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Addition of species abundance and performance predicts community primary production of macroalgae

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Abstract Understory plant assemblages are important sources of primary production in both terrestrial and marine environments, and they may exhibit different dynamics than their overstory counterparts. For example, production within dense upper canopies is typically light-limited by shading, whereas such canopy architecture effects are likely unimportant in low-light environments, such as those inhabited by sparser understory assemblages. In these assemblages, light saturation of understory production may be common as species become limited by their photosynthetic capacity, which is adapted to low-light levels. Here we show that a simple model relating species-specific light use relationships measured in the laboratory to biomass and light levels measured in nature accurately predicts community gross primary production (GPP) in a marine understory algal community. We validate the model by comparing GPP measured in situ in enclosed chambers with model estimates for the same incubations. Model estimates of GPP explained 70% of the variation in the measured estimates. The results show that GPP was accurately estimated by simple addition of the photosynthetic capacity of each species in the community based on their biomass and the available light. The difference between modeled and measured GPP did not show any relationship with community biomass or diversity, and the results suggest that diversity does not significantly affect productivity in this system. This type of model should be applicable in other environments where canopy architecture does not play a significant role in limiting photosynthesis.

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Introduction

Terrestrial and aquatic vegetation often consists of highly three-dimensional, multi-species assemblages, with complex canopy architectures shaped by inter- and intraspecific competition for light (Wierman and Oliver 1979; Ford and Diggle 1981; Gerard 1984; Ryel et al. 1990). Lower canopy layers may respond in time and space to changes in the density of upper layers driven by disturbance, phenology, or other processes (Hart and Chen 2006; Kudo et al. 2008). Understory assemblages in both terrestrial and marine habitats typically consist of shade-adapted species that can contribute significant levels of primary production to the ecosystem, particularly following disturbances that reduce the upper canopy (Alaback 1982; Hart and Chen 2006; Miller et al. 2011). There are relatively few estimates of understory production, however, particularly on temporal and spatial scales that encompass post-disturbance succession (Alaback 1982; Gower et al. 2001; Nillson and Wardle 2005), partly due to the difficulty of including understory in production models (Suchar and Crookston 2010).

The relationship between photosynthetic rate and irradiance in multi-layered assemblages of autotrophs is often positively linear within the range of natural light levels, contrasting with the saturating relationship between photosynthesis and irradiance generally seen for individual leaves and other plant elements (Hesketh and Baker 1967). This linear relationship reflects the increased light absorption by plants and plant components in lower vegetation layers with increasing light, even when the photosynthetic capacity of the upper layers is saturated, resulting

in greater community-level photosynthesis (Binzer and Middelboe 2005). Understanding the relationship between photosynthesis and light has allowed primary production models to directly relate light absorbed by the canopy to rates of photosynthetic carbon (C) fixation (McCree 1972; Gower et al. 1999). However, this overall linear relationship may mask more complex dynamics within the canopy and particularly in the understory, where shade-adapted plants may exhibit saturating relationships between photosynthesis and irradiance that differ between species or ontogenetic life stage (Young and Smith 1980; Pearcy 1987; DeLucia et al. 2003).

Models used to estimate the primary production of benthic marine macrophytes, such as those for phytoplankton and terrestrial plants, have varied in complexity from simple models based on light, biomass, and physiological data on photosynthetic response to light (Brinkhuis et al. 1977a; Jackson 1987; Burd and Dunton 2001; Binzer and Sand-Jensen 2002a; Elkalay et al. 2003) to more complex efforts incorporating physiological responses to multiple environmental variables (Duarte 1995; Duarte and Ferreira 1995, 1997). Mechanistic models based on light capture, nutrient uptake rates, and the factors that affect them have also been used to estimate benthic primary production in coastal waters (Baird et al. 2003; Zimmerman 2003). However, there are few datasets of measured primary production that can be used to validate such models, in part because of the logistical challenges of measuring primary production in shallow, wave-swept coastal habitats.

Subtidal assemblages of benthic macroalgae vary substantially in time and space due to physical disturbance (Dayton and Tegner 1984; Airoldi and Cinelli 1997; Mumby et al. 2005), grazing (Dayton et al. 1984; Chapman and Johnson 1990; Gagnon et al. 2005), and competition for light and space (Reed and Foster 1984; Santelices and Ojeda 1984). To better understand the patterns and controls of primary production by macroalgae and their ecological consequences, we developed a simple physiologically based model of benthic macroalgal production using three components: (1) taxon-specific foliar standing crop, (2) bottom irradiance, and (3) taxon-specific macroalgal photosynthesis versus irradiance (P vs. E) parameters. We also empirically measured macroalgal production by understory assemblages in giant kelp forests in enclosed chambers deployed in situ. We then applied our model to irradiance and standing crop data from the enclosed chambers and asked how well the model predicted measured community production, and whether the accuracy of model prediction varied depending on community biomass and diversity. If canopy architecture caused light limitation of lower canopy layers, then we expected the difference between modeled and measured production to increase as community biomass and species diversity increased (Binzer et al. 2006). Because light-limited communities may saturate at much higher irradiances than individual algal thalli (Binzer et al. 2006; Middelboe et al. 2006; Tait and Schiel 2011), the difference between measured and modeled production should be negatively related to irradiance if canopy architecture caused significant light limitation.

Methods

Field measurements of macroalgal biomass and production

Understory macroalgal biomass and production were measured monthly from May 2007 through September 2008 along 30-m-long fixed transects inside the giant kelp (*Macrocystis pyrifera* Linnaeus) forest at Mohawk Reef, located off Santa Barbara, California (34°23′38″N, 119°43′45″W) and in an adjacent area experimentally cleared of giant kelp (Miller et al. 2011). Understory biomass and species composition along the transects varied widely over the 17-month-long study, largely due to temporal and spatial variation in the surface canopy of giant kelp (Miller et al. 2011).

Macroalgal biomass and estimated gross primary productivity (GPP) were measured in transparent tunnel-shaped closed chambers (volume 45 L) that cover 0.1 m^2 of the sea floor (Miller et al. 2009). The chambers consisted of two U-shaped end walls made of clear rigid acrylic, with continuous side walls and ceiling made of flexible Teflon sheeting (Tefzel; DuPont, Wilmington, DE), and an open bottom framed by fiberglass-reinforced plastic that was sealed to the sea floor by a nylon gasket and a weighted flexible plastic skirt. The flexible chamber walls allowed for the transfer of water motion and algal movement. Self-contained optical probes (D-Opto; Envco, Auckland, New Zealand) logged dissolved oxygen concentration and temperature inside the chambers at a frequency of once per minute. Two chambers were set up over intact algal assemblages on each of the two transects in the morning on each sampling date and incubated from just after daybreak to just before sunset. No location on either transect was sampled more than once during the study. Chambers were incubated for 1-h periods, alternating between total darkness (using blackout cloth) and ambient light over the course of the day, and flushed with ambient seawater for 10 min every 2 h. After incubations were complete, all macroalgae inside the chambers were collected in fine mesh bags and returned to the laboratory where they were cleaned of epiphytes, sorted to genus or species (with the exception of filamentous brown algae which were grouped as Ectocarpaceae), weighed wet, and dried for at least 72 h at 60°C prior to re-weighing to

determine dry mass. Dry mass of holdfasts and stipes was measured separately from that of fronds and blades for the stipitate kelps *Pterygophora californica* Ruprecht and *Laminaria farlowii* Setchell.

Changes in dissolved oxygen within the chambers were used to calculate GPP and respiration rates by fitting a linear regression to the measured oxygen concentration over each 1-h incubation time. The regression equation was used to estimate hourly rates of oxygen production. Oxygen consumption in dark incubations was used as an estimate of community respiration. GPP was calculated as the sum of oxygen produced in the light (community production) and oxygen consumed in the dark (community respiration). GPP within a chamber was integrated across the day using calculated daylength from sunrise/sunset times for each sampling date and was converted to units of milligram carbon per square meter per day (mg C m^{-2} day^{-1}) using a photosynthetic quotient of 1 (following Rosenberg et al. 1995).

Field irradiance measurements

Logging photosynthetically active radiation (PAR, 400–700 nm) sensors with a spherical collector (MKV-L; Alec Electronics, Kobe, Japan) were mounted 10 cm from the bottom and placed between the two chambers at each of the two transects for the duration of each sampling period. Instantaneous irradiance was recorded once per second and averaged to obtain mean instantaneous irradiance values for 1- min and 1-h intervals. Because the slope and r^2 of the relationship of modeled GPP to measured GPP was not affected by the time interval over which irradiance was averaged, we used mean hourly irradiance to derive our modeled estimates of GPP.

Laboratory-measured rates of photosynthetic parameters

Eleven species of macroalgae comprising >98% of the total algal biomass measured in all chambers were collected from local reefs at a depth of 5–9 m and kept in an indoor aquarium with running seawater at ambient temperature for no longer than 2 days before photosynthesis versus irradiance (*P* vs. *E*) measurements were made. We used whole thalli in the incubation experiments to incorporate the effects of plant morphology and self-shading into production measurements (compare Littler and Arnold 1980). Each algal specimen was cleaned of all epiphytes prior to incubation. The holdfast and most of the stipe of the stipitate kelps *Pterygophora californica* and *Laminaria farlowii* were removed so the specimens could fit into the incubation tanks; most of the photosynthetic tissue in these species is in their blades. *P. californica* was represented by a much wider size spectrum of individuals than the other species (dry biomass range 1–133 g). Because weight-specific photosynthetic rates may vary with size due to self-shading and other factors (Littler 1980), we measured *P. californica* over a range of sizes and fit a power function ($y = 3.41x^{-0.53}$, $r^2 = 0.81$) to the relationship between maximum photosynthesis (P_{max}) and dry biomass to estimate P_{max} for individuals of this species.

P versus *E* relationships were obtained for each species by anchoring a specimen with modeling clay in a natural upright position to the bottom of a sealed acrylic tank (volume 35 L). The tank was submerged in a bath of running seawater. Tanks were equipped with a submersible aquarium pump (Rio model 50; 262 L h^{-1}) to provide circulation, and an optical probe (D-Opto; ENVCO) that measured dissolved oxygen at a frequency of once per minute. Specimens were incubated in the dark for 20 min to measure respiration rate. Tank seawater was then sparged with nitrogen gas (N_2) to lower initial oxygen concentrations. The nitrogen sparging had no detectable effects on seawater pH. Irradiance was provided by two 500-W halogen lamps fixed 30 cm above the tanks. Plastic mesh screens (9 in total) were sequentially removed from the incubation tank lid at 20-min intervals, creating incubation irradiances of 10 (all screens present), 19, 36, 60, 103, 178, 198, 344, 392, and 700 μmol photons m^{-2} s^{-1}, which spanned the range of irradiances measured in the field. The wet mass and volume of each specimen were measured following the completion of incubations. Wet samples were dried for at least 72 h at 60°C and re-weighed to obtain dry mass. In the calculation s of GPP, tank volumes were corrected for the volume displaced by algae, clay, pump, and oxygen probe.

Oxygen evolution rates for each light level and for dark incubations were calculated by fitting a linear regression to the measured change in oxygen concentration over incubation time. The regression equation was used to calculate hourly rates of oxygen evolution per gram of dry photosynthetic tissue. Oxygen evolution rates were converted to carbon using a photosynthetic quotient of 1 (following Rosenberg et al. 1995). The initial slope of the curve, α, was calculated by fitting a linear regression to the change in production rate over a range of non-saturating irradiance values (1–150 μmol m^{-2} s^{-1}) for each taxon (Jassby and Platt 1976). P_{max} was estimated individually for each taxon by fitting the data to the equation presented below using a least squares non-linear fitting procedure (SAS ver. 9.1.3, PROC-NLIN; SAS Institute, Cary, NC).

Physiological model of primary production

We constructed a physiologically based model incorporating biomass, photosynthetic performance, and bottom irradiance to estimate taxon-specific areal GPP (g C

m^{-2} h^{-1}) for benthic macroalgae following the hyperbolic tangent equation of Jassby and Platt (1976):

$$\mathrm{GPP} = P_{\max} \cdot \tanh(\alpha E / P_{\max}) \cdot b,$$

where $P_{\max}$ is the laboratory-calculated GPP at saturating irradiance expressed as carbon production per unit mass [mg C (mg dry mass)$^{-1}$ h^{-1}], rather than unit area, α is the laboratory-calculated initial slope of the relationship between mass-specific GPP and irradiance at non-saturating irradiance, E is the instantaneous photosynthetically active radiation on the seafloor averaged over 1 h (in μmol m^{-2} s^{-1}), and b is the naturally occurring macroalgal standing crop (not including stipes and holdfasts of the stipitate kelps) (in mg dry mass m^{-2}). We applied this model to data on bottom irradiance and macroalgal standing crop collected by Miller et al. (2011) to obtain independent estimates of daily areal GPP for each benthic chamber incubation as follows:

$$\mathrm{GPP} = \sum_{\mathrm{i,h}} P_{\max} I \cdot \tanh(\alpha E \mathrm{h} / P_{\max} I) \cdot \mathrm{b} I,$$

where I is an algal taxon and h is incubation time in hours, such that total GPP for each chamber is the sum of GPP for all algal taxa in the chamber over all incubation hours in a sampling day.

Middelboe et al. (2006) used photosynthetic parameters measured in the laboratory and species-specific biomass measured in the field to calculate the average biomass-weighted photosynthetic activity of natural algal assemblages, which they termed thallus activity. Thallus activity of the understory assemblages enclosed in our chambers was evaluated as a predictor of measured GPP and calculated as:

$$\text{Thallus activity} = \sum \left(\frac{p_I}{P}\right) \cdot \left(\frac{f_I}{F}\right),$$

where p_I is the relative abundance of species I, P is the total abundance of all species in the community, f_I is the thallus activity ($P_{\max}$ or α) of species I, and F is the mean thallus activity of all species in the chamber.

Data analysis

Because both field and modeled estimates of GPP in the plots contained within the chambers include random error, we compared estimates of GPP obtained from the two methods using Model II regression (Legendre and Legendre 1983). Additionally, because our goal was to develop a predictive model for estimating the production of understory macroalgae, we evaluated the relationship between field-measured and model-predicted GPP with ordinary least squares (OLS) Model I linear regression (Laws 1997). GPP was considered to be the most reliable estimate of in situ production because heterotrophs were present in the field-deployed chambers. Thus, we used GPP rather than net primary production (NPP) as the basis for comparison between modeled and measured production. To test whether the relationship between measured and modeled GPP was better described by a nonlinear function, we evaluated the slope of a log–log regression of the two variables to determine if the slope was significantly different from 1 (Hillebrand and Bleckner 2002).

A simple sensitivity analysis was performed to determine which parameters most influenced the output of the model. We re-ran the model using the field-collected biomass and irradiance data and each time varied one parameter ±25%. Because the field-collected biomass and irradiance data were positively correlated (see "Results"), we altered the photosynthetic parameters $P_{\max}$ and α together. The resulting output was expressed as the percentage change from the original modeled values.

We evaluated whether the difference between modeled and measured GPP varied with increasing community complexity or biomass. The difference between modeled and measured GPP was calculated as:

$$\delta\mathrm{GPP} = \frac{(\mathrm{GPP}_{\mathrm{modeled}} - \mathrm{GPP}_{\mathrm{measured}})}{(\mathrm{GPP}_{\mathrm{modeled}} + \mathrm{GPP}_{\mathrm{measured}})}.$$

δGPP therefore varied from −1 to 1, with positive values indicating larger modeled GPP compared to measured GPP. The relationship between δGPP and species richness and diversity (Shannon–Weiner index H′; Magurran 2004) was evaluated using least-squares regression, with each field incubation chamber as a replicate. The relationship between δGPP, community biomass, and irradiance was also evaluated using multiple regression. The effects of light and biomass were expected to interact to affect δGPP, such that increasing light would reduce δGPP only in high-biomass plots where shading by multiple canopy layers is greatest (Binzer et al. 2006; Middelboe et al. 2006). Thus, we used a multiple regression model of the form $\delta\mathrm{GPP} = \beta_0 + \beta_1 B + \beta_2 E + \beta_3 B \times E$, where B is biomass and E is irradiance, to evaluate the response of δGPP to varying light and biomass. The relationship between thallus activity and measured GPP was evaluated using least-squares regression. All statistical tests were performed using SAS ver. 9.1.3 (SAS Institute).

Results

Photosynthesis versus irradiance parameters

Laboratory estimates of $P_{\max}$ and α for the 11 algal taxa that comprised 98% of the biomass in all chamber incubations are shown in Table 1. P versus E relationships were

not examined for *Cryptopleura* sp., *Bossiella orbginiana* Silva, *Corallina chilensis* Linnaeus, *Nienburgia andersoniana* Kylin, *Sarcodiotheca furcata* Kylin, and *Taonia lennebackerae* Agardh, which constituted the remaining 2% of biomass in the chambers. P_{max} and α for these species were estimated using means of values for morphologically similar species.

Algal respiration was positively related to maximum gross photosynthesis [respiration = $0.7(P_{max}) - 0.84$; $r^2 = 0.73$, $P < 0.00001$]. Respiration averaged 34.8% of maximum photosynthesis across all species examined (range 10–60%; Table 1). Compensating irradiance, E_c, the light level at which photosynthesis balanced respiration, varied from 26.7 μmol photons m^{-2} s^{-1} for *Cystoseira osmundaceae* (Turner) Agardh to 64.8 μmol photons m^{-2} s^{-1} for juvenile *Macrocystis pyrifera*, and averaged 44.1 [±4 standard error (SE)] μmol photons m^{-2} s^{-1} (Table 1). Saturating irradiance, E_k, varied from 115.5 μmol photons m^{-2} s^{-1} for filamentous brown algae (Ectocarpaceae) to 304.7 μmol photons m^{-2} s^{-1} for *C. osmundaceae*, and averaged 196.7 (±16 SE) μmol photons m^{-2} s^{-1} across the 11 taxa (Table 1). E_c and E_k were uncorrelated across taxa (Spearman's ρ, $P = 0.3$). Thallus activity, in terms of either P_{max} or α, was positively related to measured GPP, but only explained a small amount of variation in GPP (GPP = $5.8 P_{max} + 779.0$; $r^2 = 0.2$, $P = 0.002$, GPP = $5.1\alpha + 765.4$; $r^2 = 0.2$, $P < 0.001$).

Species contributions to production

Five species [*Chondracanthus corymbiferus* (Kutzing), *Pterygophora californica* Kylin, *Rhodymenia californica*, *Cystoseira osmundacea*, and *Laminaria farlowii*) accounted for an average of 92% (±2 SE) of the algal biomass in the benthic chambers and 92% (±2.2 SE) of the modeled GPP (Fig. 1). Species richness varied from zero to eight in the chambers and averaged 2.8 (±0.2 SE). Although the GPP measured in a chamber was positively related to the combined biomass of all algae in the chamber (Miller et al. 2011), total algal biomass explained only about 10% of the variation in GPP. Algal species richness was positively related to total algal biomass [$r^2 = 0.15$, richness = 0.004 dry mass (g) + 2.4, $F_{1,58} = 11.3$, $P = 0.001$].

Comparison of in situ measured and modeled GPP estimates

Modeled GPP explained 70% of the variation in measured GPP when chamber incubations from all sampling dates

Table 1 Mean dry to wet mass ratio, photosynthetic parameters, and respiration rates for the 11 macroalgal taxa comprising 98% of the standing crop in the incubation chambers

Taxa	Dry mass/wet mass	P_{max}(mg C g dry mass^{-1} h^{-1})	α [mg C h^{-1} (μmol m^{-2} s^{-1}) (g dry mass)$^{-1}$]	Respiration (mg C g dry mass^{-1} h^{-1})	E_c (μmol PAR m^{-2} s^{-1})	E_k (μmol PAR m^{-2} s^{-1})
Phaeophyta						
Cystoseira osmundacea	0.15 (0.001)	0.8 (0.1)	0.003 (0.0003)	0.08 (0.02)	21.9 (5.2)	271.3 (37.5)
Ectocarpaceae	0.06 (0.003)	14.9 (3.7)	0.2 (0.04)	6.9 (3.2)	46.7 (20.0)	279.8 (115.8)
Laminaria farlowii	0.13 (0.001)	1.0 (0.6)	0.006 (0.0009)	0.2 (0.02)	25.1 (3.6)	204.3 (21.7)
Macrocystis pyrifera	0.09 (0.005)	4.5 (0.8)	0.02 (0.001)	1.3 (0.3)	61.0 (14.7)	394.9 (76.9)
Pterygophora californica	0.13 (0.001)	0.1–2.7 (0.1)	0.002 (0.0002)	0.07 (0.01)	36.0 (8.0)	181.3 (76.4)
Rhodophyta						
Callophyllis flabellulata	0.07 (0009)	3.4 (1.3)	0.03 (0.0003)	1.3 (0.8)	35.5 (14.8)	164.1 (74.3)
Chondracanthus corymbiferus	0.15 (0.001)	1.3 (0.3)	0.007 (0.001)	0.3 (0.1)	55.9 (25.0)	319.6 (78.6)
Gracilaria sp.	0.10 (0.002)	1.6 (0.3)	0.02 (0.002)	0.8 (0.3)	57.9 (20.6)	198.5 (97.1)
Polyneura latissima	0.32 (0.07)	4.1 (0.8)	0.03 (0.006)	1.6 (0.6)	38.9 (9.8)	229.2 (58.5)
Pterosiphonia dendroidea	0.07 (0.002)	8 (1.5)	0.08 (0.007)	4.8 (1.4)	80.2 (33.1)	393.0 (163.2)
Rhodymenia californica	0.16 (0.003)	3.6 (1.6)	0.03 (0.01)	1.7 (0.8)	82.9 (16.8)	359.8 (90.9)

P_{max}, Maximum gross photosynthesis [expressed in terms of gross primary production (GPP)]; E_c, compensating irradiance; E_k, saturation irradiance; PAR, photosynthetically active radiation

Data are presented as the mean, with the standard error (SE) given in parentheses

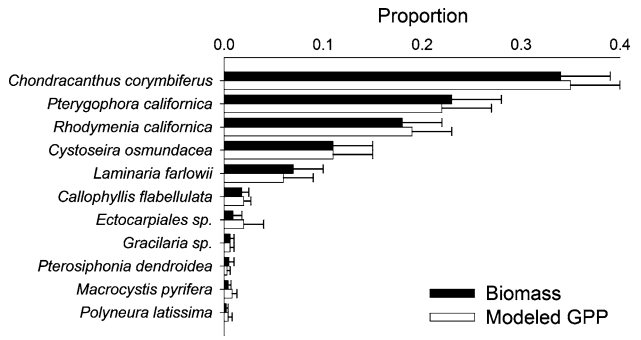

Fig. 1 The proportion of dry biomass [mean + standard error (SE), *black bars*] and modeled gross primary production (*GPP*; mean + SE, *open bars*) accounted for by 11 different algal taxa in the benthic chambers deployed at Mohawk Reef, Santa Barbara, California, USA during May 2007 through September 2008

were considered (Fig. 2). There was no evidence of non-linearity in the relationship between modeled and measured GPP; the slope of the log–log relationship was not significantly different from 1 [$m = 0.9$; 95% confidence interval (CI) 0.33]. We found no evidence that the accuracy of our model was influenced by the diversity of the algal assemblage, as the difference between modeled and measured GPP (δGPP) was unrelated to both species richness ($r^2 = 0.02$, $P = 0.3$) and to species diversity, H′ ($r^2 = 0.005$, $P = 0.7$; statistical power in both cases was >0.8). There was no evidence that community biomass and irradiance interacted to influence δGPP (multiple regression, $P = 0.3$), but δGPP was positively related to both biomass and irradiance (multiple regression without interaction term, $P < 0.0001$), with biomass having the greater explanatory power (scaled effect size of biomass 0.6, irradiance 0.4).

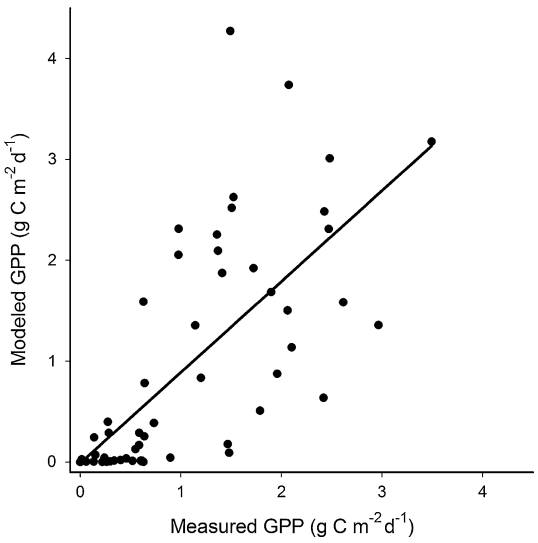

Fig. 2 The relationship between measured field estimates of areal GPP in each chamber and modeled estimates based on light and taxa specific biomass in each chamber ($y = 0.90x$, $r^2 = 0.70$)

Model sensitivity analysis

Changes in algal photosynthetic parameters and biomass resulted in proportional changes in modeled GPP (Table 2). Results were slightly less sensitive to irradiance: changing irradiance by 25% resulted in approximately a 20% change in GPP. Production changed less with added light compared to subtracted light, due to the saturation dynamics of photosynthesis in the model: once the saturation irradiance of any taxon is reached, no further increase in GPP by that taxon is possible.

Discussion

A simple physiological model based on in situ light measurements, and species-specific biomass and photosynthesis versus irradiance (*P*/*E*) parameters explained a large portion (70%) of variation in the GPP by understory algal assemblages measured in situ using sealed chambers. Moreover, the linear relationship between these two measures of production had a slope near unity, indicating that the two different methods provided a very similar estimate of production that did not vary across a large range of production rates. Previous researchers have suggested that the scaling of thallus photosynthetic rates to estimate community photosynthesis is not possible due to canopy architecture effects (Binzer and Sand-Jensen 2002b; Middelboe and Binzer 2004; Binzer and Middelboe 2005; Sand-Jensen et al. 2007). The rationale for these arguments is that thalli shaded by the canopy, and at suboptimal angles for light collection, will not be photosynthetically saturated at irradiances measured for unobstructed thalli in the laboratory and that this will lead to overestimates of modeled production (Duarte and Ferreira 1995). This phenomenon can also be expressed as large differences in the saturating irradiances of individual thalli versus multi-

Table 2 Percentage change from modeled GPP when production rates (P_{max} and α), hourly irradiance, or biomass were changed by 25%

Parameter change	P_{max} and α	*E*	*B*
−25%	25.0%	−19.5%	−25.0%
+25%	25.0%	17.6%	25.0%

α, The laboratory-calculated initial slope of the relationship between mass-specific GPP and irradiance at non-saturating irradiance; *E*, hourly irradiance; *B*, biomass

Values represent percentage change averaged over all chambers ($N = 62$)

species assemblages, with entire assemblages saturating at much higher rates than thalli, as understory thalli continue to benefit from increasing light that penetrates the canopy (Binzer and Middelboe 2005; Tait and Schiel 2011).

The reason that our results differ from these studies likely reflects differences in our methods and study system. The additive model framework we used in the study reported here, though simple, has seldom been employed in the field, and to the best of our knowledge, the modeled results has never before been compared with measurements from field incubations. Several interesting studies have been done in Denmark using shallow subtidal algal communities assembled in the laboratory (Middelboe and Binzer 2004; Binzer and Middleboe 2005) or those allowed to naturally develop on concrete tiles and brought into the laboratory for photosynthetic measurements (Middelboe et al. 2006; Binzer et al. 2006). The general conclusion from these studies was that physiological measurements on thallus pieces cannot be used to infer community-level rates (summarized in Binzer et al. 2006). In these studies, thallus pieces were fixed horizontally so that they were normal to the light source for photosynthetic measurements (Middelboe and Binzer 2004; Binzer and Middelboe 2005; Middelboe et al. 2006). Our use of naturally oriented whole plants likely resulted in estimates of photosynthetic responses to irradiance that incorporated within-plant shading effects and thus more accurately reflect photosynthesis in nature. Rather than assembling a model to estimate community production, as we have here, Middelboe et al. (2006) used "thallus photosynthetic activity" (TA) as a dependant variable in a multiple regression to explain community GPP; the result was no relationship. We found only a weak relationship between TA and the GPP measured in our chambers. Coupling photosynthetic activity with biomass and irradiance, however, resulted in reasonably accurate estimates of community GPP. Other studies that have used whole thalli or groups of thalli and similar irradiance-based models have also generated realistic estimates of primary production (Brinkhuis 1977a, b, c; Duarte and Ferreira 1993).

The subtidal setting of our study and, consequently, lower light levels and lower algal biomass may also have played a role in the results we obtained. Community standing biomass was not reported by Middelboe et al. (2006) or Binzer et al. (2006), but data from Binzer and Middelboe (2005) suggest that the shallow subtidal communities they measured attain very high standing biomass, which would likely increase the prevalence of self-shading. Similarly, Tait and Schiel (2011) found that the production of very high biomass intertidal algal communities exhibited relatively linear positive relationships with irradiance, indicating that understory biomass was light-limited. Such linear relationships are also typical of forest canopies on land (Hesketh and Baker 1967). The communities measured here cover the full range of understory macroalgal biomass found on shallow (5–10 m) subtidal reefs off the Santa Barbara coast (authors' unpublished data). Relatively low light levels and correspondingly lower algal biomasses may lessen the importance of community self-shading in the subtidal, as well as in shaded terrestrial understory communities, compared to systems in higher light environments (e.g., grasslands or the rocky intertidal). Our modeling framework may overestimate production by extremely high biomass assemblages with dense canopies that are maintained by high light levels, as reflected by the small positive effect of community biomass and irradiance on the accuracy of the model fit, as represented by δGPP. Nevertheless, oscillation of macroalgae with wave action, lensing of light by waves, and other sources of variation in the light environment may also be important in relieving self-shading effects in giant kelp forests (Gerard 1984) and other types of algal assemblages (Wing and Patterson 1993), and additional insight could be gained by testing our model across the full range of algal biomass in both intertidal and subtidal habitats.

The simple additive nature of primary production in our study, as well as the lack of any relationship between diversity and model fit, does not support enhanced productivity at higher levels of diversity beyond that which is due to higher biomass. This finding is not surprising, since controlled experiments varying richness while holding biomass constant have shown little evidence of transgressive overyielding, an emergent effect, indicating that positive effects of richness on ecosystem function are most often due to sampling effects or complementarity (reviewed by Stachowicz et al. 2007). Richness effects on productivity, moreover, are typically small, with species identity explaining most of the variation in productivity in controlled experiments (Bruno et al. 2005, 2006). This is consistent with our model results that explained most variation in productivity with species photosynthetic characteristics, combined with biomass and available light, which are controlled in most experiments.

Aquatic macrophytes have been portrayed as photosynthetically disadvantaged due to their flexible and consequently unpredictable canopy architecture, which may prevent them from achieving optimal light absorption compared to the more rigid structure of terrestrial shrubs and trees (Sand-Jensen and Krause-Jensen 1997). Despite this, studies have shown rates of NPP by aquatic macrophyte communities to be similar to those of terrestrial communities (Cebrian 1999; Laffoley and Grimsditch 2009). Our results suggest that self-shading may not be an important factor in all algal communities, particularly in the subtidal environment, the largest habitat occupied by marine macroalgae. The flexibility of algal tissues has been

shown to be an adaptation to wave and current stress (Carrington 1990), but flexibility can also impose increased stress on algae, particularly small plants (Denny et al. 1997). Koehl and Alberte (1988) showed that the ruffled blades of the kelp *Nereocystis luetkeana* Mertens decreased self-shading in this species by increasing the amplitude and variability of blade movement. Sunflecks, brief flashes of light, have been shown in some cases to provide the majority of light to terrestrial understory assemblages, and are facilitated by canopy movements due to wind (reviewed by Pearcy 1990; Chazdon and Pearcy 1991). Wave-induced rapid variations in light have been reported in kelp canopies (Gerard 1984; Wing et al. 1993) and seagrass beds (Enriquez et al. 2002) and in the intertidal habitat (Wing and Patterson 1993), and exposure to rapidly fluctuating light environments, such as that imposed via sunflecks, can increase the photosynthetic rate of macroalgae (Dromgoole 1988; Kubler and Raven 1996; Greene and Gerard 1990). Our use of chambers incorporating flexible walls that allowed undulation with wave energy (Miller et al. 2009) may have led to a better agreement with model results than other incubation methods, if canopy movement decreases self-shading. The relationship between flexibility and light harvest in algae warrants further investigation.

Our model sensitivity analysis showed that varying algal biomass or photosynthetic parameters resulted in proportional changes in production, indicating that both equally contributed to model results. Nevertheless, the most abundant species in terms of biomass (*Chondracanthus corymbiferus*) also contributed the most to modeled GPP. This result indicates that species-specific differences in photosynthetic parameters, which spanned more than an order of magnitude for P_{max} and three orders of magnitude for α (Table 1), were less important than biomass in explaining GPP. Large algae, despite their lower biomass-specific photosynthetic parameters, largely determined GPP, which is consistent with the findings of previous studies (Hatcher 1990; Westphalen and Cheshire 1997; Copertino et al. 2005; Miller et al. 2009).

Given the logistical constraints of measuring production in situ, models such as ours should prove to be useful tools for estimating benthic primary production on larger spatial and temporal scales than is possible using benthic chambers. Such modeled estimates of NPP will avoid the problem of heterotrophic respiration that is encountered in chamber incubations. Morever, building such a model for long-term coastal ecosystem studies is feasible. Measuring P versus E relationships for common species in the laboratory is straightforward. Biomass can be measured by harvesting, or non-destructively by establishing relationships between abundance (measured as percentage cover or size-specific density) and biomass (Shears and Babcock 2003; Reed et al. 2009; Harrer 2010), which allows for repeated measurements of the same plots over time. Underwater PAR sensors with a data-logging capacity are declining in cost, making the long-term collection of PAR data possible. This contrasts with the current expensive and more complex alternatives, such as eddy-correlation estimates of community production (Berg et al. 2003).

Primary production is a key measure of ecosystem function and an important driver of community structure, particularly in marine ecosystems (Cebrian 2004). Although large-scale measurements of production using remote sensing are becoming common for the open ocean (Westberry et al. 2008) and terrestrial (Hilker et al. 2008) systems, these techniques thus far are not generally applicable to the subtidal benthos and can be difficult to apply to terrestrial understory assemblages (Sakai and Akiyama 2005), which are often not accounted for in estimates of forest NPP (House et al. 2003; Sakai and Akiyama 2005). Simple predictive models of primary production, such as that provided here offer a promising means of determining the effects of environmental change on primary production in these ecosystems. Such information is needed to obtain a comprehensive understanding of the ecological consequences of climate change on some of the world's most productive habitats.

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