

Net Primary Production of Macroalgae

Overview: One potential manifestation of climate change is an increase in the frequency of severe storms. Such changes are likely to have profound effects on giant kelp forest ecosystems because storms are a major source of disturbance that removes kelp and other biota. An increase in the frequency of severe storms would likely result in large losses of giant kelp every winter. Giant kelp is the foundation species of the ecosystem and our long-term monitoring shows that the dynamics of the benthic community of understory algae and sessile invertebrates are directly linked to the dynamics of giant kelp (Arkema et al. 2009. *Ecology* 90: 3126–3137).

Experimental design: We initiated a long-term experiment (LTE) at four kelp forest sites (Arroyo Quemado, Naples, Mohawk, and Carpinteria) in 2008 to investigate the ecological consequences of regular kelp loss during winter to the structure and function of kelp forest communities in the Santa Barbara Channel (a fifth site, Isla Vista, was added in 2011). Paired 40 m x 40 m plots were established at each site and giant kelp is removed once per year in winter from one of the plots in each pair to simulate the effects of increased frequency of storm disturbance on giant kelp. The other plot in each pair is subjected to only natural disturbance and serves as a control for the experimental removal of kelp. Changes in the structure (e.g. species abundance, diversity) and function (e.g. primary production of understory algae, detrital accumulation) of the benthic community are being followed over time with seasonal monitoring in permanent 40 m x 2 m transects centered within each plot. To evaluate the effects of the constant removal of giant kelp on the benthic community we established a second 40 m x 2 m transect in the kelp removal plots at each site within which giant kelp is continually removed throughout the year. Transects are oriented parallel to shore in an eastward direction and are marked with six bolts placed at distances of 0, 8, 16, 24, 32, and 40 meters. Before each survey, divers swim a fiberglass meter tape along the transect and clip it to each permanent bolt before pulling it taut. All transects were sampled every six weeks (twice per season) from 2008 through 2012 and have been sampled once per season since then. Seasonal sampling is conducted midmonth in February, May, August, and November. Giant kelp is removed from the experimental plots immediately after the first survey of each year is completed.

Methods:

Macroalgal Abundance and Standing Biomass. Divers using SCUBA surveyed the abundance of all understory macroalgae within each 40 m x 2m transect. Abundance-derived biomass of all understory macroalgae was estimated using relationships generated from field estimates of abundance and laboratory measurements of biomass (Harrer et al. 2013). These relationships were derived for 19 taxa that accounted for 97% of the standing biomass of understory macroalgae averaged across all sampling locations during the study period.

We used different measures of abundance for macroalgae of different sizes and morphologies. Percent cover was used to measure the abundance of crustose forms, low lying turfs and foliose algae. The following taxa were included in this group: *Bossiella orbigniana* Decaisne, *Callophyllis flabellulata* Harvey, *Chondracanthus corymbiferus* Kützinger, *Corallina chilensis* Decaisne, large *Cystoseira osmundacea* Turner (defined as individuals of diameter > 10 cm), *Desmarestia ligulata* Stackhouse, *Laurencia spectabilis* Postels & Ruprecht, *Polyneura latissima* Harvey, *Rhodymenia californica* Kylin, *Dictyota* spp., family Ectocarpaceae, *Polysiphonia* spp., *Pterosiphonia* spp., *Halymenia* spp., and crustose coralline algae consisting primarily of *Pseudolithophyllum neofarlowii* Setchell & Mason. Taxon-specific relationships between percent cover and biomass were established using data collected from within 20 to 30 replicate 100 cm² quadrats strategically placed on the bottom over the course of a year at the study sites. Percent cover was estimated by divers as a proportion of 20 uniformly spaced points within the 100 cm² quadrat that contacted any foliage of the target taxon. Once points were recorded, all tissue of the targeted taxon within the quadrat was carefully collected, placed in a labeled plastic bag and returned to the laboratory for determination of biomass in units of dry mass. In the

laboratory, each sample was weighed damp, dried at 60°C for three days and then re-weighed. *C. chilensis*, *B. orbigniana* and crustose coralline algae were de-calcified using a 10% HCL bath prior to drying to obtain measurements of de-calcified dry mass.

Density (number of individuals m⁻²) was used as the measure of abundance for the understory kelps *Laminaria farlowii* Setchell and *Pterygophora californica* Ruprecht and small individuals of the fucoid *Cystoseira osmundacea*. Density was coupled with measurements of individual size to estimate biomass of these species. For large individuals of *L. farlowii* (defined as having a blade width > 15cm) and *P. californica* (defined as having a stipe length ≥ 20cm and a stipe diameter > 7mm), biomass was estimated from allometric relationships developed using individuals collected in the field and measured and weighed in the laboratory. Dry mass of large *L. farlowii* was related to total blade length, while dry mass of large *P. californica* was related to the total number of blades > 30 cm in length. Small individuals of these species can be extremely abundant and mean size calculated from a subsample of individuals was used to estimate the biomass of individuals of these species that were smaller than the sizes noted above.

We couple our derivations of biomass with time series data of abundance to estimate taxon-specific biomass through time. The abundance (percent cover or density) (and size in the case of *Laminaria farlowii*, *Pterygophora californica* and *Cystoseira. osmundaceae*) of all taxa of understory macroalgae are surveyed at each transect approximately every twelve weeks and taxon specific biomass is calculated for each sampling date. Large *P. californica* and *L. farlowii* are counted within the entire 40 m x 2 m transect area, whereas small *P. californica*, *L. farlowii*, and *C. osmundaceae* are counted in six 1 m² quadrats uniformly distributed within the 40 m x 2 m transect area. Percent cover of the remaining understory taxa are estimated using a point contact method consisting of a uniform grid of 80 points in a 40 m x 1m along each transect. This method accounts for vegetation layers of multiple taxa, however any single taxon is only recorded once at each point. All estimates of abundance are converted to units of dry mass using the relationships of Harrer et al. (2013). The biomass of rare species not mentioned above (which collectively accounted for 3% of cumulative biomass over all sites from 2008 to 2012) is determined using relationships between percent cover and biomass generated for morphologically similar taxa.

Bottom Irradiance. Surface and bottom irradiances are measured using submersible PAR sensors (MKV-L, Alec Electronics, Japan). One sensor is mounted ~30 to 100 cm above the sea surface on a moored vertical spar buoy at Arroyo Quemado and Mohawk reef and two to three sensors are mounted on a stake 30 cm above the seafloor at Arroyo Quemado, Naples, Mohawk and Carpinteria. Irradiance in units of μmol m⁻² sec⁻¹ is recorded once every two minutes and averaged to obtain hourly estimates over the course of each day.

Physiological Measurements. We used the methods of Miller et al. (2012) to measure photosynthesis versus irradiance and respiration by the 19 most common macroalgal taxa at our study sites. We incubated whole thalli (minus the woody stipe and holdfast in the case of the kelp *Pterygophora californica*) in clear acrylic tanks and measured oxygen evolution at nine levels of irradiance (19, 36, 60, 103, 178, 198, 344, 392, and 700 μmol m⁻² sec⁻¹; n = 10 to 20 whole thalli per taxon). This range of instantaneous irradiances encompassed the entire range of values that we observed on the bottom at our sites. The initial slope of the relationship between photosynthesis and irradiance at non-saturating irradiance (α) was determined using linear regression of non-saturating irradiance values for each taxon (Jassby and Platt 1976). Photosynthesis at saturating irradiance (P_{\max}) was estimated for each thallus by fitting the hyperbolic tangent function (Jassby and Platt 1976) using SAS (SAS Institute Inc., North Carolina version 9.1.3). Estimates of P_{\max} and α were averaged across replicate thalli to obtain mean estimates for each species or taxonomic group. Units of oxygen were converted to carbon using a photosynthetic quotient of 1.0 (following Rosenberg et al. 1995) and respiration and production rates were standardized to the dry mass of photosynthetic tissue.

Macroalgal Primary Production. Daily NPP ($\text{g C m}^{-2} \text{d}^{-1}$) for each taxon encountered is calculated per Miller et al. (2012), which followed a modified version of the equation of Jassby and Platt (1976):

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

Where P_{\max} is in units of $\text{mg C hr}^{-1} (\text{g dry mass})^{-1}$, α is in units of $\text{mg C hr}^{-1} (\text{g dry mass})^{-1} (\mu\text{mol m}^{-2} \text{sec}^{-1})^{-1}$, E is mean bottom irradiance ($\mu\text{mol m}^{-2} \text{sec}^{-1}$) over the course of an hour (h), R is respiration in the dark ($\text{mg C hr}^{-1} (\text{g dry mass})^{-1}$) and b is the daily estimate of standing dry biomass (g m^{-2}) of an individual taxon (i). Daily standing biomass is estimated using linear interpolation of biomass from one sampling date to the next. NPP of understory macroalgae is calculated as the sum of gross production and respiration over all daylight hours and respiration over all hours of darkness for each understory taxon at each transect for each day of the year. Density of fronds ≥ 1 meter in height is used to calculate NPP of the giant kelp, *Macrocystis pyrifera*, using the equation of Reed et al. (2009). NPP for all taxa was calculated for early and late portions of each season from 2008 to 2012. Beginning in 2013 macroalgal NPP is calculated once per season. Seasons are defined by the solar solstices and equinoxes.

References

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