NOTE

Remote monitoring of chlorophyll fluorescence in two reef corals during the 2005 bleaching event at Lee Stocking Island, Bahamas

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Abstract Zooxanthellae fluorescence was measured in situ, remotely, and in near real-time with a pulse amplitude modulated (PAM) fluorometer for a colony of *Siderastrea siderea* and *Agaricia tenuifolia* at Lee Stocking Island, Bahamas during the Caribbean-wide 2005 bleaching event. These colonies displayed evidence of photosystem II (PS II) inactivation coincident with thermal stress and seasonally high doses of solar radiation. Hurricane-associated declines in temperature and light appear to have facilitated the recovery of maximum quantum yield of PS II within these two colonies, although both corals responded differently to individual storms. PAM fluorometry, coupled with long-term measurement of in situ light and temperature, provides much more detail of coral photobiology on a seasonal time scale and during possible bleaching conditions than sporadic, subjective, and qualitative observations. *S. siderea* displayed evidence of PS II inactivation over a month prior to the issuing of a satellite-based, sea surface temperature (SST) bleaching alert by the National Oceanic and Atmospheric Administration (NOAA). In fact, recovery had already begun in *S. siderea* when the bleaching alert was issued. Fluorescence data for *A. tenuifolia* were difficult to interpret because the shaded parts of a colony were monitored and thus did not perfectly coincide with thermal stress and seasonally high doses of solar radiation as in *S. siderea*. These results further emphasize the limitations of solely monitoring SST (satellite or in situ) as a bleaching indicator without considering the physiological status of coral-zooxanthellae symbioses.

Keywords Coral bleaching alerts · PAM fluorometry · Hurricane cooling · Environmental monitoring

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Introduction

The National Oceanic and Atmospheric Administration's (NOAA's) Coral Reef Watch (CRW) utilizes satellite algorithms for predicting coral bleaching based on the deviations of sea surface temperatures (SST) above the climatological monthly maximum (Goreau and Hayes 1994; Gleeson and Strong 1995). Although effective at highlighting regions of the globe, where SSTs are warmer than average and bleaching might be expected, these products neither consider other causative or modifying factors of coral bleaching (e.g., light, hydrodynamics), nor

the functional status of coral-algal symbioses. Satellite-based alerts lack fine-scale spatial and temporal resolution (McClanahan et al. 2007) further limiting our understanding of the interactive effects these additional factors play in bleaching (Fitt et al. 2001).

NOAA's Integrated Coral Observing Network (ICON) obtains meteorological and in situ oceanographic data hourly in near real-time (via satellite relay) with high temporal resolution to complement the high spatial resolution of CRW. The ICON platform measures important secondary variables (e.g., downwelling irradiance) in addition to temperature and allows the installation of additional instruments (Hendee et al. 2006).

Both approaches rely on research divers making visual interpretations of bleaching, which are qualitative and highly subjective (Fitt et al. 2001). Pulse amplitude modulated (PAM) fluorometry measures the photosynthetic efficiency of photosystem II (PS II) within the endosymbiotic *Symbiodinium* spp. that may be used as a quantitative measure of photoinactivation during coral bleaching (Warner et al. 1999). Chronic photoinhibition is the irreversible photodamage to PS II and is hypothesized to be one of the primary mechanisms of thermally induced bleaching (Warner et al. 1999; Gorbunov et al. 2001). It is expected that a decrease in the maximal quantum yield of PS II fluorescence (F_v/F_m) will precede any visible signs of coral bleaching (Fitt and Warner 1995), improving the early detection of bleaching stress and leading to a better identification of threshold values for timely feedback of real-time conditions in situ. Zooxanthellae fluorescence was measured in situ, remotely, and in near real-time for a colony of *Siderastrea siderea* and *Agaricia tenuifolia* at Lee Stocking Island, Bahamas during the Caribbean-wide 2005 bleaching event (Donner et al. 2007). The timing of the loss in PS II activity is compared with trends in environmental data.

Materials and methods

In situ fluorometry

A specially constructed monitoring PAM fluorometer (Gademann Instruments, Germany) was deployed at the ICON station near North Norman's Patch Reef, Lee Stocking Island, Bahamas (23.791N, 76.139W) in 2005 (Fig. 1). The PAM unit consisted of a central canister connected to four monitoring heads. The unit's internal battery (12 V) was recharged via the ICON station's photovoltaic array. Each sensor was located behind an acrylic lens within a stainless steel cylinder that was kept in the proper orientation by affixing each head to a plastic frame (Fig. 1a). The sensors were oriented to ensure that they did

not shade the coral tissue being measured. A blue LED (450 nm, 18 nm full-width half-max [FWHM] bandwidth) emitted a saturating pulse (>3,500 µmol quanta m^{-2} s^{-1}) for 0.6 s every hour. The acrylic lenses were wiped clean with a soft cloth at least every 2 weeks. Fluorescence measurements were taken from two adjacent locations that experienced similar conditions on a single colony of *S. siderea* and *A. tenuifolia* (both at 6-m depth) and transmitted via satellite to NOAA's Atlantic Oceanographic and Meteorological Laboratory (AOML) in Miami from June 30, 2005 until the end of 2005. This limited sampling (i.e., two measurements on the same colony) did not provide enough data for statistical comparisons, but it did allow monitoring of two corals in a temporally intensive manner.

The maximal dark acclimated quantum yield of PS II (F_v/F_m) and the effective quantum yield of PS II ($\Delta F/F_m'$) for light acclimated corals were selected for each day. F_v/F_m and $\Delta F/F_m'$ values were then used to calculate the PS II excitation pressure ($Q_m = 1 - [(\Delta F/F_m')/(F_v/F_m)]$) (Iglesias-Prieto et al. 2004). All data were manually screened to ensure that the nighttime peak F_v/F_m was used because a dark reduction in F_v/F_m did occur during nighttime periods as recently shown by Hill and Ralph (2008). $\Delta F/F_m'$ was chosen as the minimum F_v/F_m value for each day, usually at solar noon.

Environmental variables

Sea temperature was measured with a Falmouth Scientific CTD (1 m) and wind speeds were obtained from two RM Young Model 05106C anemometers. Irradiance was measured with an in-water (1 m) BIC2104x radiometer (Biospherical Instruments) equipped with four 2 π cosine corrected sensors, oriented to record downwelling irradiance of ultraviolet (UVR) and photosynthetically active radiation (PAR): UV-305 nm with 5 nm FWHM; UV-330 and UV-380 nm with 10 nm FWHH, and integrated PAR (400–700 nm). Subsurface irradiance sensors were corrected for the immersion effect by applying the appropriate coefficients: 305 nm, 0.623; 330 nm, 0.635; 380 nm, 0.641; PAR, 0.662 (Calibration certificates, Biospherical Instruments). Hourly averages of temperature and wind measured every 6 min and light measured every 30 s were transmitted in near real-time. Hourly doses of PAR and UVR were estimated by multiplying the hourly reported averages by 3,600 s. Daily dose was estimated by summing the hourly dose values during the period of most intense solar radiation (10:00–15:00 h). Underwater light intensities were low and highly variable outside this time-frame and did not contribute substantially to the estimates.

All instruments were calibrated prior to deployment and the optical sensors were wiped clean with a soft cloth at least every 2 weeks. Plotting the light data pre/post

Fig. 1 a SCUBA diver positions PAM heads on *Siderastrea siderea* (diameter of colony ∼30 cm). **b, c** PAM heads on shaded parts of *Agaricia tenuifolia*. Note extensive bleaching on parts of colony not monitored (PAM head diameter = 2.9 cm)
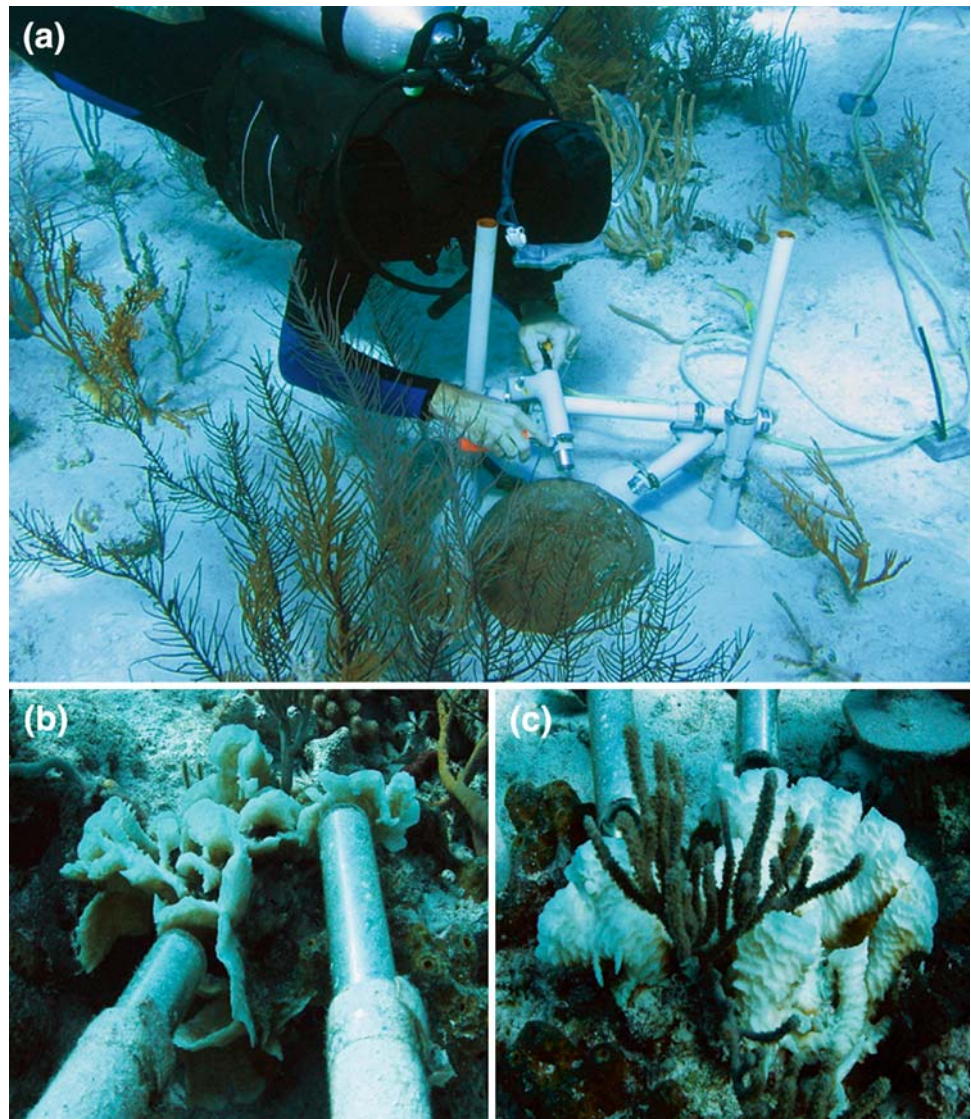
cleaning showed no observable change in the diel irradiance cycle that would indicate significant bio-fouling. Although this is not a precise way to ensure data quality, if we couple these results with the qualitative observation that there was no visible organism recruitment to the cosine collectors in between cleanings, these data are satisfactory to illustrate the trends discussed herein. Post-deployment calibrations of optical sensors have shown a maximum sensor drift due to solarization and abrasion of <0.1% per week. This drift is trivial in comparison with the diurnal range of irradiance values (0–2,000 μmol quanta m^{-2} s^{-1}) and day-to-day changes in those values.

Results and discussion

The minimum values of F_v/F_m for *S. siderea* occurred coincident with the inflection point of daily average sea temperature (Fig. 2). *S. siderea* never turned white, but rather displayed characteristic signs of bleaching for this species (i.e., paling from dark brown to blue/purple with mottled pigmentation). Conversely, the parts of the colony of *A. tenuifolia* that were not shaded (and not facing the fluorometer sensors), did show substantial paling during the late summer (Fig. 1b, c).

The intra-colony variability noted in F_v/F_m within *S. siderea* (Fig. 2b), corresponded to a higher level of PS II excitation pressure in one area of the colony from mid July to mid September as compared with the other colony section (Fig. 3). Likewise, Q_m declined substantially to ≤0.2 in both monitored sections on exceptionally cloudy days (PAR ≤ 500 μmol quanta m^{-2} s^{-1}), suggestive of some light limitation, and a seasonal trend of slowly declining Q_m was noted throughout the study (Fig. 3). Low Q_m values indicate that most PS II reaction centers remain open (i.e., light limitation), whereas high Q_m values signify
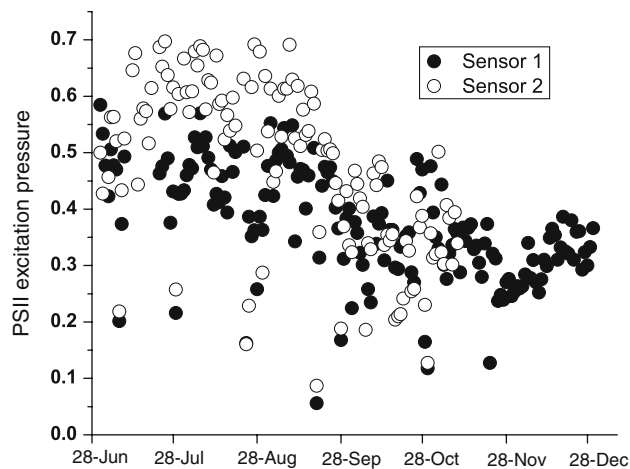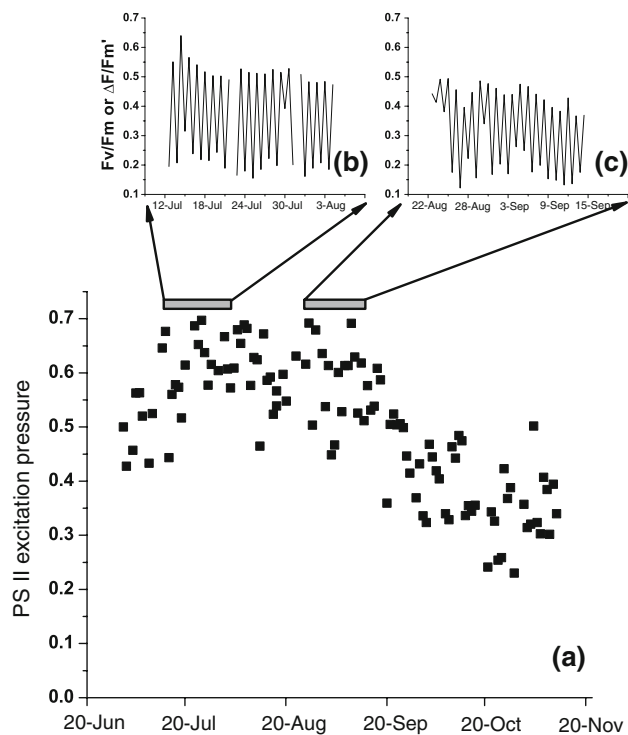
Fig. 3 PS II excitation pressure from two locations on colony of *S. siderea*
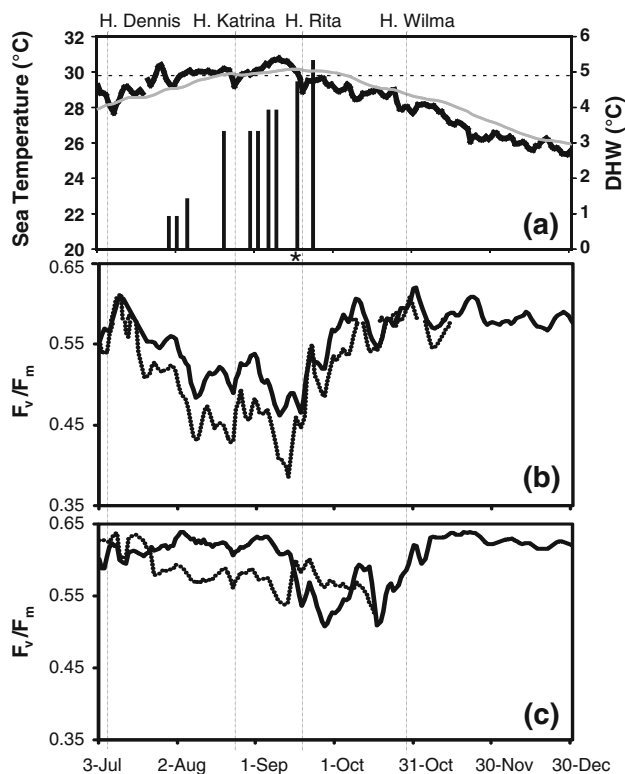
Fig. 2 a Daily average (*bold line*) and running 30-day mean (*gray line*) sea temperature (°C, 1 m) compared to degree heating weeks (DHW, *bars*). Bleaching threshold is *dashed horizontal line* (29.8°C: Manzello et al. 2007a). *Star* indicates issuing of satellite-based "Bleaching Alert Level 1" (i.e., bleaching is expected based on the accumulation of four DHW over the past 12 weeks: NESDIS 2007) on September 17 (NOAA CRW 2007). One DHW implies that SSTs have been ≥1°C than the expected annual maximum monthly SST for 1 week; thus, four DHWs indicate SSTs ≥1°C, the seasonal maximum for 1 month (Gleeson and Strong 1995). F_v/F_m reported by two sensors positioned on (**b**) *S. siderea* and (**c**) *A. tenuifolia* (*bold and dashed lines* correspond to two individual sensor heads on each coral). F_v/F_m time-series were smoothed by plotting the running 3-day mean. One of the two sensor heads on each coral failed within several weeks of each other. Timing of hurricane impacts was noted to illustrate cooling

Fig. 4 a PS II excitation pressure in one location of *S. siderea* (Low Q_m values removed for clarity). F_v/F_m and $\Delta F/F_m'$ over a period of 20 days from **b** July 12–August 3 and **c** August 22–September 15

that most reaction centers are closed suggesting photoinhibition (Iglesias-Prieto et al. 2004). Notably, the largest decline in F_v/F_m in *S. siderea* occurred while Q_m was no higher than the preceding month when F_v/F_m was high and near expected 'normal' levels (Fig. 4a). However, closer inspection of daily fluctuations in the fluorescence signal during these times indicated a lack of complete recovery in F_v/F_m for many days into early September (Fig. 4b, c); a lack of recovery suggests continued PS II photoinactivation (Warner et al. 2006).

Recovery of F_v/F_m and Q_m in *S. siderea* occurred coincident with the declines in sea temperature and solar radiation associated with the passage of Hurricane Rita (Figs. 2, 3, 4, 5). These data provide additional evidence that hurricanes can facilitate the recovery of bleached

corals (Manzello et al. 2007b). The passage of Hurricanes Dennis, Katrina, Rita, and Wilma caused declines in the daily average sea temperature from 1.0 to 1.7°C (Table 1). *A. tenuifolia* displayed a recovery response associated with Hurricane Rita, but both monitored areas continued to show signs of chronic photoinhibition shortly thereafter (Fig. 2c). One sensor stopped reporting soon after, but the remaining functional sensor output did not display persistent recovery until the seasonal decline in both temperature
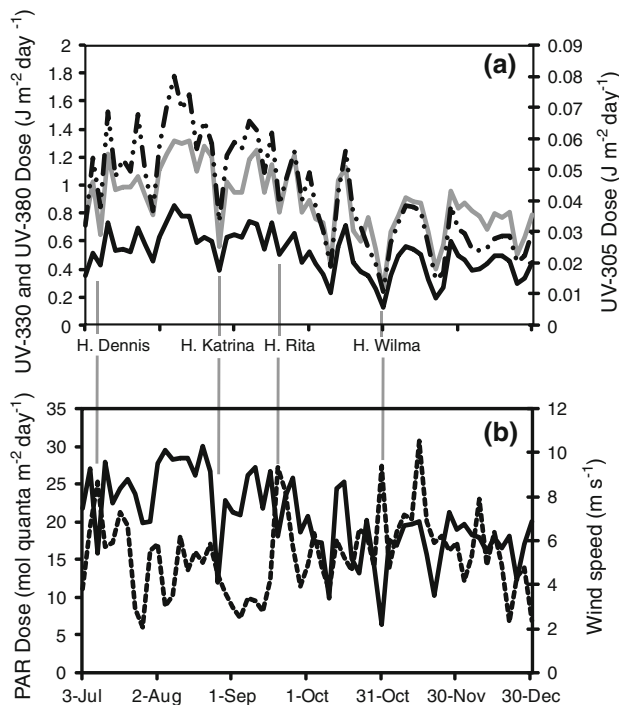
Fig. 5 **a** Daily dose of UV-305 nm (*dashed line*), UV-330 nm (*black line*) and UV-380 nm (*gray line*) at 1 m. **b** Daily dose of PAR (400–700 nm, *solid line*) and daily average wind speed (m s^{-1}, *dashed line*). Time-series were smoothed by plotting the running 3-day mean

Table 1 Nearest distance from and magnitude of cooling (Δ°C) associated with named storms that affected the Bahamas in 2005

Storm name	Distance (km)	Category	Δ°C
H Dennis	452	3	1.5
H Katrina	7	TD	1.2
H Rita	80	TS	1.0
H Wilma	539	3	1.3

Category refers to strength of the storm [Saffir–Simpson scale (Simpson and Reihl 1981)] when the distance was noted from the site. *TD* tropical depression; *TS* tropical Storm

and solar radiation was evident (Figs. 2, 5). The different trends in F_v/F_m observed between the two species are hypothesized to be a result of the different irradiances experienced by the differently oriented coral tissues, because parts of the monitored *A. tenuifolia* colony were shaded, whereas the entire *S. siderea* colony was fully exposed (Fig. 1). These two species generally harbor different *Symbiodinium* spp. within the C clade (LaJeunesse 2002), which may have been an additional factor in the differing F_v/F_m trends. The data for *A. tenuifolia* are not discussed further because they do not represent those parts of the colony that were exposed to the combined effects of temperature and light, and consequently bleached.

UVR and PAR dose declined due to the nearby passing of hurricanes and tropical storms (Fig. 5). These short-term

reductions in UVR and PAR dose are superimposed upon the characteristic trend of a summer peak followed by the seasonal decline. Declines in solar radiation corresponded with peaks in wind speed associated with Hurricanes Dennis, Katrina, Rita, and Wilma (Fig. 5). These results show that storm-related declines in solar radiation, in addition to sea temperature, occur at distances far greater (>500 km for H Wilma) than the narrow damage swath width of tropical cyclones (≤90 km from storm center) and may potentially facilitate regional bleaching recovery (e.g., Manzello et al. 2007b).

A "Bleaching Alert Level 1" [i.e., bleaching expected based on the accumulation of four degree heating weeks (DHW: Gleeson and Strong 1995) over the past 12 weeks (NESDIS 2007)] was issued for the Bahamas on September 17 (Fig. 2, NOAA CRW 2007). One DHW implies that SSTs were 1°C above the expected annual maximum monthly SST for 1 week; thus, four DHWs indicate that SSTs were 1°C above the seasonal maximum for a month (Gleeson and Strong 1995). *S. siderea* began undergoing discernible photoinactivation, indicative of chronic photoinhibition, over a month prior to the issuing of the satellite-based SST bleaching alert (Fig. 2a, b). In fact, recovery had already begun in *S. siderea* by the time the satellite-based bleaching alert was issued. The 30-day running mean in situ sea temperature reached the bleaching threshold for this site on August 18, 30 days prior to the satellite-based bleaching alert (Fig. 2a).

These results and recent work (Dunne and Brown 2001; McClanahan et al. 2007) emphasize the limitations of solely monitoring SST (both satellite and in situ) without considering the physiological status of coral-zooxanthellae symbioses. Satellite-based bleaching alerts are effective at identifying large areas where bleaching may have occurred, but they appear to be poor indicators of real-time stress. Although in situ temperature was a better indicator than satellite SST of the actual timing of photobiological 'stress' shown by the *S. siderea* data, it is still not ideal as any temperature-based 'stress' index by itself ignores the fundamental interaction of light in the bleaching response (Dunne and Brown 2001). The difficulties associated with maintaining this current setup (e.g., keeping sensor heads in proper orientation and clean from bio-fouling) prevent larger-scale implementation at this time. However, PAM fluorometry coupled with simultaneous long-term measurement of in situ light and temperature can provide much more detail for understanding coral photobiology and bleaching than sporadic point measurements and subjective assessments by researchers.

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