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Organisms Composing an Experimental Coral Reef Community from Mo'orea, French Polynesia, Exhibit Taxon-Specific Net Production: Net Calcification Ratios

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Current research on coral reefs seeks to link the responses to anthropogenic stressors (such as global warming and ocean acidification [OA]) among differing functional levels of biological organization. While experimental studies have identified *ex situ* taxon-specific responses to OA and global warming, isolating and connecting these effects *in situ* at the community-level has proved difficult. The difficulties arise from the large number of naturally varying parameters affecting corals reefs, such as light intensity and seawater residence time that affect net community production and calcification. To control variation in seawater residence time and allow light intensity to vary naturally, experimental outer reef (17-m depth) benthic communities composed of calcified algae, corals, and reef pavement were constructed in large outdoor flumes in Mo'orea, French Polynesia. Net community production (*P*), net community calcification (*G*), the ratio of *P/G* (P/G_{ratio}), and slope of *P* regressed on *G* (P/G_{slope}) were calculated for the communities, and concurrently for the constituent members under the same temperature, light, and flow conditions. *P* and *G*, for both the communities and constituent members, were correlated positively with light intensity, whereas P/G_{ratio} and P/G_{slope} were unaffected by light intensity. P/G_{ratios} and P/G_{slopes} exhibited values that were specific to each community member. These results suggest that the P/G_{ratio} and P/G_{slope} may be unaffected by natural variability in light intensity and could serve as useful metrics to relate responses at the taxon and community level, which is an important step in assessing the effects of environmental changes on coral reefs.

Keywords: ocean acidification, coral reef, calcification, photosynthesis, production:calcification ratio

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INTRODUCTION

The excess dissolution of anthropogenic CO_2 emissions into the global surface oceans, described as Ocean Acidification (OA), is decreasing surface seawater pH at 0.0017 units y^{-1} (Clarke et al., 2014), and threatens to impair physiological processes (e.g., calcification) of marine organisms (Gattuso et al., 2015). Anthropogenic CO_2 is also warming the planet, a process referred to as

global warming, which is predicted to increase sea surface temperature (SST) 1.2–3.2°C by the end of the century (Clarke et al., 2014) and may also decrease calcification in marine organisms (Hoegh-Guldberg et al., 2007). Many studies examining the effects of OA and temperature have focused on coral reefs, as this ecosystem represents the largest concentration of calcifying marine organisms on the planet (Hoegh-Guldberg et al., 2007).

The majority of OA studies have been performed *ex situ* at the cellular (e.g., Cohen and Holcomb, 2009; Venn et al., 2013), organismal (e.g., Ries et al., 2009; Erez et al., 2011), and community scales (e.g., Andersson et al., 2009; Comeau et al., 2015), and have manipulated seawater pCO_2 or pH to simulate future ocean conditions and measured rates of net production (*P*) and net calcification (*G*) as response variables. On average, the response of taxon-specific *G* to OA predict that *G* in tropical marine calcifiers will decrease 14–30% by 2100 (Chan and Connolly, 2013; Kroeker et al., 2013), while *P* has been mostly predicted to be unaffected (Schneider and Erez, 2006; Kroeker et al., 2013; Comeau et al., 2015). Likewise, seawater warming studies performed *ex situ* at the organismal scale (e.g., Reynaud et al., 2003; Comeau et al., 2016a) show that *G* and *P* in tropical marine calcifiers is enhanced until a threshold temperature (∼28°C in many organisms, but highly site specific; Pratchett et al., 2015) and then dramatically decreases thereafter due, in part, to bleaching or mortality (Hughes et al., 2017). Considering that many tropical reefs currently experience temperatures >28°C during the summer (Atkinson, 2011), there are concerns that even the minimum warming-driven increase in SST of 1.2°C will decrease *G* and *P* in tropical marine calcifiers by the end of this century (Hughes et al., 2017).

In contrast, there is little empirical research testing the effects of OA and global warming on *P* and *G* of a coral reef *in situ* at the community scale. In part, this reflects the difficulties of quantifying and predicting the response of coral reef communities to OA and warming given the logistical challenges of manipulating seawater pCO_2 or temperature over entire coral reefs (but see Albright et al., 2016). Experimental analyses of the effect of OA and warming on coral reef communities therefore are rare, and generally require taxon-specific results to predict changes *in situ* at the community level. In theory, the predicted 14–30% decrease in *G* attributed to OA at ∼800–1,000 μatm pCO_2 (as predicted by 2100; Chan and Connolly, 2013) or decline in *P* and *G* as SST rises 1.2–3.2°C (Clarke et al., 2014; Comeau et al., 2016a) should be measureable *in situ* on a coral reef given the resolution and precision of contemporary methodologies.

However, these predicted century-scale changes in *P* and *G* due to OA and global warming are small when compared to natural diel variability in *P* and *G*, which amounts to 200–300% within a day, due mainly to variation in light intensity (PAR), which modulates *P* and *G* (Falter et al., 2008). Diurnal variability in PAR drives diurnal changes in *P* and *G* that is three-to-four times greater than the predicted decline in *P* and *G* over the next century (Hofmann et al., 2011), and is thought to obscure any OA- or warming-mediated changes in coral reef community *P* and *G* that already have occurred (Atkinson, 2011). As absolute *P* and *G* are dependent on PAR, they are not well-suited to providing benchmark values against which the effects of environmental change on the same processes can be measured.

To address the effects of environmental variability on community metabolism, *P* and *G* can also be expressed as a ratio (*P/G*) that characterizes the relative rates of organic and inorganic metabolism. In the literature, this relationship can be based on the ratio of a single measurement of *P* and *G* (P/G_{ratio}), or a linear regression of *P* on *G,* when multiple measures of each response variable are available (P/G_{slope}). The P/G_{ratio} is useful in tests of the association between singular measurements of the P-G quotient and contemporaneous environmental conditions (e.g., light; Lantz et al., 2014), whereas the P/G_{slope} is valuable in examining relationships between *P* and *G* over the entire day where multiple measurements of *P* and *G* are available (Page et al., 2016). While the experimental and statistical approaches to calculating these two relationships between P and G slightly differs, both approaches express net primary production (*P*) as a function of inorganic carbon flux attributed to calcification and dissolution (*G*) (Suzuki and Kawahata, 2003). Although the physiological mechanisms linking P and G argue for a stronger connection for P driving G (rather than the other way around; Barnes and Chalker, 1990), and it would, therefore, be more appropriate to consider G as a function of P (*G/P*), the majority of the literature expresses this relationship as *P/G* (see Shaw et al., 2015). Consequently, we express the relationship as *P/G* for comparative purposes.

The *P/G* relationship is useful in establishing a benchmark against which change in community function can be measured, because, unlike individual measures of *P* or *G*, the relationship between the two potentially is unaffected by daily variability in PAR (Watanabe et al., 2006). Daily changes in PAR may amplify or depress community *P*, but because the majority of coral reef community *G* is a product of photosynthetic calcifiers (Atkinson and Cuet, 2008), *P* and *G* generally are tightly-coupled so that the ratio of *P/G* is relatively constant over diurnal timescales (Lantz et al., 2014). Therefore, it has been hypothesized that changes in community *P/G* over time reflect variation in biotic parameters, such as community composition (e.g., percent cover of calcifying organisms; Andersson and Gledhill, 2013; Page et al., 2016).

The hypothesis that community composition influences *P/G* on coral reefs relies on the assumption that each taxon within the community (e.g., corals and algae) exhibits a characteristic *P/G* relationship that contributes to the overall community *P/G*. A review of literature found that an average coral reef community exhibited a P/G_{slope} of 4.1 when coral cover was ∼20% (Shaw et al., 2015), and suggested that a benthic coral reef community with a relatively high percent cover of calcifiers (e.g., corals and calcifying algae >20%), is associated with high rates of *G* (>5 mmol $CaCO_3$ m^{-2} h^{-1}) relative to mean *P* (∼ 20 mmol C m^{-2} h^{-1}). In this case, the community may exhibit a P/G_{slope} approaching ∼2 (e.g., Albright et al., 2013). In contrast, a community with a relatively low cover of calcifiers (<20%) is predicted to have low rates of *G* (<5 mmol $CaCO_3$ m^{-2} h^{-1}) relative to mean *P* (∼20 mmol C m^{-2} h^{-1}), and a P/G_{slope} of ∼ 6 (e.g., Lantz et al., 2014; **Figure 1**). However, before *P/G*

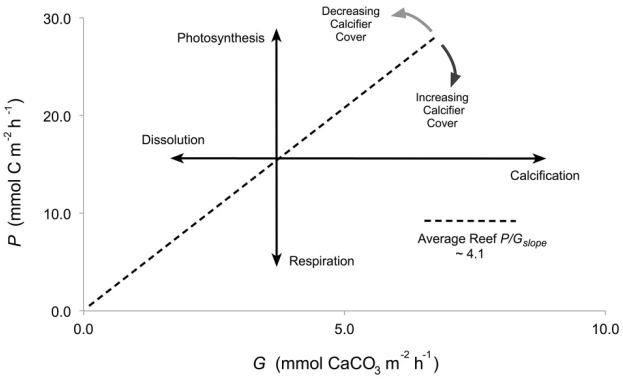

FIGURE 1 | Conceptual diagram representing reef net production (mmol C m^{-2} h^{-1}) as a function of net calcification (mmol $CaCO_3$ m^{-2} h^{-1}) with an average P/G_{slope} of 4.1 (Shaw et al., 2015). Bold arrows represent the slope for the individual processes of photosynthesis, respiration, calcification, and dissolution. Light gray arrows represent the theoretical shift to a P/G_{ratio} >4.1 for a reef with >20% cover of calcifiers. Dark gray arrows represent a shift to a P/G_{ratio} <4.1 for a reef with <20% cover of calcifiers.

relationships can be used to make accurate predictions of benthic community function on tropical coral reefs, further work is needed to evaluate if constituent organisms within a coral reef community exhibit taxon-specific *P/G* relationships.

Quantifying P/G_{ratio} or P/G_{slope} for a benthic community and its constituent members requires measurements in an experimental environment where the benthic communities are replicated and controlled over time. Where this can be accomplished, community-member P/G_{ratio} and P/G_{slope} can be calculated at a resolution lower than functional groups (i.e., corals, calcified algae), and potentially by species. To examine how P/G_{ratio} is affected by naturally varying light intensity, and how P/G_{slope} differs among the taxa composing a shallow coral reef community, the present study measured the metabolism of coral reef communities assembled in replicate experimental flumes using a controlled community composition. *P* and *G* were measured in two experimental coral reef communities, and concurrently for each of the constituent taxa of these same communities. Measurements were made during repeated 3-h incubations (09:00–12:00 h) over 3-weeks in Mo'orea, French Polynesia. Daily measured community- and taxa-level *P* was divided by *G* to derive P/G_{ratio}, and all measurements of community- and taxa-level *P* were regressed linearly against *G* to obtain P/G_{slope}.

MATERIALS AND METHODS

Experimental Design

This experiment was carried out from September 1 to October 11, 2014, in Mo'orea, French Polynesia, at the Richard B. Gump South Pacific Research Station. Coral reef communities were assembled in two replicate flumes (hereafter, Communities 1 and 2), and their composition was adjusted to match the average planar cover measured on the fore reef of Mo'orea at 17-m depth in 2006 (Edmunds, 2015). The scleractinian components of the communities were the spatially dominant corals *Pocillopora verrucosa* (11% cover), massive *Porites* spp. (*P. lobata* and *P. lutea*) (8%), and *Acropora retusa* (8%) (Comeau et al., 2016b). In addition, 5% of the floor of the flumes was covered by the crustose coralline algae (CCA) *Porolithon onkodes*, which approximated the cover of this functional group on the fore reef in 2006. Pieces of *P. onkodes,* consisting of ∼ 8 × 8 cm sections (∼ 3 cm thick), were chiseled from the reef at 17-m depth and placed in the flumes. To recreate the benthic inorganic substratum, 55% of the floor of the flume was covered by reef pavement. Pieces of reef pavement (∼20 × 20 cm) consisted of dead coral skeleton fragments naturally covered in turf algae.

The two flumes were located outdoors and each consisted of a working section of 5.0 × 0.3 × 0.3 m, through which seawater was re-circulated using pumps (W. Lim Wave II 31800 L h^{-1}) to obtain a mean flow speed of 8 cm s^{-1}, which is similar to the average flow speed on the fore reef of Mo'orea at 17-m depth (Washburn and Brooks, 2014). Seawater in the flumes was refreshed continuously at 5 L min^{-1} with seawater pumped from Cook's Bay at 12-m depth, and filtered through sand (0.45–0.55 mm nominal pore size). Clear UV-transparent acrylic covers were placed on top of the flumes to keep out rain, and blue acetate filters (Lee Filters #183 Moonlight Blue) were placed on the covers to filter ambient sunlight to simulate the photon flux density of photosynthetically active radiation (PAR, ∼500–1,200 mmol photons m^{-2} cm^{-1}; measured with a 2π quantum sensor LI-189 and a LiCor LI-1400 meter) and the spectral composition of light at 17-m depth (CA Lantz unpublished data). Temperature in the flumes was maintained at ∼27.0°C, which was the ambient seawater temperature on the fore reef at the time of the study. Light was measured at 30-min intervals with a PAR logger (2π Odyssey PAR sensor) in each flume. An average PAR value was calculated for each incubation based on the six PAR measurements taken over the 3-h incubation period.

Community metabolism (*P* and *G* arising from all community members) in each flume was measured from changes in seawater chemistry as determined during replicate 3-h incubations between 9:00 and 12:00 h on 14 days between 1 September and 11 October. With two separate flumes operated in a closed circuit for 3-h sampling periods on 14 days, this created 14 replicated measurements for each flume. To compare the response of *P* and *G* to variation in PAR for the community and the constituent taxa, the metabolism of each of the species comprising the community was measured separately for five benthic groups (*P. verrucosa*, *Porites* spp. *A. retusa*, *P. onkodes*, and pavement) using four chambers placed within each flume that were operated simultaneously. The four chambers consisted of a 2-L clear acrylic cylinder enclosed on the bottom and fitted with an individual Atman 340 L h^{-1} powerhead to create turbulent conditions (**Figure 2**). The top of each chamber (height 30-cm) remained open and above the flume water level to prevent water exchange in order to separate the chemical changes in seawater, but maintain identical temperature and PAR conditions between the chambers and flume. Trials were completed in triplicate for each community member (to provide $n = 12$ for each community member), and community members were randomly selected for each incubation.

FIGURE 2 | Picture of flumes with experimental coral reef communities 1 and 2 in place. Covers with blue filters are not in place so as to show coral reef community within the flume. Inset shows 2-L chamber, containing a *Pocillopora verrucosa* colony and a small pump for seawater circulation, which were placed within the flumes at the time of incubation.

Seawater Measurements

Seawater samples were taken from each flume and chamber at the beginning and end of each 3-h incubation (09:00–12:00 h) and analyzed for temperature, salinity, total alkalinity (TA), and pH. Temperature was measured using a ThermoFisher Scientific Traceable Thermometer (± 0.01°C) and salinity was measured using a conductivity meter (YSI 3100). Measurements of TA were made within 24 h of collection of seawater samples using open-cell potentiometric titrations (Dickson et al., 2007) on a Mettler Toledo T-50 titrator fitted with a DG115 pH electrode, and analyses were completed in duplicate using ∼50 g seawater samples. Measurements of pH were performed using a spectrophotometric procedure with m-cresol dye, and calculated on the Total Scale (pH_T). Titrations of certified reference materials (batch #140 from A. G. Dickson, Scripps Institute of Oceanography) yielded TA values ≤2.9 mmol kg^{-1} of the certified value (SE = 2.8 mmol kg^{-1}; $n = 12$). Weekly analyses of the pH of prepared Tris buffers ($pH_T = 8.096$ at 25°C) yielded an average difference of 0.009 pH units (SE = 0.004 pH_T units; $n = 12$). Values for dissolved inorganic carbon (DIC) were calculated from the measured TA, pH_T, salinity, and temperature using the R package seacarb (Lavigne and Gattuso, 2010).

Net Production and Net Calcification Measurements

Net production (P, mmol C m^{-2} h^{-1}) and net calcification (G, mmol $CaCO_3$ m^{-2} h^{-1}), were calculated from changes in DIC (ΔDIC) and TA (ΔTA) using equations from Gattuso et al. (1996):

$$P = [(\Delta DIC \times \rho \times v)/(\Delta t \times a)] - G \quad (1)$$

$$G = [(\Delta TA \times \rho \times v)/(\Delta t \times a \times 2)] \quad (2)$$

where (ρ) is the density of seawater (kg m^{-3}) at the time seawater samples were collected, calculated from temperature and salinity, (v) is the volume (L) of the flumes and incubation chambers, (a) is the projected area (m^2) of the community and community members, and (t) is time (hours) of the incubation. The ratio of P/G (mmol C mmol $CaCO_3^{-1}$), for both the community and each individual community member, was calculated by dividing each day's measured P by the contemporaneously measured G (P/G_{ratio}). The slope of P regressed on G (mmol C mmol $CaCO_3^{-1}$), for both the community and each individual community member, was calculated from a best fit type II sum of squares residual model, in which all measures of P over the course of the study were regressed on G for the respective community (P/G_{slope}), or individual community members.

Statistical Analyses

Statistical analyses were performed with SPSS software (SPSS Inc. Version 22.0, (SPSS Inc. IBM Corp., 2013)) running in a Windows environment, and the assumptions of normality and equality of variance were evaluated with graphical analyses of the residuals. An analysis of covariance (ANCOVA) was used to test the hypothesis that the relationships between P (dependent variable) and G (independent variable) differed among the flume community and community members. If P/G_{slopes} did not differ and, assuming that the null hypothesis of no differences was not rejected (for either slope or elevation), the results were pooled for the community ($n = 28$), and each community member ($n = 12$), and a new regression of P on G prepared, from which the slope of P/G was determined. To test for differences in the measured P/G_{ratio} between each flume community and each community member, an analysis of variance (ANOVA) was conducted where each community and community member were a fixed factor. A Bonferroni *post-hoc* test was used to compare the measured P/G_{ratio} among community members.

As the replicate 3-h incubations between 09:00 and 12:00 h (described above) took place on different days between 1 September 2014 and 11 October 2014, each day was characterized by different natural light regimes caused by variation in cloud cover and rain showers. The variation in PAR provided the opportunity to explore the relationship between the measured P/G_{ratio} and average PAR from each incubation period. A Pearson correlation was used to test the hypothesis that the P/G_{ratio} for each day was dependent on ambient PAR (averaged over the 3-h incubation period), and analyses were completed for each community and for the component community members.

RESULTS

Relationship between *P* and *G* in the Community and Community Members

Rates of metabolism are reported as the mean ± SE, pooled among replicates. Community P was not significantly different between flumes [$F_{(1, 26)} = 1.92$, $p = 0.311$] and, when pooled between flumes ($n = 28$ per community), was 11.9 ± 1.2 mmol C m^{-2} h^{-1}. Constituent members in the flume communities ($n = xx$), when incubated separately, exhibited a P of 7.8 ± 6.7 mmol C m^{-2} h^{-1} (pooled among all taxa), which was highest

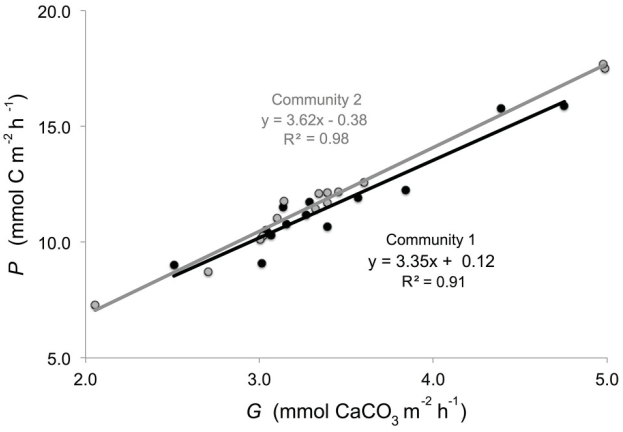

FIGURE 3 | Net production (mmol C m^{-2} h^{-1}) of reef communities as a function of net calcification (mmol $CaCO_3$ m^{-2} h^{-1}) in Community 1 (black) and Community 2 (gray). Slope and R^2 values are shown for each community.

for *P. verrucosa* (15.4 ± 1.1 mmol C m^{-2} h^{-1}), and lowest for *P. onkodes* (2.9 ± 0.1 mmol C m^{-2} h^{-1}; **Table 1**). Community *G* was not significantly different between flumes [$F_{(1, 26)} = 1.56$, $p = 0.297$] and, when pooled between flumes ($n = 28$ per community), was 3.6 ± 0.3 mmol $CaCO_3$ m^{-2} h^{-1}. Constituent members in the flume communities exhibited a *G* of 3.2 ± 2.7 mmol $CaCO_3$ m^{-2} h^{-1} (pooled among taxa), which was highest for *P. verrucosa* (6.9 ± 0.5 mmol $CaCO_3$ m^{-2} h^{-1}), and lowest for *P. onkodes* (0.7 ± 0.1 mmol $CaCO_3$ m^{-2} h^{-1}).

Community P/G_{slopes} were not significantly different between flumes [$F_{(1, 26)} = 1.21$, $p = 0.282$] and when pooled between flumes ($n = 28$ per community), yielded a slope of 3.52 ± 0.13 mmol C mmol $CaCO_3^{-1}$ (**Figure 3**). Community P/G_{ratios} did not vary between flumes [$F_{(1, 26)} = 1.057$, $p = 0.313$] and, when pooled between flumes, was 3.44 ± 0.16 mmol C mmol $CaCO_3^{-1}$ (**Table 1**). Community-member P/G_{slopes} were significantly different from one another [$F_{(4, 54)} = 19.21$, $p < 0.001$] and, for each community member ($n = 12$), slopes were maximal for the inorganic $CaCO_3$ pavement (6.21 ± 0.32 mmol C mmol $CaCO_3^{-1}$), and minimal for *P. verrucosa* (2.15 ± 0.12 mmol C mmol $CaCO_3^{-1}$; **Figure 4**). Community-member P/G_{ratios} differed among community members [$F_{(4,54)} = 22.57$, $p < 0.001$], and for each community member, were maximal for the inorganic $CaCO_3$ pavement (5.83 ± 0.37 mmol C mmol $CaCO_3^{-1}$) and minimal for *P. verrucosa* (2.21 ± 0.04 mmol C mmol $CaCO_3^{-1}$). *Post-hoc* analyses showed that P/G_{ratios} differed between community members ($p < 0.001$) except between *A. retusa* and *Porites* spp. ($p > 0.05$).

Relationship between Par and *P/G*

Over all days that metabolism was measured, PAR varied from 452 to 1,237 mmol photons m^{-2} s^{-1} during the 3-h incubation period, with a mean PAR of 996 ± 238 mmol photons m^{-2} s^{-1} ($n = 14$). Over each incubation, *P* and *G* were positively and significantly correlated with PAR in community 1 (P_1: $r = 0.86$, $df = 27$, $p = 0.01$; G_1: $r = 0.76$, $df = 27$, $p = 0.03$) and community 2 (P_2: $r = 0.78$, $df = 27$, $p = 0.032$; G_2: $r = 0.73$, $df = 27$ $p = 0.04$). At the community member-level, *P* and *G* for *A. retusa*, *P. verrucosa*, and *Porites* spp. were significantly and positively correlated ($p < 0.05$) with PAR over each incubation period, but PAR was not significantly correlated ($p > 0.05$) with *P* and *G* for *P. onkodes* or pavement. PAR from each incubation period was not significantly correlated with any of the *P/G* values either at the community level or for each individual community member ($p > 0.05$).

DISCUSSION

Comparing *P* and *G* for the communities and constituent taxa in this study revealed consistent values for P/G_{ratio} and P/G_{slope} across time (3 h) for reef communities and their community members, and a significant difference in P/G_{ratio} among community members. Correlations between the P/G_{ratio} and PAR revealed that *P* and *G* were positively correlated with PAR, which has been shown in most previous studies of these relationships (Chalker and Taylor, 1978; Barnes and Chalker, 1990; Gattuso et al., 1993). However, PAR and P/G_{ratio} were unrelated. These results are similar to previous measurements of the community metabolism of coral reefs (e.g., Lantz et al., 2014; Shaw et al., 2015), and together they support two conclusions.

First, the lack of a significant relationship between average PAR intensity and P/G_{ratio} supports the notion that the P/G_{ratio} can provide an effective benchmark for the functional performance of coral reefs that normalizes the influence of variable PAR on *P* and *G*. Studies measuring coral reef community *P* and *G* *in situ* usually go to great lengths to quantify the influence of the abiotic parameters on these factors, and typically consider reef water residence time, wind speed, and average reef water depth. The commonly used Lagrangian and Eulerian methodologies (Gattuso et al., 1996; Falter et al., 2008) for measuring community *P* and *G* depend on the quantification of these abiotic parameters, so that *P* and *G* can be normalized for residence time of reef waters in order to support comparisons among varying time periods, or among different reefs. Once measurements are normalized for residence time, previous studies of shallow coral reefs have shown a strong coupling between PAR and *P*, and between PAR and *G* on 12-h diurnal timescales (Falter et al., 2012), which supports the notion that P/G_{ratio} does not change in response to differences in PAR. An increase in PAR will enhance *P* and *G*, but because these two metabolic processes are tightly coupled on timescales of hours to days, *P/G* remains relatively constant when integrated over a day (Suzuki and Kawahata, 2003). This finding is supported by the present study given that the P/G_{ratio} and P/G_{slope} for the communities and community members, remained nearly the same among days, even though mean daily *P* and *G* differed these among days. These results indicate that *P/G* relationships can be a reflection of the coupled daily balance between *P* and *G*, and do not change among days due to variation in average PAR.

The second conclusion from these data is that each community member exhibited a characteristic P/G_{slope} and P/G_{ratio} that remained statistically indistinguishable within each

TABLE 1 | Seawater temperature [T (°C)], salinity (S), net production (*P*), and net calcification (*G*) for the experimental communities and their constituent members; values are mean ± SE.

Group	T (°C)	S	*P*	*G*	P/G_{slope}	P/G_{ratio}
Community	27.4 ± 0.6	36.7 ± 0.3	11.9 ± 1.2	3.6 ± 0.3	3.52 ± 0.13	3.44 ± 0.16
Acropora retusa	27.4 ± 0.6	36.7 ± 0.1	12.1 ± 0.8	4.7 ± 0.2	2.43 ± 0.15	2.59 ± 0.10
Pocillopora verrucosa	27.4 ± 0.6	36.7 ± 0.1	15.4 ± 1.1	6.9 ± 0.5	2.15 ± 0.12	2.21 ± 0.04
Porites spp.	27.6 ± 0.6	36.7 ± 0.2	7.6 ± 0.2	2.8 ± 0.2	2.63 ± 0.16	2.67 ± 0.16
Porolithon onkodes	27.6 ± 0.8	36.7 ± 0.2	2.9 ± 0.1	0.7 ± 0.1	3.69 ± 0.28	3.92 ± 0.31
Pavement	27.5 ± 0.7	36.7 ± 0.1	6.7 ± 0.3	1.2 ± 0.2	6.21 ± 0.32	5.83 ± 0.37

The corresponding P/G_{ratio} (calculated by dividing P by G: in units of mmol C mmol $CaCO_3^{-1}$) and slope (calculated from linear regressions of P vs. G: both in units of mmol C mmol $CaCO_3^{-1}$) are listed for the community (n = 12 incubations) and each community member (n = 3 incubations).

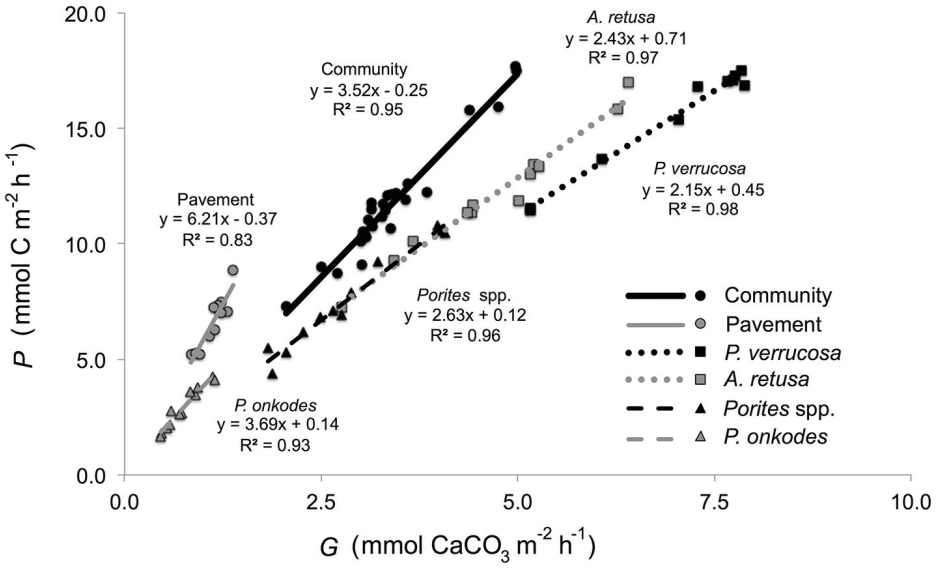

FIGURE 4 | Net production (mmol C m^{-2} h^{-1}) of reef communities as a function of net calcification (mmol $CaCO_3$ m^{-2} h^{-1}) for the community, *P. verrucosa*, *A. retusa*, *Porites* spp., *P. onkodes*, and pavement. Slope and r^2-values shown for each respective community member and the community.

member over the study. This result suggests that the P/G_{slope} and P/G_{ratio} is a community- and taxon-specific value, which characterizes the balance in *P* and *G* specific to that community or organism, respectively. It is premature to conclude that the *P/G* relationship provides a general application to scaling between organisms and community-level process for coral reefs *in situ*, given the multitude of other parameters, such as body size, temperature, and stoichiometry, which also can affect intraspecific differences in metabolism (Brown et al., 2004; Edmunds et al., 2016). It must also be noted that the P/G_{ratio} is dependent on community *P* and, therefore, it should be affected by changes in the cover of non-calcifying autotrophic organisms (e.g., macroalgae). Similarly, while the *P/G* relationship reflects the balance between organic and inorganic carbon fixation, if both processes are changing proportionately to another environmental driver (natural or anthropogenic), then the *P/G* relationship may be insensitive to these changes.

These two conclusions suggest that changes in the *in situ* *P/G* relationship for a coral reef over time (e.g., months to years) may be a function of the relative cover of constituent community members, and reflects the balance between the *P* and *G* of a coral reef regardless of daily changes in light intensity. Given these results, the use of the P/G_{ratio} or P/G_{slope} could serve as a baseline ratio of carbon production for a coral reef, against which changes on disturbed reefs can be evaluated. This hypothesis is supported by the relationship between the mean P/G_{slope} and benthic cover of calcifiers in previous studies of coral reefs. An examination of studies that have measured the P/G_{slope} and recorded the percent benthic cover of coral or calcifying taxa shows that P/G_{slope} values are higher on reefs with a lower percent cover of calcifying taxa (**Figure 5**). A linear regression of the P/G_{slope} against percent cover of benthic calcifiers is statistically significant with a negative slope ($y = -0.18x + 8.62$, $r^2 = 0.94$, $p < 0.05$; **Figure 5**). According to this relationship, the P/G_{slope} value decreases by ∼1 unit for each 5.1 ± 0.6% increase in cover of benthic calcifiers. The relationship between percent cover of calcifying taxa and the P/G_{slope} suggests that future work

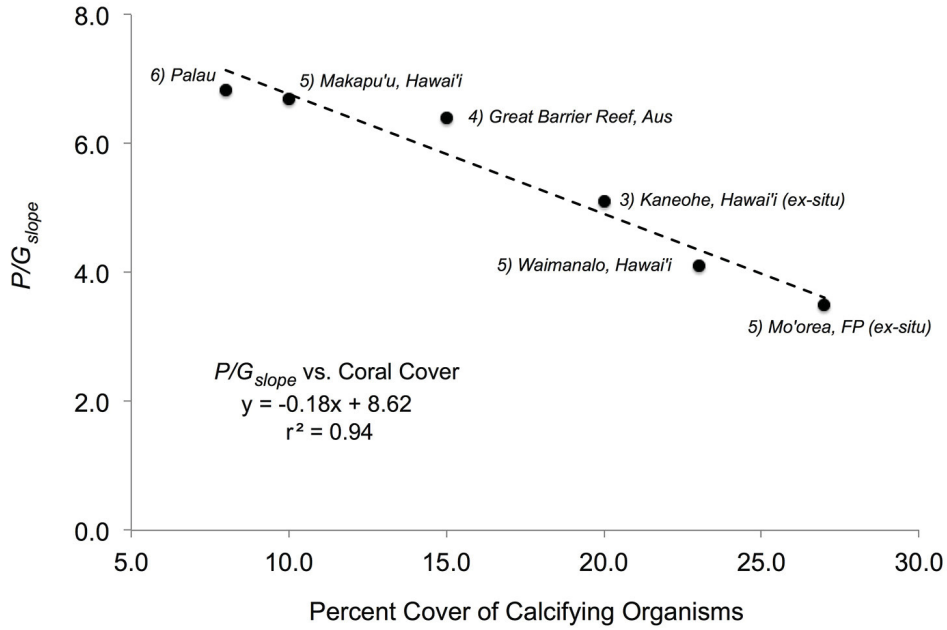

FIGURE 5 | P/G_{slope} values from different studies (which have measured net *P* and net *G* together with percent coral cover on natural reef flat communities) as a function of percent cover of calcifying organisms for each study. (1) Present study with a $P/G_{slope} = 3.52$ and 27% coral cover; (2) a natural reef community in Waimanalo (Oahu), Hawai'i, with a $P/G_{slope} = 4.1$ and 23% coral cover (Lantz et al., 2014); (3) an experimental reef community in Oahu, Hawai'i, with $P/G_{slope} = 5.10$ and 20% coral cover (Andersson et al., 2009); (4) a natural reef community on the Great Barrier Reef with a $P/G_{slope} = 6.4$ and 15% coral cover (Suzuki and Kawahata, 2003); (5) a natural reef community at Makapu'u (Oahu), Hawai'i, with a $P/G_{slope} = 6.7$ and 10% coral cover (Lantz et al., 2014), and (6) a natural reef community in Palau with a $P/G_{slope} = 6.83$ and 8% coral cover (Watanabe et al., 2006). Slope and r^2-value shown for the overall linear relationship.

need measure these two parameters in unison in order to create the opportunity to further test the hypothesis that the *P/G* relationship can serve as a baseline ratio of carbon production for coral reefs.

While the present study focused on the relationship between the P/G_{ratio} and PAR, we suggest that future work employ experimental designs that can distinguish the effects of other abiotic factors on the *P/G* relationship. These abiotic factors could include water flow (e.g., Comeau et al., 2014), temperature (e.g., Reynaud et al., 2003), or CO_2 (e.g., Schneider and Erez, 2006). For example, water flow usually is correlated positively with both *P* (Nakamura et al., 2003; Finelli et al., 2006) and *G* (Dennison and Barnes, 1988; Comeau et al., 2014) at the organism level for tropical marine calcifiers due to the enhanced flux of metabolites between the organisms and the surrounding seawater (Mass et al., 2010). However, the relationship between water flow and the ratio of *P* to *G* is unknown (i.e., if *P* and *G* change at the same rate in response to water flow). Likewise, it is unknown if a warming-driven decrease in *G* at temperatures $>\sim$28°C (Pratchett et al., 2015) will occur at the same rate. In some cases, seawater warming has actually increased rates of scleractinian calcification (e.g., McCulloch et al., 2012) and macro-algal photosynthesis (e.g., Zou and Gao, 2013). Additionally, the overall response in *G* to temperature has varied both intra- (e.g., Comeau et al., 2016a) and inter-specifically (Shaw et al., 2016). A large number of OA studies have shown that an increase in pCO_2 will decrease *G* but not *P* (Kroeker et al., 2013; Comeau et al., 2017), although some studies suggest *P* may increase in response to a CO_2-fertilization effect (Ries et al., 2009; Kroeker et al., 2010).

Therefore, it is difficult to predict how global climate change will modify the *P/G* relationships for coral reef communities given the potential for interspecific variation in the response of community members to global warming and OA. As global climate change continues to threaten the existence of coral reefs, there is a growing need for techniques to scale up results from perturbation experiments at the organism level to the community level. Building upon the present results and further quantifying community, as well as community member, *P/G* relationships for multiple reefs and community members will contribute to meeting these needs.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

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