Marine Biology (2019) 166:20
https://doi.org/10.1007/s00227-018-3459-z

SHORT NOTE

Acute effects of back-to-back hurricanes on the underwater light regime of a coral reef

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Received: 11 October 2018 / Accepted: 14 December 2018

Abstract
Some of the best-known disturbances affecting coral reefs are storms, yet their impacts on light are poorly known. Here, we describe the underwater light on a reef off St. John, US Virgin Islands (18°18′37.04N, 63°43′23.17W), during two hurricanes and multiple tropical waves that occurred between 17 August 2017 and 30 November 2017. Photosynthetically active radiation (PAR) was recorded at 19-m depth and at the surface, and rainfall was measured as a cause of turbidity affecting underwater light. Hurricanes Irma and Maria reduced maximum daily underwater photosynthetic photon flux density (PPFD) to < 14 μmol photons m^{-2} s^{-1} (< 0.001% of surface PPFD) and, from 1 September to 30 November, were associated with rainfall that was higher (107 cm) than has been recorded over this period since 1972. These reductions in underwater PPFD are unprecedented since at least 2014, and the corresponding values of the diffuse attenuation coefficients ($K_{d\text{-}PAR}$ 0.268–0.426) are among the lowest recorded on a coral reef. Our study reveals the capacity for hurricanes to render a photic habitat temporarily aphotic, and over 69 days (and relative to 2016), to contribute to a 20% reduction in summed, daily integrated underwater PPFD. Large reductions in underwater PPFD have negative implications for photosynthetic taxa, but through the turbidity that reduces underwater light, they create opportunities for population growth by suspension feeding invertebrates.

Introduction

Major storms are common disturbances in tropical regions, where they bring high winds, heavy rainfall, and waves that damage multiple ecosystems (Harmelin-Vivien 1994; Gardner et al. 2005). Distinctive signatures of destruction are created by defoliation, broken trees, mudslides, uprooted aquatic vegetation, and shattered corals (Lugo et al. 2000; Woodley et al. 1981), and while the damage is restricted to a landscape scale (sensu Mittelbach et al. 2001), the biological effects can be profound. The severity of local disturbances shifts communities to an early successional stage (Rogers 1993) and modulates diversity (Connell 1978). While the expectations of physical damage are unequivocal, this knowledge is not directly transferable to future storms because climate change increases their intensity (Cheal et al. 2017) and perhaps their frequency (Emanuel et al. 2005). Moreover, the communities they impact likely will differ from those of the recent past due to the cumulative effects of anthropogenic disturbances (e.g., Burman et al. 2012; Hughes et al. 2018).

In the tropical marine environment, coral reefs provide the best examples of an ecosystem that is strongly affected by storms (Woodley et al. 1981; Gardener et al. 2005), because colonies of their scleractinian architects are prone to breakage by waves (Madin et al. 2014). Fifty years ago, storms were considered the major physical process structuring coral reefs (Stoddart 1969) and early studies confirmed their capacity to profoundly change community structure (Stoddart 1974; Woodley et al. 1981). Similar outcomes have been recorded on numerous reefs (Gardner et al. 2005), and while communities often recovered from these disturbances in the early decades of modern coral reef research (Stoddart 1974; Pearson 1981), this outcome is less certain in an era when reefs are affected by many disturbances

Communicated by D. Gochfeld.

Reviewed by M. Slattery and T. Smith.

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including climate change and ocean acidification (Hoegh-Guldberg et al. 2007). Hurricane Allen in 1980 effectively was the catalyst that started decades of conspicuous decline in coral cover on Jamaican reefs (Woodley et al. 1981; Hughes 1994), from which recovery still has not occurred (Jackson et al. 2014), and elsewhere in the Caribbean, hurricanes now are followed by a protracted period of depressed coral cover (Gardner et al. 2005). Exceptions to these trends can be found in the tropical Pacific, with Mo'orea, French Polynesia, displaying unusually rapid recovery following a cyclone in 2010 (Adjeroud et al. 2018; Holbrook et al. 2018). The hurricanes that impacted the Virgin Islands in September 2017 were record-breaking in severity, yet surveys conducted in November 2017 showed that the impacts on coral communities between 7- and 14-m depth were modest (Edmunds 2019).

Despite the extensive study of storms on coral reefs, most analyses focus on waves, and occasionally, sedimentation, freshwater run-off, and disease (Harmelin-Vivien 1994). There have been no explicit studies of the effects of hurricanes on the underwater light regime (but see Manzello et al. 2009), even though casual observations reveal greatly enhanced turbidity following storms. Measurements of light penetration through seawater coincident with storms have rarely been made using even basic techniques (e.g., Steward et al. 2006), and opportunities to situate in situ light recorders to sample during a storm are uncommon. Remote sensing is effective at recording offshore seawater clarity (Hedley et al. 2016), but the algorithms supporting these analyses are not well developed for near-shore habitats (Barnes et al. 2013) and are unknown for the turbid conditions following storm. The paucity of information on the underwater light coincident with storms is unfortunate, because most scleractinians and octocorals, as well as macroalgae, and angiosperms, rely on light for photoautotrophic nutrition (Hatcher 1988; Muscatine 1990). Therefore, protracted reductions in underwater light intensity could create a shortfall of photosynthetically fixed carbon in these taxa, from which recovery might be slow or impossible.

In this study, we describe underwater light on a coral reef off St. John, US Virgin Islands and, using a 3.5-month record, describe the impacts of two Category 5 hurricanes on seawater clarity. The analysis also evaluates the effects on underwater light of high rainfall associated with these storms and several tropical waves, and places the results in a years-decade context of local environmental conditions. We show the large magnitude and long duration of impairment of PPFD on a coral reef that can be caused by tropical storms and discuss the likelihood that these effects push autotrophic taxa into a nutritional crisis, and reflect conditions favoring the abundance of suspension feeding invertebrates. The short-term (i.e., detected in late November 2018) biological effects of these storms are described in Edmunds (2019).

Methods

This study was completed on the coral reefs of St. John, which have been the subjects of time-series analyses for 32 years (Edmunds 2013, 2018, 2019). The measurements described herein originated from a schedule of instrument deployments initiated in 2014 to quantify variation in underwater physical environmental conditions (Edmunds et al. 2018) and, ultimately, to facilitate testing for their role in driving changes in benthic community structure (e.g., Edmunds and Lasker 2016). As part of this schedule, rainfall was recorded throughout the year, and a light meter was placed in Great Lameshur Bay in August 2017, with the objective of leaving it immersed for 6–12 months. Three weeks later, the first of two Category 5 hurricanes impacted the island, with the second arriving 14 days later. The discovery in July 2018 that this meter had survived the storms, and had remained upright and functional, created the opportunity to describe underwater light during, and immediately after, two major storms.

Rainfall was recorded on the north shore of St. John at Windswept Beach (18°21′20.95N, 64°45′57.53W), where a 20.3 cm, Standard Rain Gauge (NOAA, National Weather Service) was mounted on a roof, 1.5 m above the ground. This rain gauge was ~ 6.7 km from the underwater light sensor, and was emptied and read on a daily basis.

Underwater light was recorded with a light meter (Compact LW, JFE Advantech Co., Ltd., Japan) fitted with a cosine-corrected sensor recording photosynthetically active radiation (PAR, 400–700 nm wavelength) as photosynthetic photon flux density (PPFD). The meter was equipped with a mechanical wiper that cleaned the sensor before every measurement and it was mounted with the sensor at 19.1-m depth on the eastern side of Great Lameshur Bay (18°18′37.04N, 63°43′23.17W, Edmunds et al. 2018). The instrument was operated in burst mode during which ten measurements were recorded every 180 min, with 30 s separating measurements within a burst. This sampling regime ensured that the battery would support a deployment of 1 year. The Compact LW meter is designed for oceanographic applications to 200-m depth, is fitted with a photodiode sensor, and has an accuracy of ± 4% (over 0–2000 µmol photons m^{-2} s^{-1}) and resolution of 0.1 µmol photons m^{-2} s^{-1}. The sensors are calibrated by the manufacturer, with the calibration stable for at least 1 year. When the meter was deployed in August 2017, it had been used underwater for ~ 16 months in previous deployments (Edmunds et al. 2018) and initial records of PPFD were similar to those previously recorded at the same depth and time of year in St. John (Edmunds et al. 2018), which suggested that the calibration had not appreciably drifted.

PPFD also was measured on the surface, using two cosine-corrected sensors (S-LIA-M003, Onset Computer

Corporation) mounted ~4 m above sea level on the roof of the lab, ~0.875 km from the underwater sensor. The surface sensors were attached to weather stations (Micro Station Data Logger H21-002, Onset Computer Corporation) that recorded light every 5 min. The two sensors were calibrated by the manufacturers and were operated in a paired mode to detect spurious records and sensor drift, and to guard against equipment malfunction.

Analysis

Data were truncated to extend from 17 August to 30 November, which covered the impact of the two storms and represented the greatest period over which the in situ records of light were unaffected by fouling of the sensor. To provide context to the results from 2017 and evaluate the relative impact of the storms on underwater PPFD, comparisons were made to light recorded in 2016 over the same period of the year (Edmunds et al. 2018). Records of surface PPFD were integrated over each 5 min measurement interval, and summed by day to calculate daily integrated PPFD (mol photons m^{-2} day^{-1}). Underwater PPFD was averaged by burst, which occurred every 3 h, and the values at ~13:00 hours provided the maximum daily irradiance on most days. Average burst values of PPFD were integrated over each 180 min burst interval within each day to estimate daily in situ integrated PPFD (mol photons m^{-2} day^{-1}). To compare these values with records obtained in 2016 at the same location, but at a higher frequency (with burst sampling every 60 min, Edmunds et al. 2018), the earlier records were sub-sampled to create a burst interval of 180 min and, thereafter, were processed the same way as the results from 2017. Daily underwater integrated PPFD values in 2017 were cumulatively summed by day after Hurricane Irma (6 September) and expressed as a percentage of PPFD recorded over the same periods in 2016 to calculate the cumulative depression of in situ light in 2017.

Estimates of the transmission of surface PAR to 19.1-m depth were constrained to measurements around noon, when the high angle of the sun ensured that most of the surface light passed through the air–water interface. When sun altitudes are >46°, and wind speeds are <5 m s^{-1}, virtually all (~96%) surface light is transmitted across the air–water interface (Gregg and Carder 1990). The transmission of surface light to 19.1-m depth was calculated by day using the mean transmission recorded at 10:00 hours and 13:00 hours. PPFD measured at 19.1-m depth and on the surface at 13:00 hours were also used to calculate the diffuse attenuation coefficient for PAR ($K_{\text{d-PAR}}$) using the equation representing the Beer–Lambert Law:

$$E_d(Z) = E_d(O^-)e^{-K_d \times Z},$$

where $E_d(Z)$ is the downwelling PPFD at Z m depth, $E_d(O^-)$ is the downwelling PPFD just below the surface of the seawater, and K_d is the diffuse attenuation coefficient for downwelling irradiance; $E_d(O^-)$ was approximated from concurrent records of surface PPFD without correction for transmission across the air–water interface. This method of calculating K_d is prone to greater variance than the regression approach using downwelling PPFD quickly measured at multiple depths (Kirk 2011), but it allows a time-series of K_d to be obtained using a single instrument.

Results and discussion

The autumn of 2017 brought extreme weather to St. John, and exposed marine environments to disturbances larger than any experienced since at least 1995 (i.e., Hurricanes Marilyn and Luis), and probably since 1989 (i.e., Hurricane Hugo, Edmunds and Witman 1991; Rogers et al. 1991). Quantifying these effects remains difficult; however, despite advances in instrumenting coral reefs (e.g., Roik et al. 2016) and remote sensing of physical and chemical conditions in seawater (Zoffoli et al. 2014; Hedley et al. 2016), few data are available to describe the physical impacts of the recent storms on St. John. The only pertinent records of wave effects are available from an oceanographic buoy located 8 km southwest of Great Lameshur Bay (NOAA buoy 41052, data available at www.ndbc.noaa.gov).

On September 6th, St. John was hit by Hurricane Irma, which passed 23 km northeast with wind speeds of 298 km h^{-1}, which was close enough to cause the southern eye wall to pass along the northern shore of the island. On this day, buoy 41052 recorded mean (±SD) wind gust speeds of 66±27 km h^{-1} (n=136, with maximum gusts of 125 km h^{-1}) from a mean direction of 104±116°, and significant wave heights as high as 6 m from a mean direction of 109±55°. On the island, 17 cm of rain fell over 2 days (Fig. 1a). Eight days later, Hurricane Jose brought 14 cm of rain over 2 days (without high winds), and after a further 6 days, Hurricane Maria passed 86 km southeast of St. John (on 20th September), and brought wind speeds of 266 km h^{-1}. On September 20th at buoy 41052, mean (±SD) wind gust speeds were 69±17 km h^{-1} (n=120, with maximum gusts of 105 km h^{-1}) from a mean direction of 116±41°, and significant wave heights were as high as 8 m from a mean direction of 152±23°. On the island, 13 cm of rain fell over 2 days.

The unusual weather continued after these storms, and between September 22 and November 30, six tropical waves brought heavy rain almost every 2 weeks (Fig. 1a), adding 60 cm to the autumn rainfall total. Overall, 107 cm of rain fell between 1 September and 30 November 2017, which exceeded the 46 cm average for these months over the

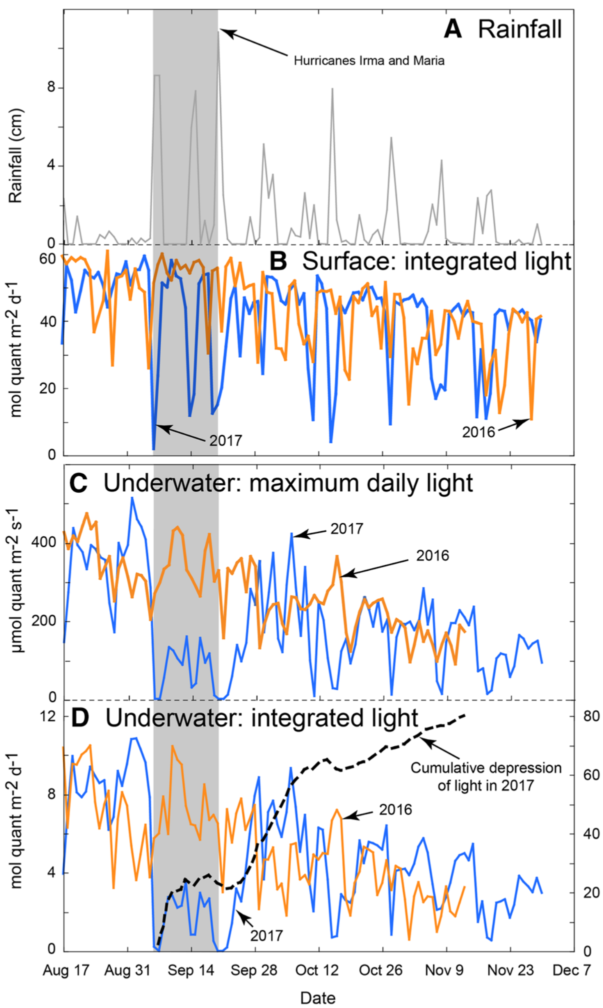

Fig. 1 Environmental conditions in St. John from 17 August to 30 November in 2016 and 2017, which included Hurricanes Irma (6 September) and Maria (20 September) in 2017 (this storm episode indicated with a shaded block). **a** Rainfall at Windswept Beach in 2017, **b** surface PPFD integrated by day for 2016 and 2017, **c** maximum daily underwater PPFD at 19.1-m depth for 2016 (limited by equipment malfunction to 17 August–13 November) and 2017, and **d** underwater PPFD at 19.1 m depth, integrated by day for 2016 (17 August–13 November) and 2017, with cumulative (i.e., summed by day from 6 September) depression of integrated daily PPFD in 2017 versus 2016 (dashed black line) as a result of Hurricane Irma and Maria and the weather that followed

previous 45 years, and was the highest rainfall ever recorded over this period in St. John. In 2017, 55% of the annual rainfall (194 cm) fell between 1 September and 30 November, and 2017 was the wettest year since at least 1972. Such heavy rainfall caused severe flooding and terrestrial erosion that was accentuated by unpaved roads (Ramos-Scharrón 2012), thereby creating extensive sediment plumes and severe coastal turbidity. These effects are accentuated by the susceptibility of mangrove communities to hurricane damage (Tilmant et al. 1994), and their impaired capacity to continue to trap sediments when severely damaged (Gedan et al. 2011). In St. John, the heavy rainfall and sedimentation recorded late in 2017 were similar to that recorded in 2010 in association with numerous storms, persistent rain, and Tropical Storm Otto (Edmunds and Gray 2014). Together, the events of 2010 brought 186 cm of rain over 12 months, high sedimentation, and multiple days of reduced surface PPFD (Edmunds and Gray 2014). One year later (2011), suspension feeding polychaetes were found at high densities on settlement tiles deployed for a year in Great Lameshur Bay, supporting the inferences that heavy rainfall and terrestrial runoff promoted the abundance of filter feeding invertebrates (Edmunds and Gray 2014).

Our sensor deployments in St. John provided the opportunity to quantify physical environmental conditions perturbed by major hurricanes. Surface PPFD was depressed by Hurricanes Irma and Maria, as well as multiple tropical waves, with daily integrated values ≤ 15 mol photons m^{-2} s^{-1} on 9 days from 17 August to 30 November (Fig. 1b). On multiple occasions, daily integrated surface PPFD was lower than over the same period in 2016 (although some days in 2016 were darker than the same days in 2017). When Hurricane Irma struck on 6th September 2017 [with maximum wave heights at buoy 41052 at 16:00 hours (UTC)], the day was dark, with a maximum surface PPFD of 118 µmol photons m^{-2} s^{-1} (cf 2311 µmol photons m^{-2} s^{-1} on September 5th, 2017). When Hurricane Maria hit on September 20th [with maximum wave heights at buoy 41052 at 07:00 hours (UTC)] the impact on maximum surface PPFD was minor (1448 µmol photons m^{-2} s^{-1}). While this reflects, in part, the nighttime occurrence on St. John of the most severe storm effects for Hurricane Maria, throughout daylight on September 20th the storm was < 275 km from the island and significant wave heights remained ≥ 2.7 m. Overall, daily integrated surface PPFD summed from 17 August to 30 November was 5.5% lower in 2017 than 2016, demonstrating the small effects on surface PPFD of two major storms, and the clouds and rain with which they were associated.

When the underwater light meter was retrieved on 27th July 2018, the wiper blade designed to clean the sensor was bent upwards, and the surface of sensor was fouled with algae, and spirorbid polychaetes (~ 2-mm diameter). While we do not know what bent the wiper, deployments of the same sensor in Mo'orea, French Polynesia, have resulted in bite damage from humphead wrasse (*Cheilinus undulatus*), and in St. John, similar damage might have been caused by parrotfish, several species of which are common in the region. More importantly, it is unknown at what point during the year-long deployment that the wiper was bent. Our in situ PPFD data revealed weak attenuation with time after 1 January 2018, and strong attenuation with time after early March 2018 (data not shown). However, PPFD records at 19.1-m depth in early December 2017 were comparable to those recorded at the same time in previous years (Edmunds et al. 2018). From these trends, we inferred that the wiper cleaned the sensor from 17 August 2017 to 30 November 2017, and that light recordings were unaffected by fouling over this period.

From 17 August to 30 November 2017, PPFD at 19.1-m depth reached maximum daily values at 13:00 hours; it varied from 512 µmol photons m^{-2} s^{-1} on 1 September to 14 µmol photons m^{-2} s^{-1} on 6 September, and declined as the sun sank lower in the sky with the approach of winter (Fig. 1c). Relative to the same deployment period in 2016, mean maximum underwater PPFD over these 109 days in 2017 was reduced by 32%. Underwater PPFD integrated by day in 2017 varied from 10.9 mol photons m^{-2} s^{-1} on 2 September, to $\leq$ 0.1 photons m^{-2} s^{-1} on September 7, 20 and 21. Hurricanes Irma and Maria resulted in large reductions in maximum and daily integrated PPFD on the day of impact, as well as on the day following impact (transmission to 19.1 m over the 48 h bracketing these events reached 0%, Fig. 1b–c). These storms were associated with a reduction in underwater PPFD that did not see a return of seasonally expected daily values until 28 September (Fig. 1). Working at 1-m depth in the Bahamas during 2005, Manzello et al. (2009) recorded four storm-related declines in daily integrated PPFD, but each downward perturbation lasted $\lesssim$ 7 days, and did not reduce light to < 5 mol quanta m^{-2} day^{-1}. Relative to the recent storms in St. John, the storms affecting the Bahamas in 2005 were modest, with Hurricane Katrina passing closest to the islands as a tropical depression, and the strongest storms (Hurricanes Dennis and Wilma, both Category 3) passing only within 452–539 km of the islands (Manzello et al. 2009).

During 2017, the heavy rain accompanying the tropical waves following Hurricanes Irma and Maria was associated with low underwater PPFD. For example, when tropical waves affected the island around 18th October and 23rd November, transmission to 19.1-m depth declined to 5% and 4%, respectively, both of which are similar to the values recorded in association with Hurricanes Irma and Maria (Fig. 2). Records of underwater light at the same location from 2014 to 2017 show that such low values are rare, with 22 such days in 2014, and 1 such day in 2016 (all from October to December) (Edmunds et al. 2018). The diffuse attenuation coefficient for PAR ($K_{\text{d-PAR}}$) allows PPFD to be calculated by depth (Kirk 2011), assuming that the seawater is vertically homogeneous for light absorption and scattering. In the autumn of 2017, $K_{\text{d-PAR}}$ was inversely related to the transmission of light to 19.1-m depth and, during the hurricanes, departed from the values expected for clear, coral reef seawater (i.e., ~ 0.100, this study also, Edmunds et al. 2018), and reached 0.397–0.426 during Hurricanes Irma and Maria (Fig. 2). High values of $K_{\text{d-PAR}}$ are characteristic of seawater with a strong ability to scatter and absorb light by water itself, as well as the material it contains (i.e., dissolved pigment, photosynthetic biota, and particulate material, Kirk 2011). $K_{\text{d-PAR}}$ records as high as these are rarely encountered in oceanic water (Kirk 2011), or over coral reefs (Edmunds et al. 2018), and were not detected in St. John over the preceding 4 years (Edmunds et al. 2018). Kirk (2011), for example, reports $K_{\text{d-PAR}}$ of 0.46 in oceanic waters upwelling at Mauritius, and numerous cases with $K_{\text{d-PAR}} \geq 0.426$ in coastal, estuarine, and inland waters. The highest $K_{\text{d-PAR}}$ values in St. John in September 2017 are exceptional and quantify for the first time the capacity for major hurricanes to render a classically photic habitat temporarily aphotic.

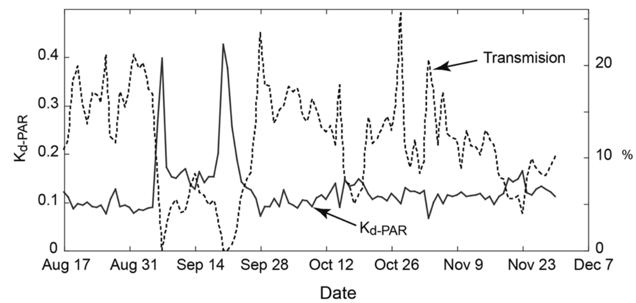

Fig. 2 Underwater PPFD from 17 August to 30 November expressed as the percentage of surface light reaching 19.1-m depth (right ordinate) and diffuse attenuation coefficient ($K_{\text{d-PAR}}$, left ordinate)

Overall, Hurricanes Irma and Maria, and the tropical waves that followed, reduced daily integrated PPFD at 19.1-m depth, summed from 6 September to 30 November, by 20% relative to 2016 (Fig. 1b). A large deficit in integrated daily PPFD (relative to 2016) began with Hurricane Irma, when a 96% deficit accrued by sunset on 6 September, and although PPFD increased in many of the days thereafter (but not in conjunction with Hurricane Maria), a 75% deficit remained on 26 September (Fig. 1d). The return of more normal seawater clarity in late September alleviated much of this deficit, although it remained detectable on 13 November 2017, which is the latest date in 2016 from which comparative data are available (Fig. 1d). Because PPFD was measured at the surface and at depth during 2017 and was reduced on the surface to only a small extent (Fig. 1b), low PPFD at depth largely was a product of scattering and absorption of light in the seawater, as quantified by $K_{\text{d-PAR}}$ (Fig. 2). While it is not possible with the present data to distinguish among the mechanisms causing $K_{\text{d-PAR}}$ to vary (Kirk 2011), they are likely to be related to the re-suspension of benthic sediments, and the addition of terrestrial sediments through runoff associated with heavy rain.

Re-suspension of benthic carbonate sediments probably was a primary cause of reduced underwater PPFD over the short period when large hurricane waves were experienced on St. John, as occurred in Great Lameshur Bay in 2010 during multiple storms (that were not hurricanes) (Edmunds and Gray 2014). Low underwater PPFD during the remainder of the present study (i.e., other than the period of immediate hurricane effects) probably was more strongly related to runoff and terrigenous sedimentation rather than benthic re-suspension. Indeed, the role of rain in reducing underwater PPFD is indicated by the positive association between daily rainfall and $K_{\text{d-PAR}}$ from 17 August to 20 November 2017 ($r = 0.502$, $df = 104$, $P < 0.001$), and following recovery of water clarity (by ~28 September), the inverse association between rainfall and the transmission of PAR to 19.1-m depth, lagged by 7 days ($r = -0.555$, $df = 32$, $P < 0.001$). Previously, we detected a similar relationship over 25 months (Edmunds et al. 2018) and have found that rainfall can explain 19–37% of the decadal variation in benthic community structure on reefs along the south shore of St. John (Edmunds and Lasker 2016). It is plausible that heavy rain increases $K_{\text{d-PAR}}$, directly through terrestrial erosion, sediment plumes, and soluble organic material, and indirectly through stimulated growth of phytoplankton and microbial flora (Fabricius 2005).

The impacts of hurricane-impaired seawater clarity on coral reefs are equivocal, especially in terms of effects that are distinct from well-known impacts, such as coral breakage, sediment deposition/erosion, and sand scour (Harmelin-Vivien 1994). With the dominance of photoautotrophs on coral reefs (e.g., scleractinians, octocorals, and macroalgae), it is reasonable to expect that reductions in PPFD will reduce the supply of photosynthetically fixed carbon, with a deficit occurring during periods of low PPFD that could precipitate a nutritional crisis (Edmunds and Davies 1989; Muscatine 1990; Fabricius 2005). Indeed, the longevity of impaired underwater PPFD during adverse weather has been a matter of speculation for decades as biologists have sought insight into the large size of the carbon reserves in shallow water corals relative to their carbon needs during periods of impaired photosynthesis (Edmunds and Davies 1989; Muscatine 1990). These kinds of effects, together with the light-dependency of coral calcification (Allemand et al. 2011), are drivers of long-term effects of reduced PPFD on coral reefs, such as depth-dependent zonation of corals (Iglesias-Prieto et al. 2004), and the changes in benthic community structure resulting from shading (Fabricius 2005). Such long-term outcomes would not arise from the short-term reductions in PPFD reported here, but it is likely that shortfalls of photosynthetically fixed carbon would develop in members of multiple taxa on the darkest days recorded in St. John.

Based on simplistic assumptions for a coral (*Porites porites*) growing in St. John from 2014 to 2017, we have shown for colonies at 10-m depth that it is unlikely that an ecologically meaningful energy deficit would develop under natural regimes of underwater PPFD extending over multiple years (Edmunds et al. 2018). A repeat of these calculations for August–November 2017 again suggested that the protracted depression of underwater PPFD would not create a meaningful energy deficit in this species at 10-m depth (results not shown). To test for the generality of this conclusion, it will be necessary to extend these calculations to different corals growing at a variety of depths and to consider the possibility that they might be able to photoacclimate to lengthy periods of reduced PPFD. Regardless of the outcome of such efforts, it is notable that Hurricane Irma and Maria did not cause statistically discernable changes in coral cover at 7- to 14-m depth, at least by November 2017 (Edmunds 2019), which suggests that mortality was not affected by a putative energy deficit resulting from the hurricanes. Large-scale scleractinian mortality within this depth range had not resulted from this (or any other) storm-related effect by August 2018. However, when these reefs were surveyed in July and August 2018, suspension-feeding invertebrates were abundant (see also Edmunds and Gray 2014). Examples include (but are not limited to) serpulid polychaetes, sponges that had quickly grown since November 2017, winged oysters (*Pteria colymbus*) on octocorals, and dense growth of bivalves on the lower surface of settlement tiles. Similar responses on coral reefs exposed to increased turbidity and nutrients are well known (reviewed in Fabricius 2005) and, in the present case, suggest that population enhancements of filter feeding invertebrates may be a delayed consequence of storm-related reductions of in situ PPFD. On present-day reefs, this trend might have important implications if spatial preemption by filter-feeding taxa accentuates progressive changes away from a benthic community dominated by scleractinians (Edmunds and Lasker 2016).

Acknowledgements This study was funded by the US National Science Foundation (Grants OCE 18-01336 and DEB 13-50146). We thank S. Prosterman, and V. Powell for logistical support in St. John, the University of the Virgin Islands and the Virgin Islands Ecological Resource Station for infrastructure that made this research possible, and two anonymous reviewers whose comments improved an earlier version of this paper. This is contribution number 282 of the CSUN marine biology program.

Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest on connection with this study.

Ethical standards This research was completed under research permits from the VI National Park (most recently VIIS-2018-SCI-0012) and did not involve experimentation with animals or plants.

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