'night-DOC') and to estimate how the contribution of this day-DOC and night-DOC release to the local DOC pool may have changed over the past 40 years on a Caribbean reef. Furthermore, we investigated the quality (i.e. C:N ratio, bio-availability and bacterial growth efficiency) of this turf-algal DOM for a natural bacterioplankton community to assess its potential contribution to the microbialization of reefs. Specifically, we (a) tested the occurrence of hypoxia at the water–turf algae interface; a prerequisite for fermentation-derived night-DOC release, (b) quantified day- and night-DOC release and net primary production by turf algae and (c) assessed the quality of these day- and night-exudates for bacterioplankton in bioassays. Lastly, we (d) extrapolated current DOC release fluxes on a coral reef site on Curaçao and (e) compared those to estimates of historic DOC release fluxes based on benthic community composition data from the 1970s at the same location.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted in August 2015 on Curaçao, Southern Caribbean. All samples were collected from a fringing reef at the site 'The Water Factory' (12°06′N, 68°57′W), on the leeward coast of the island. Turf algae and seawater for (a) dissolved oxygen (O_2) measurements at the turf algae–water interface, (b) turf-algal incubations and (c) bioassays were collected from the shallow reef terrace at 7 m water depth. At this location, sand patches are interspersed by well-developed coral communities (coral cover approx. 25%) with macro- and turf algae growing on dead coral rock. Experiments were performed at the CARMABI research station, and all collections and experimental work were carried out under the research permit (#2012/48584) issued by the Curaçaoan Ministry of Health, Environment and Nature (GMN) to the CARMABI foundation.

2.2 | O_2 concentrations at the turf algae–water interface

Dead branches thickly overgrown by turf algae were collected at 17:00 hr from a partially dead *Acropora cervicornis* colony (Figure 1) on SCUBA. Branches (mean surface area ± *SD*: 105 ± 18 cm^2) were individually packed in water-tight zippered polyethylene bags filled with seawater, and immediately transported in a cooler to the nearby (~3 km) CARMABI research station. There they were placed in a seawater tank with a circulating pump in an air-conditioned room to mimic ambient seawater temperatures (~29°C). The recirculating seawater tank was provided with seawater from the reef. After an acclimatization period of 12–18 hr in the dark, dissolved oxygen (O_2) concentrations in the turf algae–water interface (0.1–0.5 mm above the turf algae) were measured with a microsensor system (Wangpraseurt et al., 2012; Weber et al., 2007) under constant flow conditions (1.7 cm s^{-1}). Thereto, a branch with turf algae was placed in an identical tank and exposed to six consecutive periods of light (200 μmol photons m^{-2} s^{-1}) and darkness to test for the possible occurrence of hypoxia after the switch from light to dark conditions. The duration of these light and dark periods (~20 min) depended on reaching a stable maximum (i.e. local maximum) and a stable minimum (i.e. local minimum) O_2 concentration, respectively. This procedure was repeated three times, with three

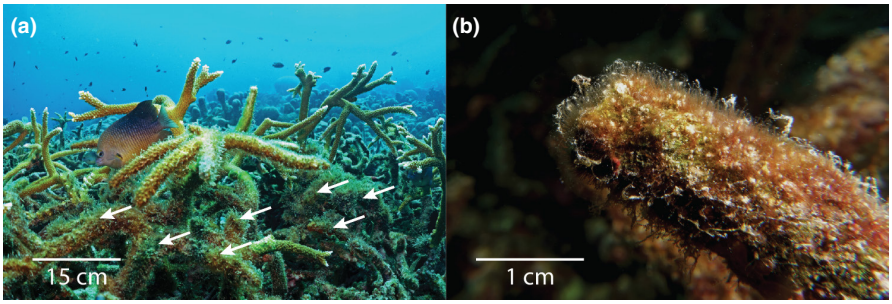

FIGURE 1 (a) Colony of live *Acropora cervicornis* with dead branches underneath that are thickly overgrown by turf algae (arrows). (b) Close-up of turf-algal community growing on dead *A. cervicornis* branch.

different branches with turf algae (i.e. $n = 3$). Prior to the measurements, a two-point calibration for the microsensor was performed using 0 and 100% oxygen-saturated seawater (confirmed by optode measurements). Analysis of dissolved oxygen data was performed using custom-made programs MPR-plotter and L@MP (Brocke, Wenzhoefer, et al., 2015).

2.3 | Day and night release of turf-algal exudates

All turf-algal fluxes determined here should be considered net community fluxes (i.e. of consortia of turf algae and their associated microbiome; sensu Barott et al., 2011). Incubation experiments with turf algae were performed between 4 and 14 August 2015 (Table S1). Four hours prior to the start of the incubations, *Acropora* branches with turf algae were collected as described above. Additionally, 38 L of reef water was sampled 1 m above the reef bottom with a modified bilge pump connected to a low-density polyethylene (LDPE) collapsible bag (19 L; Cole-Parmer; see Dinsdale et al., 2008 for technical details). Upon arrival at the CARMABI research station, water-tight zippered polyethylene bags containing branches with turf algae and reef water were stored in an air-conditioned lab. Temperature and light conditions in the laboratory mimicked those typically occurring on the collection site in the early morning and late afternoon (29°C and ~50 µmol photons m^{-2} s^{-1}).

Four transparent, airtight acrylic flow chambers (1.9 L) with magnetic stirrers to ensure proper mixing were used for the incubation experiments (see: de Goeij et al., 2013 for technical details). Prior to the incubations, flow chambers were acid-washed (0.4 mol L^{-1} HCl) and rinsed twice with reef water collected that day. Three new *Acropora* branches completely overgrown by turf algae (mean surface area ± *SD*: 105 ± 18 cm^2 determined following the advanced geometry technique; Naumann et al., 2009) were placed in each flow chamber (to ensure sufficient turf-algal biomass) and incubated in reef water (without air trapped inside the flow chamber). An additional flow chamber was filled with reef water only and served as a seawater control. Flow chambers were placed in a running seawater aquarium system (7 L min^{-1}) to keep them at temperatures similar to those on the reef (29–31°C). Daytime incubations (turf algae: $n = 9$; seawater controls: $n = 3$) were performed from 10:00 to 15:00 hr and nighttime incubations (turf algae: $n = 10$; seawater controls: $n = 4$) from 21:00 to 02:00 hr, to maintain a natural circadian rhythm (Table S1). Duration of the incubations was limited to 5 hr, to avoid accumulation of waste products and high oxygen concentrations, which may suppress photosynthesis due to photorespiration. Each incubation (i.e. flow chamber with three branches with turf algae or seawater control) was treated as an independent replicate in the statistical analyses.

Water samples (60 ml) for DOC, total dissolved nitrogen (TDN) and inorganic nutrient analysis (nitrite: NO_2^-, nitrate: NO_3^-, ammonium: NH_4^+, phosphate: PO_4^{3-}) were taken through a sampling port in the lid of the flow chamber using a polypropylene syringe at $t = 0$ and 5 hr. Syringes were acid-washed and rinsed with GF/F-filtered reef water beforehand. Samples were immediately placed in the dark and processed within 60 min after collection. O_2 concentrations were measured continuously (sampling interval: 15 s) in each flow chamber using oxygen optodes (Oxy-4, PreSens) to determine net O_2 production and dark respiration in day and night incubations, respectively. O_2 evolution during incubations served as a proxy for net primary production based on an assumed balanced molar ratio of C fixation to net O_2 production (1 mol C fixed equals 1 mol O_2 released), which also allowed us to express DOC release as percentage of net primary production (e.g. Haas et al., 2011; Mueller et al., 2016). Seawater pH was measured at the beginning and the end of each incubation with a pH meter (WTW pH 330, Cole-Parmer, USA). Natural light availability during daytime incubations was recorded using light-temperature loggers (HOBO Pendant, Onset, USA, sampling interval: 1 min) next to the incubators in the flow-through seawater system. Recorded light values were transformed to the light availability inside the incubators using a pre-determined conversion factor obtained by the empirical linear relation between the light intensity inside and outside of the flow chambers using two similar light loggers (ligh $t_{inside} = light_{outside} \times 0.469$, $R^2 = 0.314$, $p < 0.0001$). Light intensities measured in Lux were converted to µmol photons m^{-2} s^{-1} in the PAR range using the approximation by Valiela (2013, p. 64): 1 µmol photons m^{-2} s^{-1} = 51.2 Lux. Moreover, to assess the potential occurrence of stress in turf-algal communities during the course of the incubations, the change in the effective quantum yield of photosystem II ($\Delta F / F'_m$) was determined. This measure of photosynthetic efficiency is widely accepted as a proxy for the occurrence of stress and the physiological status in phototrophic organisms (e.g. Enríquez & Borowitzka, 2010; Maxwell & Johnson, 2000; Mueller et al., 2017). Thereto, three small pieces (approx. 5 cm length) of branches with turf algae were dark-adapted for 30 min before setting up the turf-algal incubations. After photochemical quenching was completely relaxed, $\Delta F / F'_m$ was measured with a waterproof PAM fluorometer (Diving PAM). This procedure was repeated after each 5-hr incubation with incubated turf algae and the change in $\Delta F / F'_m$ was calculated.

2.4 | Quality of day and night turf-algal exudates for bacterioplankton

Directly after day and night incubations were concluded, flow chambers were transported to the lab and branches with turf algae were removed using acid-washed tweezers. Subsequently, 180 ml incubation water from each flow chamber containing turf-algal exudates was filtered (GF/F, 0.7 µm) to reduce the abundance of bacterioplankton (by ~40% compared to regular reef water) and transferred to an acid-washed (0.4 mol L^{-1} HCl) glass bottle (250 ml). Hence, the number of replicates remained the same as in aforementioned flow chamber incubations. Glass bottles were then inoculated with 70 ml of unfiltered reef water (containing natural bacterioplankton

TABLE 1 Historic and present benthic cover (%; based on de Bakker et al., 2017, and average DOC release rates (mmol m^{-2} hr^{-1}) during the day and night for most abundant DOC producing functional groups on the shallow reef terrace at Buoy 0, Curaçao. The category 'other' includes other biota (e.g. sponges, fire corals, gorgonians) and bare substrate.

Benthic component	Benthic cover (%)		DOC release (mmol m^{-2} hr^{-1})		
	1973	2013	Day	Night	References
Scleractinian corals	37	1	0.8	0.07[a]	Brocke, Wenzhoefer, et al. (2015) and references therein
Macroalgae	0	16	0.9	0.05	Brocke, Wenzhoefer, et al. (2015) and references therein
Turf algae	27	25	4.6	2.7	This study
BCMs	0	41	2.7	3.5	Brocke, Wenzhoefer, et al. (2015)
Sand	10	13	–	–	
Other	26	4	–	–	

[a]Previously miscalculated nighttime rate for *O. annularis* was corrected from 3.25 to 0.075 mmol m^{-2} hr^{-1} according to Mueller et al. (2014) and reported day rates for *Manicina* sp. and *Pocillopora* sp., which were associated with stressful conditions and/or were an order of magnitude higher than all other rates, were excluded before calculating the average release rate.

communities) collected earlier that day (following procedures for dilution cultures modified from Haas et al., 2011). Seawater controls from the incubations were treated similarly and served as unamended seawater controls. An initial seawater sample for DOC, TDN and inorganic nutrient analyses was taken from each glass bottle as described above. Additionally, a 10-mL seawater sample was collected with a polypropylene syringe and immediately fixed with formaldehyde (2% end concentration) to determine initial bacterial concentrations. Bottles were subsequently closed airtight and incubated in an air-conditioned lab (29 °C) in the dark. Bottles were gently turned every 12 hr to prevent sedimentation of the bacterioplankton community. After 48 hr, bioassays were terminated and water samples for final DOC, TDN, inorganic nutrient and bacterial analyses were collected as described above. Details on DOC, TDN and inorganic nutrient analyses, as well as bacterial counts are presented in the supplementary (Text S2).

2.5 | Data analyses

Net DOC release and net O_2 production/night respiration rates were calculated as the change in concentration through time per surface area covered by turf algae. For DOC release, this change was solely based on the difference between initial and final concentrations (Figure S3), whereas changes in O_2 concentrations were analysed based on linear regressions including intermediate time points (Figure S4). Changes in DOC and O_2 concentration were further corrected by subtracting the average change in the seawater controls from respective changes in turf-algal incubations. Differences between day and night rates were determined using one-way ANOVAs. To assess the quality of turf-algal exudates for bacterioplankton, the bacterial carbon demand (BCD; removal rate of DOC), bacterial cell yield (BCY; increase in bacterial abundance) and bacterial growth efficiency (BGE; ratio increase bacterial carbon to bacterial carbon demand) were calculated for the bioassays following methods described in Haas et al. (2011). Differences between day versus night and between treatments versus controls were determined using two-way ANOVAs. Potential differences in initial concentrations/conditions between treatments and controls were tested using one-way ANOVAs followed by Tukey's HSD post-hoc tests. Differences between initial and final concentrations were assessed using paired samples *t*-tests. Prior to the analyses, assumptions of heterogeneity and normality were assessed, and if necessary, the data were log-transformed. When assumptions were still not met after transformation, non-parametric alternatives were used. All analyses were performed in SPSS 20 (IBM Corp.).

2.6 | Estimation of historic and present-day DOC release on a Caribbean reef

A dramatic phase shift from scleractinian corals and turf algae to BCMs, turf algae and macroalgae as dominant benthic taxa has been documented at the shallow reef terrace (10 m) at Buoy 0, Curaçao (12°07′N, 68°58′W) over the past decades. Historic and present benthic cover data from 1973 to 2013 (de Bakker et al., 2017) were used (Table 1) to estimate associated changes in reef-wide DOC release through time. Relative surface cover (cover %) of the most abundant DOC producing functional groups (producer) was multiplied with previously reported day and night-DOC release rates in mmol m^{-2} hr^{-1} (DOC rate). Average DOC release rates for scleractinian corals, macroalgae and BCMs were derived from Brocke, Wenzhoefer, et al. (2015). DOC release rates from this study were used for turf algae. Assuming a diurnal 12/12 hr day and night cycle (Curaçao: daytime ranging 11:27–12:52 hr throughout an annual cycle; https://www.worlddata.info/america/curacao/sunset.php), respectively, producer specific day or night-DOC release rates were multiplied by 12 hr:

$$\text{Day DOC}_{\text{producer}} = \text{cover\%}_{\text{producer}} \times \text{Day DOC rate}_{\text{producer}} \times 12\,\text{hr}, \quad (1)$$

$$\text{Night DOC}_{\text{producer}} = \text{cover\%}_{\text{producer}} \times \text{Night DOC rate}_{\text{producer}} \times 12\,\text{hr}, \quad (2)$$

Reef-wide DOC release estimates, over a 24-hr diurnal cycle (Diurnal DOC reef) for Buoy 0 in 1973 and in 2013, were approximated by combining day and night release of the most abundant DOC producing functional groups:

$$\text{Diurnal DOC reef} = \sum_{\text{producer}=1}^{n} \text{Day DOC}_{\text{producer}} + \sum_{\text{producer}=1}^{n} \text{Night DOC}_{\text{producer}}, \quad (3)$$

3 | RESULTS

3.1 | O_2 concentrations at the turf algae–water interface

O_2 concentrations at the turf algae–water interface steeply increased from hypoxic levels (11%–16% air saturation) in the dark to supersaturated levels (470%–800% air saturation) when exposed to light (Figure 2). The increase in O_2 concentrations occurred at initial rates of 80–177 μmol O_2 L^{-1} min^{-1}. Following the switch from light to dark conditions, O_2 concentrations decreased within less than 8 min to the initial hypoxic levels at a rate of −93 to −374 μmol O_2 L^{-1} min^{-1}. This pattern was consistent in all three tested turf-algal samples throughout all six consecutive light–dark cycles.

3.2 | Day and night release of turf-algal exudates

DOC release rates (mean ± *SD* throughout text, unless stated otherwise) of turf algae were not significantly different between day and night incubations, with 4.6 ± 2.4 and 2.7 ± 2.2 mmol C m^{-2} hr^{-1}, respectively (one-way ANOVA, $F(1,17) = 3.678$, $p = 0.072$; $n_{day} = 9$, $n_{night} = 10$; Figure 3).

During daytime, 36% (4.6 ± 2.4 mmol C m^{-2} hr^{-1}) of the net primary production ($NPP_{daytime}$; 12.7 ± 3.4 mmol C m^{-2} hr^{-1}) was released as day-DOC (Figure 3). At night, another 21% (2.7 ± 2.2 mmol C m^{-2} hr^{-1}) of turf-algal $NPP_{daytime}$ was released as night-DOC. After subtracting night respiration (4.2 ± 2.4 mmol C m^{-2} hr^{-1}), merely 11% (1.4 ± 10.9 mmol C m^{-2} hr^{-1}) of the net photosynthetically fixed C remained available for other physiological processes, such as growth, maintenance and reproduction over a diurnal cycle.

At the onset of the incubations with turf algae, the molar ratio of DOC to DON (i.e. C:N ratio) was similar in day (mean ± *SD*; 49 ± 13; $n = 8$) and night (49 ± 23; $n = 7$; independent sample *t*-test, $t[13] = 0.318$, $p = 0.755$; Figure 4a). Towards the end of the incubations, the C:N ratio had significantly decreased to 35 ± 8 in the day incubations (paired samples *t*-test, $t[7] = 2.753$, $p = 0.028$; $n = 8$), whereas it remained similar (54 ± 28) in night incubations ($t[6] = 70.737$, $p = 0.489$; $n = 7$).

Initial dissolved inorganic nitrogen ($DIN = NO_2^- + NO_3^- + NH_4^+$) and PO_4^{3-} concentrations were similar among all treatments (one-way ANOVA, DIN: $F(3,17) = 1.802$, $p = 0.185$, $n_{turfday} = 9$, $n_{turfnight} = 5$, $n_{controlday} = 3$, $n_{turfnight} = 4$; PO_4^{3-}: $F(3,22) = 0.165$, $p = 0.919$, $n_{turfday} = 9$, $n_{turfnight} = 10$, $n_{controlday} = 3$, $n_{turfnight} = 4$) and did not change significantly in any turf-algal incubations or seawater controls (Table 2). Initial pH of seawater was similar among all treatments (Kruskall–Wallis, $\chi^2_3 = 0.536$, $p = 0.911$, $n_{turfday} = 9$, $n_{turfnight} = 12$, $n_{controlday} = 3$, $n_{turfnight} = 4$). In turf-algal incubations, the pH increased during the day and decreased during the night as expected due to photosynthesis and respiration, respectively. In incubations with seawater controls, the pH remained unchanged.

The mean initial effective quantum yield ($\Delta F / F'_m$) for incubated turf algae was similar between day and night incubations (one-way ANOVA, $F(1,19) = 0.273$, $p = 0.607$, $n_{turfday} = 9$, $n_{turfnight} = 12$). $\Delta F / F'_m$ decreased from 0.60 ± 0.04 to 0.39 ± 0.03 during the daytime incubations (paired samples *t*-test, $t[8] = 12.265$, $p < 0.0001$; $n = 9$) and remained stable in nighttime incubations ($t[11] = 0.000$, $p = 1.000$; $n = 12$).

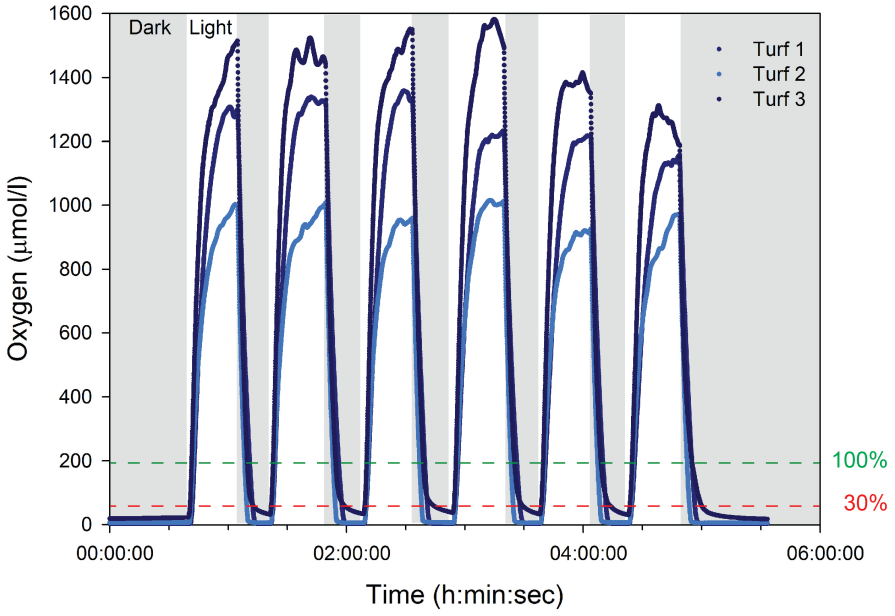

FIGURE 2 O_2 concentration at the turf algae-water interface during alternating periods of light (white) and darkness (grey). 100% and 30% (hypoxic conditions) air saturation are indicated with a green and red dashed line, respectively.

3.3 | Quality of day and night turf-algal exudates for bacterioplankton

Bacterial carbon demand (BCD; the net removal of DOC during bioassays) was significantly affected by the diel cycle (i.e. day vs. night) and by the treatment (i.e. turf-algal exudate vs. unamended seawater control (two-way ANOVA, see Table S5 for details) with nearly twice as high rates in bioassays with night turf-algal exudates (8.5 ±2.6 µmol C L^{-1} day^{-1}) compared to bioassays with day turf-algal exudates (4.8 ±3.4 µmol C L^{-1} day^{-1}; Tukey's HSD, $p = 0.038$; Figure 5a). For unamended day and night seawater controls, BCD was more than three times lower compared to respective bioassays with turf-algal exudates (Tukey's HSD, day: $p = 0.026$; night: $p = 0.001$; Figure 5a). Initial DOC concentrations were 146 ± 5 and 128 ± 7 µmol C L^{-1} for bioassays with day and night exudates, respectively, and were thereby elevated by 30 and 20 µmol C L^{-1} compared to respective unamended seawater controls (Tukey's HSD, day: $p < 0.0001$; night: $p < 0.0001$).

Bacterial cell yield (BCY; the increase in bacterial cell concentration during bioassays) was also significantly affected by the diel cycle and by the treatment (two-way ANOVA; see Table S5). BCY in bioassays with day turf-algal exudates was approximately two times higher (7.1 ±1.2 ×10^8 cells L^{-1} day^{-1}) than in bioassays with night turf-algal exudates (3.9 ±0.8 ×10^8 cells L^{-1} day^{-1}; Tukey's HSD, $p < 0.0001$; Figure 5b). Unamended seawater controls supported a twofold lower bacterial cell yield than respective day (3.4 ±1.2 ×10^8 cells L^{-1} day^{-1}; Tukey's HSD, $p < 0.0001$) and night (2.4 ±0.4 ×10^8 cells L^{-1} day^{-1}; Tukey's HSD, $p = 0.003$) turf-algal exudates. Initial bacterial concentration was 6.0 ±1.1 ×10^8 cells L^{-1} and was similar in amended and unamended bioassays (one-way ANOVA, $F(3,21) = 0.150$, $p = 0.929$).

Both the diel cycle and the treatment also had a significant effects on the bacterial growth efficiency (BGE; the ratio of bacterial carbon yield:bacterial carbon demand; two-way ANOVA; see Table S5 for details). Specifically, BGE was four times higher in bioassays with day turf-algal exudates (0.31 ± 0.20) compared to night exudates (0.08 ± 0.03; Tukey's HSD, $p = 0.004$; Figure 5c). Interestingly, BGE was similar in bioassays with turf-algal exudates and in unamended seawater controls, both during the day (Tukey's HSD, $p = 0.528$) and at night (Tukey's HSD, $p = 0.240$).

The initial C:N ratio of DOM was similar in bioassays containing day (29 ± 6) and night (34 ± 8) turf-algal exudates (independent sample t-test, $t[8] = -1.166$, $p = 0.277$; Figure 4b). The C:N ratio of DOM in turf-algal exudates released during the day remained unchanged during the course of the bioassays (paired samples t-test, $t(4) = 1.132$, $p = 0.321$). While it appeared to increase for night exudates, this increase was not significant ($t(2) = -0.908$, $p = 0.462$). Initial DIN and PO_4^{3-} concentrations were similar among all treatments and controls (one-way ANOVA, DIN: $F(3,17) = 1.030$, $p = 0.264$; PO_4^{3-}: $F(3,22) = 1.494$, $p = 0.244$) and did not change significantly during any of the bioassays (for details, see Table S6).

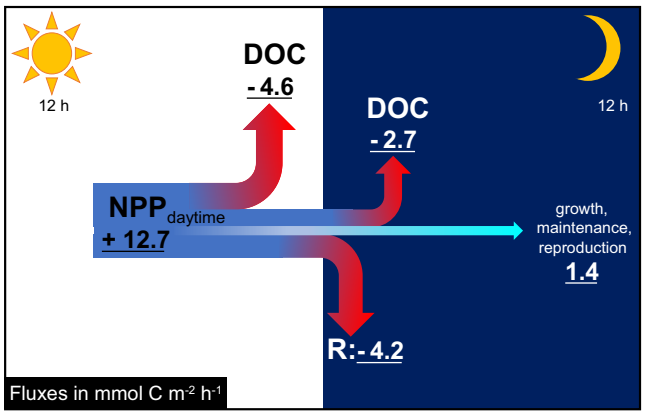

FIGURE 3 Carbon budget of turf algae over a diurnal 12/12 h day and night cycle. $NPP_{daytime}$ net primary production rate during daytime, DOC dissolved organic carbon release rate, R night respiration rate.

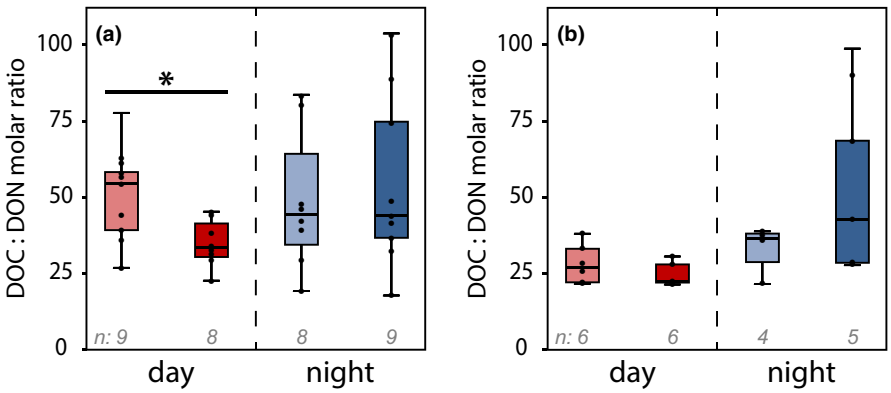

FIGURE 4 Change in DOC:DON molar ratios of (a) turf-algal incubations, and (b) subsequent bioassays with turf-algal exudates, during the day (red) and at night (blue). DOC:DON ratios at the onset and at the end of the incubation period are indicated by light and dark colours, respectively. Distribution of data is presented in boxplots (minimum, 1st quartile, median, 3rd quartile and maximum) and underlying data of the individual incubations are displayed as small dots. Number of replicates are indicated in the graphs. Boxplots marked with an asterisk are significantly different at $\alpha = 0.05$.

TABLE 2 Environmental parameters measured during day and night incubations (mean ± *SD*): light intensities (μmol photons m^{-2} s^{-1}), inorganic nutrient concentrations (μmol L^{-1}) and pH.

		Day		Night	
		Turf algae	Control	Turf algae	Control
Light		672 ± 84		0	
NO_2^-	t_0	**0.77 ± 0.34**	0.68 ± 0.27	0.71 ± 0.36	0.67 ± 0.20
	t_{end}	**0.30 ± 0.11**	0.53 ± 0.17	0.46 ± 0.17	0.59 ± 0.21
NO_3^-	t_0	0.24 ± 0.31	**0.31 ± 0.34**	0.25 ± 0.18	0.13 ± 0.08
	t_{end}	0.29 ± 0.11	**0.08 ± 0.25**	0.31 ± 0.16	0.03[a]
NH_4^+	t_0	3.01 ± 0.76	2.84 ± 0.85	3.43 ± 1.39	**3.94 ± 0.74**
	t_{end}	2.44 ± 1.06	2.43 ± 0.68	2.87 ± 0.62	**3.06 ± 0.39**
DIN	t_0	4.01 ± 1.10	3.83 ± 1.44	5.50 ± 1.66	4.75 ± 0.91
	t_{end}	3.03 ± 1.11	3.04 ± 0.87	3.63 ± 0.91	3.93[a]
PO_4^{3-}	t_0	0.101 ± 0.017	0.103 ± 0.013	0.104 ± 0.012	0.098 ± 0.017
	t_{end}	0.168 ± 0.129	0.093 ± 0.008	0.106 ± 0.020	0.097 ± 0.013
pH	t_0	**8.19 ± 0.04**	8.20 ± 0.04	**8.29 ± 0.22**	8.22 ± 0.08
	t_{end}	**8.45 ± 0.07**	8.12 ± 0.05	**7.84 ± 0.07**	7.98 ± 0.09

[a]Only one measurement available. Significant differences between t_0 and t_{end} (paired samples *t*-test) are highlighted in bold.

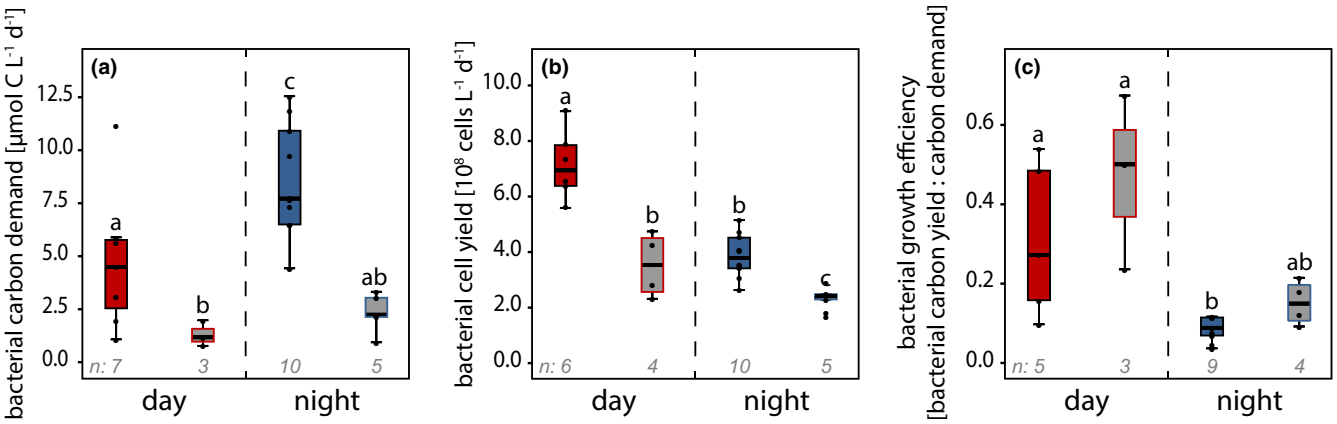

FIGURE 5 (a) Bacterial carbon demand (BCD; DOC removal in bioassays), (b) bacterial cell yield (BCY) and (c) bacterial growth efficiency (BGE; ratio of bacterial carbon yield: bacterial carbon demand) of bioassays. Day turf-algal exudates are shown in red, night exudates in blue. Unamended seawater controls are depicted in grey with red and blue outlines for day and night controls, respectively. Distribution of data is presented in boxplots (minimum, 1st quartile, median, 3rd quartile and maximum) and underlying data of the individual incubations are displayed as small dots. Number of replicates are indicated in the graphs. Boxplots with the same letter are not significantly different at $\alpha = 0.05$.

3.4 | Estimation of historic and present-day DOC release on a Caribbean reef

In 1973, scleractinian corals (37%) were the most abundant benthic component on the shallow (10 m water depth) reef terrace at Buoy 0, followed by turf algae (27%) and bare substrate (21%) within the 'other' category. Turf algae accounted for the majority of the reef-wide DOC release with 14.9 mmol m^{-2} 12 hr^{-1} during the day and 8.8 mmol m^{-2} 12 hr^{-1} at night (Figure 6). Day release by scleractinian corals (3.6 mmol m^{-2} 12 hr^{-1}) contributed to a lesser degree. Approximately one-third of the reef-wide DOC release over a 24-hr diurnal cycle was released at night. In 2013, the benthic DOC producing community consisted almost entirely of non-calcifying taxa (83%), due to the dramatic decline in scleractinian coral (37% to 1%) and bare substrate (21% to 1%), and the concomitant increase of both BCMs (0% to 41%) and macroalgae (0% to 16%) between 1973 and 2013 at this location. Turf algae and BCMs largely dominated the reef-wide DOC release during the day (13.8 and 6.9 mmol m^{-2} 12 hr^{-1}) and at night (8.1 and 17.2 mmol m^{-2} 12 hr^{-1}), whereas the contribution by corals was much smaller (Figure 6). The reef-wide DOC release during the day (22.5 mmol m^{-2} 12 hr^{-1}) had only increased slightly compared to 1973 (18.5 mmol m^{-2} 12 hr^{-1}), whereas at night the reef-wide DOC release almost tripled over this 40-year period due to the strong increase in BCMs. In 2013, nocturnal DOC release by BCMs and turf algae was estimated to contribute up to 53% of the reef-wide DOC release over a diurnal cycle.

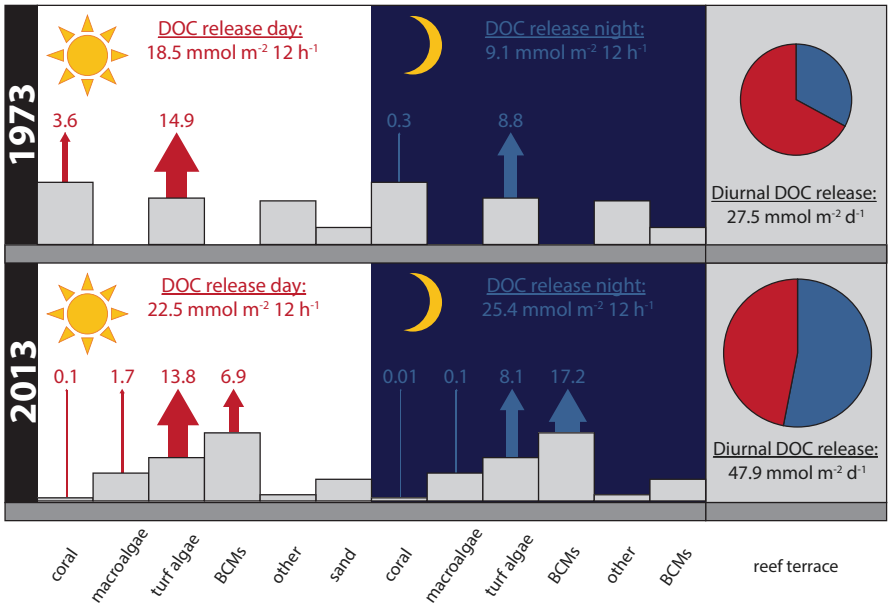

FIGURE 6 Changes in estimated DOC release on the shallow reef terrace at reef station Buoy 0, Curaçao, between 1973 and 2013. Benthic DOC producer-specific as well as reef-wide rates for day (red) and night (blue) release estimates are presented as arrows in mmol m^{-2} 12 hr^{-1} (based on a diurnal 12/12 hr day and night cycle). Width of arrows indicates the size of DOC fluxes and the abundance (in percentage cover) of benthic components is indicated by column height. Reef-wide diurnal DOC release is estimated in mmol m^{-2} day^{-1} and day (red) and night (blue) release is visualized as pie charts.

4 | DISCUSSION

In this study, we show that turf-algal communities release large quantities of DOM during the day as well as at night. The quality of this DOM for bacterioplankton differs substantially: Night exudates are utilized more rapidly, but result in a lower growth efficiency compared to day exudates. Estimations of historic and current DOC release further suggest that reef-wide DOC release over a 24-hr diurnal cycle doubled over the past 40 years, due to a strong increase in the abundance of BCMs, with night-DOC release by BCMs and turf algae accounting for >50% of the total DOC release.

4.1 | DOM release and diurnal carbon budget of turf algae

The DOC release rate of turf algae observed in this study during daytime (4.6 ± 2.4 mmol C m^{-2} hr^{-1}) is among the highest reported for coral reef benthic primary producers in general, including turf algae (Brocke, Wenzhoefer, et al., 2015 and references therein). Day-DOC release rates of turf algae vary widely from 0.1 (Mueller et al., 2016) to 5.5 mmol m^{-2} hr^{-1} (Haas et al., 2010), which can be attributed to a multitude of potential factors, including community composition and density (biomass per surface area) of turf algae (Fricke et al., 2011; Mueller et al., 2016) as well as environmental conditions (e.g. light, temperature, nutrient levels; Haas et al., 2010; Mueller et al., 2016). Highest DOC release rates are typically reported during the summer months coinciding with maximum light intensities and seawater temperatures (e.g. Haas et al., 2010; Naumann et al., 2010; Roth et al., 2021). Thus, here reported turf-algal DOC release rates measured in August might be interpreted as the summer maximum. In comparison to coral reefs with pronounced seasonality, reefs of the tropical island of Curaçao experience only mild seasonal fluctuations in environmental parameters (Haas et al., 2010; Roth et al., 2021; Vermeij & Bak, 2002). Hence, only minor seasonal variation in DOC release rates should be expected. Similar to DOC release rates, also the percentage of NPP released as DOC varies considerably for coral reef benthic primary producers, with values ranging from 4 to 51% (Brylinsky, 1977; Davies, 1984). The here reported 36% for turf algae is in the upper range of these percentages, yet considerably higher than found in earlier studies of turf algae (6%–22%; Haas et al., 2011; Haas et al., 2013; Mueller et al., 2016).

The major loss terms within the diurnal carbon budget of turf algae are day-DOC release (36% of $NPP_{daytime}$) and dark respiration (33% of $NPP_{daytime}$), but a considerably amount of C is also released as night-DOC (21% of $NPP_{daytime}$; Figure 3). This relative night-DOC release is merely half as high as reported for BCMs on Curaçao (Brocke, Wenzhoefer, et al., 2015). After subtracting all loss terms (i.e. dark respiration, day- and night-DOC release), 10% of turf algae's $NPP_{daytime}$ remains available for other physiological processes, such as growth, maintenance and reproduction. This can be considered low to exert anabolic processes, since primary producers from coral reefs and other benthic ecosystems typically show a surplus of >60% of their daily fixed C (e.g. Abdullah & Fredriksen, 2004; Haas et al., 2013; Hatcher et al., 1977). This is in line with Brocke, Wenzhoefer, et al. (2015), the only study to date where a substantial night-DOC release was reported, who found a mere surplus of 7% of $NPP_{daytime}$ after subtracting night respiration and day- and night-DOC release. This raises the question how most turf-algal communities and BCMs can be successful competitors, despite their low surplus carbon budgets?

4.2 | Night-DOM release by turf algae

Under dark and anaerobic conditions several cyanobacterial taxa, including *Oscillatoria* spp. and other benthic taxa, are known to be capable of fermentation of stored carbohydrates, resulting in the release of small organic molecules such as lactate, ethanol and

acetate (Heyer et al., 1989; Heyer & Krumbein, 1991; Moezelaar et al., 1996; Stal & Moezelaar, 1997). *Oscillatoria* spp. are widespread both in BCMs and turf-algal communities of the Southern Caribbean (Brocke, Wenzhoefer, et al., 2015; Fricke et al., 2011). Indeed, Brocke, Wenzhoefer, et al. (2015) showed that BCMs dominated by *Oscillatoria* spp. can release substantial amounts of DOC at night. Analogously, cyanobacteria in turf-algal communities may have released substantial amounts of DOC stemming from dark fermentation of carbohydrates stored in their cells. One might speculate that cyanobacterial members of the turf-algal community may even ferment organic molecules extracted from decaying organic material (e.g. from dead corals or detritus being trapped within turf-algal thalli and filaments; Figure 1b) as suggested for BCMs by Brocke, Polerecky, et al. (2015). Indeed, several cyanobacteria are capable of heterotrophic growth on external organic carbon sources (Chojnacka & Marquez-Rocha, 2004; Stal & Moezelaar, 1997; Yu et al., 2008), although anaerobic heterotrophic growth on external carbon sources seems limited to only very few cyanobacterial taxa (Richardson & Castenholz, 1987; Stal & Moezelaar, 1997). Furthermore, some chlorophytes are also capable of heterotrophic growth and dark fermentation (Atteia et al., 2013; Chojnacka & Marquez-Rocha, 2004; Kim et al., 2013; Ueno et al., 1998) and may have also contributed to the DOM release by turf-algal communities during nighttime.

Our hypothesis that the DOC release at night is at least partly driven by fermentation is supported by a rapid shift from supersaturated to hypoxic conditions following the switch from light to dark conditions in the turf algae–water interface, creating the essential conditions for fermentation processes to occur (Figure 2). Great caution was taken to exclude the possibility that night-DOM release was merely a stress-induced artefact or the result of turf algae decaying. First, the photosynthetic efficiency of incubated turf algae measured with a PAM fluorometer did not change during night incubations. This suggests no occurrence of stress or deterioration of their physiological status during the incubation period (Enríquez & Borowitzka, 2010; Maxwell & Johnson, 2000). Moreover, if the increase in DOC concentration would have been cause by decaying turf algae, this could have caused a peak in DIN and PO_4^{3-}. However, none of these concentrations increased during the night incubations (Table 2). And lastly, while pH slightly decreased during the night incubations, this change was expected as a result of respiration. The observed change in pH was less than pH changes typically occurring on coral reefs over a diurnal cycle (Anthony et al., 2011; Kleypas et al., 2011) and therefore does not indicate decomposition of turf-algal tissue.

4.3 | Quality of day and night turf-algal exudates for bacterioplankton

Given the presumed differences in the origin of turf-algal DOM produced during the day and at night (i.e. the release of photosynthates during the day and fermentation products at night), it can be expected that both types of DOM differ in composition and therefore in nutritional quality to DOM-feeding organisms. Indeed, bacterioplankton utilized night turf-algal DOC at twice the rate compared to day-DOC (Figure 5a), but day-DOM supported a two times higher bacterial growth rate compared to night-DOM (Figure 5b). In other words, bacterioplankton utilizes more turf-algal DOC produced at night, but grows less on it compared to DOC released during the day. The bacterial growth efficiencies (BGE; Figure 5c) infer that approximately 30% of the day turf-algal DOC taken up by bacterioplankton was assimilated and used to synthesize bacterial biomass, whereas the remaining 70% was respired. In contrast, night turf-algal DOC was almost entirely respired, leaving less than 10% to support new bacterial production. Bacterial growth efficiencies of bacterioplankton communities vary widely, ranging between 1% and up to 60% (Giorgio & Cole, 1998 and references therein). For exudates of coral reef benthic primary producers, BGEs appear to be at the lower end of this range, with fleshy macroalgae ranging between 6% and 2% and calcifying taxa higher with 16%–20% (Haas et al., 2011; Nelson et al., 2013; Silva et al., 2021). Night turf-algal exudates in this study compare very well to previously reported BGEs of exudates of fleshy macroalgae. BGEs of day turf-algal exudates, however, are even higher than those of calcifying taxa and are more similar to the reef water controls of these studies (27%). High BGEs are commonly associated with a high nitrogen content of the available substrates, to maintain a stable stoichiometry within bacterial cells (Fenchel & Blackburn, 1979; Goldman et al., 1987; Vallino et al., 1996). Accordingly, day turf-algal DOM—showing a higher BGE than night-DOM—was relatively enriched in N compared to the initial C:N ratio of DOM in the incubation water (Figure 4a). In contrast, night turf-algal DOM tended to be relatively depleted in N, even though this difference was not significant. Furthermore, during the course of the bioassays, DOC and DON were utilized in a balanced molar ratio for day turf-algal exudates. For night exudates on the other hand, it appeared that relatively more DON was taken up (Figure 4b), possibly indicating N-limitation of the growing bacterioplankton communities and/or a higher bio-availability of night-DON. Observed differences in BGEs of day and night exudates could additionally be explained from a bioenergetic point of view. Assuming that night-DOM originates from incomplete organic matter degradation and fermentation, resulting fermentation products (e.g. acetate, formate, lactate) are more oxidized than photosynthates (e.g. glucose, galactose, fucose) released during the day. Hence, the biologically available energy in night exudates might not be sufficient to reduce the available carbon in these substrates to the level of bacterial cell carbon (Linton & Stephenson, 1978). Consequently, those more oxidized substrates are incorporated into bacterial biomass at a lower efficiency (Figure 4c), while carbon uptake is maximized to meet maintenance energy costs from increased respiration (Figure 4a; Giorgio & Cole, 1998).

4.4 | Historic increase in reef-wide DOC release and possible consequences for ecosystem functioning

The dramatic shifts in benthic community composition that occurred on many Caribbean reefs over the past five decades have likely

caused changes in the quantity and quality of the produced DOM. For our study site, we estimated that the reef-wide DOC release of the benthic community over a diurnal 24-hr cycle has doubled between 1973 and 2013 (Figure 6). However, as turf-algal abundance appears to be comparable at both time points and the appearance of macroalgae only added marginally to the DOC release, the here reported increase in reef-wide DOC release was foremost caused by a tremendous increase in BCMs at the study site. In fact, when excluding the contribution of BCMs from our estimates, the reef-wide DOC release appears to have decreased from 27.5 mmol m^{-2} day^{-1} in 1973 to 23.9 mmol m^{-2} day^{-1} in 2013. While BCMs have certainly become a substantial component of benthic communities on Curaçaoan reefs and throughout the Caribbean (de Bakker et al., 2017; Ford et al., 2018), their actual abundance can vary enormously on short temporal and spatial scales (Brocke, Polerecky, et al., 2015; Kornder et al., 2021). Here presented reef-wide DOC fluxes from 2013 should therefore be considered as an example under very high prevalence of BCMs. Depending on the current abundance of BCMs, reef-wide DOC release can range from rates slightly lower compared to 1973, to twice this rate. Concomitantly, the contribution of night-DOC to the total diurnal 24-hr DOC release can range between 30% and >50%.

The general direction of change in benthic community composition from calcifying to non-calcifying taxa at our study site and throughout the Caribbean (Gardner et al., 2003; Jackson et al., 2014) has likely led to a substantial change in the quality of the released DOM over the past decades. During the day, the DOM released by these non-calcifying taxa stimulates the inefficient growth of opportunistic microbes (Haas et al., 2016). Large amounts of DOM need to be respired to support this growth, thereby shifting the microbial community metabolism from net autotrophy to net heterotrophy (Haas et al., 2013; Silveira et al., 2019). The lower BGE of algal-DOM compared to coral-DOM reduces the relative amount of energy and nutrients shunted into microbial biomass and thereby its transfer to higher trophic levels through the microbial loop (Haas et al., 2016; McDole et al., 2012). As turf-algal DOM released at night has a four times lower BGE than turf-algal DOM released during the day (Figure 5c), night-DOM is likely to considerably accelerate the microbialization in the water column. This will be of particular importance during periods of high prevalence of BCMs when night-DOC released by turf algae and BCMs can contribute >50% to the reef-wide DOC release (Figure 6).

Night-DOM release may also explain the high competitiveness reported for turf algae in coral–turf algae interactions (Barott et al., 2012; O'Brien & Scheibling, 2018; Vermeij et al., 2010). In general, algal-DOM increases microbial respiration in coral–algae interfaces, creating prolonged hypoxia which can harm or even kill corals (Kline et al., 2006; Roach et al., 2020; Smith et al., 2006). Deceased corals can then be overgrown by their competitor (Barott & Rohwer, 2012; Dinsdale & Rohwer, 2011). As macroalgae primarily release DOM during the day (Haas et al., 2010; Maher & Eyre, 2011; Mueller et al., 2014), microbial respiration in coral–algae interfaces is supposed to be reduced dramatically, once the day-DOM is respired and/or diluted in the course of the night. In contrast, turf algae containing cyanobacteria and/or chlorophytes continue to release DOM during the entire night, thereby prolonging the duration of hypoxia and its detrimental effect on coral health. Moreover, the aforementioned four times lower BGE of night- versus day-DOM is likely to further amplify this effect.

4.5 | Night-time DOM release beyond coral reefs

Turf-algal communities containing cyanobacteria and/or chlorophytes capable of fermenting organic material and thereby potentially releasing DOM at night are not restricted to coral reefs but are major components in a variety of intertidal and subtidal rocky habitats ranging from tropical, temperate and even polar to latitudes (Connell et al., 2014). In addition, *Oscillatoria* mats and benthic chlorophytes are also found in marine and freshwater soft bottom habitats (Guiry & Guiry, 2018; Vadeboncoeur et al., 2020). To date, ecological research into dark fermentation by cyanobacteria and chlorophytes was largely focused on the energy-providing mechanism enabling these organisms to survive and grow under dark and anaerobic conditions (Atteia et al., 2013; Stal & Krumbein, 1984; Ueno et al., 1998). Yet, the potential effect of the subsequent release of fermentation products as night-DOM on community dynamics and ecosystem processes remains to be investigated. Given its high bio-availability (Figure 5a) and low BGE (Figure 5c), night-DOM release is likely to stimulate microbial community respiration at the expense of biomass generation, which may enhance the release of CO_2 from the system (Haas et al., 2013; Silveira et al., 2019). The relative importance of night-time DOM release is likely to increase in the future as climate change has been predicted to promote the abundance of BCMs and turf-algal communities (Christie et al., 2019; Pessarrodona et al., 2022) as well as the prevalence of cyanobacteria within turf-algal communities (Bender et al., 2014; Ford et al., 2018; Paul, 2008).

5 | CONCLUSIONS

This study shows that some turf-algal communities do not only release large quantities of DOM during the day, but can also do so at night. Further evidence is provided that incomplete organic matter degradation and fermentation may underlie this night-time DOM release. As night-time DOM is consumed by bacterioplankton two times faster compared to day-time DOM, yet results in four times lower BGE, night-time DOM is likely to significantly contribute to the microbialization of reefs: (a) By increasing the competitiveness of turf algae, which solidifies or even accelerates the underlying benthic community shift from calcifying to non-calcifying taxa and (b) by further stimulating heterotrophy (i.e. respiration) in microbial communities at the expense of transfer of energy and nutrients through the microbial loop to higher trophic levels. Similar diurnal variation in the quantity and quality of DOM production may also play a role in

other ecosystems. Our results may therefore encourage further investigation of diurnal variation in DOM production and its potential effects on community structure and ecosystem functioning.

AUTHORS' CONTRIBUTIONS

B.M. conceived the ideas and designed the methodology; B.M., H.J.B. and J.M.d.G. collected the data; B.M. analysed the data and led the writing of the manuscript; F.L.R., T.D., M.J.A.V. and J.M.d.G. contributed reagents/materials/analysis tools. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

On behalf of all authors, the corresponding author states that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.1ns1rn8ww (Mueller et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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