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Partitioning of primary production among giant kelp (*Macrocystis pyrifera*), understory macroalgae, and phytoplankton on a temperate reef

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Abstract

We experimentally investigated the response of phytoplankton and understory macroalgae to canopies of giant kelp, *Macrocystis pyrifera*, by following changes in their biomass and net primary production over 17 months in 600-m^2 plots where giant kelp was continually removed or left intact and allowed to vary naturally. Production by phytoplankton was two times greater and understory algae five times greater where *Macrocystis* was removed relative to the intact forest. Understory biomass, but not phytoplankton biomass, was suppressed inside the forest, leading to a higher magnitude of effect on net primary production (NPP) by understory relative to phytoplankton. Following a natural decline of the *Macrocystis* canopy by winter storms, understory macroalgae and phytoplankton increased production in the *Macrocystis* control plot. This response was delayed for both groups, with phytoplankton production increasing in spring and understory increasing later during summer. The longer delay for understory macroalgae was likely due to restrictions in the timing of macroalgal recruitment and their slower growth rates compared with phytoplankton and with increased competition for light resulting from greater light absorption by the spring phytoplankton bloom. Surprisingly, total ecosystem production that included NPP by *Macrocystis*, phytoplankton, and understory algae did not differ between the *Macrocystis* control and removal plots for much of the study. NPP by understory algae, which comprised the bulk of the ecosystem NPP in the *Macrocystis* removal plot, can compensate to varying degrees for the loss of *Macrocystis* production following its removal by winter storms.

Coastal reefs in temperate seas are among the most productive ecosystems in the world (Mann 2000). The autotrophs in these systems can be broadly divided into pelagic phytoplankton and benthic macrophytes. Both groups can contribute substantially to ecosystem production (Gattuso et al. 1998; Cebrian 1999) and can potentially affect each other through competition for light and nutrients (Smith and Horne 1988; Kavanaugh et al. 2009). Canopy-forming kelps, particularly, can reduce the biomass of lower lying autotrophs through shading (Reed and Foster 1984; Santelices and Ojeda 1984). Patterns and controls of primary production by phytoplankton and macrophytes are generally measured and studied by separate communities of researchers: benthic ecologists and phycologists tend to study macroalgal production at relatively small spatial scales, concentrating for the most part on rocky reefs in the intertidal and shallow subtidal zones, while coastal phytoplankton production is examined by biological oceanographers generally focusing on shelf-wide or broader oceanographic scales. This separation has led to disparate views of primary production in coastal ecosystems: benthic ecologists often cite the primacy of large seaweeds such as kelps when describing coastal primary producers (Newell et al. 1982; Graham et al. 2007), whereas biological oceanographers typically ignore macroalgae altogether, focusing on phytoplankton (*see* web appendix in Cebrian 2002). These contrasting viewpoints may be reasonable given the different spatial scales of the habitats occupied by macroalgae and phytoplankton, since kelps may indeed be the most productive autotrophs on a given reef, whereas phytoplankton are distributed more broadly across continental shelves compared with macroalgae. However, these perspectives ignore the potential for interactions between benthic and pelagic autotrophs on intermediate scales, from hundreds of meters to kilometers, such as among reefs with and without kelp canopies, and much of the variation in coastal production can occur at this scale (Broitman and Kinlan 2006).

Giant kelp, *Macrocystis* spp., a foundation species and ecosystem engineer, creates dense forests that provide food and physical habitat to many animal species (Foster and Schiel 1985; Graham 2004), slow water flow (Jackson and Winant 1983; Gaylord et al. 2007), absorb light (Stewart et al. 2009), and take up nutrients (Hurd 2000), thus shaping the entire benthic community (Dayton 1985; Clark et al. 2004; Arkema et al. 2009). Controlled removal experiments have shown that giant kelp suppresses the biomass of understory macroalgae (Dayton et al. 1984; Reed and Foster 1984; Clark et al. 2004). Standing crop biomass of giant kelp varies dramatically both seasonally and interannually, with much of the variation driven by wave disturbance (Graham et al. 2007; Reed et al. 2008).

The extent to which variability in *Macrocystis* biomass alters the production of other autotrophs to influence the magnitude and variability of kelp forest ecosystem net primary production (NPP) is largely unknown. If *Macrocystis* dominates NPP of the entire reef ecosystem, then variation in *Macrocystis* biomass will drive corresponding variation in total ecosystem NPP. Alternatively, if NPP of understory algae and/or phytoplankton increases in re-

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sponse to reduced *Macrocystis* canopy, then variability in total reef ecosystem NPP will be reduced. The amount of such compensatory productivity will depend upon the magnitude and temporal lag of the response of understory algae and phytoplankton NPP to the more favorable light conditions associated with removal of the *Macrocystis* canopy. Phytoplankton are likely able to respond rapidly, since their biomass in the kelp forest is influenced by larger scale processes that affect the regional production and transport of phytoplankton (Otero and Siegel 2004) with only their local productivity possibly affected by shading from *Macrocystis*. In contrast, both the biomass and productivity of understory algae are influenced by conditions within the forest, and their slower growth rates and seasonal recruitment may cause their NPP to lag behind that of phytoplankton following a reduction of the *Macrocystis* canopy.

Here we compare rates of primary production of understory macroalgae and phytoplankton beneath and outside of a canopy of *Macrocystis* in a giant kelp forest off Santa Barbara, California, over a 17-month period during which *Macrocystis* standing crop and production varied substantially. We hypothesized that the *Macrocystis* canopy would negatively affect the productivity of understory macroalgae and phytoplankton and that these effects would vary with *Macrocystis* standing crop. We predicted that unlike phytoplankton, the response in the productivity of understory macroalgae would lag reductions in *Macrocystis* shading, due to restrictions in the timing of macroalgal recruitment and their slower growth rates compared with phytoplankton. Finally, we compared NPP by *Macrocystis* with that by the other primary producers in the forest (i.e., understory macroalgae and phytoplankton) to determine whether natural fluctuations in *Macrocystis* biomass led to similar fluctuations in NPP of the entire kelp forest ecosystem. We postulated that large temporal declines in *Macrocystis* NPP could be dampened by increased NPP from understory macroalgae and phytoplankton in response to higher light levels arising from declines in the *Macrocystis* canopy.

Methods

Study site—This study was done at Mohawk Reef off Santa Barbara, California (34°23′38″N, 119°43′45″W), a shale reef at 5–9-m depth that supported a giant kelp (*Macrocystis pyrifera*) forest. The surface canopy of giant kelp was patchy at the beginning of the study, and a lush assemblage of understory kelps (*Pterygophora californica* and *Laminaria farlowii*) and red algae (principally *Chondracanthus corymbiferus* and *Rhodymenia californica*) occupied the bottom underneath the gaps in the *Macrocystis* canopy. We measured primary production by understory algae and phytoplankton approximately monthly from May 2007 through September 2008 at two locations on the reef: at the offshore edge of the forest in a patch with sparse *Macrocystis* and a lush assemblage of understory macroalgae (area $\sim$ 1000 m^2) and at 30-m inshore of the offshore edge, under a dense *Macrocystis* canopy with a sparse understory assemblage. *Macrocystis* was beginning to reinvade the location at the offshore edge, and we forestalled this by removing *Macrocystis* in March 2007, two months before the study began and by maintaining this area clear of *Macrocystis* throughout the study period. We quantified the extent of the *Macrocystis* surface canopy at both sites in the year prior to our study from *SPOT* satellite imagery of Mohawk Reef per the methods of Cavenaugh et al. (2010).

Both locations (hereafter referred to as the *Macrocystis* removal [MR] and *Macrocystis* control [MC] sites) were at similar depth and in areas of relatively flat, low-relief rock substrate. To quantify these physical attributes, we measured depth and rugosity at the two sites along 30-m permanent transects that we established to locate measurements of understory production (*see* below). We measured depth every meter at two points spaced 0.5 m perpendicular to the transect (n = 124 points transect^{-1}). Rugosity was measured as the length of chain (links 1 cm) required to contour the substrate across a 1-m horizontal distance. This was done perpendicular to the transects every 1 m (n = 30 transect^{-1}). The variation in depth (as characterized by the coefficient of variation among the 60 points) and the rugosity measurement were used to characterize the topographic relief of the MR and MC sites.

The large influence of *Macrocystis* on light and flow in the Mohawk kelp forest (Gaylord et al. 2007; Fram et al. 2008; Stewart et al. 2009) coupled with the close proximity and similar biological and physical features of the MR and MC sites (*see* Results) greatly reduced the chance that factors other than the presence of giant kelp would cause differences in NPP between the two sites. NPP and biomass of *Macrocystis* were measured monthly at a similar depth $\sim$ 10 m west of the MC site as part of the Santa Barbara Coastal Long-Term Ecological Research Program's ongoing investigations. Briefly, mean daily biomass and NPP were calculated from monthly measurements of *Macrocystis* biomass and loss rates of tagged individuals and fronds. NPP was estimated using a simple model of kelp dynamics, which assumed that, within a sampling period, biomass was produced and lost at rates proportional to existing foliar standing crop (for detailed description of methods *see* Rassweiler et al. 2008).

Understory algal biomass, production, and community structure—Primary production by the understory algal assemblage was measured each month along permanent 30-m transects at both the MC and MR sites. Primary production was estimated from oxygen evolution measured in tunnel-shaped closed chambers (25 cm wide $\times$ 40 cm long $\times$ 40 cm tall), that 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) and an open bottom framed by fiberglass-reinforced plastic that was sealed to the seafloor by a nylon gasket and a weighted flexible plastic skirt (Miller et al. 2009). Observations using rhodamine dye indicated that this made a highly effective seal (Miller et al. 2009). The flexible side walls and ceiling permitted wave energy to be transmitted through the walls of the chambers, allowing macrophytes inside to oscillate naturally with wave-

generated flow (sensu Gust 1977; Yates and Halley 2003). Chamber volume was ~ 45 liters and was measured for each chamber for production calculations. Water circulation was provided with a battery-powered submersible pump to ensure mixing of oxygen and prevent mass-transfer limitation of algal photosynthesis (Rule 500 baitwell pump, 1890 L h^{-1}). Self-contained optical probes (D-Opto, ENVCO) within each chamber logged dissolved oxygen concentration and temperature inside the chambers at a frequency of once per minute.

Oxygen measurements were taken simultaneously in four chambers per sampling date. Two chambers were placed randomly by divers along the control and removal transects on the morning of each sampling date and incubated for the majority of the day to capture diurnal variability in production rates (10 h March–November, 8 h December–February). The placement of chambers along the transects differed on each sampling date such that no plot was sampled more than once during the study. Conditions within the chambers were alternated between ambient light and dark on an hourly basis with darkness created by draping blackout cloth over the chamber. Chambers were flushed with outside water after each pair of light and dark incubations (every 2 h) by opening two stoppered ports and using the circulation pump to exchange water for 10 min. Oxygen saturation levels inside the chambers never exceeded those of ambient seawater by more than 10%.

After all incubations for the day were complete, the biomass of macroalgae enclosed by the chambers was collected by gently scraping it from the bottom into a fine mesh bag. Macroalgae were separated from animals and other material in the laboratory and sorted by taxon. The algae were cleaned of animal epiphytes, blotted dry, weighed, and then dried at 60°C and reweighed to obtain dry weight. Subsamples of dried tissue of each algal taxon were ground and analyzed for carbon content, and these values were used to convert dry weight to carbon weight. To evaluate the potential for differences in nutrient availability between the MR and MC sites, tissue samples from species of understory algae that were present within at least one chamber at both sites on the same date were also analyzed for carbon and nitrogen content using a Carlo-Erba (Flash EA 1112 series) automated organic elemental analyzer.

Production and respiration rates were calculated by plotting oxygen concentration over incubation time, fitting a linear regression line to the data, and using the regression equation to calculate hourly rates of oxygen change. Net community production (NCP) was estimated as oxygen production in the light incubation. We report estimates of NCP per 12-h period, since we did not measure nighttime community respiration, which is likely to be lower and nonlinearly related to daytime respiration (Barron and Duarte 2009). Oxygen consumption in the dark incubation was used as an estimate of community respiration (CR). Gross primary production (GPP) was calculated as the sum of oxygen produced in the light and that consumed by respiration in the dark, and GPP was converted to NPP using mass-specific respiration rates obtained in laboratory dark incubations of 11 of the common understory species representing > 97% of the understory biomass (R.J. Miller unpubl. data). Briefly, algal specimens were collected and kept in running seawater, and within 1 d were incubated for 30 min in the dark to obtain respiration rates, after which the algae were dried at 60°C and weighed. For rare species that were not measured, average respiration rates of related species were used to estimate NPP. Middelboe et al. (2006) found that separate measurements of thallus respiration, weighted by biomass, accurately predicted community respiration in mixed-species heterotrophy-free algal assemblages. While we do not know the degree to which respiration in the light is different from respiration in the dark, the carbon-concentrating capacity of aquatic plants should minimize this difference (Falkowski and Raven, 2007). Direct measures of the effect of oxygen concentration on dissolved inorganic carbon (DIC) uptake and compensation point in marine macroalgae have supported this view (Cook and Colman 1987).

NPP, NCP, and CR were integrated across the day for each plot, using daylengths calculated with sunrise and sunset times for each sampling date, and are expressed in milligrams of carbon per meter per day, which was obtained using photosynthetic and respiratory quotients of 1, following Rosenberg et al. (1995), who found that photosynthetic quotients did not consistently relate to nutrient source or taxonomy and recommend using a value of 1 for the sake of inconvertibility when DIC uptake is not directly measured. Near-bottom rates of phytoplankton NPP were low, averaging less than 1% of benthic production, and were not corrected for, since measurements of phytoplankton and benthic algae were not simultaneous.

Abundance of understory algae was monitored approximately monthly starting in summer 2007 to document dynamics of algal community structure at the two sites. Ten 1-m^2 quadrats were placed at even intervals along the transects, and the presence or absence of benthic species was recorded at 20 evenly spaced points at the intersections of a grid of thin nylon lines. Larger species of understory kelps (*P. californica* and *L. farlowii*) were counted and measured (*P. californica*, number blades; *L. farlowii*, blade length). Species-specific relationships between percentage cover and biomass (Miller et al. 2009), and morphometrics and biomass for the understory kelps (R.J. Miller and D.C. Reed, unpubl. data), were used to convert these data to biomass (grams dry weight per square meter).

Light availability at each site was measured using photosynthetically active radiation (PAR, 400–700 nm) sensors. Bottom irradiance was measured every second during the chamber incubations using logging meters with spherical collectors (Mark V-Light, Alec Electronics) mounted ~ 10 cm above bottom near the chambers. Light was also recorded each minute from June 2007 to September 2008 by sensors mounted on stakes ~ 60 cm above the bottom at the MC and MR sites, and, after September 2007, measurement of surface irradiance was added using a single sensor mounted above the seawater surface. We calculated water column extinction coefficients (K_d) in the MC and MR sites using irradiance values from the surface sensor and the bottom sensors.

Phytoplankton biomass and production—Phytoplankton production was measured at the MR and MC sites using in situ ^{13}C-bicarbonate tracer incubations according to the methods of Shipe and Brzezinski (2003). Briefly, a pair of 500-mL polycarbonate light and dark bottles were filled with water collected at five depths (1, 2, 3, 4, 6 m) at each site (MC and MR) using an 8-liter Go-Flo bottle (General Oceanics). Following addition of 0.5 ml of 0.167 mol L^{-1} $H^{13}CO_3^-$ (99.9 atom%), experimental bottles were incubated for ~ 24 h at each site on a moored line at the collection depths, placed in a dark cooler upon collection, and filtered through precombusted (450°C for 2 h) glass fiber filters. ^{13}C atom percentage of the particulate matter was measured using a Thermo Finnigan Delta-Plus Advantage isotope mass spectrometer coupled with a Costech EAS elemental analyzer. Carbon fixation in the incubation bottles was calculated as

$$POC_{new} = \frac{(A\%_{sam} - A\%_{nat})}{(A\%_{enr} - A\%_{sam})} \times POC_0 \quad (1)$$

where $A\%_{sam}$ is atom percentage ^{13}C measured on the filtered sample after incubation, $A\%_{nat}$ is the average natural abundance of ^{13}C in suspended particulate organic carbon (POC, 1.112%, Fernandez et al. 2005), and $A\%_{enr}$ is the atom percentage ^{13}C of the labeled substrate. POC_0 is the preincubation concentration of POC (μmol C L^{-1}). Production was corrected for dark uptake, including any that occurred between collection and filtration, and integrated through the water column (to 6-m depth). Twenty-four hour carbon tracer uptake best represents NPP, although high heterotrophic activity during the night may lead to an underestimation of production (Marra 2009). POC and chlorophyll *a* (Chl *a*) concentrations (surrogates for phytoplankton biomass) were measured for each sampling depth. POC concentrations were measured in 630-mL water samples filtered through precombusted glass fiber filters and analyzed with a Leeman Labs (Model 440) carbon–hydrogen–nitrogen analyzer. Chl *a* was measured in 200-mL water samples filtered through 0.45-μm, 47-mm cellulose ester Millipore filters following Parsons et al. (1984).

Ecosystem production—To explore the differences in ecosystem NPP (i.e., NPP of understory algae + phytoplankton + *Macrocystis*) between the MC and MR sites, we summed our estimates of NPP for these three groups of primary producers for months where we measured all three ($n = 15$); these were assigned to the six seasonal periods of the study (spring, summer, and autumn in 2007 and winter, spring, and summer in 2008). *Macrocystis* NPP was assumed to be zero for the MR site.

Data analysis—Irradiance values collected each minute within the chambers were averaged over each incubation time for correlation with benthic production rates. We used ANOVA to test the hypothesis that the *Macrocystis* canopy would negatively affect the productivity and biomass of understory macroalgae and phytoplankton and that these effects would vary seasonally, with *Macrocystis* standing crop. Biomass and production of understory benthos (NPP and NCP) and phytoplankton (NPP), benthic respiration rates (CR), and total ecosystem NPP were analyzed, with season (six levels, spring 2007–summer 2008) as a random factor (replicated temporal block) and site (two levels, MC and MR) as a fixed factor. Seasons were defined by solar solstices and equinoxes. Since we predicted a priori that *Macrocystis* would negatively affect nonkelp production and biomass, we used planned comparisons using the ANOVA matrix (1 degree of freedom *F* tests) to compare treatments within seasons. Levene's test was used to test for heteroscedasticity prior to ANOVA; this test was met in all cases without the need for transformation. Statistical analyses were done using JMP (SAS Institute, Windows version 7.0).

Results

Site characteristics—The mean depths at MR and MC sites were identical (7.6 m below mean lower low water; *t*-test, $t = 0.52$, df = 246, $p = 0.5$). The coefficient of variation of the 60 depth measurements was similar (CV = 4.2 and 3.8 for the removal and control sites, respectively). Moreover, the mean bottom rugosity of the two sites was identical (chain length to contour 1 m = 2.6 ± 0.2 m standard error [SE]). Taken collectively these results show that the average depth and topographic relief of the MR and MC sites were very similar.

Analysis of *SPOT* satellite imagery revealed that the MR site was clear of significant *Macrocystis* canopy for at least 1 yr prior to the initiation of this study (Fig. 1), indicating that the established understory assemblage at this site developed in the absence of shading from giant kelp. In contrast, a canopy of *Macrocystis* was present intermittently at the MC site in the year prior to our study.

Understory algal biomass, production, and community structure—We found no evidence of a midday depression in rates of primary production by understory algae as would be expected from light inhibition; production usually peaked around midday throughout the year at both the MR and MC sites (Fig. 2). Areal rates of GPP (mg C m^{-2} h^{-1}) were positively correlated with mean bottom irradiance during incubations (least squares regression [LSR] $F_{1,283} = 83.1$, $p < 0.0001$, $r^2 = 0.23$). In contrast, biomass-specific rates of GPP (mg C mg dry weight^{-1} h^{-1}) were not correlated with mean bottom irradiance ($F_{1,283} = 0.13$, $p = 0.7$).

The biomass of *Macrocystis* in the MC site steadily declined for the first 12 months of the study due to sloughing of the canopy during summer and autumn 2007 and the removal of entire plants during a large storm in winter 2008 (Fig. 3A). Favorable conditions for the recruitment and growth of new kelp led to an increase in *Macrocystis* biomass beginning in spring 2008. As a result of these temporal trends in kelp abundance, the effects of its removal on understory algal biomass varied among seasons ($F_{5,52} = 3.13$, $p < 0.01$ for kelp × season interaction) as did its effect on understory NPP ($F_{5,52} = 5.45$, $p = 0.0004$ for kelp × season interaction). For most of the study, understory algal biomass in the MC site was

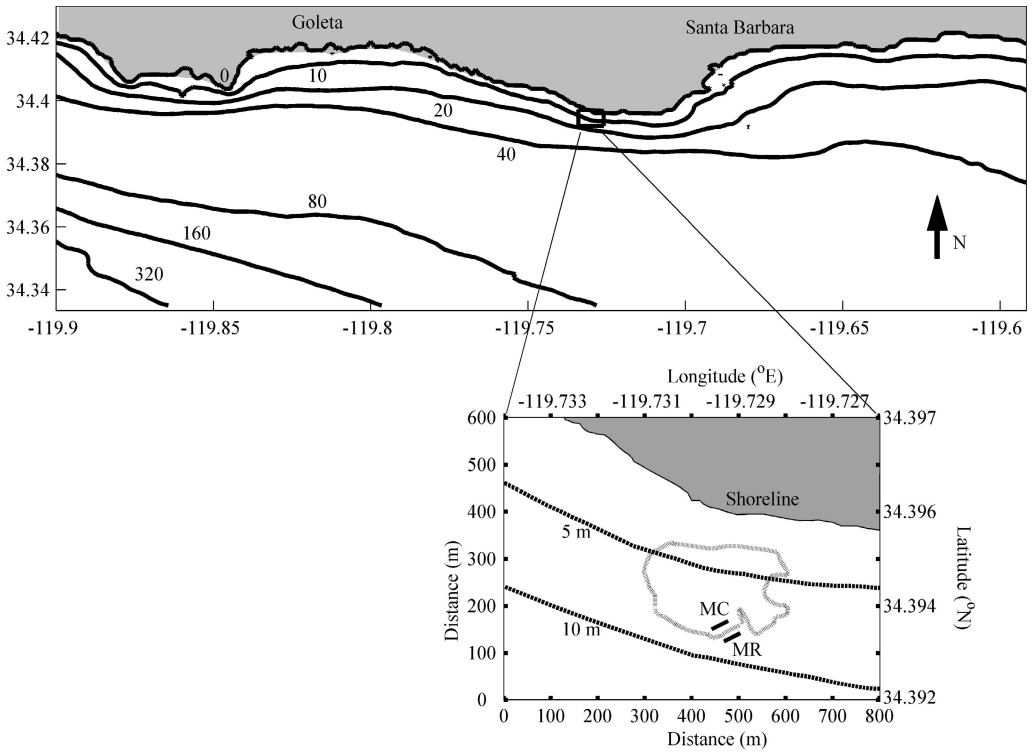

Fig. 1. Bathymetric map of Mohawk Reef showing the coverage (dotted outline) of *M. pyrifera* in September 2005 as determined from *SPOT* satellite imagery (Cavenaugh et al. 2010). The locations of the *Macrocystis* removal (MR) and *Macrocystis* control (MC) transects are marked.

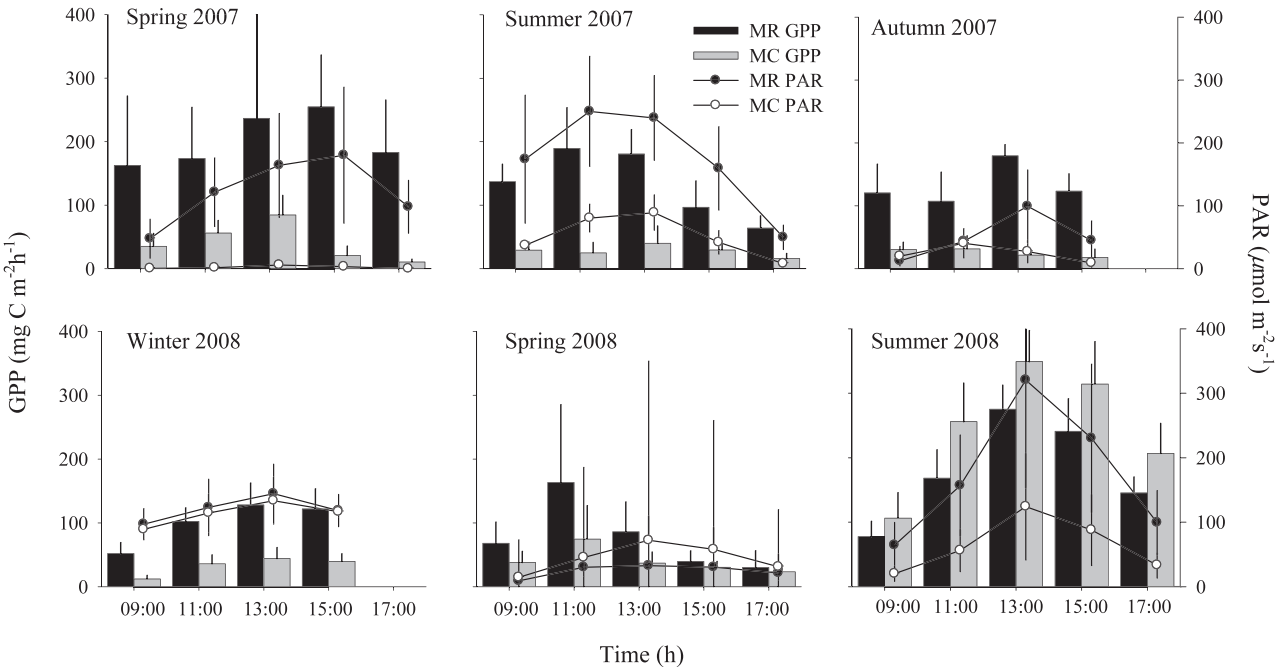

Fig. 2. Mean (± 1 SE) diurnal patterns by season in gross primary production (GPP) rates of understory algal communities at the *Macrocystis* removal (MR) and *Macrocystis* control (MC) sites. Bars represent rates measured over 2-h periods (1 h light and dark incubations) centered on the labeled time of day, and are means averaged over measurements taken on three separate days, except for spring 2007 and spring 2008, which are means averaged over 2 d. Open and closed circles represent mean irradiances for the periods when GPP was measured at the MR and MC sites.

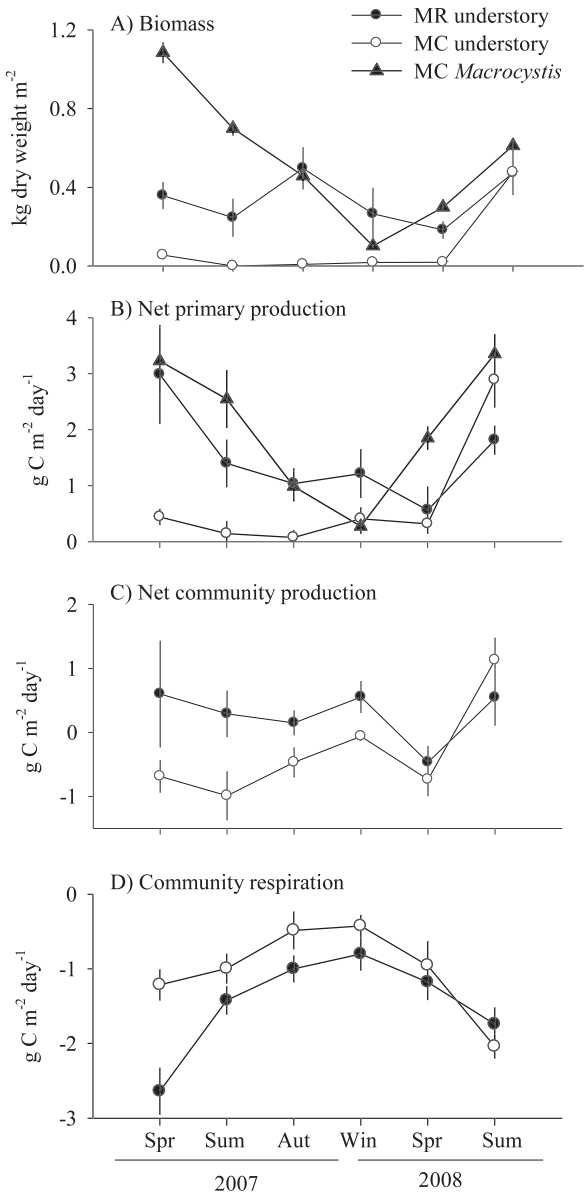

Fig. 3. Mean (± 1 SE) values for benthic understory algae and the giant kelp *Macrocystis* at the *Macrocystis* removal (MR) and *Macrocystis* control (MC) sites. (A) biomass, (B) net primary production, (C) net community production, and (D) community respiration. Spr, spring; Sum, summer; Aut, autumn; Win, winter.

extremely low and significantly less than that in the MR site (spring 2007–winter 2008, planned comparisons, $F_{1,52} > 4.0$, $p < 0.05$). Although the biomass of *Macrocystis* in the control site had declined drastically by winter 2008, a corresponding increase in the understory was not observed until summer 2008 (Fig. 3A), when bottom irradiance at the MC site peaked (Fig. 2; Table 1) and understory biomass reached levels similar to that in the MR site ($F_{1,52} = 0.002$, $p = 0.97$).

Patterns of NPP by the understory in the MC site closely matched those of its biomass, remaining low throughout the study until summer 2008, when it rose dramatically to a level that was actually higher than that observed in the MR area (Fig. 3B; $F_{1,52} = 4.96$, $p = 0.03$). In contrast, NPP by the understory at the MR site showed a temporal trend that was more similar to that observed for *Macrocystis* in the MC site with highs in the spring and summer and lows during autumn and winter (Fig. 3B). The relationship of seasonal NPP with irradiance (Fig. 4) shows that the understory algae in the MC site responded more rapidly to the higher light levels in summer 2008 than did the established understory community at the removal site.

Understory algal NPP at the MR site averaged 1.5 ± 0.3 (SE) g C m^{-2} d^{-1} across the entire study period (spring 2007–summer 2008), a value near the median of published values for macroalgae, including kelps (Duarte and Cebrian 1996). *Macrocystis* NPP at Mohawk Reef during the same period was estimated as 1.9 ± 0.4 (SE) g C m^{-2} d^{-1}. Seasonal NPP of the understory was correlated with understory algal biomass across both sites (LSR, $F_{1,10} = 17.8$, $p = 0.002$, $r^2 = 0.64$). Understory turnover time (here defined as doubling time in the absence of grazing), measured as the ratio of carbon standing crop biomass to daily NPP, averaged 93 ± 60 (SE) d.

NCP by the benthos was not significantly affected by *Macrocystis* or time of year (Fig. 2C; $p > 0.07$ for the main and interactive effects of *Macrocystis* and season). However, NCP was greater than zero at the MR site for all sampling seasons except spring 2008; the difference, however, was not statistically different from zero (*t*-tests, $t \geq 0.7$, df = 5 except for spring 2007, 2008, df = 3, p = 0.1–0.3), except in winter 2008 (*t*-test, $t = 2.3$, df = 5, p = 0.04). In contrast, NCP was significantly less than zero at the control site during all seasons except summer 2008 (*t*-tests, $t \geq 0.2.0$, df = 5 except for spring 2007, 2008, df = 3, $p \leq 0.05$). The effects of MR on benthic community respiration differed significantly among seasons ($F_{5,52} = 3.05$, $p = 0.02$ for kelp × season interaction). In contrast to that observed for understory algal biomass and NPP, CR was generally higher at the MC site but differed significantly from the MR site only in spring 2007 (Fig. 2D; $F_{1,52} = 16.80$, $p < 0.01$).

Community structure of the understory algae differed substantially between the two sites. Phylum-level composition of the understory community at the MR site was relatively stable, with Phaeophyta dominating biomass (64.8% ± 3% SE) and the remainder composed of Rhodophyta (Fig. 5). The opposite pattern was seen at the MC site, with Rhodophyta generally dominating (73.6% ± 9% SE; Fig. 5). Red algal turf made up less than 1% of biomass at the MR site but was relatively more abundant at the MC site, making up 5.0% ± 2% SE of biomass (Fig. 5). In summer 2008 Phaeophyta biomass increased at both sites, but this increase was particularly dramatic at the MC site (Fig. 5), where Phaeophytes overtook Rhodophytes in biomass. The dominant Phaeophytes responsible for this increase at the MC site were *P. californica*, *Cystoseira osmundaceae*, and *Desmerestia ligulata* (Table 2).

Three understory species were sampled in both the MR and MC sites on the same dates and analyzed for carbon and nitrogen content to evaluate possible differences in nutrient availability: *C. corymbiferus* (spring 2007 $n = 4$,

Table 1. Mean bottom irradiance (± SE) at the *Macrocystis* removal (MR) and *Macrocystis* control (MC) sites and the percent of surface light reduction by giant kelp at the MC site. Means are based on continuous data described in methods.

Year	Season	MR (μmol m^{-2} s^{-1})	MC (μmol m^{-2} s^{-1})	% kelp reduction
2007	summer	229.4±0.7	17.1±0.1	92.5
2007	autumn	90.6±0.5	15.0±0.1	83.4
2008	winter	84.4±1.0	32.7±0.4	61.3
2008	spring	169.8±0.7	66.9±0.5	60.6
2008	summer	230.6±0.7	140.5±0.6	39.1

winter 2008 $n = 2$, spring 2008 $n = 4$, summer 2008 $n = 6$), *R. californica* (spring 2007 $n = 2$, summer 2007 $n = 2$, spring 2008 $n = 4$, summer 2008 $n = 4$), and *P. californica* (autumn 2007 $n = 2$, summer 2008 $n = 4$). C : N ratios of these species did not significantly differ between the MC and MR sites (*t*-tests of mean difference between sites against expected value of zero: *C. corymbiferus*, mean C : N 11.9 ± 0.3 SE, $t = -0.9$, df = 8, $p = 0.4$; *R. californica*, mean C : N 7.0 ± 0.2, $t = 1.0$, df = 6, $p = 0.4$; *P. californica*, mean C : N 15.1 ± 0.6, $t = 0.8$, df = 2, $p = 0.5$).

Phytoplankton biomass and production—Unlike the biomass of understory macroalgae, the biomass of phytoplankton, as estimated by the concentration of POC and suspended Chl *a*, was not affected by the *Macrocystis* canopy, but instead showed pronounced seasonal variation in both the MR and MC sites with highs in spring and autumn and lows in summer and winter (Fig. 6A,B; $F_{5,24} = 35.03$, $p = 0.0007$ and $F_{5,24} = 94.05$, $p < 0.00001$ for POC and Chl *a*, respectively).

The effects of kelp on phytoplankton NPP varied inconsistently among seasons (Fig. 6C; $F_{5,24} = 2.08$, $p = 0.04$ for kelp × season interaction). Phytoplankton NPP showed a typical pattern of spring and fall blooms, with NPP magnitudes in the order spring > fall > summer ≫ winter. Phytoplankton NPP averaged 1.5–2 times higher where *Macrocystis* was experimentally removed compared with where it was left in place. The exception to this pattern occurred in spring 2007, when phytoplankton NPP was 36 times higher at the MR site compared with the MC site. This large difference between the two sites occurred when the biomass of *Macrocystis* at the MC site was at its highest level during the study (Fig. 3A).

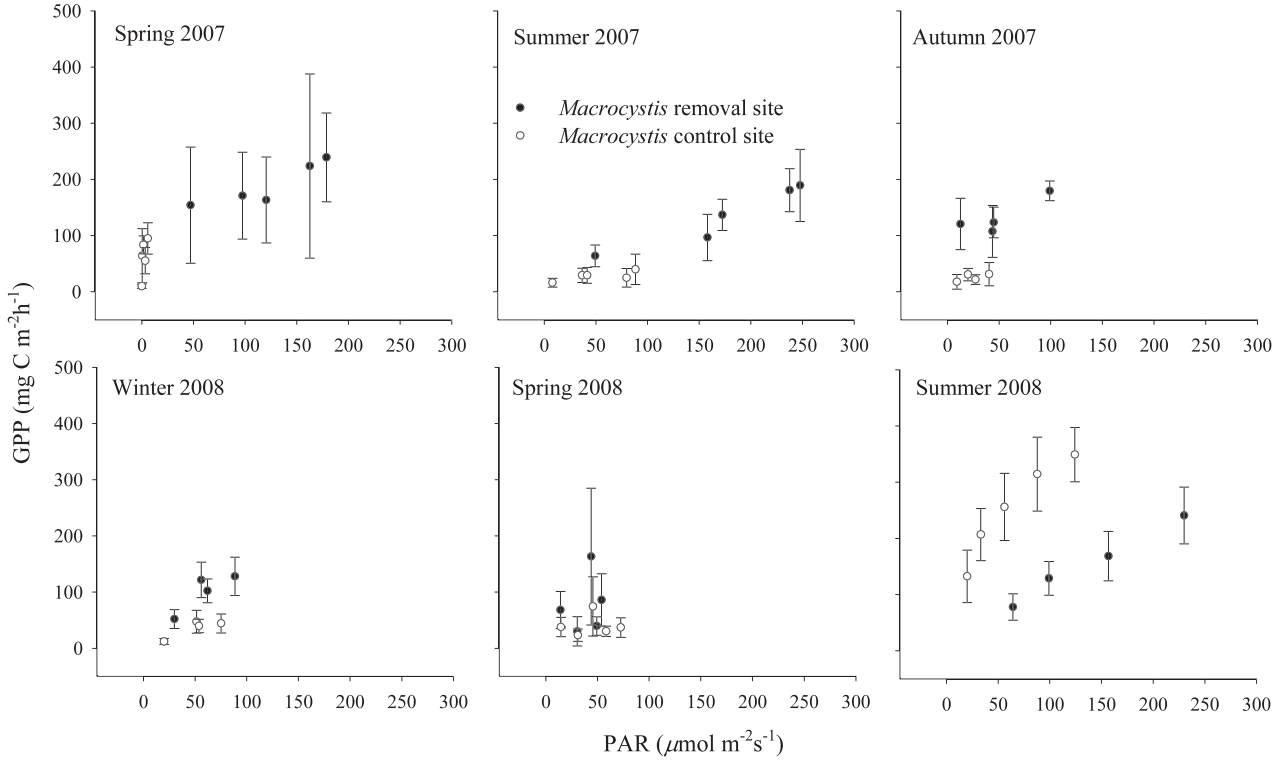

Fig. 4. Mean (± 1 SE) of hourly gross primary production (GPP) rates of understory algal communities measured over 2-h periods (1 h light and dark incubations) at the *Macrocystis* removal (MR) and *Macrocystis* control (MC) sites, plotted against mean irradiances for the periods when GPP was measured at the MR and MC sites.

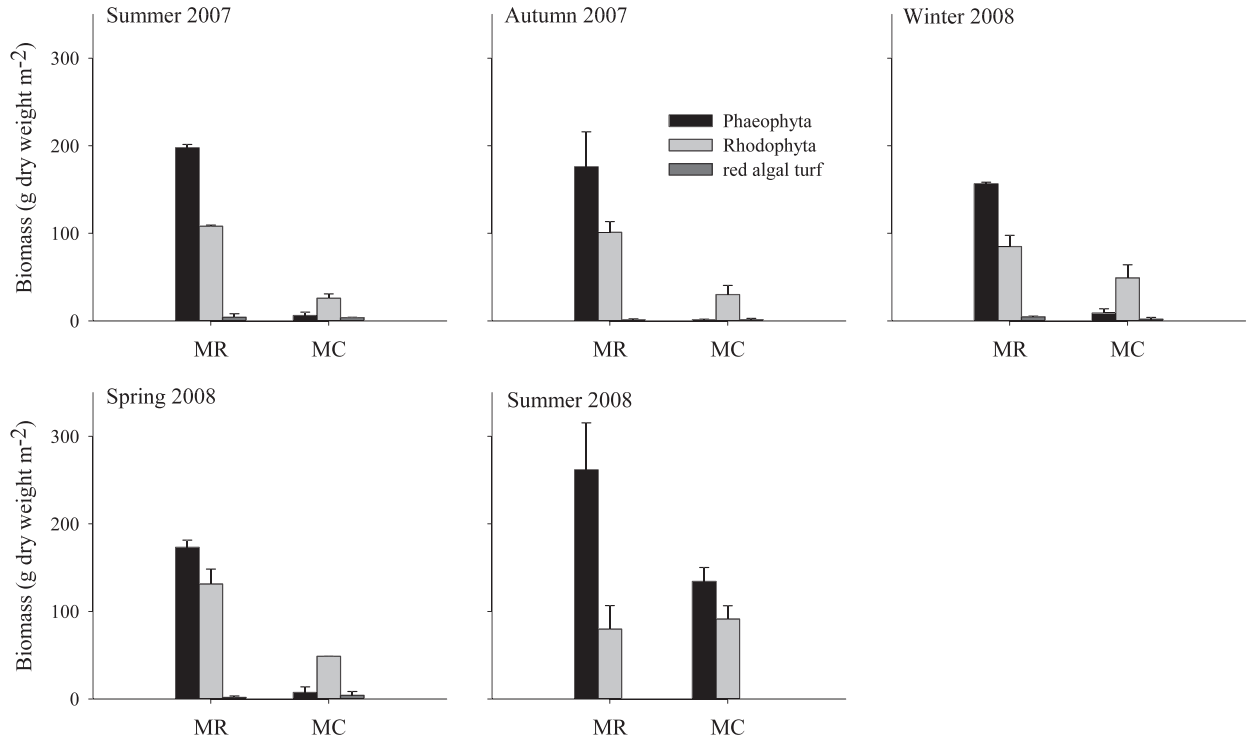

Fig. 5. Seasonal biomass of major taxonomic groups of understory macroalgae at the *Macrocystis* removal (MR) and *Macrocystis* control (MC) sites. Red algal turf is composed of a mix of low-growing Rhodophytes (Miller et al. 2009).

The generally higher phytoplankton NPP at the MR site reflected higher chlorophyll-specific production rates (Fig. 6D), as evidenced by the similar concentration of Chl *a* at the MC and MR sites (Fig. 6B) and the strong correlation between chlorophyll concentration and phytoplankton NPP at the MR site (LSR, $F_{1,16} = 69.9$, $p < 0.0001$, $r^2 = 0.81$, slope = 0.03). At the MC site, where phytoplankton exhibited lower chlorophyll-specific rates of NPP (Fig. 6D), phytoplankton NPP was also significantly related to Chl *a* concentration, although the relationship was correspondingly weaker, with a shallower slope (LSR, $F_{1,16} = 7.9$, $p = 0.01$, $r^2 = 0.33$, slope = 0.01). Phytoplankton turnover time, as estimated by the ratio of daily integrated carbon NPP to integrated POC, averaged 9 ± 4 (SE) days. This is a conservatively long estimate as only a portion of the POC pool consists of living phytoplankton.

Ecosystem production—Ecosystem NPP, as defined by the sum of NPP by *Macrocystis*, understory algae and phytoplankton, showed a seasonal trend at both the MC and MR sites with highs in spring and summer and lows in autumn and winter (Fig. 7A). There was no significant effect of the presence of a *Macrocystis* canopy on total ecosystem production at Mohawk Reef when averaged over the six seasons of our study ($F_{1,2} = 1.07$, $p = 0.30$). The only difference in ecosystem NPP that we observed between the two sites occurred during summer 2008, when NPP at the MC site was nearly three times higher than that at the MR site (Fig. 5A; $F_{1,16} = 6.46$, $p = 0.0217$). The overall biomass of macroalgae (*Macrocystis* + understory) in the MC site was relatively high at this time, since a well-developed understory algal assemblage coexisted with a newly developed *Macrocystis* canopy (Fig. 3A).

Ecosystem NPP averaged over the study period at each of the two sites was very similar (MC site 2.8 ± 0.6 [SE] and MR site 2.4 ± 0.5 [SE] g C m^{-2} d^{-1}). Non-*Macrocystis* NPP contributed 19% to 64%, of ecosystem NPP at the MC site (mean average across all seasons = 32.9% ± 8%, SE; Fig. 7B). On average, understory NPP was more than five times higher than that of phytoplankton NPP, and this proportion did not differ significantly between the MC and MR sites ($F_{1,30} = 0.9$, $p = 0.4$). In the absence of a *Macrocystis* canopy, understory NPP was almost always higher than that of phytoplankton except during spring 2008 when phytoplankton production was nearly twice that of the understory (Fig. 3B vs. Fig. 6C). The relative amount of production by understory macroalgae and phytoplankton was more variable at the MC site, where phytoplankton contribution to NPP was similar to or greater than that of understory macroalgae during three of the six seasons sampled (Fig. 7B).

Bottom irradiance—Mean seasonal PAR on the bottom at the MR site ranged from 84 to 231 μmol m^{-2} s^{-1}, with the highest values in summer 2007 and the lowest values in summer 2008 (Table 1). As predicted, bottom irradiance at the MC site was 1.6 to 13 times lower than the MR site; average seasonal light reduction by the *Macrocystis* canopy was as high as 93% (Table 1). Daily extinction coefficients (K_d) varied from 0.1 to 1.4 and averaged 0.40 (± 0.01 SE) in spring 2008 and 0.34 (± 0.01 SE) in summer 2008 (Fig. 8).

Table 2. Mean seasonal biomass (g dry weight±SE) of dominant macroalgal taxa at the *Macrocystis* removal (MR) and *Macrocystis* control (MC) sites.

	Summer 2007 (n=2)		Autumn 2007 (n=4)		Winter 2008 (n=3)		Spring 2008 (n=2)		Summer 2008 (n=4)	
Taxon	MC	MR	MC	MR	MC	MR	MC	MR	MC	MR
Phaeophyceae										
Pterygophora californica	5.4±3	116.8±2	0.7±1	83.7±22	2.1±2	63.0±9	1.5±2	54.6±30	48.1±23	129.1±43
Laminaria farlowii	0.3±0	67.6±7	—	31.5±8	0.9±1	30.3±3	0.5±1	34.2±1	0.3±1	63.9±11
Cystoseira osmundaceae	—	13.1±13	—	59.8±14	5.8±6	60.3±12	—	72.2±28	48.2±17	47.9±18
Desmerestia ligulata	—	—	—	—	—	—	—	6.5±7	37.0±31	34.8±20
Taonia lennebackerae	—	—	—	—	—	—	2.7±3	—	—	—
Rhodophyceae										
Chondracanthus corymbifera	9.5±1	32.9±1	7.7±3	36.1±1	11.3±1	36.6±5	21.7±6	47.8±1	36.6±8	35.7±13
Rhodymenia californica	10.9±1	19.8±1	8.1±3	11.5±1	14.2±2	11.8±1	8.3±8	9.3±9	—	—
Nienburgia andersonia	—	13.3±3	2.1±2	11.2±2	—	5.5±1	—	8.2±1	8.2±8	2.1±2
Callophyllis flabellulata	—	8.2±8	—	10.0±1	2.7±3	9.1±1	—	12.7±3	—	6.2±4
Gracilaria sp.	—	5.3±5	—	—	—	—	13.4±3	10.7±1	7.1±4	6.0±3
Halymenia sp.	—	—	2.7±2	7.2±4	—	—	—	4.0±4	3.6±4	10.8±1
Acrosorium ciliolatum	—	—	—	—	—	—	—	—	2.7±3	—
Cryptopleura farlowianum	—	—	—	—	13.6±14	—	—	4.2±4	8.5±9	14.8±12
Corallina officinalis	5.4±5	18.4±3	9.5±3	14.8±2	7.2±4	3.6±4	—	13.6±3	12.7±7	15.6±7
Bossiella orbigniana	—	10.1±0	—	10.1±6	—	11.8±2	—	11.1±1	10.1±6	15.2±5
Red algal turf	3.7±0	4.1±4	1.4±1	1.1±1	2.0±2	4.7±1	4.2±4	1.7±2	—	—

Discussion

Influence of Macrocystis on ecosystem NPP—Strikingly, we found that the presence of giant kelp (*Macrocystis* sp.) on Mohawk Reef most often did not result in significantly higher ecosystem NPP (Fig. 7A). On average, NPP by understory algae and phytoplankton at the MR site was similar to ecosystem NPP at the MC site over the 17-month study, supporting empirical and theoretical evidence from both aquatic and terrestrial systems that primary productivity should not vary with autotroph community composition and body mass (Niklas and Enquist 2001). It should be noted, however, that unlike our estimates of NPP by the algal understory, our estimates of NPP by *Macrocystis* and phytoplankton did not account for exudate (dissolved organic matter [DOM]) loss. Ongoing studies in the Mohawk kelp forest indicate that DOM may account for approximately 30% of NPP by *Macrocystis* (E. Halewood pers. comm.), and about 5–15% by phytoplankton (J. Goodman pers. comm.). Incorporating these values of DOM loss into our estimates of NPP would diminish the combined proportion of total ecosystem NPP contributed by understory algae and phytoplankton relative to giant kelp. Nonetheless, our results strongly suggest that *Macrocystis* should not be the sole focus of studies of primary production in giant kelp forests.

The presence of giant kelp at the MC site substantially reduced subsurface irradiance, which undoubtedly contributed to the lower rates of NPP by both phytoplankton and understory algae during times of high *Macrocystis* biomass. Evidence for this comes from the observation that the magnitude of the difference in nonkelp production between the two otherwise matched sites was greatest when *Macrocystis* biomass was at its peak (in spring 2007). Seasonal patterns of irradiance at the MC site never approached that in the MR site, even when *Macrocystis* biomass was at its lowest (Fig. 2). These results suggest that *Macrocystis* should dominate ecosystem NPP in forests with well-developed canopies and that NPP by nonkelp producers should increase to similar levels only after the *Macrocystis* canopy is absent long enough to allow significant increases in understory algal biomass.

The delay between canopy loss and the response of understory algae was evident in 2008, when significant increases in understory NPP occurred during summer several months after the reduction in kelp canopy at the MC site. This delay may be a function of the influence of phytoplankton blooms on bottom irradiance and the life history characteristics of the understory algae. Light absorption by dense concentrations of phytoplankton may limit understory algal production, which may have delayed the release of understory algae from light limitation in spring 2008 despite a sparse *Macrocystis* canopy (Fig. 3). In addition, seasonal patterns in the growth of understory algae may have contributed to the delayed response of the understory. For example, *P. californica*, a dominant understory kelp at our sites, has highest growth rates in summer (Reed 1990); of course, this seasonal pattern could very well be due to typically low bottom irradiance caused by dense phytoplankton populations during spring upwelling. Community composition data, moreover, do not support a dominant role for seasonal patterns of macroalgal community dynamics in driving the delay: biomass of the strongly seasonal phaeophytes *C. osmundaceae* and *D. ligulata* rose sharply at the MR site by Spring 2008, whereas they did not achieve significant biomass at the MC site until summer (Table 2).

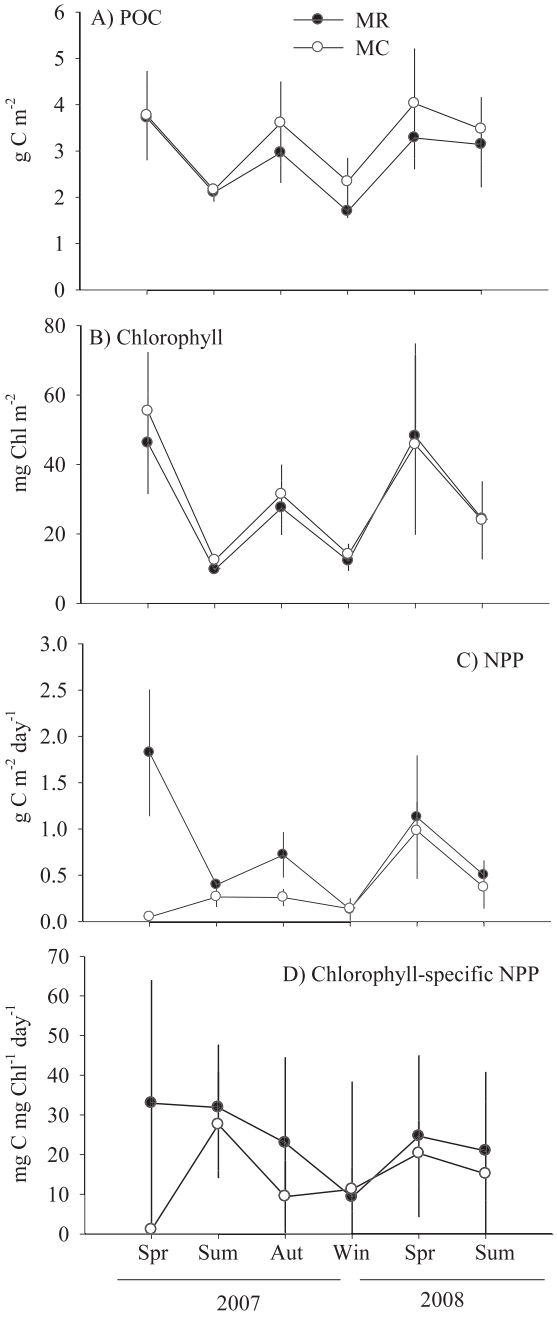

Fig. 6. Mean (± 1 SE) values at the *Macrocystis* removal (MR) and *Macrocystis* control (MC) sites for (A) concentration of suspended particulate organic carbon, (B) concentration of suspended chlorophyll, (C) phytoplankton net primary production, and (D) phytoplankton growth rate (i.e., chlorophyll-specific NPP).

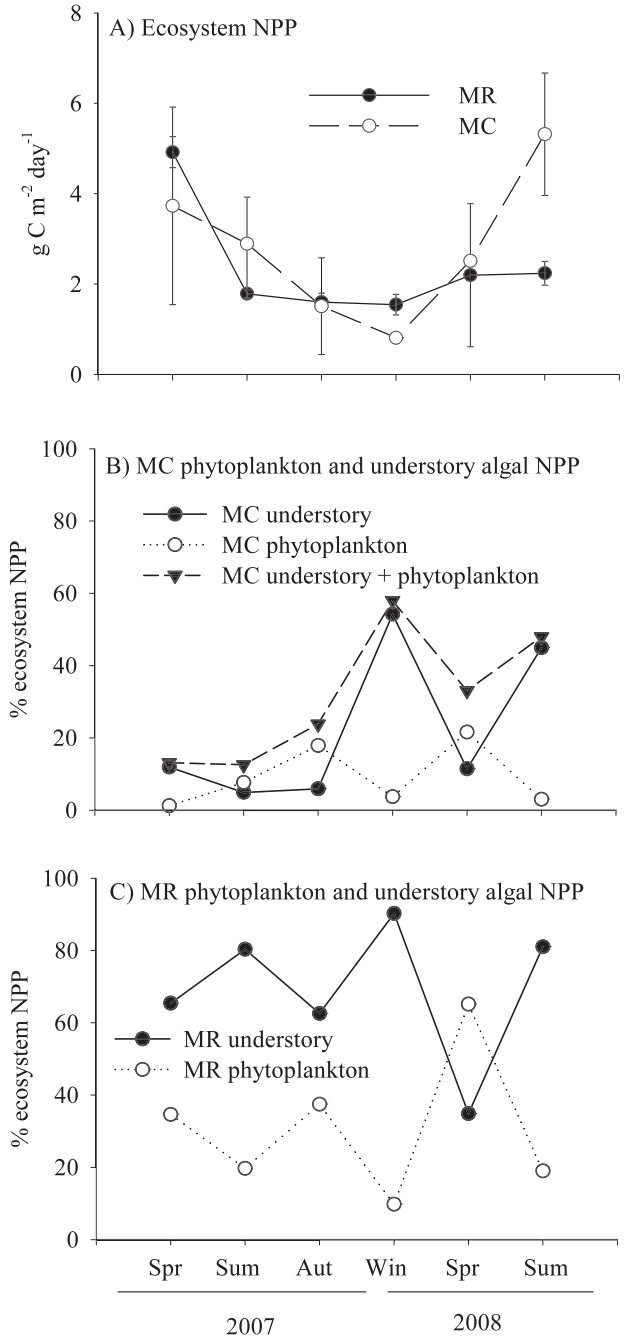

Fig. 7. Time series of (A) mean ecosystem NPP (the combined NPP of *Macrocystis*, understory algae, and phytoplankton) at the *Macrocystis* removal (MR) and *Macrocystis* control (MC) sites at Mohawk Reef. Error bars are 1 SE. (B) Percentage of ecosystem NPP attributed to understory algae, phytoplankton, and the sum of understory algae and phytoplankton at the *Macrocystis* control site (MC). (C) Percentage of ecosystem NPP attributed to understory algae and phytoplankton at the *Macrocystis* removal site (MR).

The one-season lag in understory response to increasing light levels approximately equals the 3-month turnover time of the understory. Nevertheless, light levels did not reach their maximum until summer, and the balance of evidence suggests that the understory at the MC site remained light limited. Although attenuation by phytoplankton also affected the MR site, higher initial biomass of the understory there likely lessened its effect relative to the MC site, where the understory community was recovering from very low biomass (Table 1).

Subtidal rocky reefs typically consist of patch mosaics of different macroalgal assemblages with varying combinations of surface canopy kelps, subsurface foliose algae, and

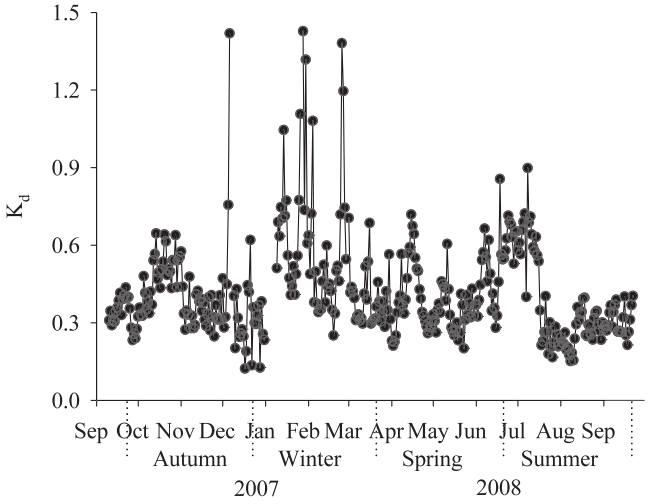

Fig. 8. Daily extinction coefficient for the water column at Mohawk Reef for autumn 2007–summer 2008. Hourly K_ds were calculated for 10 daylight hours (08:00–18:00 h) each day based on mean hourly PAR measured at a frequency of 1 min, and averaged to obtain daily K_d. Dotted lines represent season boundaries.

low-lying algal turfs and crusts (Dayton 1985; Foster and Vanblaricom 2001) that are bathed in waters containing seasonally abundant phytoplankton. Our results highlight the dynamic nature of giant kelp forests and the interactive role of disturbance and oceanographic conditions in determining the relative contributions of the component primary producers to NPP of the kelp forest ecosystem.

Other factors besides light that may be affected by a dense kelp canopy include nutrients and water flow (Hurd 2000). Extensive prior work at Mohawk Reef has shown that the kelp forest does slow water flow going through it (Gaylord et al. 2007; Stewart et al. 2009) but that this dampening of flow does not limit nutrient uptake for kelp inside the forest (Fram et al. 2008). Moreover, nitrate concentrations were not consistently lower inside the forest compared with outside the forest at the offshore edge (Fram et al. 2008). These findings, along with our observations that understory algae in the MC and MR sites had similar C : N ratios, indicate that nutrient limitation was not an important factor driving the site differences in the production of understory algae and phytoplankton observed in this study.

The lack of consistent differences in ecosystem NPP between the MC and MR sites suggests that ecosystem NPP was limited by one or more factors that affected all three groups of producers similarly. One such factor is light, which is harvested by organisms occurring higher in the water column thus impeding photosynthesis by organisms below. Nonetheless, our results showed that in the MR site areal rates of NPP by understory algae on the bottom were typically five times higher than those by phytoplankton residing in the water column above. This likely reflects the fact that local phytoplankton production and biomass can be limited by short residence times (Cloern 1996), whereas the sessile life form of understory algae allows their biomass to accumulate over time on the bottom, enhancing their NPP. Consequently, at the MR site where understory algae became established without interference from the kelp canopy, the contribution of understory algae to ecosystem NPP was greater than that of phytoplankton except during the bloom in phytoplankton biomass in spring 2008 (Fig. 7C). In contrast, at the MC site where understory biomass was usually suppressed, the relative contributions of phytoplankton and understory algae to ecosystem NPP were more temporally variable.

Implications for the dynamics of ecosystem NPP—The positive responses by understory algae and phytoplankton NPP to MR suggests that production by these three groups of primary producers is potentially complementary in space and time. Our results indicate that at locations or times when *Macrocystis* is absent or diminished, production by understory algae and phytoplankton can eventually increase to levels that compensate for the loss of production by *Macrocystis*. Such compensation has the potential to significantly dampen variability in NPP by the kelp forest ecosystem that arises from large interannual fluctuations in *Macrocystis* biomass (Reed et al. 2008). To evaluate the potential for such dampening in interannual variation, we compared annual *Macrocystis* production at Mohawk Reef for the 5 yr preceding this study, using data from the Santa Barbara Coastal Long-Term Ecological Research Program, with an estimate of annual production by phytoplankton and understory algae at the MR site based on our seasonal averages for 2007 (Fig. 9). Despite the limited temporal extent of our data, they clearly show that production by phytoplankton and understory algae can be substantial and can act to greatly reduce interannual variation in NPP by the kelp forest ecosystem. This conclusion remains even if the estimates of kelp NPP are adjusted upward by 30% to compensate for production lost as DOM.

Interactions among the principal primary producers likely caused the observed lag in the response of understory algal NPP to the natural removal of *Macrocystis* at the MC site in winter 2008. Development of the understory algal assemblage inside the forest was delayed until the following summer, when bottom irradiance increased to more than twice that measured in spring (Table 1; Fig. 4). Aside from shorter days and smaller solar azimuths, high water column attenuation caused by phytoplankton blooms may also cause bottom irradiance in spring to be lower than that in summer. Data on surface and bottom irradiance are consistent with the hypothesis that the development of the understory assemblage in the MC site was delayed in the spring by competition for light with phytoplankton. Water column attenuation during the spring of 2008 was high and diminished markedly after the third week of summer (Fig. 8). Phytoplankton blooms in spring may extend the low-light winter period when kelp forests are often thinned by storms. Such phenomena may inhibit benthic production and diminish the ability of understory macroalgae to compensate for reductions in ecosystem NPP caused by the seasonal loss of *Macrocystis*.

Similar lags in NPP by phytoplankton following the removal of the *Macrocystis* canopy do not appear to exist,

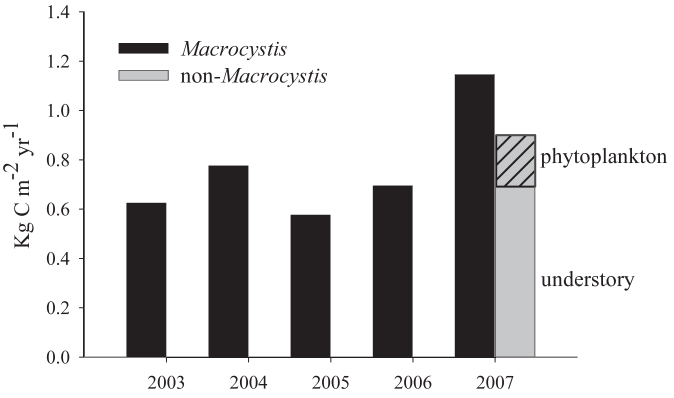

Fig. 9. Annual *Macrocystis* NPP at Mohawk Reef as measured by the Santa Barbara Coastal Long-Term Ecological Research Program (*see* Rassweiler et al. 2008 for methods) and nonkelp production (understory algae + phytoplankton) for 2007 measured in this study in the *Macrocystis* removal area.

since phytoplankton biomass (represented by Chl *a* concentration) was not affected by *Macrocystis* (Fig. 6B). Consequently, phytoplankton NPP increased unimpeded by kelp in spring 2008 following the removal of the *Macrocystis* canopy the previous winter (Fig. 6C). The ability of phytoplankton to rapidly respond allows it to compensate in part for the seasonal reduction in kelp forest NPP caused by the winter reduction in *Macrocystis* biomass. This is evidenced by the fact that phytoplankton contributed most to total ecosystem NPP at the MC site in spring 2008. This compensation, however, was short lived, since the contribution of phytoplankton to kelp forest NPP dropped to near its lowest level in summer 2008. The increase in phytoplankton biomass and NPP observed in spring 2008 is typical off southern California, where spring upwelling events promote phytoplankton blooms (Otero and Siegel 2004; McPhee-Shaw et al. 2007).

When reduction of the *Macrocystis* canopy is sustained long enough, the establishment of a well-developed understory can contribute substantially to ecosystem NPP. The biomass of *Macrocystis* can be limited by wave disturbance (Graham et al. 2007; Reed et al. 2008) and nutrients (Jackson 1977; Gerard 1982), particularly during El Niño events when resulting thermal stratification can suppress *Macrocystis* canopies for multiple years (Zimmerman and Kremer 1986; Dayton et al. 1999). At least some understory algal species appear to be less susceptible to nutrient limitation during El Niño events, possibly due to lower nutrient requirements or resistance to low-nutrient conditions, combined with lower temperatures and higher nutrient concentrations near the bottom (Dayton et al. 1999). Moreover, the low profile of most understory algae offers less drag to hydrodynamic forces compared with *Macrocystis*. Consequently, understory algae are less vulnerable to wave disturbances that remove *Macrocystis* (Dayton and Tegner 1984). This greater resistance of understory algae to disturbances and ocean conditions that diminish *Macrocystis* biomass acts to increase the probability that understory algae will compensate in part for the reduction in ecosystem NPP caused by the loss of *Macrocystis*.

Trophic influences—The similar levels of ecosystem NPP observed between the MR and MC sites during most of our study might lead one to conclude that the composition of producer biomass on rocky reefs is of little ecological importance. It is important to recognize, however, that *Macrocystis*, understory algae and phytoplankton have distinct ecological roles that are not interchangeable. As a foundation species, *Macrocystis* provides structural habitat to a diverse community of organisms, most of which do not, at least directly, depend on giant kelp for food (Foster and Schiel 1985; Graham 2004). Much *Macrocystis* biomass is transported to beaches (Dugan et al. 2003) or bathyal environments (Harrold et al. 1998; Vetter and Dayton 1999), where it provides an important source of allochthonous production to these ecosystems. Understory algae provide reef fishes with foraging habitat and refuge from predators (Laur and Ebeling 1983; Ebeling and Laur 1985; Holbrook and Schmitt 1992), and phytoplankton is an important food source for a diverse array of benthic suspension feeders (Gili and Coma 1998; Page et al. 2008), a trophically dominant group on many coastal reefs (Newell et al. 1982). Thus, the compensation of *Macrocystis* NPP by understory algae and phytoplankton would likely not be matched in terms of NCP, because the high export rate of *Macrocystis* would result in much higher NCP : NPP ratios. Shading, in this case by a Macrocystis canopy, can benefit sessile suspension feeders by reducing competition for space with understory algae (Miller and Etter 2008; Arkema et al. 2009) and can also suppress the growth and reproduction of mobile predators that forage in understory algae (Holbrook et al. 1990). Similar interactions can occur between other species of canopy-forming kelps and the autotrophs living beneath them (Johnson and Mann 1988; Kennelly 1989; Clark et al. 2004). The very different ecological roles of giant kelp, understory algae, and phytoplankton means that factors affecting their relative abundance in space or time will likely have complex ecosystem ramifications. Future studies that seek to identify interactions among different producers and consumers in kelp forests will lead to a more comprehensive understanding of how changes in the relative and absolute amounts of NPP by the principal producer groups alter the biotic structure of kelp forests and the ecological functions that they provide.

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