

Short-term coherency between gross primary production and community respiration in an algal-dominated reef flat

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Received: 3 December 2009 / Accepted: 10 August 2010 / Published online: 2 September 2010
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Abstract Rates of net community carbon production ($\text{mmol C m}^{-2} \text{ h}^{-1}$) were measured continuously in an algal-dominated reef flat community on the Kaneohe Bay barrier reef, Hawaii, for 12 days at the end of October 2006. The weather became increasingly cloudy during the last 5 days of measurements, resulting in a sevenfold decline in daily incident light ($28\text{--}4 \text{ Ein m}^{-2} \text{ d}^{-1}$). In response, gross primary production (P) for the reef flat community also decreased sevenfold, varying linearly with light ($r^2 = 0.92$, $n = 12$). Community respiration (R) decreased fivefold over this same period and was highly correlated with changes in P ($r^2 = 0.84$, $n = 12$). We reason that this short-term coherence between P and R indicates that most of the carbon fixed during this period was rapidly metabolized via plant respiration. We further conclude that the dominance of autotrophic respiration under general conditions of nutrient-limited growth can explain much of the balance between P and R that is commonly observed in shallow reef communities.

Keywords Biogeochemistry · Community · Production · Respiration

Communicated by Biology Editor Dr. Mark Warner

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Introduction

Gross primary production (P) and respiration (R) of shallow coral reef communities are generally equal, indicating that these communities consume roughly the same amount of organic carbon as they produce (Kinsey 1985; Crossland et al. 1991; Atkinson and Falter 2003). These observations led early investigators to hypothesize that reef communities were closed systems in which high rates of carbon production by autotrophs were balanced by equally high rates of consumption by heterotrophs and that this trophic balance was sustained by the tight recycling of nutrients (Pomeroy 1970). Most estimates of P and R reported in the literature have been derived from discrete measurements of net production made over a few weeks. For some reef communities, these measurements were repeated more than once, at intervals ranging from months to years (Kinsey 1979; Gattuso et al. 1996). In contrast, Falter et al. (2001) measured day-to-day changes in both P and R of the Biosphere II reef mesocosm over a three-year period and found a significant correlation between P and R at timescales of days to weeks, changes that were much faster than seasonal variations in community biomass (Bymers et al. 2005). They concluded that much of the short-term variation in R was being driven by short-term variation in P , and thus light. In a later study, Langdon et al. (2003) demonstrated that rates of light respiration within the Biosphere II mesocosm were 1.2 to 2.1 times higher than rates of dark respiration, results consistent with prior studies of primary producers (Bender and Grande 1987; Weger et al. 1989). This further reinforced the notion that increases in production drive increases in respiration at short timescales (hours to days).

Similar short-term coherency between P and R had never been observed in natural, open reef communities

because of the difficulty in making fast enough measurements over a well-defined reef area. We have demonstrated that continuous measurements of net production can be made over a reef community using a modified Eulerian approach (Falter et al. 2008). This same approach allowed us to measure day-to-day changes in P and R over the same reef flat community for 12 consecutive days. During the last 5 days of the deployment, increasing cloud cover caused an 85% reduction in daily integrated light. This fortuitous weather event provided a natural perturbation experiment in which to study the effects of rapid and extreme changes in light on both community production and respiration.

Methods

Kaneohe Bay is located on the northeast, or windward, side of the island of Oahu, Hawaii. The Kaneohe Bay Barrier Reef is approximately 2 km wide and 10 km long, separating the interior bay from the adjacent coastal ocean (Fig. 1a). Our study site is a completely lithified reef surface 1.5–2 m deep located on the reef flat near the island of Kapapa, just shoreward of the surf zone (Fig. 1b). The community inhabiting this section of the reef is comprised mainly of mixed macrophytes from the phyla chlorophyta, phaeophyta, rhodophyta, and cyanophyta. The taxonomic composition of the community can vary with season in terms of biomass per area but is perennially dominated by *Sargassum*, *Microdictyon*, and *Halimeda* (Table 1). Prior surveys have demonstrated that coral cover within the study area is less than 10%. Waves incident to the reef generally drive the movement of water across the reef flat and through the study area while semi-diurnal tides

typically vary ± 0.3 m in height. Wave heights in the study area are generally depth-limited to heights <0.5 m (Lowe et al. 2005) and are rarely subject to secondary breaking as a result of its position landward of the reef crest and surf zone.

The following data were collected between October 20 and November 2, 2006. Planar downwelling photosynthetically active radiation (PAR) irradiance (E_d in $\mu\text{Ein m}^{-2} \text{s}^{-1}$) was measured at the center of the study area using a Biospherical Instruments cosine PAR collector (QCP-2300) logging into a Seabird Electronics 16 + CTD. The CTD was also used to record temperature and salinity. Daily integrated light (ΣE_d in $\text{Ein m}^{-2} \text{d}^{-1}$) was calculated by integrating daily light curves from sunrise to sunset. Vertical profiles of current speed and direction were measured at each vertex of a triangular control volume using three RD Instruments 1200 kHz acoustic Doppler current profilers (ADCPs). The ADCPs were programmed to sample velocity and pressure at 1 Hz in 10-minute bursts every 20 min (mode 12). The purpose of a triangular control volume is that it required the least number of instruments to enclose a fixed planar area of the reef. The resulting mean profiles were then integrated to calculate the total 2-D Eulerian transport ($\text{m}^3 \text{s}^{-1} \text{m}^{-1}$), \vec{q}_E , for each burst. Wave height spectra were calculated from pressure data recorded by the ADCPs using linear wave theory. The magnitude of the Stokes transport due to waves, \vec{q}_S , was estimated from the wave height spectra following the approach of Kenyon (1969). The total transport was calculated as the sum of the Eulerian and Stokes transport ($\vec{q} = \vec{q}_E + \vec{q}_S$).

Dissolved oxygen and temperature were measured at the vertices of the control volume with In Situ Troll 9000 loggers equipped with Aanderaa RDO dissolved oxygen

Fig. 1 **a** Quickbird image of Kaneohe Bay courtesy of Digitalglobe© with the study area bounded by a red box. **b** Close-up image of the study area showing the location of the control volume vertices

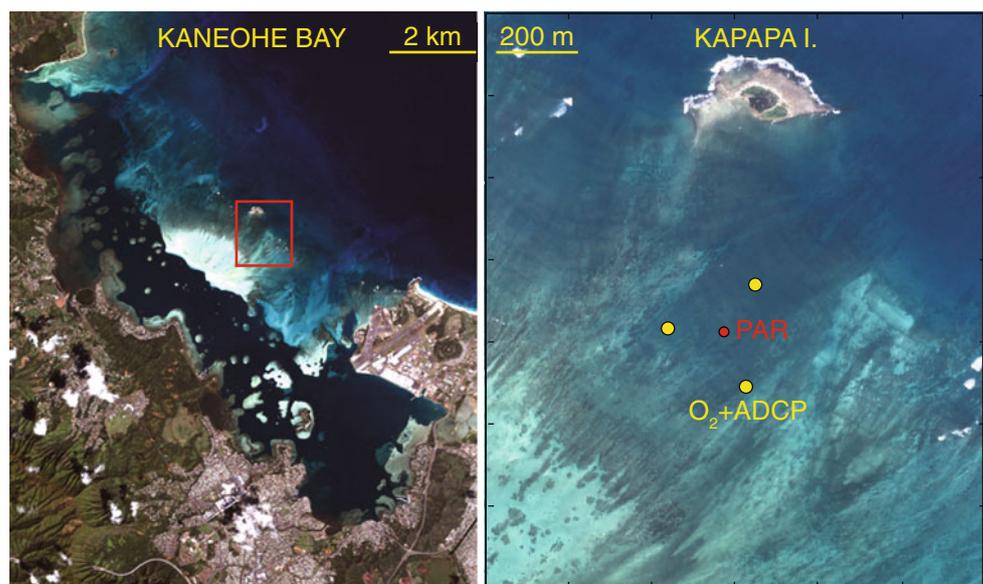


Table 1 Biomass per area of macrophytes inhabiting the study site in winter and summer

	Algae	gDW m ⁻²
Winter	<i>Acanthophora spicifera</i>	2.3
	<i>Halimeda discoidea</i>	31
	<i>Microdictyon setchellianum</i>	22
	<i>Sargassum polyphyllum</i>	22
Summer	<i>Acanthophora spicifera</i>	3.8
	<i>Dictyota acutiloba</i>	5.2
	<i>Hypnea cervicornis</i>	3.8
	<i>Lyngbya majuscula</i>	8.6
	<i>Padina sanctae-crucis</i>	2.9
	<i>Turbinaria ornata</i>	1.7
	<i>Halimeda discoidea</i>	15
	<i>Microdictyon setchellianum</i>	28
	<i>Sargassum polyphyllum</i>	86

Values represent the average biomass per area measured in 16 randomly deployed quadrats (0.5 × 0.5 m). Late autumn species distributions (this study) are between the winter and summer values shown

optodes sampling every 5 min. All three oxygen sensors were calibrated in the laboratory (±2 μM O₂) before deployment over a range of 20 to 350 μM O₂ at 25°C and a salinity of 35 by Winkler titration (± 0.5 μM O₂). When the oxygen sensors were deployed on the reef flat, duplicate water samples were collected every day using a 2-L Van Dorn bottle and immediately fixed for analysis by Winkler titration; resulting data were used to correct for drift in each of the sensors. All three sensors drifted less than 10 μM over the course of their deployment.

Fluxes of dissolved oxygen (J_{O_2}) to the benthos were calculated using a vertically integrated form of the advection–dispersion–reaction equation according to (Falter et al. 2008):

$$J_{O_2} = -K \nabla_h^2 C_{O_2} + h \frac{\partial C_{O_2}}{\partial t} + \vec{q} \cdot \vec{\nabla}_h C_{O_2} - J_{gas} \quad (1)$$

where h is water depth, K is the horizontal dispersion coefficient, and J_{gas} is the flux of oxygen across the air–water interface. We have already shown that the dispersion term is negligible and the gas flux term is minor in our study area (Falter et al. 2008). Hourly rates of net community production of organic carbon (NP in mmol C m⁻² h⁻¹) were calculated from continuous measurements of J_{O_2} , assuming a photosynthetic and respiratory quotient equal to 1 (1.05 ± 0.1, Smith and Marsh 1973; Carpenter and Williams 2007). Community respiration (R in mmol C m⁻² d⁻¹) for a given day was calculated as the average of night-time hourly net community production from the preceding and following nights multiplied by 24. Gross primary production (P in mmol C m⁻² d⁻¹) was calculated from integrating net

community production between sunrise and sunset and adding them to hourly rates of community respiration (Falter et al. 2001). While this approach does not account for differences between rates of light and dark respiration, it is consistent with prior approaches for calculating P and R in reef flat communities made over the past 50 years and, thus, provides us with an unbiased means of comparing our data with values reported in the literature.

Results

During the first 7 days of measurement, maximum daily irradiances ranged 800–1100 μEin m⁻² s⁻¹ as a result of changes in cloud cover, variations typical for the windward side of Oahu (Fig. 2). Hourly net production ranged between -30 mmol C m⁻² h⁻¹ at night and 70 mmol C m⁻² h⁻¹ during the day (Fig. 3). P averaged 520 mmol C m⁻² d⁻¹ and R averaged 500 mmol C m⁻² d⁻¹ over this 7-day period (Fig. 4), values within 10% of the average for reef flat communities worldwide (580 mmol C m⁻² d⁻¹, Kinsey 1985). During the last 5 days of the deployment, a less typical weather system formed over the windward side of Oahu causing cloud cover to become increasingly thicker. Maximum light intensities at the solar zenith on the last 2 days were similar to early morning and late afternoon intensities earlier in the study (~200 μEin m⁻² s⁻¹; Fig. 2), while daily integrated light decreased by 86%, from 26.6 Ein m⁻² d⁻¹ to just 3.7 Ein m⁻² d⁻¹ (Fig. 4). During this 5-day period, rates of daytime net production and night-time respiration decreased proportionately (Fig. 3). Thus, there was an 85% decrease in P , from a maximum of 670 to a minimum of 100 mmol C m⁻² d⁻¹ (Fig. 4), which was highly correlated with light ($r^2 = 0.92$,

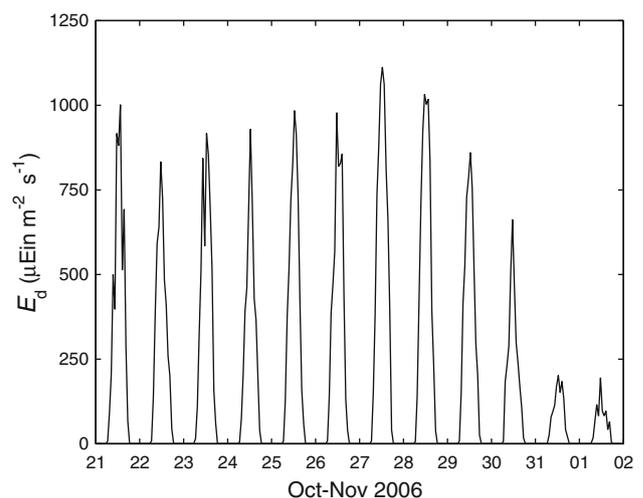


Fig. 2 Instantaneous downwelling light (PAR) incident to the reef flat versus time after application of a 1-hour moving average

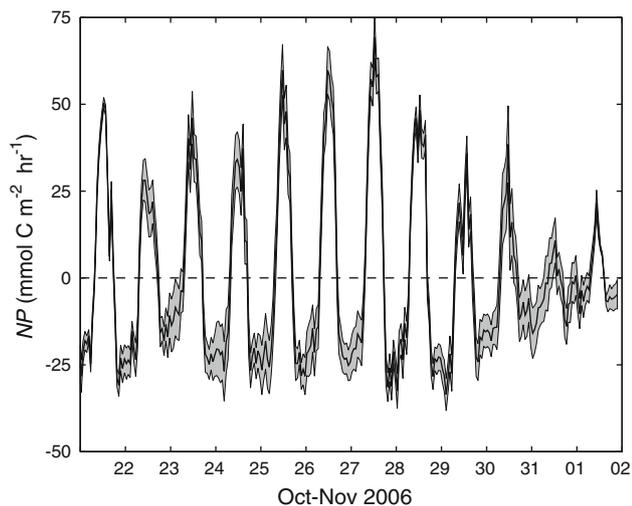


Fig. 3 Hourly rates of net production (*heavy line*) versus time in October and November of 2006. The *gray* boundaries represent the standard error in estimates of *NP*, and the *dashed line* represents zero net production

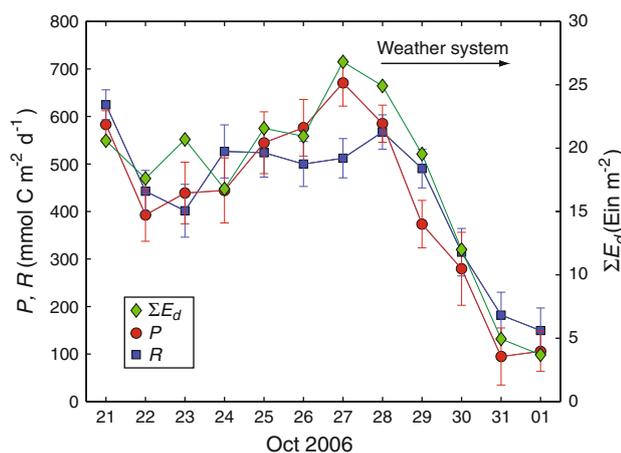


Fig. 4 Cumulative daily light incident to the reef flat, gross primary production (*P*), and community respiration (*R*) at the end of October 2006

$n = 12$). In addition, there was a 77% decrease in *R*, from a maximum of 570 to a minimum of 150 $\text{mmol C m}^{-2} \text{d}^{-1}$ (Fig. 2), which was highly correlated with *P* ($r^2 = 0.84$, $n = 12$). Finally, rates of night-time respiration in the present community decreased on average by 30% from just after sunset to just before sunrise, or $\sim 2.5\%$ per hour (Fig. 5).

Discussion

The strong correlation between decreasing community production and decreasing respiration indicates tight coupling between the production and consumption of fixed carbon on timescales of days, behavior which is consistent

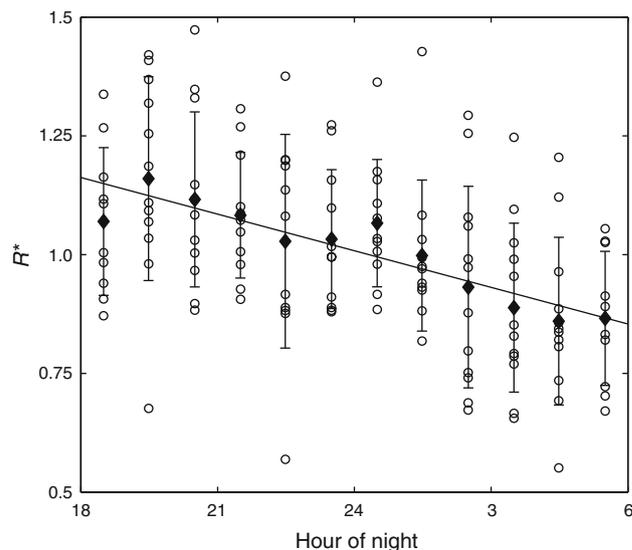


Fig. 5 Hourly night-time respiration rates normalized by the average respiration rate for their respective nights (R^*). *Circles* represent individual values, whereas *diamonds* represent values averaged over each hour of night (*error bars* represent ± 1 SD). *Line* shown is the best-fit linear regression between mean R^* versus hour of night ($y = -0.027x + 1.7$, $n = 12$, $r^2 = 0.81$) whose slope is significantly less than zero ($p < 0.01$)

with results from the algal-dominated community in the Biosphere II reef mesocosm (Falter et al. 2001). This short-term coherence has not previously been observed in the field, probably for two reasons. First, given measurement errors in *P* and *R* of at least 10–15%, it would take an unusually rapid and severe change in light levels ($>50\%$) to observe significant correlations between *P* and *R* on the timescale of days. Second, prior studies integrated diel curves of hourly net production collected over weeks, thus obscuring any short-term changes in *P* and *R*.

There are three explanations for the decrease in night-time respiration from sunset to sunrise: (1) community respiration rates fell with declining water column oxygen concentrations as indicative of microbial and invertebrate heterotrophic respiration (Johnson 1967; Newton and Atkinson 1991); (2) there was elevated crepuscular respiration in reef heterotrophs as a result of diurnal shifts in feeding behavior; and (3) light-enhanced respiration of plants extended into the twilight hours. The first explanation is attractive because respiration rates of sediment microbial and infaunal communities are often proportional to water column oxygen concentration (Jorgensen and Revsbech 1985; Jorgensen and Des Marais 1990). In our data set, however, there was no correlation between rates of night-time respiration and oxygen concentration. Furthermore, given that respiration rates of coral reef sand communities are an order of magnitude lower than this algal-reef flat community (Atkinson and Falter 2003), it is even more unlikely that changes in the sediment respiration

drove the observed 77% change in community respiration. It is well known that grazers are more active in the evening; however, there are no studies that quantify the change in respiration associated with this behavior. The third explanation, that the higher respiration rate in the evening reflects higher rates of light-driven respiration in the afternoon following the cumulative buildup of fixed carbon during the day is well documented for benthic reef primary producers (Gao et al. 1993; Al-Horani et al. 2003; Hoo-genboom et al. 2006). Daily rates of community respiration should also take into account elevated respiration rates in the light; however, rates of light respiration are only directly measurable using specialized chemical tracers (Langdon et al. 2003). Although it is not possible to make light respiration measurements in the field, higher rates of light versus dark respiration would result in even greater coherency between daily changes in production and respiration than we report here. Regardless, conventional methods of estimating gross primary production based on dark respiration rates are valid for evaluating the balance between fixed carbon production and respiration over periods of days, weeks, months, or years because it is unlikely that carbon fixed and respired within the same light period has any meaningful role in community energy or mass budgets on longer timescales.

Plants, both free-living and symbiotic, constitute 85–90% of the total biomass in shallow reef communities and therefore are the dominant component of community metabolism (Odum and Odum 1955). It is unlikely that the rapid changes in community respiration measured in this study were driven by changes in the biomass and/or metabolic activity of reef heterotrophs. No such changes in faunal abundance were observed in response to the short-term changes in community production and respiration that occurred within the Biosphere II reef mesocosm. Given that the study site is located landward of the surf zone, it would also be impossible for any physical disturbance to alter the biomass of algae during the study period. Furthermore, given that most of the grazers at the study site consist of small (<10–20 cm) crustaceans, fish, and echinoderms, we doubt that the 77% decline in community respiration occurred as a result of a rapid and massive migration of grazers off the reef flat.

Plant growth in shallow reef flat communities is generally nutrient-limited (Hatcher and Larkum 1983; Schaffelke and Klumpp 1998), indicating that these communities supply fixed carbon in excess of what is needed for the growth of new biomass. Prior work on this reef has shown that rates of nutrient uptake are mass-transfer limited indicating nutrient limitation of plant growth in this community (Falter et al. 2004). Consequently, C:N:P ratios of the this macrophyte community are high (660:30:1–770:37:1, Falter et al. under review). Thus, it is likely that much of the fixed carbon is

used to support catabolic pathways via respiration rather than anabolic pathways such as growth. Some of the algal-dominated communities reviewed by Kinsey (1985) exhibited *P*:*R* ratios much greater than one, indicating their ability to direct much of their fixed carbon into the growth of new tissue. Many of these values were not for intact algal communities, but for fragments of algae removed from the reef and incubated in closed containers with little control on the spatial structure and magnitude of the local light field (Rogers and Salesky 1981; Vooren 1981; Hawkins and Lewis 1982). Few of these studies also measured production and respiration at time- and space-scales comparable to those measured for intact reef communities; thus, the measured *P*:*R* probably represented only a transient imbalance between rates of carbon production and consumption. In contrast, field measurements indicate that the *P*:*R* of natural algal-dominated communities are close to one (Kinsey 1979; Gattuso et al. 1997). Furthermore, Binzer et al. (2006) demonstrated that the *P*:*R* ratios for experimental macrophyte communities were close to one (median = 1.2) when integrated over a typical diurnal light curve even though the *P*:*R* ratios of tissue fragments from the same community were very high (median = 6.6). This work was based on 190 measurements of light and net production that spanned 20 different genera of marine and freshwater macrophytes. They concluded that their results were due to the higher ratios of biomass per absorbed light in whole macrophyte canopies versus freely suspended tissue fragments. Thus, both nutrient limitation and high biomass per area can constrain the *P*:*R* in real macrophyte communities.

The *P*:*R* ratio for the present reef flat community averaged 1.04 ± 0.06 over the eight days leading up to the arrival of the weather system, thus indicating high carbon turnover and little net production under more normal conditions (Fig. 2). More recent data indicate that the *P*:*R* ratio for this same community was modestly greater than one in summer when environmental conditions were more favorable for growth (*P*:*R* = 1.25; Falter et al. pers. obs.). Nonetheless, such relatively low *P*:*R* indicate that the production and respiration of fixed carbon in this community is tightly coupled all year round and that net growth is generally just a fraction of gross primary production. Such marginal net productivity can help explain how grazers are still able to control the standing biomass of reef algae even despite the high rates of light-driven carbon fixation, and therefore influence the competition for space between coral and algae (McCook et al. 2001).

In summary, we observed rapid coherent changes in both community production and respiration of a shallow reef community due to a drastic reduction in light over a 5-day period. These changes reflect the dominance of autotrophic respiration where most of the fixed carbon is shunted toward autotrophic respiration, rather than to the

growth of new tissue. Thus, this result provides further evidence that carbon metabolism in shallow reef communities is dominated by plants, the growth of these plants is nutrient-limited, and a substantial portion of the carbon they fix is quickly metabolized via autotrophic respiration. Therefore, we expect that $P:R$ ratios for many algal-dominated shallow reef communities to be much closer to one than predicted from experimental incubations of algal fragments. More importantly, this simple trophic model can explain much of why production and respiration are commonly so well balanced in reef communities worldwide.

Acknowledgments The work presented in this manuscript was supported by a collaborative grant from the NSF Chemical (OCE-0453117) and Physical (OCE-0622967) Oceanography Programs as well as the Alliance for Coastal Technologies, award #CA 07-10.

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