

Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests

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Abstract. We took advantage of regional differences in environmental forcing and consumer abundance to examine the relative importance of nutrient availability (bottom-up), grazing pressure (top-down), and storm waves (disturbance) in determining the standing biomass and net primary production (NPP) of the giant kelp *Macrocystis pyrifera* in central and southern California. Using a nine-year data set collected from 17 sites we show that, despite high densities of sea urchin grazers and prolonged periods of low nutrient availability in southern California, NPP by giant kelp was twice that of central California where nutrient concentrations were consistently high and sea urchins were nearly absent due to predation by sea otters. Waves associated with winter storms were consistently higher in central California, and the loss of kelp biomass to winter wave disturbance was on average twice that of southern California. These observations suggest that the more intense wave disturbance in central California limited NPP by giant kelp under otherwise favorable conditions. Regional patterns of interannual variation in NPP were similar to those of wave disturbance in that year-to-year variation in disturbance and NPP were both greater in southern California. Our findings provide strong evidence that regional differences in wave disturbance overwhelmed those of nutrient supply and grazing intensity to determine NPP by giant kelp. The important role of disturbance in controlling NPP revealed by our study is likely not unique to giant kelp forests, as vegetation dynamics in many systems are dominated by post-disturbance succession with climax communities being relatively uncommon. The effects of disturbance frequency may be easier to detect in giant kelp because it is fast growing and relatively short lived, with cycles of disturbance and recovery occurring on time scales of years. Much longer data sets (decades to centuries) will likely be needed to properly evaluate the role of disturbance relative to other processes in determining patterns of NPP in other systems.

Key words: consumer pressure; *Macrocystis pyrifera*; NPP; nutrient limitation; regional comparison; resource availability; sea urchin grazing; trophic cascade; wave disturbance.

INTRODUCTION

With few exceptions primary production derived from photosynthesis fuels the energy demands of higher trophic levels and plays a key role in virtually all ecosystem processes. Not surprisingly, scientists have been interested in patterns of primary production and the factors that control them since the time of Aristotle (Lieth 1973). At the most basic level primary production is controlled by characteristic features of the physical environment (e.g., temperature, pH, and soil type) that determine how well plants can survive in a particular locale. Once these basic requirements are met, the availability of resources (e.g., light, nutrients, and water) dictates how fast plants grow. In the absence of

disturbance, these factors determine the standing biomass of actively growing vegetation, and ultimately the amount of material fixed by photosynthesis that becomes available to higher trophic levels (Rosenzweig 1968, Webb et al. 1983).

Coexisting with this bottom-up flow of primary production driven by the abiotic environment are top-down consumptive forces that alter producer biomass (Hairston et al. 1960, Terborgh and Estes 2010). Primary producers are consumed by grazers, which in turn are fed upon by their predators. When such trophic interactions are strong the balance between predators and grazers can effectively determine the amount and type of plant biomass and resulting levels of primary production (Pace et al. 1999, Terborgh et al. 2010). Superimposed upon these bottom-up processes and top-down forces are various forms of physical disturbance that alter the biomass of producers and consumers to varying degrees depending on the type of disturbance

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and the structure of the community prior to its occurrence (Sousa 1984, Pickett and White 1985).

There has been much discussion and debate over the relative importance of resource availability (bottom-up), consumer pressure (top-down), and disturbance in controlling the structure and dynamics of natural communities (Connell 1978, Matson and Hunter 1992, Polis 1999). Perhaps nowhere has this debate been more ardent than in discussions of shallow benthic marine systems dominated by large kelps (e.g., Jackson et al. 2001, Foster et al. 2006, Halpern et al. 2006, Steele et al. 2006, Foster and Schiel 2010). The notable discovery by Estes and Palmisano (1974) that kelp forests in the Aleutian Islands are largely controlled by sea otter foraging was followed by reports of trophic cascades and strong top-down control in other kelp forest systems (Mann 1977, Shears and Babcock 2002, Lafferty 2004). By contrast, the unprecedented ENSO events of the 1980s and 1990s served to heighten an awareness of nutrient limitation and storm disturbance as important drivers of kelp forest structure (Dayton and Tegner 1989) and led to subsequent studies that argued for the primacy of larger scale bottom-up oceanographic processes in controlling kelp biomass and production (Dayton et al. 1999, Broitman and Kinlan 2006). Notwithstanding these arguments, Reed et al. (2008) found that variation in biomass and NPP of giant kelp in southern California was most readily explained by wave disturbance, possibly because of an absence of nutrient poor El Niño conditions in the region and period studied.

There is wide acknowledgement that biotic and abiotic forces act simultaneously to influence populations and communities and that the critical challenge for ecologists is to measure the relative strengths and interactions of these forces as a means of explaining the distribution and abundance of species in nature (Hunter and Price 1992). This has proven to be problematic for many systems due to the difficulty of mimicking natural disturbances and manipulating resources and large predators at the spatial scales appropriate for testing meaningful hypotheses. Regional comparisons and natural experiments have been advocated as an effective means for overcoming these challenges (Menge 2000, Terborgh and Estes 2010, Wernberg et al. 2010). In the kelp forest, manipulating even one of the potential controls of NPP in a realistic way is a huge challenge; there are legal and logistical challenges to transplanting sea otters and other large predators, spatial and temporal patterns of nutrient delivery are difficult to simulate, and the powerful water movements associated with large waves cannot be reproduced on the scale of a kelp forest. A regional comparison is the most (or perhaps only) practical approach to examining the relative importance of these three factors.

Here we make use of known regional differences in environmental forcing and predator abundance in

California kelp forests (Graham et al. 2008) to examine the relative importance of grazing pressure (top-down), nutrient availability (bottom-up), and storm waves (disturbance) on the standing biomass and net primary production of the giant kelp *Macrocystis pyrifera*, which is the dominant biomass producer of kelp forests in this region (Foster and Schiel 1985, Graham et al. 2007). We use time series data to show that there are consistent differences in grazers, nutrients and waves between central and southern California. These differences indicate that top-down control should cause reefs in central California to support more kelp biomass and higher production than reefs in southern California because of the near absence of sea urchin grazers in central California due to the presence of sea otters. Bottom-up control should also lead to more kelp in central California due to kelp's rapid growth in the cold, nutrient rich waters of central California, and slower growth on the more oligotrophic reefs of southern California. Surprisingly, we found that patterns of kelp biomass and production did not match either of these predictions. Using a nine-year time series of net primary production (NPP) by giant kelp at long-term study sites in southern and central California we show that NPP was consistently lower in central California, apparently because the more intense wave disturbance on the central coast overwhelmed top-down and bottom-up forces.

METHODS

Data for this study were collected from eight kelp forest sites in central California and nine kelp forest sites in southern California during the period 2001–2009 (Fig. 1). The sites in central California spanned 80 km of coast south of Monterey, while the sites in southern California covered an 80-km stretch of the mainland coast of the Santa Barbara Channel. Biological surveys of giant kelp, understory algae, macro-invertebrates and fish were done annually in the summer at the eight sites in central California by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) and at the nine sites in southern California by the Santa Barbara Coastal Long Term Ecological Research project (SBC LTER).

The focal species of this study was the giant kelp *Macrocystis pyrifera*, which is the world's largest known alga. Individuals are made up of many (up to 100 or more) fronds that originate from a common holdfast on the bottom and extend vertically in the water column to form a canopy at the sea surface. The density of giant kelp fronds provides a good estimate of its standing biomass, and when measured in the summer, frond density has been shown to account for 70–80% of the interannual variation in giant kelp NPP (Reed et al. 2009).

Measures of top-down control

Sea otters are a top predator in kelp forests of the North Pacific. They were historically abundant across

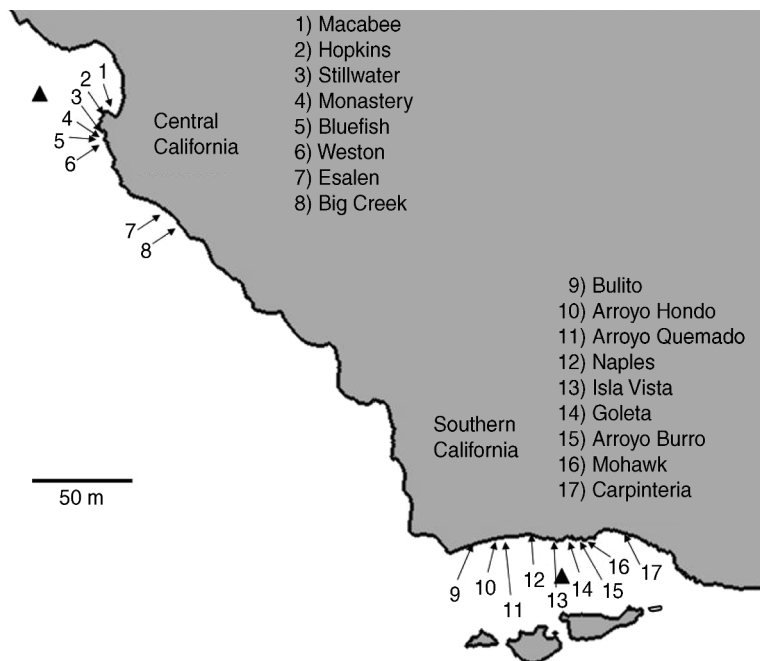


FIG. 1. Map showing the locations of the eight study sites in central California and nine sites in southern California. Solid triangles mark the locations of the NOAA buoys where wave height data were collected.

the Pacific Rim from northern Japan to central Baja California, but the fur trade in the 18th and 19th centuries greatly reduced their population size and distribution (Estes 1980). In California they have been largely confined to the central portion of the state since the early 1900s with a present day population of approximately 2700. Sea otters have been termed a keystone species because of their ability to exert strong influence on the structure and function of kelp forests through top-down predation on sea urchins (Estes and Palmisano 1974), which are responsible for the vast majority of algal biomass lost to herbivory in kelp forests worldwide (Harrold and Pearse 1987).

We made use of the modern day distribution of sea otters to examine regional differences in top-down control in giant kelp forests at our study sites in central and southern California. The red and purple sea urchins (*Strongylocentrotus franciscanus*, *S. purpuratus*) are the most abundant sea urchins on reefs off California and their extensive grazing on giant kelp has been well documented (reviewed in Foster and Schiel 1985, Graham et al. 2007). The grazing rates of other species of invertebrates and fish in California kelp forests are generally low (Foster and Schiel 1985) with estimates on order of 3–6% of giant kelp NPP (Gerard 1976). We used the combined density of red and purple urchins as an indicator of top-down control of giant kelp biomass and productivity. Red and purple urchins were counted by divers in replicate 30×2 m transects ($n = 8–10$) at each of the eight sites in central California and in six 1-m^2 quadrats uniformly spaced along fixed 40×2 m

transects ($n = 2–8$) at each of the nine sites in southern California. Data were collected once per year in summer at each site and the mean combined density of red and purple sea urchins for each site year was used as the measure of urchin density in our analyses. Because red and purple urchins are long-lived, annual sampling is sufficient for characterizing their population dynamics. Differences between regions in the mean densities of sea urchins were evaluated with a *t* test. Data were log transformed to meet the assumption of equality of variances.

Measures of bottom-up control

Nitrogen is considered to be the nutrient that most frequently limits the productivity of giant kelp in California (Jackson 1977). We used the concentration of nitrate + nitrite (hereafter referred to as dissolved inorganic nitrogen) in waters < 10 m deep as an indicator of bottom-up control of giant kelp biomass and productivity. Dissolved inorganic nitrogen data for central California were obtained from the Monterey Bay Aquarium Research Institute's mooring 1 site located in Monterey Bay (36.747° N, -122.022° W). Water samples were collected approximately every 21 days at this site during the nine-year study period (data available online).⁶ Dissolved inorganic nitrogen data for southern California were obtained from monthly water samples collected by the SBC LTER at five sites (Arroyo

⁶ (http://www.mbari.org/bog/Projects/CentralCal/summary/ts_summary.htm)

Quemado, Naples, Arroyo Burro, Mohawk, and Carpinteria; see Fig. 1 for site locations) during the study period. For each region we calculated the mean value of dissolved inorganic nitrogen for each month using all samples collected from 2001–2009. We used these mean monthly values to compare intra-annual patterns in dissolved inorganic nitrogen concentrations among regions. Differences between regions in the overall mean concentration of dissolved inorganic nitrogen were evaluated with a *t* test of regional means averaged across all months of the year.

Measures of physical disturbance

We documented the contrasting wave climate in the two regions using wave heights measured by buoys operated by the National Oceanic and Atmospheric Administration. Southern California waves were measured at the East Santa Barbara buoy (No. 46053) located offshore within 45 km of all southern California sites. Central California waves were measured at the Monterey buoy (No. 46042) located offshore within 55 km of six of the eight central California sites (Fig. 1). The proximity of these two buoys to the study sites make them appropriate for characterizing regional differences in wave climate. Each buoy reports significant wave heights every hour; significant wave height represents the mean of the largest one-third of the waves recorded during a 20-minute sampling period. For each region we used all observations from 2001 through 2009, first finding the mean significant wave height in each month, then averaging those monthly means across all years to yield aggregate seasonal trends. Different metrics of wave height (e.g., median significant wave height or the 95th percentile of significant wave height) showed seasonal and intra-regional patterns similar to those exhibited by the mean significant wave height.

Large waves associated with winter storms account for the vast majority of standing kelp biomass removed by physical disturbance in central and southern California (Graham et al. 1997, Reed et al. 2008). We estimated the amount of disturbance to kelp during winter as the proportional decrease in giant kelp canopy biomass from the autumn maximum to winter minimum. Canopy biomass of giant kelp was estimated at each of the 17 study sites at 30-m resolution every one to two months during the study period using multispectral imagery from the Landsat 5 Thematic Mapper (TM) sensor (methods used to process and calibrate the Landsat 5 images into giant kelp canopy biomass are described in detail in Cavanaugh et al. [2011] and are summarized here). Each Landsat image was geometrically corrected with ground control points and atmospherically corrected using the empirical line correction method. Spectral mixture analysis was then used to calculate the percentage of each pixel's spectral reflectance signal that was influenced by giant kelp within the bounding regions delineated for each site. The kelp fractions were transformed into canopy biomass using a

relationship generated from comparisons of Landsat kelp fraction indices to diver collected measurements of canopy biomass (canopy biomass (kg wet mass/m²) = 5.1 Landsat kelp fraction + 0.75; $r^2 = 0.64$, $n = 96$). We used these measurements of disturbance-related loss of canopy biomass to calculate the mean and interannual variability (as estimated by the among year coefficient of variation) in winter reduction in kelp canopy biomass for each region. Differences between regions in the mean and coefficient of variation in winter reduction of canopy biomass were evaluated with *t* tests.

Net primary production

Because giant kelp fronds in central and southern California are similar in size, the density of fronds is considered to be a good predictor of biomass density of giant kelp throughout central and southern California (reviewed in North 1994). Frond density is also a good predictor of NPP in giant kelp, especially when it is measured in the summer (Reed et al. 2009). In this paper, we applied the relationships between frond density in a given month and annual NPP generated by Reed et al. (2009) to data on frond densities measured in summer to determine annual NPP by giant kelp at each of our study sites for each year of the study. We then calculated the interannual variation in NPP (as estimated by the among year coefficient of variation). The relationships between frond density and NPP developed by Reed et al. (2009) were derived from data collected at only three of our 17 study sites (Arroyo Burro, Arroyo Quemado, and Mohawk in the Santa Barbara Channel). These relationships, however, are expected to apply equally well across all our sites because (1) frond density is a good predictor of biomass density across the geographic range of our study (North 1994) and (2) seasonality in the main biological processes contributing to primary production by giant kelp (i.e., recruitment, growth, and biomass loss) is similar in central and southern California (Gerard 1976, Graham et al. 1997, Reed et al. 2008). We used *t* tests to evaluate potential regional differences in the mean and interannual variation in giant kelp NPP ($n = 9$ years for each region). Data were log-transformed to meet the assumption of equality of variances.

RESULTS

Top-down and bottom-up forcing

The mean density of red and purple sea urchins in southern California was 7.1 ± 1.2 individuals/m² (mean \pm SE) when averaged over all sites and years. Sea urchin densities in this region varied over three fold among years and nearly 30 fold among sites (as evidenced by the large standard errors for southern California in Fig. 2a). As expected, mean sea urchin densities were significantly lower in central California where sea otters are abundant ($t = -20.37$, $df = 16$, $P < 0.0001$), averaging only 0.06 ± 0.009 individuals/m² across all sites and years. The highest density of sea urchins ever

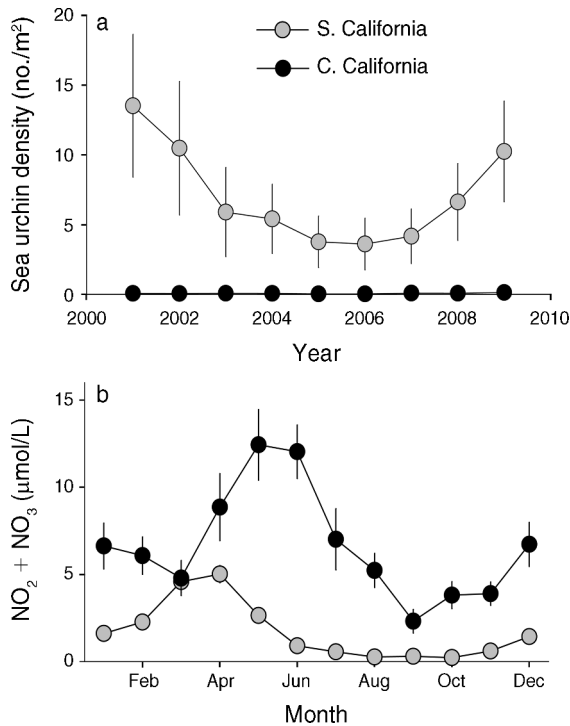


FIG. 2. Mean (\pm SE) of (a) annual density of sea urchins (*Strongylocentrotus franciscanus* + *S. purpuratus*) in central and southern California ($n = 8$ sites in central California and 9 sites in southern California) and (b) monthly concentration of nitrate + nitrite in surface waters for central and southern California ($n = 9$ years). Standard errors that are not visible are smaller than the diameter of the symbol.

recorded at any central California site in any year was 0.21 individuals/m² at Macabee in 2007. In contrast, urchin densities averaged 27.8 ± 4.1 individuals/m² at Carpinteria in southern California over the nine-year study period. These data support the contention that stronger top-down control of sea urchin grazing occurs in central California compared to southern California.

The concentration of dissolved inorganic nitrogen showed strong seasonal patterns in both central and southern California with the greatest concentrations in the spring in both regions (Fig. 2b). On average, the spring peak in central California occurred one month later (i.e., April instead of March) and lasted several months longer than in southern California. Despite this variation, September was the only month in central California where the mean concentration of dissolved inorganic nitrogen was below 3 $\mu\text{mol/L}$. By contrast, concentrations of dissolved inorganic nitrogen averaged $< 1 \mu\text{mol/L}$ for six consecutive months (June through November) in southern California. Concentrations of dissolved inorganic nitrogen were nearly four times higher in central California compared to southern California when averaged over the entire year for the nine-year time series ($t = 4.84$, $df = 22$, $P < 0.0001$). These data are consistent with stronger bottom-up

limitation of giant kelp in southern California compared to central California.

Disturbance and net primary production

Significant wave heights followed the same seasonal pattern in central and southern California with the largest waves occurring in winter and the smallest waves in summer (Fig. 3a). Importantly, significant wave heights in central California during the winter (December through March) were on average nearly twice as high as they were in southern California (2.7 m vs. 1.5 m; $t = 12.7$, $df = 6$, $P < 0.0001$). As might be expected given this difference in wave heights, the mean proportional reduction in canopy biomass observed during the winter in central California was nearly twice that observed in southern California (Fig. 3b; $t = 6.18$, $df = 15$, $P < 0.0001$), which is consistent with the commonly held belief that wave disturbance causes the winter reduction in canopy biomass (see Plate 1). While the mean reduction in canopy biomass due to waves in central California was nearly double that of southern California, the year-to-year variation in the amount of canopy reduction was only about one-quarter as much (Fig. 3c; $t = -4.48$, $df = 15$, $P = 0.0004$). Waves consistently removed large portions of the canopy biomass each year in central California, but did so only sporadically in southern California.

Patterns of net primary production were consistent with the hypothesis that regional differences in wave disturbance overwhelmed those of grazing and nutrients in controlling primary production by giant kelp. In the highly disturbed forests of central California annual NPP by *Macrocystis* was low every year, averaging only half that of southern California (Fig. 4a; $t = 6.72$, $df = 15$, $P < 0.0001$). Furthermore, patterns of year-to-year variation in NPP reflected those of winter canopy loss due to wave disturbance as interannual variation in kelp NPP in southern California was significantly greater than that in central California (Fig. 4b; $t = -4.96$, $df = 15$, $P = 0.0002$).

DISCUSSION

Our study demonstrates the potential for physical disturbance to overwhelm the effects of top-down and bottom up forces in determining NPP. Patterns of NPP by giant kelp in southern and central California were best explained by inter-regional differences in wave disturbance, and run counter to the patterns that would be expected if grazing by urchins or availability of nutrients controlled NPP. These results are consistent with our earlier findings that wave disturbance from winter storms was a major determinant of giant kelp biomass in southern California and that the effects of wave disturbance on biomass explained much more of the year-to-year variation in giant kelp NPP than did variation in kelp growth rates (Reed et al. 2008).

Our results do not imply that grazing and nutrient limitation are unimportant in California kelp forests.

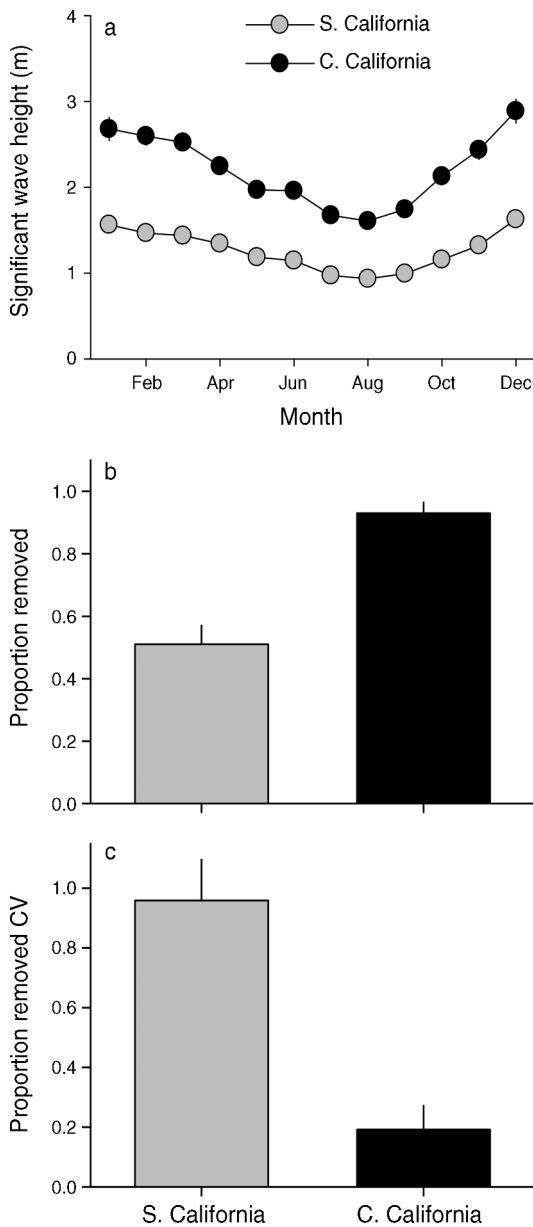


FIG. 3. (a) Mean (\pm SE) monthly significant wave height for central and southern California ($n = 9$ years). (b) Proportional reduction in the canopy biomass during winter attributed to waves. Data represent regional nine-year means (\pm SE) averaged over sites within each region ($n = 8$ sites in central California and 9 sites in southern California). (c) Interannual variation in the proportional reduction in the canopy biomass during winter. Plotted are regional mean coefficients of variation (%; \pm SE) averaged over sites within each region ($n = 8$ sites in central California and 9 sites in southern California). Coefficients of variation for each site were calculated from annual means averaged over the period 2001–2009. Standard errors that are not visible are smaller than the diameter of the symbol.

There are many well documented examples of severe grazing and of nutrient limited growth in giant kelp forests, especially in southern California (see Foster and Schiel [1985] and Graham et al. [2007] for reviews). In

fact, these factors are present at our study sites in southern California, some of which were repeatedly deforested by sea urchin grazing during the period of our study and all of which experienced extremely low nutrients for 6 months of the year (June through November). The nutrient stress observed during our study period did not match that experienced during strong El Niño conditions; such events can decimate

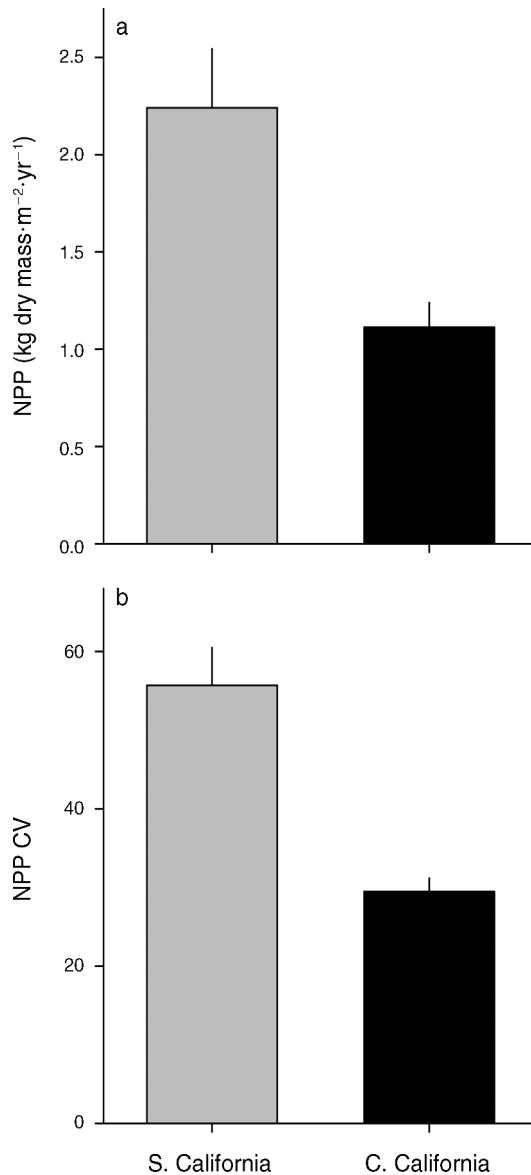


FIG. 4. (a) Annual net primary production (NPP) by giant kelp. Data represent regional nine-year means (\pm SE) averaged over sites within each region ($n = 8$ sites in central California and 9 sites in southern California). (b) Interannual variation in net primary production by giant kelp. Plotted are regional mean coefficients of variation (%; \pm SE) averaged over sites within each region. Coefficients of variation for each site were calculated from annual means averaged over the period 2001–2009.



PLATE 1. Mounds of beached giant kelp (*Macrocystis pyrifera*) torn loose by large waves during a winter storm off Santa Barbara, California, USA. Photo credit: Shane Anderson.

giant kelp throughout its range, but particularly in the more southern regions (Dayton and Tegner 1989, Edwards and Estes 2006). Although these stressful conditions are well documented, they are short-lived (~ 2 years) and relatively rare (there were only three strong El Niños that had a sustained impact on giant kelp in southern California during the period 1930–2000; Foster and Schiel 2010). Hence, the nutrient stresses experienced by giant kelp during our study were typical for southern California, even though they did not attain the maximum stress that can occur. Despite our observations of strong locally imposed grazing pressure and the seasonally oligotrophic conditions in southern California, we found that NPP by giant kelp at our southern sites was on average twice that of our central California sites.

The dominating influence of wave disturbance on giant kelp is due in large part to its massive growth form; it extends throughout the water column with the majority of its biomass residing in the canopy at the sea surface. This morphology creates tremendous drag that makes fronds and entire plants highly susceptible to removal by wave-induced water motion. Not all kelp forests are dominated by species with floating canopies and the importance of wave disturbance relative to top-down and bottom-up processes almost certainly varies among kelp forest systems due to differences in their susceptibility to disturbance, grazing, and nutrient limitation.

Our analysis concerned NPP by giant kelp, and so did not account for all sources of NPP on these reefs. In particular, we did not consider primary production by understory species of macroalgae, which are also present

in most giant kelp forests. The low profile of these species makes them less vulnerable to wave disturbances that remove giant kelp and less susceptible to nutrient limitation due to higher concentrations of nutrients near the bottom (Dayton et al. 1999). These characteristics allow understory macroalgae to compensate in part for the seasonal reduction in NPP caused by the loss of giant kelp to winter waves (Miller et al. 2011). The understory assemblages of central California kelp forests consist largely of perennial species, which raises the possibility that the intra-regional patterns in NPP reported here for giant kelp may differ from those for the entire kelp forest ecosystem.

While other species of macroalgae may compensate in part for the loss of primary production resulting from the removal of *Macrocystis* they cannot replace its ecological role as a foundation species (reviewed in Foster and Schiel 1985, Graham et al. 2007). Giant kelp provides structural habitat to a diverse community of organisms, most of which do not depend directly on it for food (Graham 2004, Graham et al. 2008). Recent studies show that the frequency at which giant kelp is removed by wave disturbance is a primary determinant of the diversity and complexity of the kelp forest food web (Byrnes et al. 2011). Thus disturbances affecting foundation species such as giant kelp are likely to have impacts that cascade through entire ecosystems.

The important role of physical disturbance in controlling vegetative biomass, NPP and the structure of the resulting ecosystem is by no means restricted to giant kelp forests. Mechanical damage and sedimentation associated with floods is an important control of vegetative biomass in streams (Peterson and Stevenson

1992, Biggs 1996) and riparian habitats (Stromberg et al. 1997, Cavalcanti and Lockably 2006), while fire, hurricanes, and avalanches greatly alter the landscape and productivity of terrestrial forests (Veblen et al. 1994, Lugo and Scatena 1996). Vegetation dynamics in these and other systems are dominated by post disturbance succession (Sousa 1984, Pickett and White 1985), which can have profound consequences for NPP (Scatena et al. 1996, Miller et al. 2011). The extent to which spatial and temporal patterns of NPP are controlled by physical disturbance depends on the frequency and intensity of disturbance events relative to recovery time for the dominant vegetation and resource availability, grazing pressure and the direct and indirect effects of the disturbance on these factors (Biggs 1996, Reed et al. 2008). Our results highlight the need expressed by others (Dayton and Tegner 1984, Menge and Olson 1990) to account for the spatial and temporal scales over which different biotic and abiotic processes operate and to integrate their respective roles when assessing the causes of observed patterns of variation. The physical and biological characteristics of many systems dictate that long-term (decades to centuries), spatially extensive data be used to evaluate the importance of disturbance in accounting for variation in NPP and community structure relative to that of other factors.

More generally, our results highlight the role of physical disturbance in structuring natural communities. Studies of kelp forests have more often focused on the relative importance of top-down and bottom-up forces. Here we have shown that physical disturbance is more important than either of these processes in explaining regional differences in the biomass and productivity of giant kelp in California. Physical disturbance is likely to play a similar role in other systems. This role is evolving as many sources of physical disturbance are expected to be affected by climate change; storms, floods, and fires have all been predicted to change in frequency or intensity (Webster et al. 2005, Flannigan et al. 2006, Lehner et al. 2006). If physical disturbances become more frequent or intense as often predicted, then disturbances may begin to limit NPP even in systems where they had previously been less important, with profound consequences for the global carbon cycle (Peng and Apps 1999). Regardless of such predicted changes, understanding when and where physical disturbance overwhelms other factors will help us to explain and predict NPP, vegetative biomass, and the myriad of ecosystem properties that depend on them.

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