## Macroalgal NPP Methods

*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) 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 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 (*Macrocystis pyrifera*) in these plots.

*Study Sites.* Macroalgal biomass and irradiance data were collected at five reefs as part of a long-term experiment designed to evaluate the effects of disturbance to giant kelp on the structure and productivity of the benthic community (Reed and Foster 1984, Castorani et al. 2018). 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 subtidal macroalgal assemblages in the region. A common (but not always persistent) feature on these reefs was the presence of the giant kelp, which forms a dense canopy at the sea surface that suppresses recruitment and growth of understory algae below it.

Beginning in 2008, *M. pyrifera* was removed from a 2000 m$^2$ plot once per year in early winter at four reefs (Arroyo Quemado, Carpinteria, Mohawk and Naples) to simulate the effects of winter storm disturbance. An adjacent unmanipulated 2000 m$^2$ plot served as a control. Beginning in winter 2010, *M. pyrifera* was removed 1 to 2 times per season in a 600 m$^2$ area at each of these reefs to create a "continuous kelp removal" plot . In fall 2010 we established a fifth site at Isla Vista with 2000 m$^2$ annual kelp removal and kelp control plots (a 600 m$^2$ continuous kelp removal plot was not established at this site). The experimental removal of kelp ceased in winter 2016 or winter 2017 depending on the site (Table 1). Data collection in all plots is ongoing.

Table 1: Establishment date and manipulation schedule at the five study reefs from 2008 - present.

| Reef | Manipulation | First Sampling Date | '08 | '09 | '10 | '11 | '12 | '13 | '14 | '15 | '16 | '17 | '18 - present |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Arroyo Quemado | Control | January 2008 | Not manipulated | | | | | | | | | | |
| | Annual removal in winter | January 2008 | 1 x per year in winter | | | | | | | | | | Not manipulated |
| | Seasonal removal within annual removal plot | May 2010 | 1 x per year in winter | | 2 x per season starting May 2010 | | | 1 x per season | | | | | Not manipulated |
| Ca rpi | Control | January 2008 | Not manipulated | | | | | | | | | | |

<table>
<tr><td rowspan="2"></td><td>Annual removal in winter</td><td>January 2008</td><td colspan="5">1 x per year in winter</td><td>Not manipulated</td></tr>
<tr><td>Seasonal removal within annual removal plot</td><td>May 2010</td><td>1 x per year in winter</td><td colspan="2">2 x per season starting May 2010</td><td colspan="2">1 x per season</td><td>Not manipulated</td></tr>
<tr><td rowspan="2">Isla Vista</td><td>Control</td><td>October 2011</td><td colspan="6">Not Manipulated</td></tr>
<tr><td>Annual removal in winter</td><td>October 2011</td><td colspan="2">Not manipulated</td><td colspan="2">1 x per year in winter</td><td colspan="2">Not manipulated</td></tr>
<tr><td rowspan="3">Mohawk</td><td>Control</td><td>January 2008</td><td colspan="6">Not manipulated</td></tr>
<tr><td>Annual removal in winter</td><td>January 2008</td><td colspan="5">1 x per year in winter</td><td>Not manipulated</td></tr>
<tr><td>Seasonal removal adjacent to annual removal plot</td><td>May 2010</td><td>Not manipulated</td><td colspan="2">2 x per season starting May 2010</td><td colspan="2">1 x per season</td><td>Not manipulated</td></tr>
<tr><td rowspan="3">Naples</td><td>Control</td><td>January 2008</td><td colspan="6">Not manipulated</td></tr>
<tr><td>Annual removal in winter</td><td>January 2008</td><td colspan="4">1 x per year in winter</td><td colspan="2">Not manipulated</td></tr>
<tr><td>Seasonal removal within annual removal plot</td><td>May 2010</td><td>1 x per year in winter</td><td colspan="2">2 x per season starting May 2010</td><td>1 x per season</td><td colspan="2">Not manipulated</td></tr>
</table>

*Macroalgal Abundance and Standing Biomass.* Divers surveyed the abundance of all macroalgae and its relevant data packages are listed here:

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

All macroalgae were surveyed 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. 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 taxa.

Divers also counted the density of *M. pyrifera* fronds $\geq$ 1 m in height in the 40 m x 2 m transects. The density of *M. pyrifera* fronds $\geq$ 1 m in height was converted to the biomass of giant kelp 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). These relationships allowed us to use our measurements of frond density to estimate total standing biomass of giant kelp in any given month and account for variation in biomass associated with experimental treatments (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 caused periodic data gaps in seafloor irradiance in some of the study plots. 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. Because attenuation varied among sites and kelp removal treatments, and because kelp removal treatments were discontinued later in the time series, we used the logic below to determine the best estimate of attenuation for approximating missing seafloor irradiance at a given sampling location and time:

1) Approximate seafloor irradiance using average attenuation for that sampling location calculated as the average for that hour, on that specific day of the year, averaged over all years when the experimental design was the same (e.g., years encompassing ongoing manipulations vs. years following the discontinuation of manipulations). If data are still missing, then:
2) For sampling locations that have been manipulated, approximate seafloor irradiance using attenuation of a nearby treatment sampling location for that specific date and hour of the day. If data are still missing, then:
3) Approximate seafloor irradiance using average attenuation for that sampling location calculated as the average for that hour, on that specific day of the year, averaged over all years.

Estimates of attenuation were also coupled with sea surface irradiance measurements 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 *Cystoseira 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 study reefs (data package name: SBC LTER: Reef: Macroalgal photosynthetic parameters). Additionally, we measured photosynthesis versus irradiance for the reproductive fronds of *Cystoseira osmundaceae*, which can exhibit seasonally high biomass. These estimates of net production at saturating irradiance ($P_{max}$), net production 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 2.

Table 2. Directly measured (Proxy) taxa. Physiological measurements from Proxy taxa were used for less common species that were not directly 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 | *Cystoseira* | *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 | *Eisenia* | *arborea* - large | PTCA | *Pterygophora* | *californica* - large |
| EAJ | *Eisenia* | 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* |

| | | | | | |
|---|---|---|---|---|---|
| PHTO | *Phyllospadix* | *torreyi* | DP | *Dictyota* | spp. |
| 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 | *Cystoseira* | *osmundaceae* - large |
| UEC | Unidentified erect coralline | spp. | CO | *Corallina* | *officinalis* |
| UV | *Ulva* | spp. | DP | *Dictyota* | spp. |
| ZOMA | *Zostera* | *marina* | DL | *Desmarestia* | *ligulata* |

*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 *C. 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* > 1 m tall was estimated by multiplying the daily interpolated value of its biomass by the slope of the relationship between biomass and mean daily NPP developed for a specific month by Rassweiler et al (2018).

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

*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

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

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

Reed, D. C. and M. S. Foster. 1984. The Effects of Canopy Shadings on Algal Recruitment and Growth in a Giant Kelp Forest. Ecology


Reference 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)