

Diurnal variability in turbidity and coral fluorescence on a fringing reef flat: Southern Molokai, Hawaii

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Abstract

Terrigenous sediment in the nearshore environment can pose both acute and chronic stresses to coral reefs. The reef flat off southern Molokai, Hawaii, typically experiences daily turbidity events, in which trade winds and tides combine to resuspend terrigenous sediment and transport it alongshore. These chronic turbidity events could play a role in restricting coral distribution on the reef flat by reducing the light available for photosynthesis. This study describes the effects of these turbidity events on the Hawaiian reef coral *Montipora capitata* using in situ diurnal measurements of turbidity, light levels, and chlorophyll fluorescence yield via pulse-amplitude-modulated (PAM) fluorometry. Average surface irradiance was similar in the morning and the afternoon, while increased afternoon turbidity resulted in lower subsurface irradiance, higher fluorescence yield ($\Delta F/F'_m$), and lower relative electron transport rates (rETR). Model calculations based on observed light extinction coefficients suggest that in the absence of turbidity events, afternoon subsurface irradiances would be 1.43 times higher than observed, resulting in rETR for *M. capitata* that are 1.40 times higher.

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1. Introduction

Changing water quality poses a worldwide threat to coral reefs. Terrestrial runoff alters water quality in four ways: inorganic nutrients, particulate organic matter, light reduction from turbidity, and sedimentation (Fabricius, 2005). Highly turbid waters do not necessarily lead to net sediment accumulation (Woolfe and Larcombe, 1999), and in some cases corals can flourish in naturally turbid environments (Ayling and Ayling, 1991; McClanahan and Obura, 1997; Anthony, 2000, 2006; Te, 2001). However, human activity has generally increased sediment loading on coral reefs (e.g. McCulloch

et al., 2003). In Hawaii, changing land-use patterns increases sediment delivery to the coastal ocean and results in chronic sediment stress to coral reefs (Jokiel et al., 2004). This problem often occurs in heavily populated areas, but it can also be a concern in areas devoted to agriculture or grazing, or in protected embayments. For example, sediment from an agricultural field deposited in Honolulu Bay, Maui during a runoff event in 2002 persisted for over 6 months, and periodic sediment damage decreased coral cover in the bay by 33% between 1992 and 2002 (Dollar and Grigg, 2004). On the south coast of Molokai, historical overgrazing has increased the delivery of terrigenous sediment to nearshore waters (Roberts, 2001). The wharf at Kaunakakai further inhibits longshore transport and removal of sediment from the Molokai reef flat, resulting in some of the lowest coral cover in the state of Hawaii (Jokiel et al., 2004).

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Sediment events can be acute or chronic, and can affect corals through multiple pathways. Sedimentation effects occur largely through direct deposition on the coral surface, while turbidity effects are from suspended sediments that reduce light availability in the water column or abrade coral tissue. Elevated sediment loads can bury corals, decrease coral cover, alter species composition and colony morphology, and inhibit photosynthesis, calcification, growth, and recruitment (see reviews by Pastorok and Bilyard, 1985; Rogers, 1990; Fabricius, 2005). Predicting effects of, or acclimatization to, chronic sediment stress is predicated on demonstrating specific mechanistic relationships between physical factors and physiological responses (Anthony and Larcombe, 2002). As light, water motion, and sediment often co-vary, true experimental field tests of sediment impacts are exceedingly difficult; notable exceptions include sedimentation studies by Rogers (1983) and Philipp and Fabricius (2003) that demonstrated species-specific physical tolerance and reductions in quantum yields, respectively. However, energy budgets and modeling efforts (e.g. Edmunds and Spencer Davies, 1989; Anthony et al., 2002, 2004; Anthony and Hoegh-Guldberg, 2003; Anthony and Connolly, 2004) can be used to link laboratory observations with field conditions to describe the mechanisms by which corals physiologically cope with sediment stress, particularly with respect to turbidity. For example, a primary effect of turbidity is to reduce light for coral photosynthesis. Physiologically corals respond to elevated turbidity by increasing chlorophyll concentrations, increasing photosynthetic efficiency, and decreasing saturation irradiance (Anthony and Fabricius, 2000; Te, 2001; Anthony and Hoegh-Guldberg, 2003). High turbidity decreases coral photosynthesis:irradiance ratios, which could be due to reduced photosynthesis (Anthony and Fabricius, 2000; Te, 2001) or increased respiration (Telesnicki and Goldberg, 1995). The net result is to reduce the photosynthetic energy available for coral growth or reproduction. Corals may acclimatize to turbidity-induced energetic restrictions by rapidly replenishing energy between turbidity events, shifting from autotrophy to heterotrophy, photoacclimation, and/or reduced energy expenditure (Anthony and Larcombe, 2002).

This project is part of an ongoing research program by the United States Geological Survey to understand the influence of oceanographic and geologic processes on the health and sustainability of Hawaiian coral reef systems. The objective of this paper is to describe diurnal patterns in fluorescence yield of *Montipora capitata* colonies subjected to natural daily turbidity events on the South Molokai reef flat, using non-invasive pulse-amplitude-modulated (PAM) fluorometry. Diurnal variability in coral photobiology in the field has been documented with fast-repetition rate (FRR, Lesser and Gorbunov, 2001; Levy et al., 2004) and PAM fluorometry (Winters et al., 2003), and acute, sublethal sediment stress on corals has been described with PAM in the field and the laboratory (Philipp and Fabricius, 2003; Weber et al., 2006; Piniak, 2007). Here we describe the effects chronic turbidity events on the in situ photobiology of a dominant coral, *M. capitata*, on the coral reefs of Molokai, Hawaii.

2. Materials and methods

2.1. Study site

A reef flat extends almost 50 km along the southern coast of Molokai, Hawaii, forming a shallow (<1.5 m), roughly horizontal surface between the shoreline and the reef crest 0.5–1.0 km offshore. The reef flat sediment is up to tens of centimeters thick; the sand is predominantly marine carbonates (58–65%) while the silts and clays are mostly (40–70%) terrigenous in origin (Calhoun and Field, 2002). The inner reef flat is primarily terrestrial mud, giving way to sandy and hardbottom habitats further from shore (Cochran-Marquez, 2005). Macroalgal cover can locally exceed 75%, and can play a significant role in trapping terrigenous sediment on the reef flat (Stamski and Field, 2006). Small seagrass (*Halophila hawaiiiana*) patches are occasionally present on the reef flat. Corals are found both as solitary colonies and as patch reefs. Average coral cover increases from 1.6% at 400 m offshore to 11.2% at 700 m (Rodgers et al., 2005). *Montipora capitata* and *Pocillopora damicornis* are the dominant corals on the inner reef flat; *Porites compressa*, *Porites lobata*, *Pocillopora meandrina*, and *Montipora patula* become more abundant on the outer reef flat (Jokiel et al., in press). Beyond the reef crest is a well-developed, moderate relief (1–3 m) spur-and-groove system to a depth of 30 m (Storlazzi et al., 2003). Most of the south Molokai fore reef has extremely high (80–98%) coral cover, but between Kaunakakai and Kawela (including offshore of the study site) coral cover is 0–20% (Jokiel et al., in press).

The Molokai reef flat experiences mixed semi-diurnal tides with a mean range of 0.6 m and a maximum spring range of 0.9 m (Ogston et al., 2004; Storlazzi et al., 2004). High tides have cooler water temperatures, lower salinity, and higher suspended sediment concentrations than low tides (Storlazzi et al., 2004). Daily cycles of solar radiation heat the island, lowering atmospheric pressure and increasing trade wind velocities (Fletcher et al., 2002). Strong (>10 m s⁻¹) trade winds occur for the majority of the year, producing longshore currents to the west and slightly offshore (Storlazzi et al., 2004; Presto et al., 2006). Wave formation on the reef flat is depth-limited, and as the tide rises deep-water energy propagates onshore from the fore reef and large trade wind-driven waves develop on the reef flat (Storlazzi et al., 2004). Suspended sediment concentrations are <1 mg l⁻¹ during calm conditions but increase to 10–25 mg l⁻¹ during these daily resuspension events and up to 100 mg l⁻¹ in extreme events (Ogston et al., 2004; Presto et al., 2006). High suspended sediment concentrations on the fore reef are linked to resuspension events on the reef flat (Storlazzi et al., 2004; Bothner et al., 2006). Elevated turbidity on the reef flat occurs for ~30% of the daylight hours during the trade wind months, and the resulting light attenuation may limit coral cover and diversity on the reef flat (Ogston et al., 2004). Patch reef communities on the Molokai reef flat also have low daily gross photosynthetic rates (2.4–2.8 g O₂ m⁻² d⁻¹, Yates and Halley, 2003).

In May 2005, turbidity and coral fluorescence measurements were made at a series of patch reefs on the Molokai

reef flat at 21°04.537'N, 157°00.211'W, about 500 m from shore and slightly west of a relic fish pond. The patch reefs were shallow (<2 m) relatively low-relief (0.5–0.6 m) shore-normal outcrops several meters in length along a north–south axis and surrounded by a flat sandy bottom, which facilitated instrument placement. These patch reefs were colonized primarily by *Montipora capitata* and *Pocillopora damicornis*; *M. capitata* was chosen for this experiment because it predominates inshore turbid reef environments in Hawaii (Te, 2001; Dollar and Grigg, 2004), is physiologically resistant to sedimentation (Hodgson, 1989), has a flattened, plate-like colony morphology (making fluorescence probe placement easier), and has been shown to decrease in fluorescence yield in response to acute sediment stress (Piniak, 2007). The experiment was conducted during the trade wind season and around the new moon so as to maximize the tidal range and thus the potential for sediment resuspension.

2.2. Instrumentation

Two instrument packages were deployed for this experiment. The first consisted of three Aquatec/Seapoint 200-TY self-contained optical backscatter sensors (SCOBS), mounted horizontally at ~0.10, 0.40, and 0.65 m above the bed. The SCOBS were not fitted with cleaning wipers as biofouling was expected to be minimal during the short deployment period, which was confirmed by visual inspection at the end of the deployment. The SCOBS recorded an eight-sample burst every 5 min; these eight samples were averaged to produce one measurement of turbidity, in units of NTUs, every 5 min. The vertical array measured turbidity throughout the water column; as data from all three sensors were highly auto-correlated, for clarity only the data from the lower unit are reported here. A self-contained Dobie-A strain gauge pressure sensor (National Institute of Water & Atmospheric Research Ltd.) was mounted vertically so that the pressure sensor was ~0.5 m above the bed, sampling for 512 s at a 2 Hz frequency every 30 min; this sensor thus provided measurements of wave height (m), wave period (s) and water depth (m) every 30 min. Photosynthetically active radiation above the water surface (PAR_s) during the experiment was measured at 15-min intervals with a flat LICOR LI-192SA quantum sensor mounted ~2.0 m above the bed on a stainless steel pole; light data were recorded with a LICOR LI-1400 logger housed in a waterproof Pelican case mounted to the instrument rack.

The second instrument package included a Seabird SBE-37SM MicroCat conductivity temperature sensor (CT) and a pulse-amplitude-modulated fluorometer (DIVING-PAM, Walz GmbH, Germany). The CT sensor was mounted ~0.4 m above the bottom, and recorded single-point measurements of salinity (PSU) and water temperature (°C) every 5 min. The DIVING-PAM was anchored to the instrument mount, and the fiber-optic probe fixed in place 3 mm from and perpendicular to a *Montipora capitata* colony with a custom-built sample holder (fabricated from transparent Plexiglas to reduce shading of the colony surface; light attenuation through the holder was ~3.4% but the reduction was not statistically significant).

The PAM was calibrated daily so that the settings for each individual coral produced initial chlorophyll fluorescence measurements (F) of ~300–500 units when a weak pulsed blue light was applied to the surface of the corals (measuring intensity usually ranged between 3 and 5; gain was fixed at 2). Maximum fluorescence (F'_m) was measured using a saturating light pulse (0.8 s, >2000 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$), and the change in fluorescence ($\Delta F = F'_m - F$) was used to calculate effective quantum yield ($\Delta F/F'_m$) for light-adapted corals (Genty et al., 1989). For dark-adapted (e.g. nocturnal) samples, effective quantum yield is the same as the maximum quantum yield ($F_m - F_0/F_m$, or F_v/F_m). Light near the surface of the coral colony (PAR_c) was measured with the PAM's cosine-corrected quantum sensor, which was attached to the fiber-optic probe holder and calibrated against the LI-192SA. The relative electron transport rate (rETR) was calculated as:

$$\text{rETR} = \Delta F/F'_m \times PAR_c \times 0.5;$$

where 0.5 is the result of an assumed equal distribution of photons absorbed by the two photosystems (Walz, 1998). The rETR does not account for the fraction of light absorbed by the photosynthetic tissue (Hoegh-Guldberg and Jones, 1999). Yield and PAR_c measurements were made every 30 min using the DIVING-PAM's internal timer. Data collection ran from just after sunrise to just before sunset over a period of 5 days. On two occasions (6–7 and 8–9 May) data collection continued throughout the night; this was not done routinely because the 30-min sampling interval created battery power constraints. Each morning shortly after sunrise the PAM instrument package was moved to a new coral colony ($n = 5$). Only *Montipora capitata* colonies on the northern or southern edge of the reef patches (to minimize shading over the course of the day) that had flat, upward-facing surfaces ~0.3 m above the bed were used for the experiment.

2.3. Statistical analysis

The full time series of physical parameters is presented below, but only data collected simultaneously with coral fluorescence parameters were analyzed statistically. The physical parameters were pooled into two groups: morning (sunrise to noon), and afternoon (noon to sunset). Fluorescence data from all five corals were pooled for analysis. Statistical tests were conducted using STATISTICA 7.1 (StatSoft, 2006). Data were tested for homogeneity of variance using Levene's test (StatSoft, 2006), and normality assumptions were tested using a Kolmogorov–Smirnov test for goodness of fit (Zar, 1984). Data that did not meet these assumptions were transformed as appropriate (log or arcsin-square root) and re-tested. Temporal differences in parameters were tested using one-way analysis of variance using time of day (morning or afternoon) as categorical factors. Data that failed to meet assumptions after transformations were analyzed using nonparametric Mann–Whitney tests. Predictive effects of physical parameters on fluorescence data were tested using regression.

3. Results

3.1. Physical parameters

Photosynthetically active radiation incident at the water surface (PAR_s) typically reached a maximum at $\sim 2200 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ shortly after noon (Fig. 1a). Average photoperiod during the study was 13.0 h; the average PAR_s from sunrise to noon was not significantly different than the average between noon and sunset (Mann–Whitney $U = 1224.0$, $p = 0.172$). Light at the coral colony surface (PAR_c) was $57.7 \pm 1.0\%$ (average \pm SE) of PAR_s in the morning (Fig. 1a), but only $44.2 \pm 2.2\%$ in the afternoon, a significant difference (arcsin-square root transformed for ANOVA, $F_{1,106} = 74.450$, $p < 0.001$). This reduction was related to two factors: the significant difference in water clarity between relatively calm mornings and turbid trade wind dominated afternoons (Fig. 1b, log-transformed for ANOVA, $F_{1,106} = 125.78$, $p < 0.001$), and greater light attenuation by significantly greater water depths (45 cm on average) during the afternoon high tide (ANOVA,

$F_{1,106} = 356.31$, $p < 0.001$). The afternoon turbidity increase tracked the high tide, but there was no turbidity increase with the smaller of the semi-diurnal high tides that occurred during the night due to a lack of wind-driven waves (Fig. 1b). During the short duration of this study, water temperatures followed a diurnal rather than a tidal pattern; temperatures were highest during the high tide while the lower of the high tides did not affect temperatures at all (Fig. 1c). Salinity was lowest during the lowest of the semi-diurnal tides, likely due to the offshore advection of terrestrial freshwater inputs by the falling tide (Fig. 1c). PAR_s , turbidity, and depth at the coral surface (D_c) were significant predictors of PAR_c in a forward stepwise linear regression ($F_{2,105} = 140.747$, $p < 0.001$), but turbidity was a much weaker predictor of PAR_c than were the other two factors (Table 1).

3.2. Coral fluorometry

The *Montipora capitata* colonies in this experiment showed diurnal variability in effective quantum yield (Fig. 2a) and relative electron transport rate (Fig. 2b). Yields were considerably

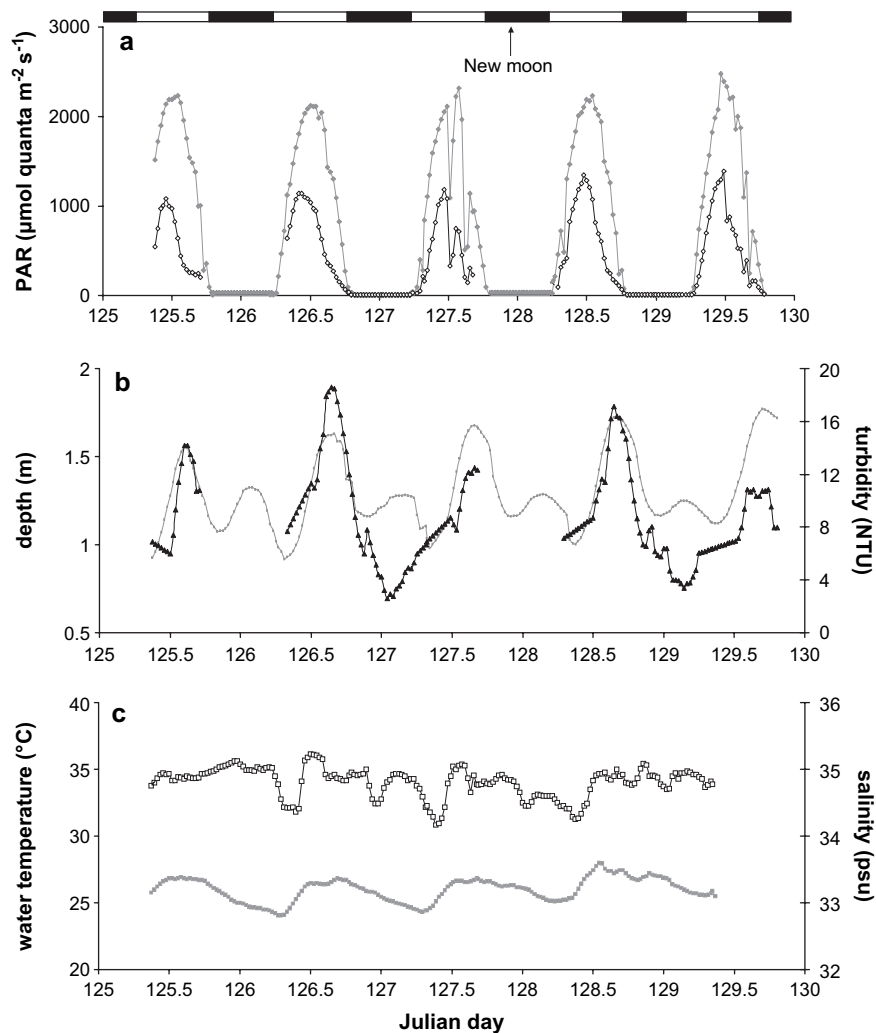


Fig. 1. Physical conditions at the study site from 5 to 9 May, 2005, at half an hour intervals. The black and white bar at the top of the figure represents the light:dark cycle and appearance of the new moon. (a) Incident light above the water surface (PAR_s , gray diamonds) and adjacent to the coral colony surface (PAR_c , open diamonds); (b) total water depth (gray line) and turbidity of the lower optical backscatter unit ~ 0.10 m above the bed (black triangles); (c) water temperatures (gray rectangles) and salinity (open rectangles).

Table 1
Results of a forward stepwise linear regression with PAR_c dependent on PAR_s , water depth above the coral surface (D_c), and turbidity at the lower backscatter sensor

Factor	Regression slope	R^2	p
PAR_s	0.713	0.68	<0.001
D_c	-0.27	0.11	<0.001
Turbidity	-0.12	0.01	0.049
Total		0.80	

higher for corals dark-adapted at night than those under natural solar irradiance, but as night-time yields were only measured for two of the five corals due to battery re-charging requirements only the daytime patterns were analyzed statistically. Effective quantum yield was lower in the morning (average \pm SE: 0.410 ± 0.012) than in the afternoon (0.455 ± 0.012 ; ANOVA, $F_{1,106} = 6.755$, $p = 0.011$), and decreased as irradiance at the coral surface increased (yield = $-0.0067 \times \log PAR_c + 0.587$; $F_{1,106} = 74.052$, $p < 0.001$, $R^2 = 0.41$). Relative electron transport rate (rETR) increased significantly with irradiance at the coral surface (rETR = $130.598 \times \log PAR_c - 243.73$; $F_{1,106} = 662.520$, $p < 0.001$, $R^2 = 0.86$), and rETR was higher in the morning (average \pm SE: 135.2 ± 9.3) than the afternoon (69.6 ± 5.9 ; ANOVA, $F_{1,106} = 38.245$, $p < 0.001$). However, plots of rETR against PAR_c (Fig. 3) showed little indication of hysteresis; that is, when light intensities were similar, rETR was the same in the morning as in the afternoon.

4. Discussion

4.1. Physical parameters

As described by Beer–Lambert’s law, PAR_c was strongly dependent on PAR_s and depth; however, turbidity was

expected to have a stronger effect than was observed. For example, seasonal periodicity in turbidity in Cleveland Bay, Australia accounts for >75% of the variation in light reaching the seafloor, producing alternating conditions of light limitation and light stress in shallow benthic ecosystems (Anthony et al., 2004). The Anthony et al. (2004) study used average daily conditions, whereas the present study was based on measurements at 30-min intervals over a 5-d period and lacked the requisite forcing data (wind speed, cloud cover, etc.) to replicate their analysis. However, the daily turbidity patterns observed in the present study are typical of those on the Molokai reef flat during trade wind season, which persist for the majority of the year (Ogston et al., 2004; Storlazzi et al., 2004; Presto et al., 2006). These moderate turbidity events occur for $\sim 30\%$ of the daylight hours during trade wind months, with higher suspended particulate concentrations occurring for several days during storm events (Ogston et al., 2004). The light conditions observed during this study may therefore be representative of chronic low-level sediment stress. Conditions likely differ during the winter months, when light variable winds produce lower turbidity, with occasional acute high turbidity events during periods of large waves and heavy precipitation.

4.2. Coral fluorometry

To make the in situ measurements described here, the probe of the DIVING-PAM was fixed in place for sampling periods of 8–25 h. The sample holder was made of clear plastic, and did not significantly attenuate light ($\sim 3.4\%$ reduction, Mann–Whitney $U = 9.00$, $p = 0.465$). Point measurements in outdoor tanks found no significant difference in fluorescence yield when the probe was perpendicular to the coral

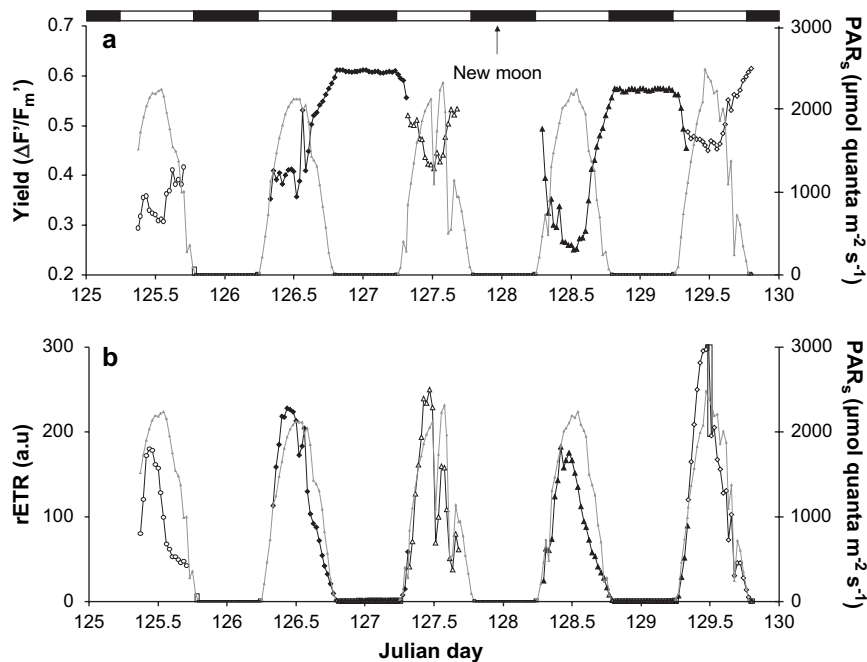


Fig. 2. Effective quantum yield $\Delta F/F_m$ (a) and relative electron transport rate (rETR, a.u. = arbitrary units) (b) for five different *Montipora capitata* colonies (open circle, filled diamond, open triangle, filled triangle, and open diamond). The gray line in each figure is the incident light at the coral surface (PAR_c).

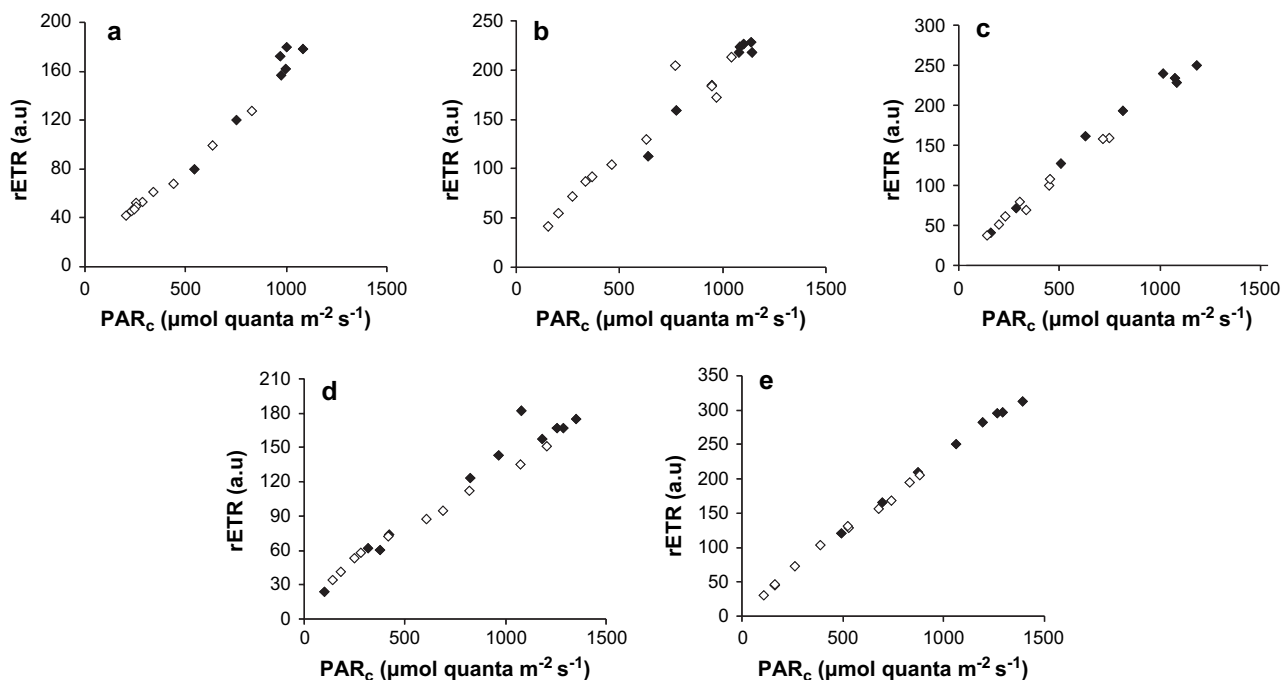


Fig. 3. Daytime relative electron transport rate (rETR, a.u. = arbitrary units) as a function of photosynthetically active radiation at the colony surface (PAR_c), for five different *Montipora capitata* colonies: (a) 5 May 05, (b) 6 May, (c) 7 May, (d) 8 May, and (e) 9 May. Filled diamonds indicate morning hours, open diamonds indicate afternoon.

surface or at a 60° angle (Mann–Whitney $U = 29.00$, $p = 0.753$). Placing the probe at an angle might have helped to reduce any effects of probe placement (self-shading, changes in flow, etc.) during longer-term in situ measurements; nevertheless, the overall fluorescence patterns observed in *Montipora capitata* were typical of corals in situ and in the laboratory. Yield was highest at night, decreased in the morning, reached a low around noon, and increased again in the afternoon (Brown et al., 1999; Ralph et al., 1999; Jones and Hoegh-Guldberg, 2001; Lesser and Gorbunov, 2001; Winters et al., 2003). However, the decoupling of surface and subsurface irradiance during the afternoon turbidity events resulted in higher rETR in the morning than in the afternoon. In contrast, Hoegh-Guldberg and Jones (1999) found higher afternoon rETRs than in the morning for *Porites cylindrica* and *Stylophora pistillata*. The difference in the results may be due to the fact that Hoegh-Guldberg and Jones (1999) report light-saturated ($>1000 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$) rETR, while the *M. capitata* colonies may not have been light-saturated at the low afternoon irradiances that were observed (average afternoon $PAR_c = 405 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$).

An additional way to consider diurnal effects is to directly plot rETR against irradiance and look for hysteresis: differences in electron transport at different times of the day but at the same light intensity. The most common pattern is that fluorescence parameters or oxygen production are higher in the morning than in the afternoon (i.e. clockwise hysteresis, sensu Levy et al., 2004), though the opposite pattern (counter-clockwise, or morning $<$ afternoon) has also been observed (Levy et al., 2004). In a similar in situ study with *Stylophora pistillata*, Winters et al. (2003) observed

considerable depression in afternoon ETR for shallow colonies (2 m), but deeper colonies (11 m) at lower light levels showed no daily hysteresis. In the present study *Montipora capitata* at water depths and PAR_c similar to the shallow corals of Winters et al. (2003) showed minimal hysteresis effects (Fig. 3). It is possible that the lack of hysteresis observed here may simply be due to the fact that hysteresis patterns are species-specific or can vary among individual colonies of a given species (Levy et al., 2004). An alternative explanation for this discrepancy is that the turbidity events could have reduced light levels at the coral surface enough to prevent the normal afternoon shallow-water dynamic photoinhibition seen in other reef systems (Gorbunov et al., 2001). This study was not specifically designed to measure dynamic photoinhibition, but there was some indication that nonphotochemical quenching ($NPQ = [F_m - F'_m]/F'_m$) was higher in the morning than in afternoon for the two corals for which nocturnal yields were measured (data not shown). Decreased nonphotochemical quenching in the afternoon likely indicates undersaturation of the reaction centers and potentially reduced productivity. However, during extremely stressful conditions it is possible that the turbidity could have a photoprotective effect: bleaching effects of solar radiation and increased water temperatures may be reduced in some reef systems due to the shading from turbidity (Phongsuwan, 1998) or clouds (Mumby et al., 2001).

4.3. Effects of turbidity and light on coral fluorescence

Daily afternoon turbidity events are characteristic of the Molokai reef flat, and may limit development of corals in these areas (Jokiel et al., 2004; Ogston et al., 2004; Presto et al.,

2006). Most of the sediment types on the Molokai reef flat that are likely to be resuspended during turbidity events (e.g. silt and clay) are primarily terrigenous in origin (Calhoun and Field, 2002). Terrigenous sediment causes greater reduction in photosynthesis than does reef sediment (Te, 2001). While some corals can derive energy from ingested sediment (e.g. Anthony, 2000), energetic costs of turbidity include increased mucus production (Riegl and Branch, 1995), increased respiration (Telesnicki and Goldberg, 1995; Te, 2001), and possibly tissue loss from abrasion.

To try and understand effects of turbidity on photo-physiological processes, coral fluorometric patterns observed in this study were compared with those predicted to occur in the absence of afternoon turbidity events (Table 2). Based on surface irradiance and water depth above the coral surface (D_c), an extinction coefficient (k) was calculated for the observed morning and afternoon conditions with the nonlinear estimation module in STATISTICA, using Beer's Law:

$$\text{PAR}_c = \text{PAR}_s e^{-kD_c}$$

and a least squares fit (morning $k = 0.7613 \text{ m}^{-1} \pm 0.0322 \text{ m}^{-1}$ (SE), $p < 0.001$, $R^2 = 0.81$; afternoon $k = 0.9641 \text{ m}^{-1} \pm 0.0299 \text{ m}^{-1}$ (SE), $p < 0.001$, $R^2 = 0.80$). The resulting extinction coefficients were used to calculate expected afternoon PAR_c in the absence of turbidity [no differences were expected between observed and predicted values for the morning as turbidity events occur primarily during the trade wind dominated afternoons; instead, morning data were used to check the validity of the calculations, and there were no significant differences between observed and predicted morning values (Table 2)]. Predicted PAR_c values in the absence of afternoon turbidity were 1.43 times higher than those observed, a significant difference (Wilcoxon matched pairs test, $Z = 5.19$, $p < 0.001$). Predicted yield values were not significantly different than those observed (Wilcoxon matched pairs test, $Z = 1.95$, $p = 0.051$), but predicted rETR in the absence of

turbidity were 1.40 times higher than observed values (Wilcoxon matched pairs test, $Z = 4.97$, $p < 0.001$).

The effect of turbidity on rETR calculated here is consistent with decreased photosynthesis rates due to turbidity for *Montipora capitata* reported by Te (2001). In some systems ETR and oxygen production can be positively correlated at low to moderate irradiance (Beer and Axelsson, 2004), and ETR has been used as a proxy for photosynthesis in terrestrial plants (Silva and Santos, 2004). However, those assumptions may not hold in corals. For example, photosynthesis and rETR are decoupled in *Pocillopora damicornis*, with the degree of non-linearity depending on whether the colonies were dark- or light-adapted (Ulstrup et al., 2006). Hoogenboom et al. (2006) demonstrated that diurnal changes in photochemical efficiency were unrelated to net photosynthesis in *Turbinaria mesenterina*. Diurnal reductions in rETR may therefore have little short-term photosynthetic consequence for *M. capitata* on the turbid Molokai reef flat. However, long-term turbidity effects may still occur; irradiance-induced changes in chlorophyll concentration can negatively affect photosynthesis on the scale of days to weeks (Hoogenboom et al., 2006), and corals can photoacclimatize within 1–2 weeks (Anthony and Hoegh-Guldberg, 2003). In addition to turbidity effects, daily resuspension events can deposit sediment on the coral surface. Sedimentation decreases fluorescence yield (Philipp and Fabricius, 2003; Weber et al., 2006; Piniak, 2007), but in the present study turbidity reduced light and increased yield, suggesting that changes in rETR were due to light and turbidity rather than changes in yield.

5. Conclusions

The corals on the Molokai reef flat face unusual challenges: high light levels during the calm morning hours, and reduced light levels during afternoon trade wind-driven resuspension of terrigenous sediment. This experiment was specifically conducted so that the high spring tides would occur in the afternoons during trade wind season, so that the synergy between afternoon trade winds and propagation of deep-water wave energy over the reef crest maximize sediment resuspension on the reef flat (Ogston et al., 2004; Storlazzi et al., 2004). However, future research is needed to describe the effects of turbidity on light availability and coral fluorescence during other time periods. Turbidity events are somewhat weaker during the remainder of the month when tides are lower (Ogston et al., 2004; Storlazzi et al., 2004), and in the winter when variable winds occur on the Molokai reef flat more often than trade winds (Presto et al., 2006). The relative effect of acute storm events and chronic resuspension events should also be addressed.

Predicting effects of or acclimatization to chronic sediment stress is predicated on demonstrating specific mechanistic relationships between physical factors and physiological responses (Anthony and Larcombe, 2002). PAM and other fluorometers can offer useful physiological insights on turbidity effects, although the data should be interpreted with caution as PAM data and oxygen production are decoupled in

Table 2

Average values for physical factors and coral fluorescence on the Molokai reef flat in the morning (07:00–12:00) and afternoon (12:00–18:00) during the study, and values predicted from regressions of yield on light (morning yield = $-0.1412 \times \log \text{PAR}_c + 0.8095$, $R^2 = 0.31$; afternoon yield = $-0.1579 \times \log \text{PAR}_c + 0.8436$, $R^2 = 0.46$) and the calculated morning extinction coefficient ($k = 0.7613 \text{ m}^{-1}$). Parentheses are standard error

	Observed	Predicted
Morning		
PAR_s	1587 (83)	—
PAR_c	825 (55)	855 (42)
D_c	0.80 (0.01)	—
Yield	0.410 (0.012)	0.401 (0.004)
rETR	161.1 (11.0)	167.3 (7.4)
Afternoon		
PAR_s	1359 (94)	—
PAR_c	405 (38)	533 (40)
D_c	1.27 (0.02)	—
Yield	0.455 (0.012)	0.434 (0.009)
rETR	83.0 (7.0)	106.7 (7.1)

corals (Hoogenboom et al., 2006; Ulstrup et al., 2006). The relatively high cost and short battery life of fluorometers may limit their utility for long-term in situ monitoring. However, short-term deployments or diver measurements of fluorescence could be combined with long-term water quality monitoring to test the effects of mitigation actions (revegetation of the Molokai coastal slope, restoration of water flow through the wharf) that would alter turbidity and light on the Molokai reef flat.

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References

- Anthony, K.R.N., 2000. Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). *Coral Reefs* 19, 59–67.
- Anthony, K.R.N., 2006. Enhanced energy status of corals on coastal, high-turbidity reefs. *Marine Ecology Progress Series* 319, 111–116.
- Anthony, K.R.N., Connolly, S.R., 2004. Environmental limits to growth: physiological niche boundaries of corals along turbidity-light gradients. *Oecologia* 141, 373–384.
- Anthony, K.R.N., Connolly, S.R., Willis, B.L., 2002. Comparative analysis of energy allocation to tissue and skeletal growth in corals. *Limnology and Oceanography* 47, 1417–1429.
- Anthony, K.R.N., Fabricius, K.E., 2000. Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. *Journal of Experimental Marine Biology and Ecology* 252, 221–253.
- Anthony, K.R.N., Hoegh-Guldberg, O., 2003. Kinetics of photoacclimation in corals. *Oecologia* 134, 23–31.
- Anthony, K.R.N., Larcombe, P., 2002. Coral reefs in turbid waters: sediment-induced stresses in corals and likely mechanisms of adaptation. *Proceedings of the Ninth International Coral Reef Symposium Bali* 1, 239–244.
- Anthony, K.R.N., Ridd, P.V., Orpin, A.R., Larcombe, P., Lough, J., 2004. Temporal variation of light availability in coastal benthic habitats: effects of clouds, turbidity, and tides. *Limnology and Oceanography* 49, 2201–2211.
- Ayling, A.M., Ayling, A.L., 1991. The effect of sediment runoff on the coral populations of fringing reefs at Cape Tribulation. In: Great Barrier Reef Marine Park Authority Research Publication 26. Great Barrier Reef Marine Park Authority, Townsville.
- Beer, S., Axelsson, L., 2004. Limitations in the use of PAM fluorometry for measuring photosynthetic rates of macroalgae at high irradiances. *European Journal of Phycology* 39, 1–7.
- Bothner, M.H., Reynolds, R.L., Casso, M.A., Storlazzi, C.D., Field, M.E., 2006. Quantity, composition, and source of sediment collected in sediment traps along the fringing coral reef off Molokai, Hawaii. *Marine Pollution Bulletin* 52, 1034–1047.
- Brown, B.E., Ambarsari, I., Warner, M.E., Fitt, W.K., Dunne, R.P., Gibb, S.W., Cummings, D.G., 1999. Diurnal changes in photochemical efficiency and xanthophyll concentrations in shallow water reef corals: evidence for photoinhibition and photoprotection. *Coral Reefs* 18, 99–105.
- Calhoun, R.S., Field, M.E., 2002. Beach and reef-flat sediments along the south shore of Molokai, Hawaii. In: Magoon, O.T., Robbins, L.L., Ewing, L. (Eds.), *Carbonate Beaches 2000, Proceedings of the First International Symposium on Carbonate Sand Beaches*. American Society of Civil Engineering, Reston, VA, pp. 163–171.
- Cochran-Marquez, S.A., 2005. Molokai Benthic Habitat Mapping. U.S. Geological Survey Open-File Report 2005-1070. Available from: <http://pubs.usgs.gov/of/2005/1070/> (accessed 01.07.07).
- Dollar, S.J., Grigg, R.W., 2004. Anthropogenic and natural stresses on selected coral reefs in Hawaii: a multidecade synthesis of impact and recovery. *Pacific Science* 58, 281–304.
- Edmunds, P.J., Spencer Davies, P., 1989. An energy budget for *Porites porites* (Scleractinia), growing in a stressed environment. *Coral Reefs* 8, 37–43.
- Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50, 125–146.
- Fletcher, C.H., Richmond, B.M., Grossman, E.E., Gibbs, A.E., 2002. Atlas of Natural Hazards in the Hawaiian Coastal Zone. U.S. Geological Survey Geological Investigations Series I-2716. USGS, Reston, VA.
- Genty, B., Briantais, J.M., Baker, N.R., 1989. The relationship between quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochimica et Biophysica Acta* 990, 87–92.
- Gorbunov, M.Y., Kolber, Z.S., Lesser, M.P., Falkowski, P.G., 2001. Photosynthesis and photoprotection in symbiotic corals. *Limnology and Oceanography* 46, 75–85.
- Hodgson, G., 1989. The effects of sedimentation on Indo-Pacific reef corals. Ph.D. thesis, University of Hawaii, Honolulu, HI.
- Hoegh-Guldberg, O., Jones, R.J., 1999. Photoinhibition and photoprotection in symbiotic dinoflagellates from reef-building corals. *Marine Ecology Progress Series* 183, 73–86.
- Hoogenboom, M.O., Anthony, K.R.N., Connolly, S.R., 2006. Energetic cost of photoinhibition in corals. *Marine Ecology Progress Series* 313, 1–12.
- Jokiel, P.L., Brown, E.K., Friedlander, A., Rodgers, K.S., Williams, W.R., 2004. Hawaii coral reef assessment and monitoring program: spatial patterns and temporal dynamics in reef coral communities. *Pacific Science* 58, 159–174.
- Jokiel, P.L., Brown, E.K., Rodgers, K.S., Smith, W.R. Reef corals and the coral reefs of South Molokai. In: Field, M.E., Storlazzi, C.D., Cochran-Marquez, S.A., Logan, J.B. (Eds.), *Atlas of a Fringing Coral Reef: Molokai, Hawaii – The Longest Fringing Reef in the Hawaiian Chain*. USGS Scientific Investigations Report 2007-5101, In press.
- Jones, R.J., Hoegh-Guldberg, O., 2001. Diurnal changes in the photochemical efficiency of the symbiotic dinoflagellates (Dinophyceae) of corals: photoprotection, photoinactivation and the relationship to coral bleaching. *Plant, Cell, and Environment* 24, 89–99.
- Lesser, M.P., Gorbunov, M.Y., 2001. Diurnal and bathymetric changes in chlorophyll fluorescence yields of reef corals measured in situ with a fast repetition rate fluorometer. *Marine Ecology Progress Series* 212, 69–77.
- Levy, O., Dubinsky, Z., Schneider, K., Achituv, Y., Zakai, D., Gorbunov, M.Y., 2004. Diurnal hysteresis in coral photosynthesis. *Marine Ecology Progress Series* 268, 105–117.
- McClanahan, T.R., Obura, D., 1997. Sedimentation effects on shallow coral communities in Kenya. *Journal of Experimental Marine Biology and Ecology* 209, 103–122.
- McCulloch, M., Fallon, S., Wyndham, T., Hendy, E., Lough, J., Barnes, D., 2003. Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. *Nature* 421, 727–730.
- Mumby, P.J., Chisholm, J.R.M., Edwards, A.J., Andrefouet, S., Jaubert, J., 2001. Cloudy weather may have saved Society Island coral reefs during the 1998 ENSO event. *Marine Ecology Progress Series* 222, 209–216.
- Ogston, A.S., Storlazzi, C.D., Field, M.E., Presto, M.K., 2004. Sediment resuspension and transport patterns on a fringing reef flat, Molokai, Hawaii. *Coral Reefs* 23, 559–569.
- Pastorok, R.A., Bilyard, G.R., 1985. Effects of sewage pollution on coral reef communities. *Marine Ecology Progress Series* 21, 175–189.
- Philipp, E., Fabricius, K., 2003. Photophysiological stress in scleractinian corals in response to short-term sedimentation. *Journal of Experimental Marine Biology and Ecology* 287, 57–78.

- Piniak, G.A., 2007. Effects of two sediment types on the fluorescence yield of two Hawaiian scleractinian corals. *Marine Environmental Research* 64, 456–468.
- Phongsuwan, N., 1998. Extensive coral mortality as a result of bleaching in the Andaman Sea in 1995. *Coral Reefs* 17, 70.
- Presto, M.K., Ogston, A.S., Storlazzi, C.D., Field, M.E., 2006. Temporal and spatial variability in the flow and dispersal of suspended sediment on a fringing reef flat, Molokai, Hawaii. *Estuarine, Coastal and Shelf Science* 67, 67–81.
- Ralph, P.J., Gademann, R., Larkum, A.W.D., Schreiber, U., 1999. In situ underwater measurements of photosynthetic activity of coral zooxanthellae and other reef-dwelling dinoflagellate endosymbionts. *Marine Ecology Progress Series* 180, 139–147.
- Riegl, B., Branch, G.M., 1995. Effects of sediments on the energy budgets of four scleractinian corals (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. *Journal of Experimental Marine Biology and Ecology* 186, 259–275.
- Roberts, L.M., 2001. Historical land use, coastal change, and sedimentation on south Molokai. In: Saxena, N. (Ed.), *Recent Advances in Marine Science and Technology*, 2000. PACON International, Honolulu, Hawaii, pp. 167–176.
- Rodgers, K.S., Jokiel, P.L., Smith, W.R., Farrell, F., Uchino, K., 2005. Biological Survey in Support of USGS Turbidity and Sediment Baseline Survey on South Molokai Reef Flat, April 2005. U.S. Geological Survey Open-File Report 2005-1361. Available from: <http://pubs.usgs.gov/of/2005/1361/> (accessed 01.07.07).
- Rogers, C.S., 1983. Sublethal and lethal effects of sediments applied to common Caribbean reef corals in the field. *Marine Pollution Bulletin* 14, 378–382.
- Rogers, C.S., 1990. Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* 62, 185–202.
- Silva, J., Santos, R., 2004. Can chlorophyll fluorescence be used to estimate photosynthetic production in the seagrass *Zostera noltii*? *Journal of Experimental Marine Biology and Ecology* 307, 207–216.
- Stamski, R.E., Field, M.E., 2006. Characterization of sediment trapped by macroalgae on a Hawaiian reef flat. *Estuarine, Coastal and Shelf Science* 66, 211–216.
- StatSoft, 2006. STATISTICA Data Analysis Software System, Version 7.1. StatSoft, Inc., Tulsa, OK.
- Storlazzi, C.D., Logan, J.B., Field, M.E., 2003. Quantitative morphology of a fringing reef from high-resolution laser bathymetry: Southern Molokai, Hawaii. *Geological Society of America Bulletin* 115, 1344–1355.
- Storlazzi, C.D., Ogston, A.S., Field, M.E., Presto, M.K., 2004. Wave- and tidally-driven flow and sediment flux across a fringing coral reef: Southern Molokai, Hawaii. *Continental Shelf Research* 24, 1397–1419.
- Te, F.T., 2001. Responses of Hawaiian Scleractinian Corals to Different Levels of Terrestrial and Carbonate Sediment. Ph.D. thesis, University of Hawaii, Honolulu, HI.
- Telesnicki, J.G., Goldberg, W.M., 1995. Effects of turbidity on photosynthesis and respiration of two South Florida reef coral species. *Bulletin of Marine Science* 57, 527–539.
- Ulstrup, K.E., Ralph, P.J., Larkum, A.W.D., Kuhl, M., 2006. Intra-colonial variability in light acclimation of zooxanthellae in coral tissues of *Pocillopora damicornis*. *Marine Biology* 149, 1325–1335.
- Walz, 1998. Underwater Fluorometer Diving-PAM Handbook of Operation. Heinz Walz GmbH, Effeltrich.
- Weber, M., Lott, C., Fabricius, K.E., 2006. Sedimentation stress in a scleractinian coral exposed to terrestrial and marine sediments with contrasting physical, organic and geochemical properties. *Journal of Experimental Marine Biology and Ecology* 336, 18–32.
- Winters, G., Loya, Y., Rottgers, R., Beer, S., 2003. Photoinhibition in shallow-water colonies of the coral *Stylophora pistillata* as measured in situ. *Limnology and Oceanography* 48, 1388–1393.
- Woolfe, K.J., Larcombe, P., 1999. Increased sediment supply to the Great Barrier Reef will not increase sediment accumulation at most coral reefs. *Coral Reefs* 18, 163–169.
- Yates, K.K., Halley, R.B., 2003. Measuring coral reef community metabolism using new benthic chamber technology. *Coral Reefs* 22, 247–255.
- Zar, J.H., 1984. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ.