Macroalgal Net Primary Production

Overview. Macroalgae are important primary producers in many subtidal habitats, yet little information exists on the temporal and spatial dynamics of net primary production (NPP) by entire assemblages. Here we modelled net primary production by intact assemblages of understory macroalgae (including juvenile giant kelp *Macrocystis pyrifera*) in permanent plots on subtidal reefs off Santa Barbara, California by combining time series data on taxon-specific biomass and hourly irradiance with taxon-specific relationships between irradiance and photosynthesis and irradiance and respiration. To understand the contribution of these assemblages to total macroalgal production we also present time series estimates of NPP by the overstory formed by giant kelp in these plots.

Study Sites. Time series data of reef biota (i.e., algae, invertebrates and fish) and irradiance were collected at five reefs as part of a long-term experiment designed to evaluate the effects of disturbance to giant kelp (*Macrocystis pyrifera*) on the structure and productivity of the benthic community. The five reefs (Arroyo Quemado 34^0 28.048'N, 120^0 07.031'W; Carpinteria 34^0 23.474'N, 119^0 32.510'W; Isla Vista 34^0 23.275'N, 119^0 32.792'W; Mohawk 34^0 23.649'N, 119^0 43.762'W; and Naples 34° 25.342'N, 119° 57.102'W) ranged in depth from 5.8 m to 8.9 m (MLLW) and were chosen to represent a range of physical and biological characteristics known to influence the structure and productivity of subtidal reef communities in the region. A ubiquitous (but not always persistent) feature on these reefs was the presence of giant kelp, which forms a dense canopy at the sea surface that alters the biomass, diversity and temporal stability of reef biota (Castorani et al. 2018, Miller et al. 2018, Lamy et al. 2020).

Beginning in 2008, giant kelp was removed from a 2000 m^2 plot once per year in winter at four reefs (Arroyo Quemado, Carpinteria, Mohawk and Naples) to simulate the effects of winter storm disturbance (referred to as "annual removal" treatment). An adjacent unmanipulated 2000 m^2 plot served as a control. Beginning in winter 2010, giant kelp was removed 1 to 2 times per season within a 600 m^2 area within (or in the case of Mohawk adjacent to) each of the annual removal plots to create a "continual removal" treatment. In fall 2011, a fifth site was established at Isla Vista with 2000 m^2 annual removal and control plots (a 600 m^2 continual removal treatment was not established at this site). The reef community of algae (including giant kelp), invertebrates and fish were surveyed in annual removal and continual removal plots prior to each experimental removal of giant kelp. Thus, data collected on the date following the first kelp removal represents the first sampling period of the annual and continual removal treatments. The last experimental removals of giant kelp occurred in winter 2016 or winter 2017, depending on the site. The last sampling of reef communities under experimental conditions for annual and continual kelp removal treatments occurred ~12 months following the last kelp removal. Control, annual removal, and continuous removal plots continue to be sampled seasonally to document the recovery of the reef community in the absence of experimental kelp removal. Dates of the initiation and cessation of kelp removal in the experimental plots are provided in Table 1.

Table 1: Dates, in the format yyyy/mm/dd, of the first and last kelp removal for the annual and continual giant kelp removal treatments at the five reef sites.

Reef	Treatment	Date of First Removal	Date of Last Removal
Arroyo Quemado	Annual	2008/01/30	2017/03/02
	Continual	2010/02/04	2017/03/02
Carpinteria	Annual	2008/02/12	2017/02/15
	Continual	2010/01/29	2017/02/15
Isla Vista	Annual	2011/10/26	2016/02/18
Mohawk	Annual	2008/01/17	2017/02/13
	Continual	2010/05/05	2017/02/13
Naples	Annual	2008/01/10	2016/02/09
	Continual	2010/01/28	2016/02/09

Macroalgal Abundance and Standing Biomass. All macroalgae were surveyed by divers along permanent 40 m x 2 m transects located in the center of each plot twice per season (approximately every six weeks) from January 2008 through December 2012 and once per season (approximately every 12 weeks) beginning in the winter of 2013. The methods and data from these surveys are contained in the following data packages:

SBC LTER: Reef: Long-term experiment: Kelp removal: Abundance and size of Giant Kelp dataset

SBC LTER: Reef: Long-term experiment: Kelp removal: Invertebrate and algal density dataset

SBC LTER: Reef: Long-term experiment: Kelp removal: Cover of sessile organisms, Uniform Point Contact dataset

These data packages and all other provenance data packages listed in this document are available through the data portal of the Environmental Data Initiative (https://portal.edirepository.org/nis/home.jsp).

Time series data of the abundance of all understory species including small *M. pyrifera* (< 1 m in height) were converted to dry mass using species-specific relationships generated from field measurements of abundance and laboratory measurements of mass (data package name: *SBC LTER: Reef: Coefficients for calculating biomass of benthic kelp forest invertebrate, algal,* *and fish species from body size and percent cover*). These relationships were combined with taxon-specific measurements of abundance and size to estimate standing biomass for each taxon. Divers also counted the density of *M. pyrifera* fronds $\geq$ 1 m in height in the 40 m x 2 m transects, which was converted to the biomass by applying month-specific relationships between frond density (no. m^{-2}) and dry mass density (dry kg m^{-2}) developed by Rassweiler et al. (2018). The methods and data for the algal biomass from the long-term kelp removal experiment are contained in the data package *SBC LTER: Reef: Long-term experiment: biomass for kelp forest species, ongoing since 2008)*.

Irradiance - Irradiance at the seafloor and sea surface were recorded once or twice per minute at the study sites using PAR sensors (data package name: *SBC LTER: Kelp Removal Experiment: Hourly photon irradiance at the surface and seafloor*). Sensor malfunction and availability caused data gaps in seafloor irradiance in some of the study plots (Table 2). To account for these missing data in our calculations of NPP we estimated seafloor irradiance by calculating water column attenuation from sea surface irradiance and seafloor irradiance in other plots during the period of missing data. All estimates of attenuation were constrained to be positive and below infinity by converting to very low values (0.01 µmol m^{-2} s^{-1}) in cases where sea surface irradiance was positive, but seafloor irradiance was measured to be 0. In situations where sea surface irradiance was low ($\leq$ 100 µmol m^{-2} s^{-1}), we constrained attenuation to be positive by converting seafloor irradiance to 6% of measured sea surface irradiance.

Table 2: Chronology of PAR sensor deployments for the experimental treatments at the five reef sites of the long-term kelp removal experiment

Reef	Treatment (experimental kelp removal)	Period of PAR sensor deployment
Arroyo Quemado	Control	01/30/2008 - present
	Annual	01/30/2008 – 08/09/2010, 05/08/2017 - present
	Continual	08/09/2010 – 05/18/2017
Carpinteria	Control	01/11/2008 - present
	Annual	01/11/2008 – 09/03/2010, 05/19/2017 - present
	Continual	09/03/2010 – 08/10/2017
Isla Vista	Control	01/19/2012 - present
	Annual	01/19/2012 - present
Moha wk	Control	10/16/2008 - present
	Annual	10/16/2008 - present

	Continual	06/14/2010 – present
Naples	Control	01/30/2008 - present
	Annual	01/30/2008 - 05/16/2017 - present
	Continual	NA

Because attenuation varies in space and time due to variation in kelp biomass and other factors, we used the logic below to determine the best estimate of attenuation for filling data gaps in seafloor irradiance:

1) Hourly seafloor irradiance for a given plot was estimated using the mean attenuation for that hour and day of the year averaged over the years for a given kelp treatment in that plot.
2) If data gaps remained in a continuous kelp removal plot after implementing the above procedure, then hourly seafloor irradiance was estimated using attenuation data collected from the adjacent annual kelp removal plot at that site. Similarly, if data gaps remained in an annual kelp removal plot then hourly seafloor irradiance was estimated using attenuation data collected from the adjacent continuous kelp removal plot at that site. Analyses showed that on average seafloor irradiance did not differ significantly between annual kelp removal and continuous kelp removal plots
3) If data gaps still remained in a given plot after performing the above two procedures, then hourly seafloor irradiance was estimated using the mean attenuation for that hour and day of the year averaged over all the years for that plot.

Estimates of attenuation were coupled with measurements of sea surface irradiance to approximate midwater irradiance (i.e., irradiance at ½ of the sampling location depth) used to estimate NPP of the kelp *Egregia menziesii* and the reproductive fronds of the fucoid *Stephanocystis osmundacea*, which extend into the water column (see *Estimating Net Primary Production* below). For low values of sea surface irradiance ($\leq$ 100 umol m^{-2} s^{-1}), we assumed midwater irradiance to be 20% of sea surface irradiance.

Physiological Measurements. We used the methods of Miller et al. (2012) to measure photosynthesis versus irradiance and respiration by the 22 most common macroalgal taxa observed at the study reefs (data package name: *SBC LTER: Reef: Macroalgal photosynthetic parameters*). Additionally, we measured photosynthesis versus irradiance for the reproductive fronds of *Stephanocystis osmundaceae*, which can exhibit seasonally high biomass. These estimates of net photosynthesis at saturating irradiance (P_{max}), net photosynthesis at non-saturating irradiance (α) and respiration were used in our calculations of hourly net primary production. Physiological measurements for less common taxa were estimated using parameters for the morphologically similar species given in Table 3.

Table 3. Common "proxy" taxa used to estimate photosynthetic parameters for less common species for which the parameters were not measured.

SP_CODE	GENUS	SPECIES	PROXY SP_CODE	PROXY GENUS	PROXY SPECIES
AMZO	*Amphiroa*	*zonata*	CO	*Corallina*	*officinalis*
ANPA	*Anisocladella*	*pacifica*	R	*Rhodymenia*	*californica*
AU	*Acrosorium*	*uncinatum*	CF	*Callophyllis*	*flabellulata*
BLD	Unidentified brown blade	spp.	MPJ	*Macrocystis*	*pyrifera* - < 1m tall
BO	*Bossiella*	*orbigniana*	CO	*Corallina*	*officinalis*
BR	Blady red	spp.	CC	*Chondracanthus*	spp.
BRA	Branching Red Algae	spp.	R	*Rhodymenia*	*californica*
CAL	*Calliarthron*	*cheilosporioid*	CO	*Corallina*	*officinalis*
CG	Cladophora	graminea	RAT	Red Algal Turf	spp.
COF	*Codium*	*fragile*	GS	*Gracilaria*	spp.
CP	*Colpomenia*	spp.	POLA	*Polyneura*	*latissima*
CRYP	*Cryptopleura*	spp.	BF	*Cryptopleura*	*farlowianum*
CYJ	*Stephanocystis*	*osmundaceae* - small	MPJ	*Macrocystis*	*pyrifera* - < 1m tall
CZ	*Chondracanthus*	*spinosa*	CC	*Chondracanthus*	spp.
DIAT	Diatom	Mat	FB	Filamentous brown	spp.
DU	*Dictyopteris*	*undulata*	DP	*Dictyota*	spp.
EA	*Ecklonia*	*arborea* - large	PTCA	*Pterygophora*	*californica* - large
EAJ	*Ecklonia*	arborea - *small*	PTCA	*Pterygophora*	*californica* - large
EGJ	*Egregia*	*menziesii* - small	MPJ	*Macrocystis*	*pyrifera* - < 1m tall
ER	Encrusting	red	EC	Encrusting	coralline
FASP	*Fauchea*	spp.	R	*Rhodymenia*	*californica*
FG	Filamentous green	spp.	FB	Filamentous brown	spp.
FR	Filamentous red	spp.	RAT	Red Algal Turf	spp.
FTHR	*Neoptilota Ptilota Rhodoptilum*	spp.	RAT	Red Algal Turf	spp.
GEL	*Gelidium*	spp.	GS	*Gracilaria*	spp.
GR	*Gelidium*	*robustum*	GS	*Gracilaria*	spp.
GYSP	*Gymnogongrus*	spp.	CC	*Chondracanthus*	spp.
HAGL	*Halosaccion*	glandiforme	POLA	*Polyneura*	*latissima*
IR	*Iridaea*	spp.	CC	*Chondracanthus*	spp.

LFJ	*Laminaria*	*farlowii* - small	MPJ	*Macrocystis*	*pyrifera* - < 1m tall
LI	*Lithothrix*	spp.	CO	*Corallina*	*officinalis*
LX	*Osmundea*	*spectabilis*	LS	*Laurencia*	spp.
NA	*Nienburgia*	*andersoniana*	CF	*Callophyllis*	*flabellulata*
NEO	*Neoagardhiella*	*baileyi*	GS	*Gracilaria*	spp.
PHSE	*Phycodrys*	*setchellii*	CF	*Callophyllis*	*flabellulata*
PL	*Prionitis*	*lanceolata*	CF	*Callophyllis*	*flabellulata*
PRSP	*Prionitis*	spp.	CC	*Chondracanthus*	spp.
PTJ	*Pterygophora*	*californica* - small	MPJ	*Macrocystis*	*pyrifera* - < 1m tall
PTL	*Pterygophora*	*californica - small*	MPJ	*Macrocystis*	*pyrifera* - < 1m tall
SAFU	*Sarcodiotheca*	*furcata*	CF	*Callophyllis*	*flabellulata*
SAHO	*Sargassum*	*horneri - large*	SHJ	*Sargassum*	*horneri* - small
SCCA	*Scinaia*	*confusa*	GS	*Gracilaria*	spp.
SELO	*Scytosiphon*	*lomentaria*	DP	*Dictyota*	spp.
SMJ	*Sargassum*	*muticum* - small	SAMU	*Sargassum*	*muticum* - large
STIN	Stenogramme	interrupta	R	*Rhodymenia*	*californica*
TALE	*Taonia*	*lennebackerae*	DP	*Dictyota*	spp.
UBB	Unidentified brown blade	spp.	CYOS	*Stephanocystis*	*osmundaceae* - large
UEC	Unidentified erect coralline	spp.	CO	*Corallina*	*officinalis*
UV	*Ulva*	spp.	DP	*Dictyota*	spp.

Estimating Net Primary Production. Daily NPP (g C m^{-2} d^{-1}) was calculated for each taxon (with the exception of large *M. pyrifera*) as per Miller et al. (2012), which followed a modified version of the equation of Jassby and Platt (1976):

$$NPP_i = \sum_h P_{\max} * \tanh\left(\alpha_i E_h / P_{\max_i}\right) * b_i - \sum_h R * b_i$$

Where P_{max} is in units of mg C hr^{-1} (mg dry mass)$^{-1}$, α is in units of mg C hr^{-1} (g dry mass)$^{-1}$ (µmol m^{-2} sec^{-1})$^{-1}$, E is mean irradiance (µmol m^{-2} sec^{-1}) over the course of an hour (h), R is respiration in the dark (mg C hr^{-1} (g dry mass)$^{-1}$) and b is the daily estimate of standing dry biomass (g m^{-2}) of an individual taxon (i). Mean midwater irradiance was used to calculate NPP of reproductive fronds of *S. osmundaceae* and *E. menziesii,* while mean seafloor irradiance was used to calculate NPP of all other taxa. Daily standing biomass of a taxon was estimated using linear interpolation of its biomass from one sampling date to the next. Taxon-specific NPP at each sampling location was calculated as the sum of gross production and respiration over all daylight hours and respiration over all hours of darkness for each group at each sampling location for each day of the year over the time series. For days in which summed respiration was greater than production, daily NPP was constrained to 0. NPP by *Macrocystis pyrifera* $\geq$ 1 m tall on a given day was estimated by multiplying the interpolated value of its biomass for that day by the slope of the relationship between biomass and mean daily NPP developed for that month by Rassweiler et al (2018). For days during sampling periods that began immediately following experimental removal of kelp, the interpolated value of giant kelp biomass was calculated using an initial value of =0.

Taxon-specific estimates of daily NPP in each study plot were averaged over all days in a season (defined by the solar solstices and equinoxes) to produce mean daily values of NPP (g C m^{-2} d^{-1}) by season for each taxon in each year of the time series.

Relationships Between Standing Biomass in Summer and Annual NPP

For each taxon that was recorded in summer, we a developed linear regression to predict its average daily net primary production for a given year (g C m^{-2} d^{-1}) from its standing biomass measured during the summer of that year. Linear relationships were not developed for ephemeral taxa that were absent in summer, but present during other seasons of the year. Data used in the linear regressions included observations from all transects at all five sites during the period 2008-present. Exceptions were made for data collected in 2010 in all continuous removal transects and data in 2011 in all the Isla Vista transects because these transects were established in mid-year of 2010 and 2011, respectively, and consequently lacked complete data for the year they were established. Regression parameters and summary statistics for the regressions for each taxon are provided.

References

Castorani, M. C. N., D. C. Reed and R. J. Miller. 2018. Loss of foundation species: disturbance frequency outweighs severity in structuring kelp forest communities. Ecology, 99: 2442-2455

Lamy, T., C. Koenigs, S. J. Holbrook, R. J. Miller, A. C. Stier, and D. C. Reed. 2020. Foundation species promote community stability by increasing diversity in a giant kelp forest. Ecology, e02987

Miller, R. J., S. Harrer and D. C. Reed. 2012. Addition of species abundance and performance predicts community primary production of macroalgae. Oecologia, 168: 797-806

Miller, R. J., K. Lafferty, T. Lamy, L. Kui, A. Rassweiler and D. C. Reed. 2018. Giant kelp, *Macrocystis pyrifera*, increases faunal diversity through physical engineering. Proc. R. Soc. B, 285: 20172571.

Rassweiler, A., D. C. Reed, S. L. Harrer and J. Clint Nelson. 2018. Improved estimates of net primary production, growth, and standing crop of *Macrocystis pyrifera* in Southern California. Ecology, 99: 2132

References for data packages:

SBC LTER: Reef: Long-term experiment: Kelp removal: Abundance and size of Giant Kelp (https://portal.edirepository.org/nis/mapbrowse?scope=knb-lter-sbc&identifier=29)

SBC LTER: Reef: Long-term experiment: Kelp removal: Invertebrate and algal density (https://portal.edirepository.org/nis/mapbrowse?scope=knb-lter-sbc&identifier=34)

SBC LTER: Reef: Long-term experiment: biomass for kelp forest species, ongoing since 2008 (https://portal.edirepository.org/nis/mapbrowse?scope=knb-lter-sbc&identifier=119)

SBC LTER: Reef: Macroalgal photosynthetic parameters (https://portal.edirepository.org/nis/mapbrowse?scope=knb-lter-sbc&identifier=57)

SBC LTER: Kelp Removal Experiment: Hourly photon irradiance at the surface and seafloor (https://portal.edirepository.org/nis/mapbrowse?scope=knb-lter-sbc&identifier=36)

SBC LTER: Reef: Coefficients for calculating biomass of benthic kelp forest invertebrate, algal, and fish species from body size and percent cover (https://portal.edirepository.org/nis/mapbrowse?scope=knb-lter-sbc&identifier=127)