RESEARCH ARTICLE

Diel versus time-integrated (daily) photosynthesis and irradiance relationships of coral reef organisms and communities

Yvonne Sawall [ORCID]*, **Eric J. Hochberg**

Coral Reef Ecology and Optics Laboratory (CREOL), Bermuda Institute of Ocean Sciences (BIOS), St. George's, Bermuda

* yvonne.sawall@bios.edu

Abstract

The most important source of energy to tropical shallow water coral reefs is light, the transformation of which ultimately limits reef biomass and growth. Therefore, measurements of productivity (primary production, P) for benthic reef organisms and communities are critical to understand reef functioning. Short-term (minutes to hours) P measurements of reef photosynthesizers virtually always produce the classic hyperbolic tangent (or similar) P-E (irradiance) relationship, with P rapidly rising to a saturation point as E increases. Longer-term (days to weeks), larger-scale investigations of natural reef communities typically do not explore P-E relationships, but the few that do show no saturation of *time-integrated* P with high *time-integrated* E. In this paper we present a modeling study to reconcile this apparent contradiction. We used 52 published short-term (*instantaneous*) P-E curves of organisms (corals, algae) and communities (corals, mixed corals and algae) from different reefs in the Indo-Pacific and the Caribbean, each coupled with 928 diel light curves comprising a wide range of cloud cover scenarios. The diel light curves provided *instantaneous* E at 1-minute intervals, from which we calculated corresponding *instantaneous* P using the different published P-E relationships. We integrated both variables to calculate *time-integrated* E and P. *Time-integrated* E varied up to 18-fold due to changes in cloud cover and season. We found that, despite routine saturation of *instantaneous* P, day-scale P-E relationships were near linear in all cases, with slightly decreased linearity in cases where instantaneous light saturation occurred very early during the day. This indicates that the Functional Convergence Hypothesis (FCH) developed by terrestrial ecologists may also apply for reef photosynthesizers. The FCH states that despite short-term light saturation, plants on average do not absorb more light than they can use, since resource allocations are strictly coordinated and tailored towards an optimal use. Thus, there is no contradiction: At the growth time scale ($\geq$ day), P should be expected to be a near linear function of E. One implication is that reef P can be estimated using rapid optical measurements, as opposed to traditional, laborious respirometry methods. The requirement going forward is to derive appropriate values for light-use efficiency, which is the rate at which the plant or community converts absorbed light into fixed carbon.

Introduction

Light is the most important source of energy for shallow water benthic coral reef communities, where corals and algae are highly productive (e.g., [1, 2]). Most corals (hard and soft) strongly depend on the productivity of their photosynthesizing endosymbionts, dinoflagellates of the genus *Symbiodinium* (zooxanthellae), which cover most of the energy demands of corals and hence determine coral growth (calcification in the case of hard corals; [3–6]). Free-living algae form another important group of primary producers in reefs and include, for example, crustose coralline red algae (CCA), "fleshy" calcifying (e.g., *Halimeda*) and non-calcifying algae and turf algae. CCA contribute to reef growth as well as to substrate stabilization (e.g., by cementing coral rubble; [7]), while fleshy macroalgae and turf algae serve as an important food source for herbivores [8, 9]. Microalgae (e.g., diatoms) and cyanobacteria contribute to reef productivity, as well [10, 11]. Since primary production (P) of shallow water reef organisms ultimately determines reef biomass and growth [12, 13], measurement of P for individuals and communities is of high priority to understand reef functioning.

Current approaches to measure P of coral reef organisms and communities in-situ are all based on respirometry. These include organism [14, 15] or community enclosures [16, 17], flow respirometry over reef communities [18,19], and the gradient flux approach [20, 21]. These methods each feature different logistical restrictions and are generally very laborious, which makes large-scale (>1 km) and repetitive measurements (e.g., for monitoring purposes) very difficult. Another challenge is interpreting in-situ P measurements under light conditions that vary day to day; the very nature of photosynthesis means that changes in sky conditions lead to changes in absolute rates of P. This makes it difficult to conduct comparative studies, where measurements are made for reefs in different locales or across seasons/years. Optical tools, as employed to measure P for terrestrial plant and ocean phytoplankton ecosystems via remote sensing (e.g., [22–25]), do not have these limitations and may therefore be a promising alternative to measure coral reef P [26]. An important prerequisite to expand optical-based P measurement to coral reefs is that reef photosynthesizers follow the same principle of photosynthesis adjustment as plants in other biomes, which would be reflected in a (near-) linear relationship of *time-integrated*, day-scale P and irradiance (E) of reef organisms and communities.

P measurements for terrestrial systems via remote sensing are based on the concept of light-use efficiency (LUE) introduced by Monteith [27] and Monteith and Moss [28], where LUE is the ratio of P to absorbed photosynthetically active radiation (APAR). Consequently, P can be calculated by multiplying measured APAR and *known* LUE (e.g., [26]):

$$\text{P} = \text{LUE} \int_{\lambda=400}^{700} E_d(\lambda)A(\lambda)d\lambda = \text{LUE} \times \text{APAR}, \tag{1}$$

where spectral downwelling plane irradiance [$E_d(\lambda)$] is the light flux (photons area^{-1} time^{-1} wavelength^{-1}) incident to the organism or community at a given wavelength (λ), and spectral absorptance [$A(\lambda)$] describes the fractional amount of light absorbed by the community (non-dimensional). LUE has units oxygen or carbon photon^{-1}. The optical terms are integrated across the wavelengths of photosynthetically active radiation (PAR; 400–700 nm). $A(\lambda)$ is determined using reflectance spectroscopy, where a spectrometer measures the fraction of light reflected by the organism or community; the fraction *not* reflected is absorbed [$A(\lambda) = 1 - R(\lambda)$]. Similar expressions have also been developed with respect to marine systems [29, 30]. (Table 1 lists parameters used in this publication and provides a brief description for each.)

Table 1. Description of parameters used or mentioned in the publication.

Parameter	Description
P	Primary production
P_{max}	Maximum primary production
NP	Net primary production
GP	Gross primary production
E	Irradiance
E_k	Saturation irradiance, derived from P-E curves
E_{max}	Maximum irradiance
LUE	Light-use-efficiency; P / APAR [e.g., O_2 photon^{-1}]
APAR	Absorbed photosynthetically active radiation
$E_d(\lambda)$	Spectral downwelling plane irradiance (photons area^{-1} time^{-1} wavelength^{-1})
$A(\lambda)$	Spectral absorptance, the fraction of incident light absorbed by the organism(s) or substrate
$R(\lambda)$	Spectral reflectance, the fraction of incident light reflected by the organism(s) or substrate
λ	Wavelength

The linear form of Eq (1) is in apparent contradiction to the very well known non-linear, hyperbolic tangent (and similar) relationship between P and E [31]:

$$P = P_{max}\tanh(E/E_k),\qquad(2)$$

where E is (photosynthetically available) irradiance, E_k is the saturation irradiance, and P_{max} is the horizontal asymptote of photosynthetic capacity. Under Eq (2), P increases rapidly as E increases to E_k; beyond E_k, P increases slowly until reaching P_{max}.

The contradiction between Eqs (1) and (2) is explained by the time frame of reference. Eq (2) considers *instantaneous* P and E at seconds to hours, while Eq (1) considers *time-integrated* P and E (or APAR) at the day scale and longer. These time-scale-varying patterns in the P-E relationship are borne out by observation in terrestrial plant systems [32, 33]. The reason for the different P-E relationships is that it is not energetically cost-effective for plants to adjust pigment levels at time scales of milliseconds to an hour, where light intensity can rapidly vary by more than an order of magnitude. It is advantageous, however, for plants to adjust pigment levels to best utilize the long-term, prevailing light field. A classic example is the difference between light- and shade-acclimated corals [34]. The result is that, although light saturation may occur on short time scales and on small spatial scales, plants *on average* do not absorb more light than they can use. That is, plants optimize their photosynthetic capacity to prevailing conditions, e.g., general availability of light, nutrients, CO_2, and temperature [33].

This ability of plants to adjust photosynthetic capacity forms the basis of the Functional Convergence Hypothesis (FCH), which states that resource allocations are strictly coordinated and tailored towards an optimal use [33, 35] and that these fundamental optimization processes are similar across different species [36, 37]. If the FCH holds true, for a given set of environmental (temperature, nutrients, etc.) conditions, LUE—the plant's capacity to convert absorbed light to fixed carbon—is expected to be relatively constant over time, independent of normal variations in day-to-day light availability. LUE should be also similar for different species that share similar life histories and resource limitations. Ultimately, a constant LUE in Eq (1) means that P is mainly determined by APAR, which varies with light availability and the plant's capacity to harvest light (e.g., abundance of light-harvesting pigments).

The aim of this study is to examine whether coral reef benthic organisms and communities feature a (near-) linear relationship of *time-integrated* P and E (or APAR). To date, there are no suitable APAR—and hence LUE—data available, but we can assume that APAR is

proportional to E. Thus, P-E curves should show the same type of relationship as P-APAR curves. This assumption is based on the fact that pigment concentrations typically change slowly over time and, hence, the organism's ability to absorb light remains practically constant over the course of a day and between successive days.

In order to obtain *time-integrated* P and E (or APAR) curves, we used the following modeling approach. First, we identified published, empirical *instantaneous* P-E curves for a range of different coral reef benthic organisms and communities. Next, we acquired several years' worth of solar irradiance (E or PAR) diel curves at 1-minute intervals. Then, we applied *instantaneous* PAR to each P-E curve, thus modeling *instantaneous* P. We integrated these data to calculate daily P and E. The resulting *time-integrated* P thus encompassed a wide range of E scenarios (overcast to sunny, and short winter days to long summer days). We found that the *time-integrated* P-E relationships (daily rates), in contrast to *instantaneous* P-E relationships, were near linear in all cases.

Material and methods

Fifty-two published *instantaneous* P-E curves were chosen, representing a number of (although not all) studies conducted on a wide range of benthic reef organisms (corals and algae) and communities (coral dominated, turf algae dominated, sand with microalgae), as well as environmental conditions. The latter was determined by season, depth (0 to 65 m), distance from land, biogeographic region (Red Sea, Great Barrier Reef, Central Pacific, Caribbean, Mediterranean) and latitude (14° to 44°). Studies were either conducted under natural light conditions over a daily cycle or under artificial light conditions in the laboratory using different light intensities. The publications and relevant information for all *instantaneous* P-E curves are listed in S1 Table, which includes species/community type, location, depth, date of measurement, environmental conditions, P_{max}, E_k and maximum E (E_{max}).

To gain a large range of *time-integrated* (daily) E values representing different cloud intensities and day lengths, we gathered all the available, valid diel insolation curves during 2012–2014 (total 928 curves) from the National Weather Service pyranometer stationed at L. F. Wade International Airport in Bermuda (S2 Table). These curves included all conditions from virtually clear to heavy overcast throughout all seasons and covered an 18-fold range of daily E. The wide range of daily E in Bermuda likely exceeds the range occurring in other coral reef regions, since Bermuda is situated at a particularly high latitude (32.3°N) for warm water coral reefs. However, use of this range allows a conservative modeling approach, providing day-scale light variability beyond that expected in most locations of this study, except the Mediterranean. For each P-E simulation, we scaled the maximum E value across all diel curves to 110% of the reported (or estimated) E_{max} (μmol photons m^{-2} s^{-1}). The resulting diel E curves had the correct magnitudes for each given study, and cloud effects were based on actual cloud patterns (examples in Fig 1C and 1D).

To determine P, we simply applied the modeled E to the appropriate measured *instantaneous* P-E curve (examples in Fig 1A and 1B). This produced 928 diel curves of *instantaneous* P (examples in Fig 1E and 1F). The diel E and P curves were numerically integrated (trapezoid rule), providing 928 rates at the day scale for each study. Plotted against each other, this resulted in conservative *time-integrated* P-E curves (examples in Fig 1G and 1H), with daily E for each case ranging from values slightly higher than measured in-situ (110% of E_{max}) to values somewhat lower than expected in the corresponding season (6% of E_{max}). Expected minimum values are ~10–15% of maximum daily E, based on Falter et al. [38], who found a 7-fold change (14%) in daily E within one week due to changes in cloud cover.
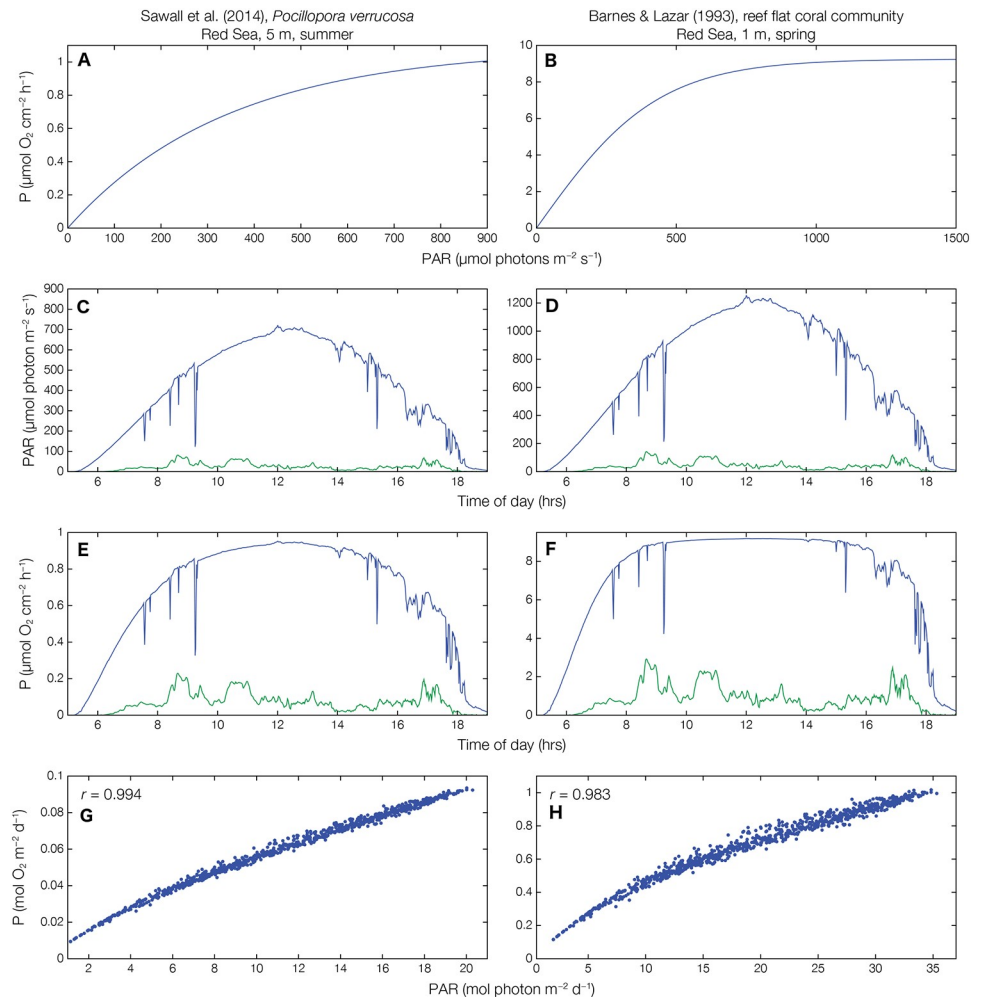
Fig 1. Results of the different steps of the model for a late saturating [15] and early saturating [2] *instantaneous* P-E curve. *Instantaneous* P-E curves reconstructed from the equations and parameters described in the respective publications (see specifics in Table 1) (**A, B**). Maximum (green line) and minimum (green line) *instantaneous* PAR of the Bermuda light curves adjusted to local maximum PAR of published P-E curve (**C, D**). Derived *instantaneous* P corresponding to adjusted PAR at different times of day and under different cloud cover scenarios (**E, F**). *Time-integrated* P-E curves representing daily rates of P and daily PAR for 928 different days with different cloud cover scenarios (**G, H**).

https://doi.org/10.1371/journal.pone.0208607.g001

Results

Model demonstration

The results of the different steps of the *time-integrated* P-E modeling are demonstrated in Fig 1 with two examples, one for an *instantaneous* P-E curve saturating late (left column) and one saturating early (right column) in the day. Both examples show the modeled variability of *instantaneous* E and P, with E ranging between 100% on a cloudless day to 6% on a heavily overcast day. The *time-integrated* P-E curves show a near-linear relationship in both examples; only the lower ends of the curves (low light intensities) exhibit slightly steeper slopes, in particular where the *instantaneous* P-E curves saturate earlier (Fig 1; see [2]). The earlier saturating *instantaneous* P-E curves also result in a slightly higher scatter of points in the *time-integrated* P-E curve.
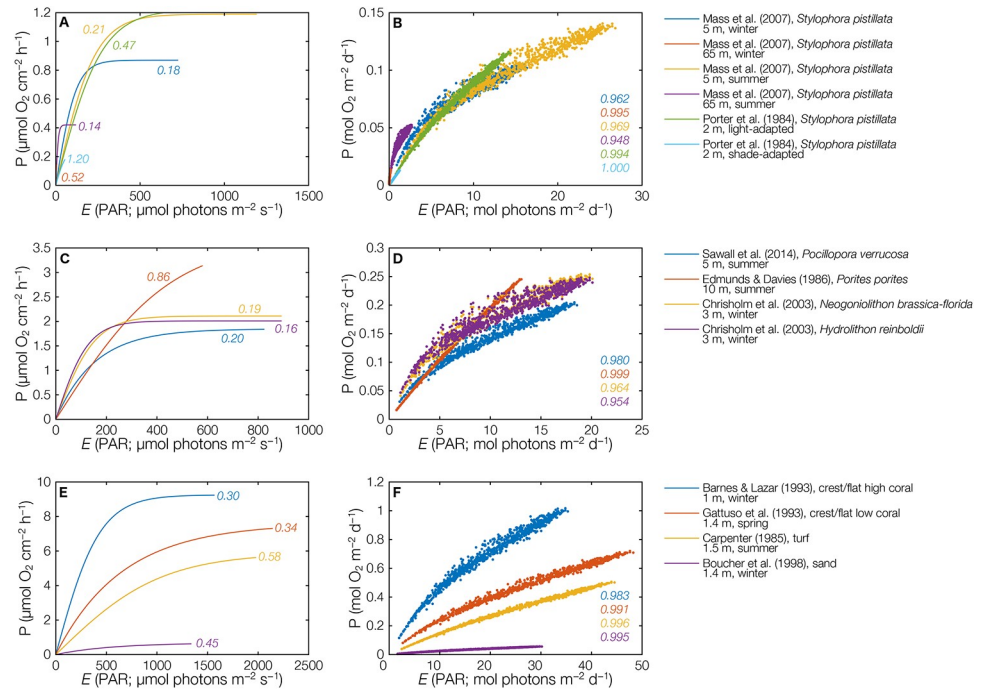
Fig 2. *Instantaneous* **P-E curves (left column: A, C, E) and corresponding** *time-integrated* **P-E curves (right column: B, D, F) of the coral species** *Stylophora pistillata* **(A, B), of different individual reef corals and algae (C, D) and of different reef communities (E, F).** P = photosynthesis or productivity, E = irradiance, PAR = photosynthetically available radiation, values within the graphs A, C and E = E_k/E_{max}, values within the graphs B, D and F = correlation coefficient *r*.

https://doi.org/10.1371/journal.pone.0208607.g002

Model results

All *time-integrated* P-E curves revealed statistically significant linear relationships with $r > 0.89$ (p < 0.001, S1 Table). Those *time-integrated* P-E curves with $r < 0.98$ (comparatively lower linearity) exhibited a slightly steeper initial slope, where daily E was ≤25% of maximum daily PAR (Fig 2B, 2D and 2F). This is related to the rather low E_k of the corresponding *instantaneous* P-E curve (Fig 2A, 2C and 2E), as indicated by the relationship between the *instantaneous* E_k/E_{max} ratios and *r* of the *time-integrated* P-E slopes (Fig 3). In particular, when E_k/E_{max} dropped below 0.2, which occurs in 13 of the 52 curves, the linearity of the *time-integrated* P-E curve decreased markedly (Fig 3).

Comparison of P-E curves of different species and communities in different habitats

In order to visualize the *time-integrated* P-E relationship between different species, communities, and environmental settings, we plotted a selection of P-E curves. Fig 2A shows the *instantaneous* P-E relationships for the coral *Stylophora pistillata* in the Gulf of Aqaba (Red Sea) in two different seasons, in different depths, and under different local light conditions due to shading (light exposed versus shaded). Fig 2B shows the corresponding *time-integrated* (daily-scale) P-E relationships, which are linear in all instances when E_k is higher than ~25% of E_{max}, such as at 65 m depth in winter ($E_k/E_{max} = 0.52$) and in shaded location at 2 m depth ($E_k/E_{max} = 1.2$).

Fig 2C and 2D present *instantaneous* and *time-integrated* P-E curves of different species, including the corals *Pocillopora verrucosa* (Red Sea, 5 m, summer) and *Porites porites* (Jamaica,
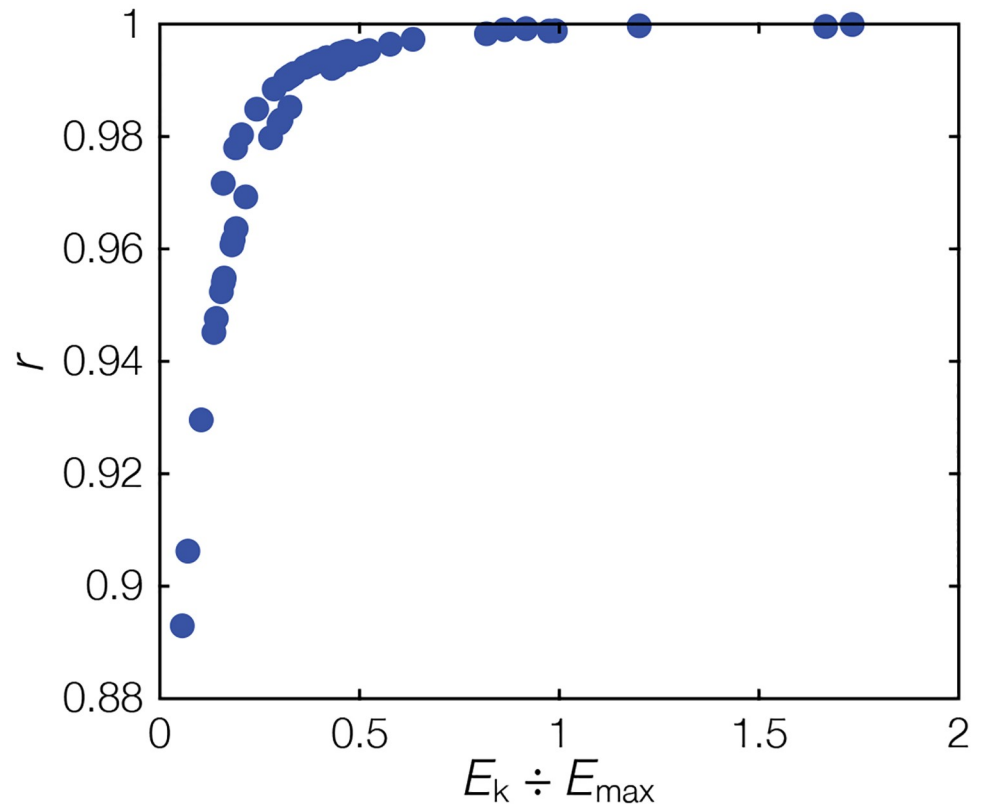
Fig 3. Relationship of light saturation / maximum irradiance ratio (E_k/E_{max}) of the 52 published *instantaneous* P-E curves and the correlation coefficient (*r*) of the corresponding *time-integrated* P-E curves.

https://doi.org/10.1371/journal.pone.0208607.g003

10 m, summer) and the crustose coralline red algae (CCA) *Neogoniolithon brassica-florida* and *Hydrolithon reinboldii* (both Great Barrier Reef, 3 m, winter). Here, the differences between species with low and high E_k/E_{max} values are particularly evident, where the two CCA species saturate very early (E_k/E_{max} ~0.18), resulting in a large scatter of points and a steeper initial slope. In contrast, *P. porites* at 10 m depth saturates late (E_k/E_{max} ~0.86), resulting in a strong linear P-E relationship throughout.

Fig 2E and 2F show the *instantaneous* and *time-integrated* P-E curves of different shallow water whole reef communities (1–1.5 m depth). Those include (*i*) a reef flat close to the reef edge in the Gulf of Aqaba, Red Sea, with a high coral cover, (*ii*) a reef flat with a comparatively low coral cover and increased algal abundance in Moorea (transect from the reef edge [31% live coral cover] into the lagoon [<2%]), (*iii*) a turf algae community in the US Virgin Islands, and (*iv*) a microalgae community inhabiting a sandy area in the Moorea lagoon. The coral-dominated community exhibits the steepest slope and the largest scatter, owing to a comparatively lower E_k/E_{max} value. The two macroalgae communities show very similar slopes, both slightly less than the coral community, and the low-biomass microalgae community has a very shallow P-E slope.

Discussion

Without exception, all modeled *time-integrated* P-E curves revealed a much stronger linear relationship than their respective *instantaneous* P-E curves within their natural range of light intensities. Day-scale P-E relationships for organisms/communities with a low E_k value relative
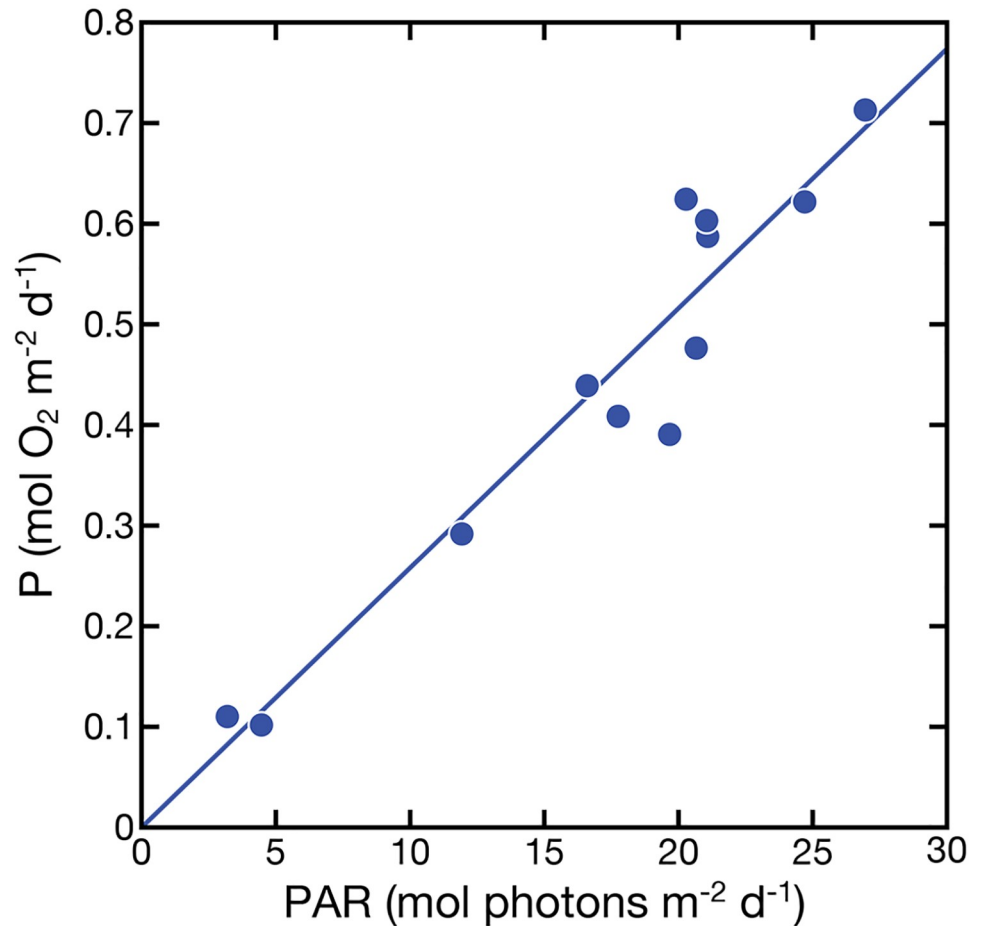
Fig 4. Measured daily gross photosynthesis rate P vs. PAR for the Kaneohe Bay reef flat showing that P does not saturate at higher irradiances at the day scale. $R^2 = 0.92$. Data for P and PAR provided by courtesy by J. Falter. Data is presented in different way in Falter et al. 2011 [38].

https://doi.org/10.1371/journal.pone.0208607.g004

to E_{max} (early saturation) showed a slightly steeper initial slope, which transitioned into a less steep slope that was strongly linear at daily E > ~25% of maximum. Conversely, organisms/communities with higher E_k relative to E_{max} exhibited a stronger linear fit of *time-integrated* P-E curves across the entire range of daily E. This was equally valid for individual colonies of corals and coral fragments, for different algal species, and for different coral reef benthic communities measured in-situ as well as under laboratory conditions. Hence, the pattern is independent of individual, community, and environment. Our modeled results are corroborated by a study of Falter et al. [38], whose data exhibit a strong linear relationship between measured daily gross production rates and measured daily E on an algal-dominated reef flat in Kaneohe Bay, Hawaii, where daily E varied 7-fold (Fig 4, r = 0.96).

These results indicate that reef organisms (corals and algae) most likely optimize photosynthesis to the same degree as terrestrial plants—at the day scale and longer—and therefore possess an important prerequisite of functional convergence. This optimization allows short-term light saturations at high mid-day irradiance, where an excess of absorbed light is dissipated through photo-protective mechanisms (as heat or fluorescence). However, *on average*, the photosynthetic machinery is tuned so that no more light is absorbed than the plant requires or is able to process efficiently. Theoretically, this would result in equal daily LUEs independent

of light availability [32, 33, 35]. In other words, reef organisms and communities scale their investment in photosynthetic capacity to average light availability [35]. The fact that this can be observed across various reef species points toward the second part of the FCH, which implies that LUEs are similar across different species [33, 36, 37].

Optimization of light absorption and utilization (CO_2 fixation) is, on one hand, determined by the carbon requirement of the plant or coral, which includes respiration to maintain cell functioning, production of biomass (growth), reproduction, and defense against predation and pathogens. On the other hand, it is limited by resource availability such as nitrogen, CO_2 and light [39–43]. For example, in many systems, nitrogen, an element essential for various enzymes and structural components, is a limiting resource [44, 45]. Assuming optimal nitrogen utilization, an organism should allocate as much nitrogen to the photosynthetic apparatus (e.g., light harvesting pigments, RuBisCo, enzyme D1, etc.) as necessary to meet the demand of carbon acquisition to maintain plant functioning under prevailing nitrogen and light conditions [46]. As another example, light limitation leads to stronger nutrient allocation to the photosynthetic machinery, in particular for the construction of light harvesting pigments and pigment-protein complexes, in order to maintain photosynthetic gain [34, 47, 48, 49]. In turn, excess light availability can lead to resource allocation for mechanisms that reduce light absorption (e.g., production of fluorescent pigments in corals; [50]) and in the decomposition of light harvesting pigments and complexes [34, 47]. These examples demonstrate that the adjustments of the photosynthetic apparatus, and hence P, are the product of the optimized use of resources. P can therefore also be regarded as an ecological integrator, meaning that photosynthetic performance integrates all prevailing growth conditions [33, 35].

Interestingly, the near linearity of the *time-integrated* P-E relationship seems to be even more pronounced in a reef system than in a terrestrial system. Haxeltine and Prentice [32] showed that in terrestrial systems the linearity is particularly evident when P is measured on a larger spatial scale, meaning on the level of a canopy instead of on the leaf level (part of a plant). In contrast, we have found a near-linear *time-integrated* P-E relationship for coral fragments (e.g., [15, 51]) and even for small coral nubbins [52]. A potential explanation for this is based on differences in the complexity of a tree and a coral or alga. A tree is divided into different compartments (e.g., roots, stem, branches, leaves adapted to shaded and to light-exposed conditions), where each compartment has a certain function, and only the tree as a whole can work efficiently adjusted to local (resource) conditions. Reef photosynthesizers, on the other hand, are structured on a much smaller scale. Coral colonies consist of a number of small, more or less independent entities, the polyps, which are often only few millimeters in diameter. Hence, a fragment or even a small nubbin of coral consists of a number of polyps harboring millions of photosynthesizing zooxanthellae and is therefore able to work as efficiently (per unit area) as a whole coral colony or even a coral community.

It should be mentioned that, while most P-E curves used for this study represent net productivity (NP), some represent gross productivity (GP) (S1 Table). In Fig 2, this includes *P. porites* in Jamaica (Fig 2C and 2D; [3]), the coral-dominated reef flat in the Gulf of Aqaba (Fig 2E and 2F; [2]), and the microalgal community of the sand in a lagoon of Moorea (Fig 2E and 2F; [10]). However, employing either NP or GP has no influence on the shape and slope of the P-E relationship, only on the position of the modeled data points, since the published GP rates were usually calculated by simply adding night respiration rates to the NP rates. (Note, that NP versus GP would have an effect on calculated LUE and the hypothesized similarities between LUEs between species; [35]).

The result of our model is promising with respect to optics-based (APAR-based) P measurements in coral reefs, although some potential limitations have been identified for early-light-saturated reef organisms and communities. In cases where light saturation occurs later in

the day ($E_k/E_{max} > 0.25$), the near-linearity of the *time-integrated* P-E relationship implies a steady and reliable LUE across all light intensities. Early-light-saturated organisms and communities ($E_k/E_{max} < 0.25$), in contrast, exhibit a steeper slope between day-scale P and E at low light intensities. A single LUE would be less representative across the full range of day-scale E, though still useful, especially for day-scale E ≥ ~25% of full range. Early-light-saturated organisms and communities also exhibit more scatter in the *time-integrated* P-E relationship, which will inevitably result in less accurate APAR-based P rates. The error estimated from our modeled *time-integrated* P-E curves can be as high as 30% in extreme cases (e.g., shallow-water crustose red algae [7]).

Keeping these limitations in mind, optics-based P measurements may have a range of advantages over traditional respirometry-based techniques. Namely, optical measurements are independent of local topography, and they can be used across spatial scales. The next step toward optics-based P measurements is to determine actual LUEs for different reef photosynthesizers. These LUEs should be based on GP instead of NP in order to gain LUEs independent of respiration. LUEs based on NP would otherwise underestimate the actual LUE and would reflect potential variability in respiration. Furthermore, it is known that P rates and photo-inhibitory processes vary between morning and afternoon at equal E (e.g., [53, 54, 55]). Hence, daily LUE should not be derived from *instantaneous* P-E curves, but by integrating multiple *instantaneous* P rates measured throughout the entire day. If LUE is fairly constant between species as suggested by the FCH [35], variability in P would thus derive from concomitant variability in APAR, which is dependent on an organism's capacity to absorb light [$A(\lambda)$]. Dubinsky et al. [40] found that about 33% of E is absorbed by the Red Sea coral *Stylophora pistillata* under natural low-nutrient conditions, while absorption increased up to 85% under nutrient enrichment. Enriquez et al. [56] found absorption rates up to more than 90% in healthy *Porites branneri* in the Caribbean. Hochberg et al. [57] have shown that, worldwide, typical coral and algal $R(\lambda)$ is ~10%, which equates to $A(\lambda)$ of ~90%. LUE, in contrast, is defined by the ability of the organism to process the captured light, meaning the conversion of energy gained by photons into cellular energy (ATP) and carbon fixation via the electron transport chain and within the Calvin Cycle. This is a rather standardized process across species, although variability may occur. For example, temperature or water velocity changes may influence enzyme activity and CO_2 availability, respectively [58]. These changes may affect different species to different degrees, and those species may differ in their abilities to adjust to these changes. However, if a rather narrow range of LUEs can be proven and/or LUE can be modeled based on environmental conditions, optics-based P measurements, even on remote sensing scale, are very feasible. This would have the potential to advance our understanding on reef functioning over space and time significantly.

Supporting information

S1 Table. Summary of information of all *instantaneous* P-E curves used for modeling and results of corresponding *time-integrated* P-E curves. Gross photosynthesis (GP) and net photosynthesis (NP) refers to what was measured in the corresponding study. Maximum photosynthetic rate (P_{max}), light saturation point (E_k), maximum irradiance reaching measured individuals or communities (E_{max}). Slope of *time-integrated* P-E curve is the ratio of daily P / daily E in mol O_2 m^{-2} d^{-1} / mol photons m^{-2} d^{-1} in cases where *instantaneous* P was reported as μmol O_2 cm^{-2} h^{-1}. In case *instantaneous* P was reported in another unit, the original unit was maintained. Note that the slope is not the actual light-use efficiency (LUE), since LUE describes the ratio of *time-integrated* P / APAR, not P / PAR.
(XLSX)

S2 Table. Mat lab file containing all the normalized diel PAR curves used for modeling.
The variable "Normalized_PAR" contains 928 diel curves of normalized PAR. Each column is
a single diel curve. These curves represent the range from cloudy days with short photoperiod
to sunny days with long photoperiod. These values can be scaled by E_{max} for use in each spe-
cific instantaneous P-E curve, as given in S1 Table. The variable "Time_of_Day" is a single col-
umn vector with time of day from midnight to midnight in decimal days, at one-minute
intervals. The file was written using Matlab version R2017a.
(MAT)

Author Contributions

Conceptualization: Yvonne Sawall, Eric J. Hochberg.

Data curation: Yvonne Sawall.

Formal analysis: Eric J. Hochberg.

Funding acquisition: Eric J. Hochberg.

Methodology: Eric J. Hochberg.

Visualization: Eric J. Hochberg.

Writing – original draft: Yvonne Sawall.

Writing – review & editing: Eric J. Hochberg.

References

1. Crossland CJ, Hatcher BG, Smith SV. Role of coral reefs in global ocean production. Coral Reefs 1991; 10:55–64

2. Barnes DJ, Lazar B. Metabolic performance of a shallow reef patch near Eilat on the Red Sea. Journal of Experimental Marine Biology and Ecology 1993; 174:1–13

3. Edmunds PJ, Davies PS. An energy budget for *Porites porites* (Scleractinia). Marine Biology 1986; 92:339–347

4. Riegl B, Branch GM. Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. Journal of Experimental Marine Biology and Ecology 1995; 186:259–275

5. Muller-Parker G, Davy SK. Temperate and tropical algal-sea anemone symbioses. Invertebrate Biology 2001; 120:104–123

6. Davy SK, Allemand D, Weis VM. Cell biology of cnidarian-dinoflagellate symbiosis. Microbiology and Molecular Biology Reviews 2012; 76: 229–261 https://doi.org/10.1128/MMBR.05014-11 PMID: 22688813

7. Chisholm JRM. Primary productivity of reef-building crustose coralline algae. Limnology and Oceanography 2003; 48:1376–1387

8. Ogden JC, Lobel PS. The role of herbivorous fishes and urchins in coral reef communities. Environmental Biology of Fishes 1978; 3:49–63

9. Russ GR. Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. Coral Reefs 2003; 22:63–67

10. Boucher G, Clavier J, Hily C, Gattuso JP. Contribution of soft-bottoms to the community metabolism (primary production and calcification) of a barrier reef flat (Moorea, French Polynesia). Journal of Experimental Marine Biology 1998; 225:269–283

11. Jantzen C, Schmidt GM, Wild C, Roder C, Khokiattiwong S, Richter C. Benthic reef primary production in response to large amplitude internal waves at the Similan Islands (Andaman Sea, Thailand). PLoS ONE 2013; 8, e81834. https://doi.org/10.1371/journal.pone.0081834 PMID: 24312365

12. Atkinson MJ, Grigg RW. Model of a coral reef ecosystem. II. Gross and net benthic primary production at French Frigate Shoals, Hawaii. Coral Reefs 1984; 3:13–22

13. Grigg RW, Polovina JJ, Atkinson MJ. Model of a coral reef ecosystem. III. Resource limitation, community regulation, fisheries yield and resource management. Coral Reefs 1984; 3:23–27

14. Sawall Y, Teichberg MC, Seemann J, Litaay M, Jompa J, Richter C. Nutritional status and metabolism of the coral Stylophora subseriata along a eutrophication gradient in Spermonde Archipelago (Indonesia). Coral Reefs 2011; 30:841–853

15. Sawall Y, Al-Sofyani A, Banguera-Hinestroza E, Voolstra C. Spatio-temporal analyses of zooxanthellae physiology of the coral Pocillopora verrucosa along large-scale nutrient and temperature gradients in the Red Sea. PLoS ONE 2014; 9. e103179 https://doi.org/10.1371/journal.pone.0103179 PMID: 25137123

16. Kinsey DW. Productivity and calcification estimates using slack water periods and field enclosures. In: Stoddart DR, Johannes RE (editors) Coral reefs: research methods. UNESCO, Paris. 1978; p. 439–468

17. Yates KK, Halley RB. Measuring coral reef community metabolism using new benthic chamber technology. Coral Reefs 2003; 22:247–255

18. Marsh JA, Smith SV. Productivity measurements of coral reefs in flowing waters. In: Stoddart DR, Johannes RE (editors) Coral reefs: research methods. UNESCO, Paris. 1978; p. 361–378

19. Falter JL, Lowe RJ, Atkinson MJ, Monismith SG, Schar DW. Continuous measurements of net production over a shallow reef community using a modified Eulerian approach. Journal of Geophysical Research: Oceans 2008; 113

20. McGillis WR, Langdon C, Loose B, Yates KK, Corredor J. Productivity of a coral reef using boundary layer and enclosure methods. Geophysical Research Letters 2011; 38. https://doi.org/10.1029/2010GL046179

21. Takeshita Y, McGillis W, Briggs EM, Carter AL, Donham EM, Martz TR, et al. Assessment of net community production and calcification of a coral reef using a boundary layer approach. Journal of Geophysical Research: Oceans 2016; 121:5655–5671

22. Longhurst A, Sathyendranath S, Platt T, Caverhill C. An estimate of global primary production in the ocean from satellite radiometer data. Journal of plankton Research 1995; 17:1245–1271

23. Running SW, Nemani RR, Heinsch FA, Zhao M, Reeves M, Hashimoto H. A continuous satellite-derived measure of global terrestrial primary production. BioScience 2004; 54:547–560

24. Fensholt R, Sandholt I, Rasmussen MS, Stisen S, Diouf A. Evaluation of satellite based primary production modelling in the semi-arid Sahel. Remote Sensing of Environment 2006; 105:173–188.

25. Behrenfeld MJ, O'Malley RT, Siegel DA, McClain CR, Sarmiento JL, Feldman GC, et al. Climate-driven trends in contemporary ocean productivity. Nature 2006; 444:752 https://doi.org/10.1038/nature05317 PMID: 17151666

26. Hochberg EJ, Atkinson MJ. Coral reef benthic productivity based on optical absorptance and light-use efficiency. Coral Reefs 2008; 27:49–59

27. Monteith JL. Solar radiation and productivity in tropical ecosystems. Journal of Applied Ecology 1972; 9:747–766

28. Monteith JL, Moss CJ. Climate and the efficiency of crop production in Britain [and Discussion]. Philosophical Transactions of the Royal Society of London. B. Biological Sciences 1977; 281:277–294

29. Morel A. Available, usable and stored radiant energy in relation to marine photosynthesis. Deep Sea Research 1978; 25:673–688

30. Platt T. Primary production of the ocean water column as a function of surface light intensity: algorithms for remote sensing. Deep Sea Research 1986; 33:149–163

31. Chalker BE. Simulating light-saturation curves for photosynthesis and calcification by reef-building corals. Marine Biology 1981; 63:135–141

32. Haxeltine A, Prentice IC. A general model for the light-use efficiency of primary production. Functional Ecology 1996; 10:551–561

33. Goetz SJ, Prince SD. Modelling terrestrial carbon exchange and storage: Evidence and implications of functional convergence in light-use efficiency. In: Fitter AH, Raffaelli D (editors) Advances in Ecological Research. Academic Press. 1999; p. 57–92

34. Falkowski PG, Dubinsky Z (1981) Light-shade adaptation of Stylophora pistillata, a hermatypic coral from the Gulf of Eilat. Nature 1981; 289:172–174

35. Field CB. Ecological scaling of carbon gain to stress and resource availability. In: Mooney HA, Winner WE, Pell EJ (editors) Response of plants to multiple stresses. San Diego Academic Press. 1991; p. 35–65

36. Reich PB, Walters MB, Ellsworth DS. From tropics to tundra: Global convergence in plant functioning. Proceedings of the National Academy of Sciences 1997; 94:13730–13734

37. Meinzer FC. Functional convergence in plant responses to the environment. Oecologia 2003; 134:1–11 https://doi.org/10.1007/s00442-002-1088-0 PMID: 12647172

38. Falter JL, Atkinson MJ, Schar DW, Lowe RJ, Monismith SG. Short-term coherency between gross primary production and community respiration in an algal-dominated reef flat. Coral Reefs 2011; 30:53–58

39. Dustan P. Depth-dependent photoadaption by zooxanthellae of the reef coral *Montastrea annularis*. Marine Biology 1982; 68:253–264

40. Dubinsky Z, Stambler N, Ben-Zion M, Mccloskey LR, Muscatine L, Falkowski PG. The effect of external nutrient resources on the optical properties and photosynthetic efficiency of *Stylophora pistillata*. Proceedings of the Royal Society of London. B. Biological Sciences 1990; 239:231–246

41. Dubinsky Z, Jokiel PL. Ratio of energy and nutrient fluxes regulates symbiosis between zooxanthellae and corals. Pacific Science 1994; 48:313–324

42. Heikoop JM, Dunn JJ, Risk MJ, Sandeman IM, Schwartz HP, Waltho N. Relationship between light and the δ15N of coral tissue: Examples from Jamaica and Zanzibar. Limnology and Oceanography 1998; 43:909–920

43. Teichberg M, Fricke A, Bischof K. Increased physiological performance of the calcifying green macroalga *Halimeda opuntia* in response to experimental nutrient enrichment on a Caribbean coral reef. Aquatic Botany 2013; 104:25–33

44. Delgado O, Lapointe BE. Nutrient-limited productivity of calcareous versus fleshy macroalgae in a eutrophic, carbonate-rich tropical marine environment. Coral Reefs 1994; 13: 151–159

45. Marubini F, Davies PS. Nitrate increases zooxanthellae population density and reduces skeletogenesis in corals. Marine Biology 1996; 127:319–328

46. Titlyanov EA, Titlyanov TV, Yamazato K, van Woesik R. Photo-acclimation of the hermatypic coral *Stylophora pistillata* while subjected to either starvation or food provisioning. Journal of Experimental Marine Biology and Ecology 2001; 257:163–181 PMID: 11245874

47. Porter JW, Muscatine L, Dubinsky Z, Falkowski PG. Primary production and photoadaptation in light- and shade-adapted colonies of the symbiotic coral *Stylophora pistillata*. Proceedings of the Royal Society of London. B. Biological Sciences 1984; 222:161–180

48. Warner M, Chilcoat G, McFarland F, Fitt W. Seasonal fluctuations in the photosynthetic capacity of photosystem II in symbiotic dinoflagellates in the Caribbean reef-building coral *Montastraea*. Marine Biology 2002; 141:31–38

49. Dubinsky Z, Stambler N. Photoacclimation processes in phytoplankton: mechanisms, consequences, and applications. Aquatic Microbial Ecology 2009; 56:163–176

50. Salih A, Larkum A, Cox G, Kuhl M, Hoegh-Guldberg O. Fluorescent pigments in corals are photoprotective. Nature 2000; 408:850–853 https://doi.org/10.1038/35048564 PMID: 11130722

51. Davies PS. Effect of daylight variations on the energy budgets of shallow-water corals. Marine Biology 1991; 108:137–144

52. Ferrier-Pagès C, Gattuso JP, Dallot S, Jaubert J. Effect of nutrient enrichment on growth and photosynthesis of the zooxanthellate coral *Stylophora pistillata*. Coral Reefs 2000; 19:103–113.

53. Ralph PJ, Gademann R, Larkum AWD, Schreiber U. In situ underwater measurements of photosynthetic activity of coral zooxanthellae and other reef-dwelling dinoflagellate endosymbionts. Marine Ecology Progress Series 1999; 80:139–147

54. Gorbunov M Y, Kolber Z. S, Lesser MP, Falkowski PG. Photosynthesis and photoprotection in symbiotic corals. Limnology and Oceanography 2001; 46:75–85

55. Levy O, Dubinsky Z, Schneider K, Achituv Y, Zakai D, Gorbunov MY. Diurnal hysteresis in coral photosynthesis. Marine Ecology Progress Series 2004; 268:105–117

56. Enriquez S, Méndez ER, Iglesias-Prieto R. Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. Limnology and Oceanography 2005; 50:1025–1032

57. Hochberg EJ, Atkinson MJ, Andréfouët S. Spectral reflectance of coral reef bottom-types worldwide and implications for coral reef remote sensing. Remote Sensing of Environment 2003; 85:159–173

58. Kirk JTO Light and photosynthesis in aquatic ecosystems. Cambridge, UK: Cambridge University Press 2010