

## BIOMASS RATHER THAN GROWTH RATE DETERMINES VARIATION IN NET PRIMARY PRODUCTION BY GIANT KELP

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**Abstract.** Net primary production (NPP) is influenced by disturbance-driven fluctuations in foliar standing crop (FSC) and resource-driven fluctuations in rates of recruitment and growth, yet most studies of NPP have focused primarily on factors influencing growth. We quantified NPP, FSC, recruitment, and growth rate for the giant kelp, *Macrocystis pyrifera*, at three kelp forests in southern California, USA, over a 54-month period and determined the relative roles of FSC, recruitment, and growth rate in contributing to variation in annual NPP. Net primary production averaged between 0.42 and 2.38 kg dry mass·m<sup>-2</sup>·yr<sup>-1</sup> at the three sites. The initial FSC present at the beginning of the growth year and the recruitment of new plants during the year explained 63% and 21% of the interannual variation observed in NPP, respectively. The previous year's NPP and disturbance from waves collectively accounted for 80% of the interannual variation in initial FSC. No correlation was found between annual growth rate (i.e., the amount of new kelp mass produced per unit of existing kelp mass) and annual NPP (i.e., the amount of new kelp mass produced per unit area of ocean bottom), largely because annual growth rate was consistent compared to initial FSC and recruitment, which fluctuated greatly among years and sites. Although growth rate was a poor predictor of variation in annual NPP, it was principally responsible for the high mean values observed for NPP by *Macrocystis*. These high mean values reflected rapid growth (average of ~2% per day) of a relatively small standing crop (maximum annual mean = 444 g dry mass/m<sup>2</sup>) that replaced itself approximately seven times per year. Disturbance-driven variability in FSC may be generally important in explaining variation in NPP, yet it is rarely examined because cycles of disturbance and recovery occur over timescales of decades or more in many systems. Considerable insight into how variation in FSC drives variation in NPP may be gained by studying systems such as giant kelp forests that are characterized by frequent disturbance and rapid rates of growth and recruitment.

**Key words:** biomass; disturbance; giant kelp; growth; *Macrocystis pyrifera*; net primary production; nutrients; recruitment; resource supply; standing crop.

### INTRODUCTION

Primary production by photosynthetic organisms provides the energetic and material basis for the vast majority of life on earth (Lieth and Whittaker 1975). Most ecological studies of primary production have focused on “net primary production” (NPP), which is that portion of gross primary production from photosynthesis that remains after plant respiration. Net primary production may represent different processes depending upon the methods used to measure it, but in most cases it signifies the dry mass of plant matter (or plant carbon) produced per unit area of the earth's surface per unit time (Reichle et al. 1975, Webb et al. 1983, Fahey and Knapp 2007). It is the product of the density of actively growing plant mass (hereafter foliar standing crop [FSC]) and its rate of increase due to growth and recruitment. Foliar standing crop is

determined by morphological properties of the vegetation (e.g., plant size, meristem density) and the proportion of habitat area that it occupies, whereas rates of growth and recruitment are functions of the intrinsic physiological properties and life-history characteristics of the component species and their responses to extrinsic environmental conditions (e.g., resource availability, temperature).

To date, most research aimed at identifying sources of interannual variation in NPP has focused on environmental conditions that affect the rate of growth. Temporal and spatial variation in NPP in many systems has been causally linked to meteorological variables that influence the availability of water, nutrients, and light, which frequently limit plant growth (Brylinsky and Mann 1973, Runyon et al. 1994, Jobbagy and Sala 2000, Knapp and Smith 2001). Disturbance may also affect plant growth (and hence NPP) by altering resource availability (Sprugel 1985, McNaughton et al. 1989, Hobbs and Mooney 1995, Knapp et al. 1998).

In addition to its effects on growth rate, disturbance may dramatically alter the landscape and cause large

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reductions in the standing crop of primary producers (Sprugel and Bormann 1981, Dayton and Tegner 1989). However, the contribution of disturbance to temporal variation in NPP via the reduction in FSC has rarely been investigated. Such effects are likely to be most dramatic when NPP is examined over timescales that are long enough to capture multiple cycles of disturbance and recovery. Few published data sets on NPP are long enough to capture these cycles, as the return times for large disturbances are relatively long (e.g., on order of decades in the case of most wildfires, hurricanes, mudslides, and outbreaks of disease or grazing; Sousa 1984, Pickett and White 1985). Consequently, ecosystem modeling has been the primary means for investigating how disturbance affects vegetation dynamics to influence variability in NPP (Chen et al. 2000, Li et al. 2003).

Submarine forests of giant kelp (*Macrocystis pyrifera*) offer a promising system for field-based investigations of the relative importance of vegetation dynamics and growth rate to interannual variation in NPP. Not only are giant kelp forests believed to be one of the most productive systems on earth (Mann 2000), but frequent disturbance from a variety of sources causes substantial temporal and spatial variation in the standing crop of giant kelp at both local and regional scales (Graham et al. 1997, Dayton et al. 1999, Edwards 2004). Moreover, giant kelp forests are a tractable system to study because rapid growth coupled with a high propensity for recruitment following disturbance allows most *Macrocystis* populations to recover from disturbance within a couple of years (Reed et al. 2006).

In contrast to the wealth of information on patterns and causes of *Macrocystis* population dynamics, surprisingly little is known about temporal and spatial variation in *Macrocystis* growth and NPP and the factors that control them. Our knowledge of the environmental processes that control growth in *Macrocystis* is derived largely from short-term studies of small juvenile plants (Dean and Jacobsen 1984) and of individual blades and stipes of large mature plants (van Tussenbroek 1989, Brown et al. 1997, Hepburn and Hurd 2005). Data from such studies are difficult to extrapolate to entire populations that have spatially and temporally variable age and size structures. Similarly, most empirical studies of primary production in *Macrocystis* have been relatively short term, of limited spatial scale, and difficult to compare either because they used methods that measured different processes or because they expressed NPP in different metrics (reviewed in Coon 1982, North 1994). Such eclectic information has limited value when attempting to understand and predict patterns and causes of spatial and temporal variation in the growth and production of giant kelp forests.

In this study we documented patterns of temporal variation in NPP of *Macrocystis* at three kelp forests in southern California over 4.5 years. We measured the vital rates underlying NPP (i.e., growth, biomass loss,

and recruitment) and the extent to which variation in them was influenced by abiotic factors, such as ocean swell height (the primary source of physical disturbance), ocean temperature (a surrogate for nitrate, which is the nutrient thought to most frequently limit growth), and biological processes such as density dependence (inferred from FSC). We used these data to determine the relative contributions of disturbance-driven fluctuations in FSC and resource-driven fluctuations in rates of recruitment and growth to variation in annual NPP of giant kelp.

#### SPECIES DESCRIPTION AND STUDY SITE CHARACTERISTICS

The giant kelp, *Macrocystis pyrifera*, is the world's largest alga. An individual (hereafter referred to as a plant) consists of a bundle of fronds (often totaling more than 100) anchored by a common holdfast. Each frond consists of a cylindrical rope-like stipe along which many leaf-like blades are attached via small gas bladders that serve to buoy the frond. Unlike land plants, kelp has no belowground parts and nutrient uptake and photosynthesis occur throughout the organism. New fronds originate in the basal foliage just above the holdfast, grow vertically in the water column, and form a dense canopy at the sea surface. They routinely attain lengths over 20 m, and the stipes commonly elongate at rates of 50 cm/d, which is among the fastest elongation rates on record for any terrestrial or marine autotroph (Clendenning 1971). The average life span of a frond in southern California is three to five months, and adult plants live an average of two to three years (North 1994; D. C. Reed, A. Rassweiler, and K. K. Arkema, unpublished data).

Data for this study were collected at three kelp forests located off the coast of Santa Barbara, California, USA: Mohawk Reef (34°23'40" N, 119°43'48" W), Arroyo Burro (34°24'00" N, 119°44'40" W), and Arroyo Quemado (34°28'08" N, 120°07'17" W). These forests occur on low-relief bedrock reefs whose dimensions range from ~300 m (Mohawk and Arroyo Burro) to 1500 m (Arroyo Quemado) in length (alongshore dimension) and ~200 m to 300 m in width (cross-shore dimension). All data on kelp were collected in permanent plots located in the middle of each forest at 6–8 m depth using scuba.

#### METHODS

##### *Net primary production calculations*

We investigated spatial and temporal variation in NPP of *Macrocystis pyrifera* using field measurements and a simple model of kelp dynamics, which assumed that, within a sampling period, biomass was produced and lost at rates proportional to existing FSC. Using this model we calculated the NPP and specific growth rate (i.e., rate at which new kelp tissue is produced per unit of existing kelp tissue) for each month that accounted for the observed change in FSC given independently measured loss rates. We calculated mean daily NPP

and mean daily specific growth rate of giant kelp at the three study sites for each season (i.e., winter, spring, summer, and autumn as defined by the winter solstice, spring equinox, summer solstice, and autumnal equinox) from spring 2002 through autumn 2006 (see Rassweiler et al., *in press*, for detailed description of the methods). Net primary production and specific growth were expressed as daily rates to account for slight variations in the length of the sampling intervals.

At each site we sampled *M. pyrifera* plants in a permanent plot that was either 200 m<sup>2</sup> (Arroyo Quemado and Mohawk) or 480 m<sup>2</sup> (Arroyo Burro) in area. Our estimates of the FSC of giant kelp at the beginning and end of each monthly sampling interval were based on measurements taken of all individuals >1 m tall in each plot. We characterized each individual that we measured using three distinct plant sections: (1) the “subsurface” section consisted of fronds that did not reach the surface, (2) the “water column” section was the subsurface portion of fronds that reached the surface, and (3) the “canopy” section was the portion of the fronds at the sea surface. For each plant within the permanent plots we counted the number of fronds 1 m above the holdfast ( $N_{1m}$ ), and the number of fronds at the surface ( $N_{srfc}$ ), and we measured the water depth at the top of the holdfast ( $D$ ) and the length of the canopy portion of the longest frond ( $MAX$ ). We use these measurements to calculate the length of each plant section, according to the following equations:

$$\text{subsurface length} = (N_{1m} - N_{srfc})[1 + 0.5(D - 1)] \quad (1)$$

$$\text{water column length} = (N_{srfc})(D) \quad (2)$$

$$\text{canopy length} = (N_{srfc})(0.5MAX). \quad (3)$$

We tested the accuracy of Eqs. 1, 2, and 3 in estimating the total frond length by comparing estimates of length obtained using these equations to actual lengths. To do this we collected 55 plants between June 2002 and June 2003 from our three study sites. In the laboratory we measured the length of all fronds on each plant and compared the sum of these lengths to the total frond length obtained by summing the values given by Eqs. 1, 2, and 3. Total frond length estimated using Eqs. 1, 2, and 3 was an excellent predictor of actual total frond length ( $r^2 = 0.993$ , slope = 1.02).

Relationships generated from length and mass measurements of the 55 adult *M. pyrifera* collected from our study sites were used to convert the total length of each of the three plant sections measured in the permanent plots to total wet mass. Holdfasts and basal sporophylls were not included in measurements of total wet mass. The ratio of frond wet mass (in kilograms) to frond length (in meters) was 0.117 for the subsurface section, 0.105 for the water column section, and 0.259 for the canopy section. The wet mass of each plant was converted to dry mass based on the ratio of wet/dry

mass of blades collected from 10–15 plants at each site during each survey to obtain an estimate of FSC in units of kelp dry mass. A 5-cm<sup>2</sup> disk was taken from the central portion of each blade and used to form a composite sample that was dried and analyzed using an elemental analyzer to estimate the percentage of carbon and percentage of nitrogen of the FSC for each site every month. Values were adjusted to account for differences in the carbon and nitrogen content of stipes and blades (Rassweiler et al., *in press*).

During each monthly sampling interval we also calculated instantaneous loss rates for entire plants and for fronds on surviving plants using 10–15 tagged plants at each site. Loss rates of plants were based on the fraction of tagged plants that survived from one sampling date to the next. New plants were tagged to replace plants that were lost during the previous sampling interval to maintain a sample size of 10–15 plants. Loss rates of fronds were based on the fraction of tagged fronds on tagged plants that survived during each sampling interval. Estimating losses resulting from the removal of parts of a frond and from the excretion of dissolved substances was beyond the scope of this study. Thus we estimated the total instantaneous loss rate  $l$  as the sum of the loss rates of plants and fronds.

Using our estimates of the initial and final FSC ( $S_0$ ,  $S_t$ ) and loss rate ( $l$ ) for each monthly sampling interval we calculated the mean growth rate ( $g$ ) of *M. pyrifera* as

$$g = \frac{1}{T} \ln \left( \frac{S_t}{S_0} \right) + l \quad (4)$$

where  $T$  is the number of days in the sampling interval. This calculation was based on an exponential growth model, but using a linear or logistic growth model to calculate NPP produced nearly identical results (Rassweiler et al., *in press*). This exponential model implies that NPP at any moment is the product of  $g$  and  $S$ . We assumed that growth was constant over the monthly sampling interval and expressed  $S$  at any time  $t$  as a function of initial FSC, growth rate, and loss rate ( $S_t = S_0 e^{(g-l)t}$ ). Daily NPP for each monthly sampling interval was obtained by integrating instantaneous NPP over the interval and dividing by  $T$ :

$$\text{NPP} = \int_0^T g S_t dt. \quad (5)$$

Mean daily NPP and mean daily growth rate of *M. pyrifera* for each season were calculated as the mean NPP and mean growth rate for all days in the season.

Each of the variables included in our calculations of growth rate and NPP has an error associated with its measurement. We accounted for observer error, sampling error, and regression error for each variable in our calculations of NPP and growth rate using a Monte Carlo approach that drew randomly from the distributions of each of the component variables (Harmon et al. 2007). These distributions were derived from actual data

and from independent estimates of the error associated with each variable. The standard error for each value of NPP and growth rate was based on values observed in 1000 Monte Carlo simulations. We used this same approach to estimate errors associated with our measurements of FSC and loss rate.

#### *Environmental data*

We used seawater temperature as a surrogate for the ambient concentration of nitrate to investigate the relationship between nutrient availability and specific growth rate in giant kelp. Temperature and nitrate are inversely correlated at our sites and at other locals in southern California (Jackson 1977, Zimmerman and Kremer 1984, McPhee-Shaw et al. 2007). We measured temperature every 10 min using loggers (Stowaway Onset tidbits, accuracy  $\pm 0.2^\circ\text{C}$ ; Onset Computer, Bourne, Massachusetts, USA) fastened to the bottom at each site. The ambient concentration of dissolved inorganic nitrogen (DIN = nitrate + nitrite) was calculated from temperature using a relationship reported in McPhee-Shaw et al. (2007) that was based on 3137 data points collected at Arroyo Quemado ( $\text{DIN} = 0.00628747\text{Temp}^4 + 0.32811\text{Temp}^3 - 5.7165\text{Temp}^2 + 33.833\text{Temp} - 9.7322$  for  $\text{Temp} < 15.5^\circ\text{C}$ , with  $\text{DIN} = 0.22$  for  $\text{Temp} > 15.5^\circ\text{C}$ ; total error  $\pm 0.79 \mu\text{mol/L}$ ). Dissolved inorganic nitrogen values were averaged to obtain a mean DIN concentration for each season.

We investigated the relationship between wave height and loss rates of *Macrocystis* plants and fronds (as a fraction of FSC) using wave data from the Goleta Point Buoy (Coastal Data Information Program station 107, data *available online*)<sup>4</sup> located 11 km offshore of our study sites in the Santa Barbara Channel ( $34^\circ 20' 00'' \text{ N}$ ,  $119^\circ 48' 13'' \text{ W}$ ). We used the maximum value of the significant wave height ( $H_S$ ) recorded during each monthly sampling interval to examine the relationship between wave disturbance and monthly estimates of the two different types of biomass loss (i.e., fronds and plants). Significant wave height is commonly used to describe wave height and represents the mean of the largest one-third of the waves recorded during a 30-min sampling period.

#### *Statistical analyses*

We examined whether annual NPP was related to the FSC at the start of the growth year (hereafter initial FSC), the density of plants that recruit during the year, and the annual rate of kelp growth. We considered the start of the growth year to be the winter solstice since this is the time of year when FSC is most commonly at or near its minimum (see *Results*, Fig. 1). The density of recruits for each month was estimated as the increase in plant density from the previous month. Recruitment was assumed to be zero in months when plant density did not

increase. Recruitment can be greatly underestimated using this approach if the appearance of new plants largely coincides with the loss of established plants. Our independent estimates of plant loss indicate that this was not the case as the loss rate of established plants was typically lowest during months that showed the greatest increase in plant density (see *Results*, Fig. 2 vs. Fig. 3a). Annual growth and annual NPP were calculated as the sum of daily growth or daily NPP over the growth year. Single regressions were done to obtain the best independent estimates of the contributions of initial FSC, annual recruitment, and annual growth to variation in annual NPP using annual estimates from four years at each of the three sites. Stepwise multiple regression was used to estimate the relative contribution of each of the independent variables to variation in annual NPP. We tested for collinearity among the independent variables by evaluating tolerance variables (Quinn and Keough 2002) and condition indices (Belsley et al. 1980) and found that it was not significant.

## RESULTS

### *Foliar standing crop*

The FSC of giant kelp peaked at all three sites during the first three months of the 54-mo study, with maximum values of 1.28, 1.12, and 1.66 kg dry mass/m<sup>2</sup> at Arroyo Burro, Arroyo Quemado, and Mohawk, respectively (Fig. 1). Maximum plant densities during this period averaged 0.3 plants/m<sup>2</sup> at Arroyo Burro and 0.61 plants/m<sup>2</sup> at Arroyo Quemado and Mohawk. These peaks were followed by abrupt declines at all three sites beginning in November 2002. The initiation of this decline coincided with a period of large oceanic swells that led to a >90% reduction in FSC over the ensuing three months (November 2002 to January 2003). Kelp dynamics behaved differently at the three sites following this decline. Most notable was the lack of recovery by *Macrocystis* at Arroyo Burro where FSC rarely increased above 0.15 kg dry mass/m<sup>2</sup> during the next four years. The sustained reduction in FSC at Arroyo Burro was due to a persistent decrease in the availability of reef habitat needed for kelp recruitment and growth. This decrease in reef habitat resulted from movement of sand during the November 2002 swells that buried >80% of the rocky habitat for the remainder of the study (D. C. Reed, A. Rassweiler, and K. K. Arkema, *unpublished data*). In contrast to Arroyo Burro, the reefs at Arroyo Quemado and Mohawk were not inundated by sand and the kelp forests at these sites recovered relatively quickly from the large swells of 2002 (Fig. 1). Nevertheless, the FSC at these sites never reached the high levels observed at the start of the study, in part because wave-induced disturbance occurred during each winter of the study. Substantial variability in giant kelp FSC was observed both within and among years at these two sites, with peaks generally occurring in late summer to autumn (August to November) and minima in winter (January to March). The FSC averaged  $0.444 \pm 0.036$

<sup>4</sup> (<http://cdip.ucsd.edu>)

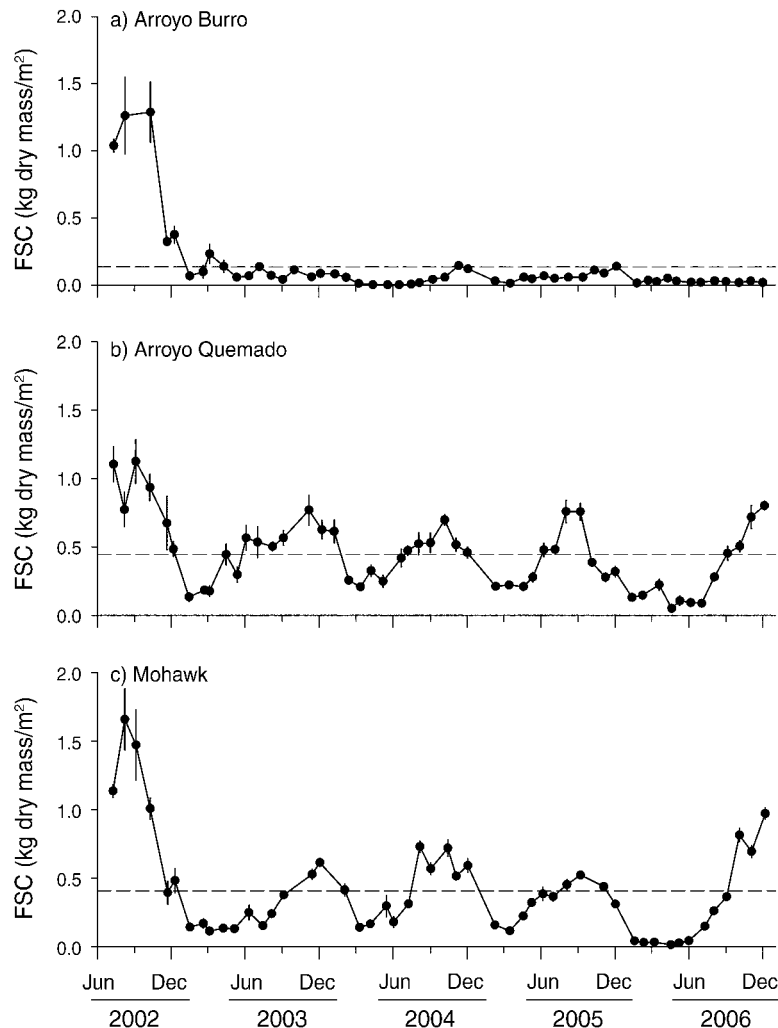


FIG. 1. Monthly estimates ( $\pm$ SE) of the foliar standing crop (FSC) of giant kelp (*Macrocystis pyrifera*) at the three study sites located off the coast of Santa Barbara, California, USA. Horizontal dashed lines represent the time-averaged means for each site.

and  $0.408 \pm 0.051$  kg dry mass/m<sup>2</sup> ( $0.126 \pm 0.011$  and  $0.115 \pm 0.014$  kg C/m<sup>2</sup>; mean  $\pm$  SE) at Arroyo Quemado and Mohawk, respectively, over the 54-month study.

Decreases in FSC reflected losses of entire plants and portions of plants (i.e., fronds) due to senescence and dislodgement. Frond loss occurred continuously throughout the year, though the rate of frond loss varied as much as fivefold within any given year (Fig. 2). Highest loss rates were observed in the winter, with frond loss during some months averaging as much as 4% of the FSC per day. Unlike fronds, the loss of entire plants was relatively episodic, with most tagged plants disappearing in winter and early spring and little to no plant loss occurring in summer. Losses at each of the three sites were related to oceanic swells; the maximum significant wave height observed during a given sampling interval explained a significant amount of the variation in the loss rates of both fronds and plants

during that sampling interval (Fig. 2). The lone exception to this pattern was at Arroyo Burro, where frond loss varied independently of wave height. Rates of frond loss and plant loss at each site were unrelated to the densities of fronds and plants at the site prior to the loss ( $r^2 < 0.04$  and  $P > 0.17$  for both frond loss and plant loss at all three sites). While the loss rates of fronds and plants varied among sites during any given month, the 54-month means were similar across the three sites, averaging  $\sim 1.3\%$  and  $0.5\%$  of the FSC per day, for fronds and plants, respectively (Fig. 2).

#### Recruitment

The recruitment of new plants to a size of at least 1 m tall occurred primarily in the summer (June through September; Fig. 3a). Recruitment rates differed greatly among sites and years. Relatively little recruitment was observed at Arroyo Burro during the study, whereas substantial recruitment was observed in four of the five

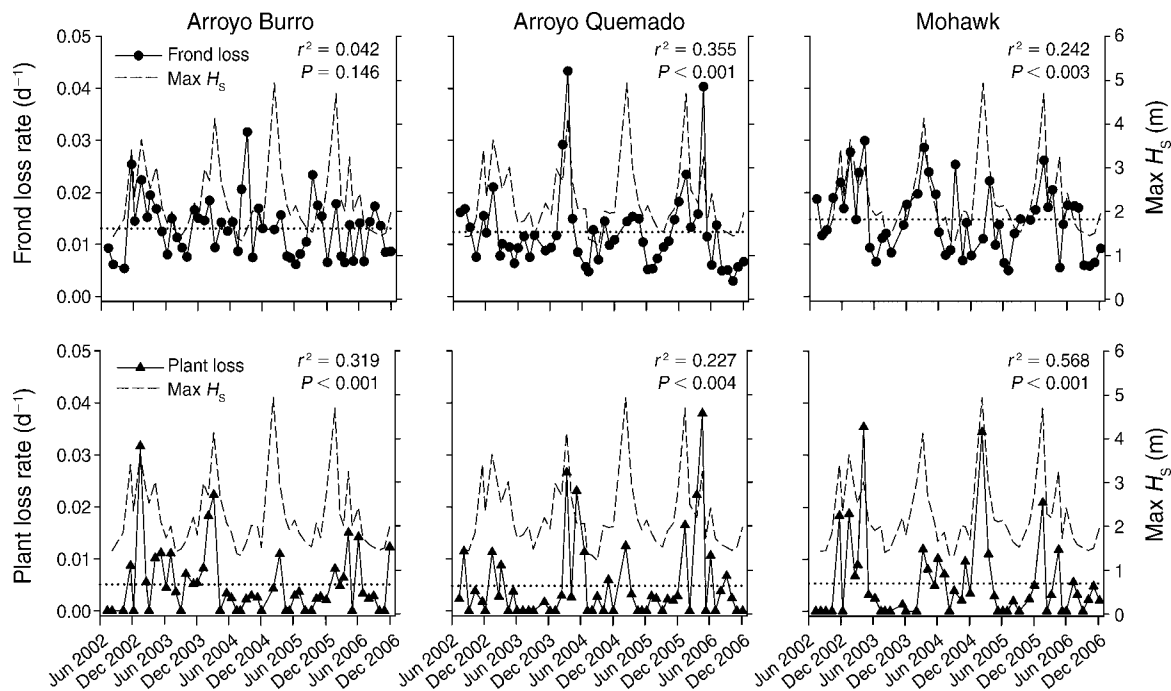


FIG. 2. Instantaneous loss rates for giant kelp (*Macrocystis pyrifera*) fronds (top row) and plants (bottom row) and maximum significant wave height (max  $H_s$ ) vs. time. Labels on the far right and far left y-axes apply to all panels within a row. Horizontal dotted lines represent the time-averaged means of frond and plant loss rates. Statistics are from the linear regressions examining the relationship between instantaneous loss rate (fronds or plants) during a sample period and the max  $H_s$  during the sample period.

summers at Mohawk (2002 being the exception) and in two summers (2004 and 2006) at Arroyo Quemado. Pulses in recruitment (i.e., periods when the density of recruits  $> 0.4$  recruits/m<sup>2</sup>) occurred only when the initial FSC was  $< 0.4$  kg dry mass/m<sup>2</sup> (Fig. 3b), and peaks in recruitment were always followed by increases in FSC (Fig. 3a vs. Fig. 1).

### Growth

Growth rates of giant kelp on a dry-mass basis averaged  $\sim 2\%$  of the FSC per day at each of the three sites over the period of study (Fig. 4). At this rate the FSC had the potential to double every 34 d, assuming no biomass loss. Although mean growth was similar among the sites, patterns of temporal variation in growth differed among them. Seasonal variation in growth was most evident at Arroyo Quemado, where it cycled between high rates in winter and spring and low rates in summer and fall (Fig. 4b). This seasonal pattern in growth rate varied inconsistently among years at Mohawk, where it showed a winter/spring peak in 2003 and 2005 and a spring/summer peak in 2004 and 2006 (Fig. 4c). In contrast to Arroyo Quemado and Mohawk, growth rates at Arroyo Burro fluctuated sporadically in time with no apparent seasonality (Fig. 4a). The large spike in growth at Arroyo Burro observed in summer 2004 occurred at a time when the low FSC consisted of a relatively high proportion of

small young plants. Growth rates at this site reached a minimum the following winter (2005), when these young plants were lost during a large wave event (Fig. 1a).

The highest growth rates were most frequently observed at times and locations when FSC was relatively low (i.e.,  $< 0.5$  kg dry mass/m<sup>2</sup>; Fig. 5a). A small standing crop, however, was not the sole requisite for rapid growth as slow growth was also frequently observed at low standing crops. Growth varied with the size structure of the standing crop as growth rate was positively related to the proportion of the FSC that consisted of small, young individuals, suggesting younger plants grew at a faster rate than older plants (Fig. 5b). Growth rate was positively related to the concentration of DIN at Arroyo Quemado, where seasonal trends in growth rate were most apparent (Fig. 6a). No such relationship was found at either Arroyo Burro or Mohawk. Moreover, growth rate was unrelated to the nitrogen content of the standing crop at all three sites (Fig. 6b). The nitrogen content of the standing crop followed a power function with DIN at each of the sites (Fig. 6c), indicating that the acquisition of nitrogen by kelp was generally dependent upon the concentration of nitrate in seawater.

### Net primary production and turnover

The highest values of NPP were recorded at the beginning of the study prior to the large swells in

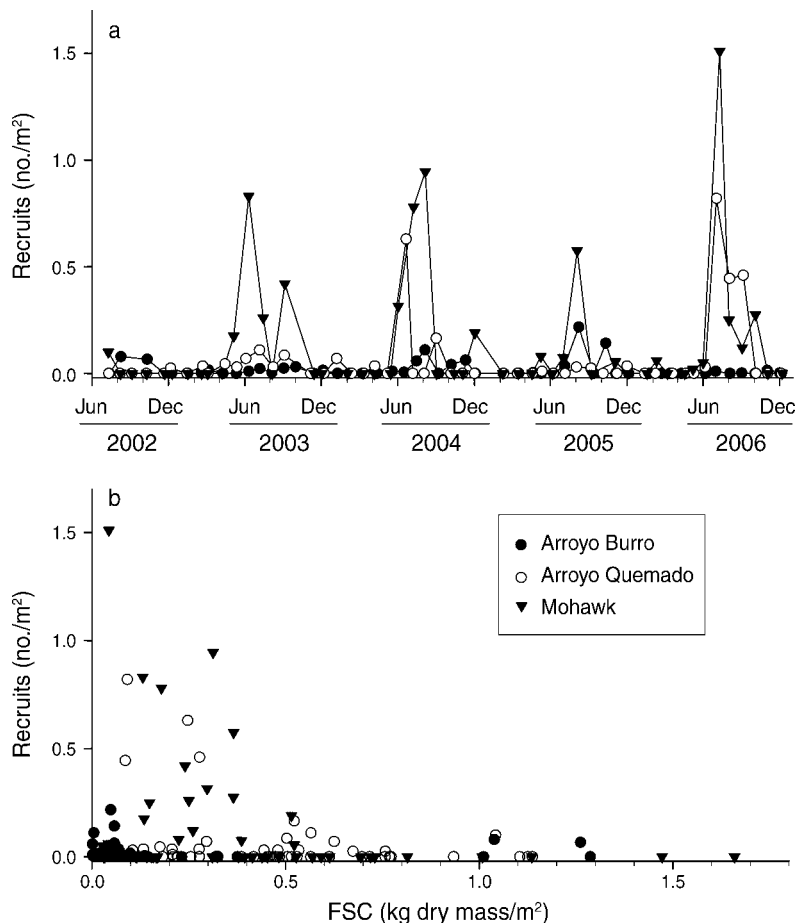


FIG. 3. (a) Spatial and temporal variation in the density of newly recruited giant kelp (*Macrocystis pyrifera*) >1 m tall. (b) Relationship between the density of recruits at the end of the sampling interval and foliar standing crop (FSC) at the beginning of the sampling interval. Data are monthly values for Arroyo Burro (solid circles), Arroyo Quemado (open circles), and Mohawk (solid triangles).

November 2002 (Fig. 7). The loss of kelp biomass caused an abrupt decline in NPP at all three sites. Net primary productivity remained relatively low at Arroyo Burro, averaging  $2.0 \text{ g dry mass}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  ( $0.6 \text{ g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) over the 54-month study, despite periods of rapid growth (Fig. 3a). In contrast, NPP varied sporadically at Arroyo Quemado and Mohawk, with no apparent seasonality. Overall, NPP was substantially higher at these two sites, averaging  $\sim 7.5 \text{ g dry mass}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  ( $2.2 \text{ g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ; Fig. 7b, c). These relatively high mean values of NPP resulted from consistently high growth rates (Fig. 4) of a relatively small amount of kelp biomass (Fig. 1) that turned over on average 6.8 times per year (as estimated by the ratio of annual NPP to mean annual FSC). Annual rates of biomass turnover were similar among sites (mean annual turnover rate = 7.3, 5.9, and 7.2 for Arroyo Burro, Arroyo Quemado, and Mohawk, respectively;  $F_{2,11} = 3.37$ ,  $P = 0.081$ ) and were largely independent of the mean annual FSC ( $F_{1,11} = 3.60$ ,  $r^2 = 0.265$ ,  $P = 0.087$ ).

#### Sources of variation in annual net primary production

On an annual basis NPP averaged  $0.42 \text{ kg dry mass}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  ( $0.12 \text{ kg C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ) at Arroyo Burro and 2.31 and  $2.38 \text{ kg dry mass}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  ( $0.66$  and  $0.68 \text{ kg C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ) at Arroyo Quemado and Mohawk, respectively. Annual NPP was positively related to both initial FSC ( $F_{1,11} = 16.76$ ,  $r^2 = 0.626$ ,  $P = 0.002$ ) and annual recruitment ( $F_{1,11} = 8.96$ ,  $r^2 = 0.473$ ,  $P = 0.014$ ). Surprisingly, no correlation was found between annual growth and annual NPP ( $F_{1,11} = 0.21$ ,  $r^2 = 0.021$ ,  $P = 0.653$ ). Multiple regression analysis revealed that initial FSC and annual recruitment contributed 62% and 22% of the interannual variation in NPP, respectively (Table 1a). The greater influence of initial FSC and recruitment compared to growth rate resulted in large part from differences in the dynamic range of variation in these variables. Interannual variability in initial FSC and recruitment (as indicated by the coefficient of variation among years) was 78.0% and 69.2%, respectively, compared to 19.2% for growth rate.

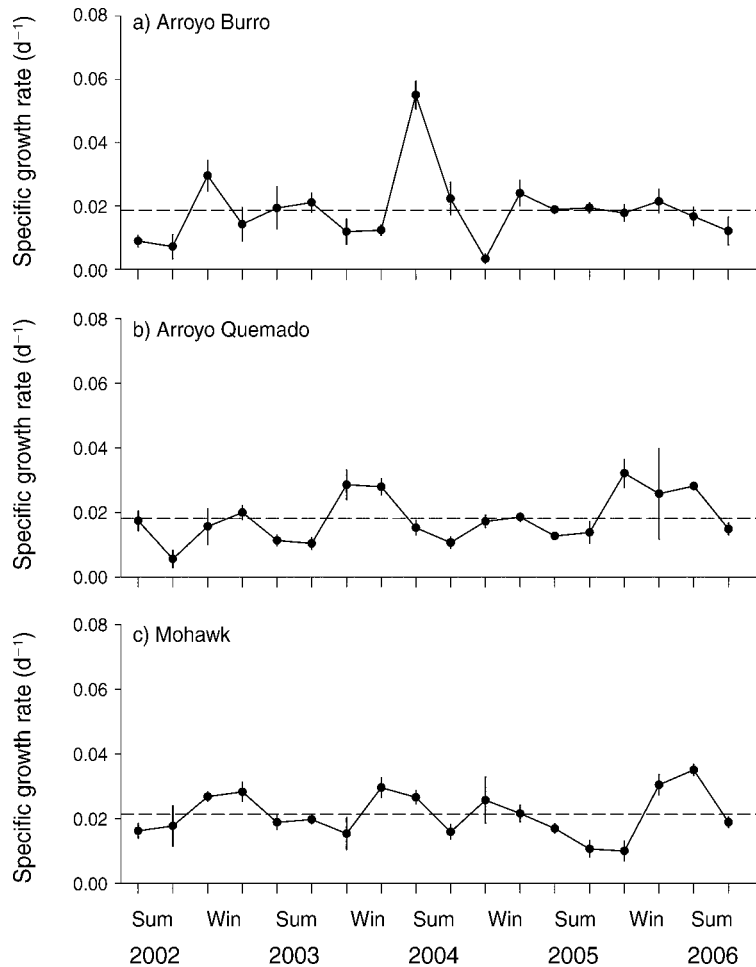


FIG. 4. Estimates ( $\pm$ SE) of the specific growth rate of giant kelp (*Macrocystis pyrifera*) at the three study sites by season (Sum, summer; Win, winter). Horizontal dashed lines represent the time-averaged means for each site.

Additional regression analyses revealed a positive feedback between initial FSC and NPP, as initial FSC (the primary determinant of NPP) was positively related to NPP in the previous year ( $F_{1,11} = 13.67$ ,  $r^2 = 0.578$ ,  $P = 0.004$ ) and negatively related to the loss rate of kelp biomass at the end of the previous year (i.e., autumn;  $F_{1,11} = 5.29$ ,  $r^2 = 0.346$ ,  $P = 0.044$ ). Collectively, these two variables accounted for 79.5% of the interannual variation in initial FSC (Table 1b).

#### DISCUSSION

One of the most striking results of our study was the insignificance of growth rate in explaining variation in annual NPP. We believe that this was due in part to an oceanographic climate that was relatively favorable for kelp growth during our study. Nitrate has been identified as the nutrient that most frequently limits growth of giant kelp in many parts of the world, and variation in climatic factors that influence the supply of nitrate to giant kelp forests is believed to be a leading cause of variability in kelp growth (Jackson 1977,

Zimmerman and Kremer 1986, van Tussenbroek 1989, Brown et al. 1997). For instance, in southern California nitrogen-limited growth in *Macrocystis* is most pronounced during extended periods of low nutrient availability, such as those that occur during El Niños (Gerard 1982, Zimmerman and Robertson 1985). However, kelp growth rates during more nutrient-rich conditions can be highly variable, with no clear correlation to ambient nitrate concentrations or tissue nitrogen content (Wheeler and North 1981). Our observations of continuously high nitrogen content in kelp (generally above 1%; Fig. 6b, c) coupled with our finding that growth was unrelated to the concentration of DIN in seawater at two of our three sites (Fig. 6a) suggest that growth was rarely nitrogen limited during our study. The contrasting results between our study and those done during prolonged conditions of nutrient stress (Gerard 1982, Zimmerman and Robertson 1985) lend support to the contention that the importance of intra-annual variation in nitrogen supply in determining



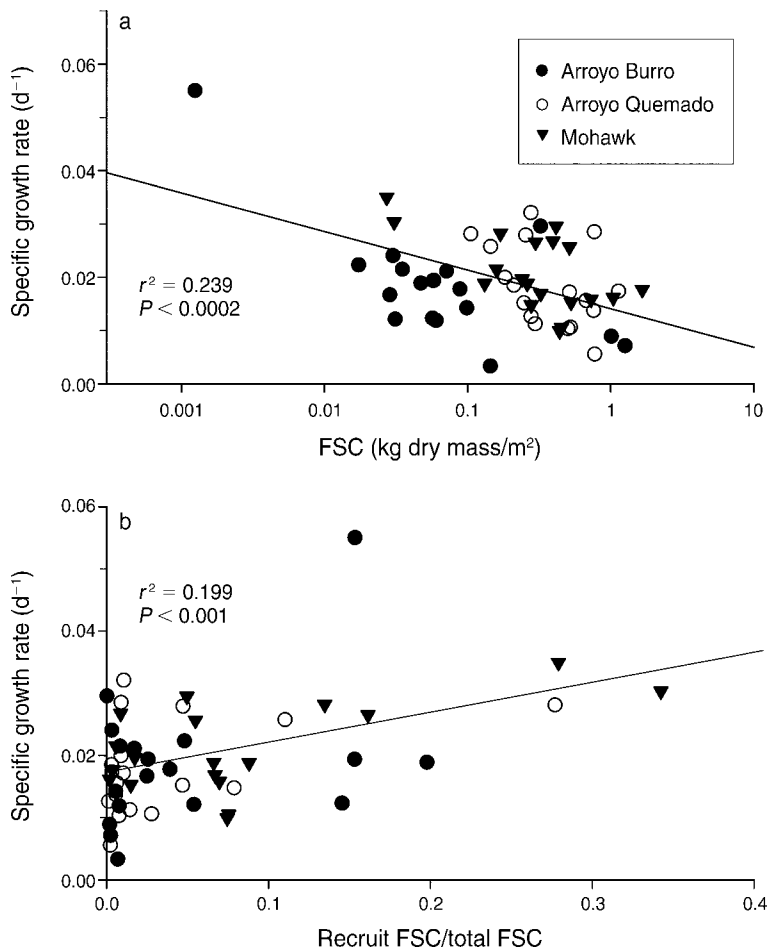


FIG. 5. The relationship between the specific growth rate of giant kelp (*Macrocystis pyrifera*) and (a) the foliar standing crop (FSC) of kelp at the start of each season and (b) the proportion of the standing crop consisting of new recruits (recruit FSC/total FSC). The regression in (a) remained significant ( $P < 0.0146$ ) when the outlier at Arroyo Burro was excluded from the analysis. Recruits in (b) were defined as subsurface plants with four or fewer fronds. Data are seasonal means for Arroyo Burro (solid circles), Arroyo Quemado (open circles), and Mohawk (solid triangles).

kelp growth depends on the state of longer-term oceanographic conditions (Graham et al. 2007).

The reduction in light due to density-dependent shading is widely regarded as a critical determinant of plant growth. Not surprisingly, light limitation is believed to be a very important constraint on growth in giant kelp (Jackson 1987), and it may have contributed to the seasonal variation in growth that we observed. The inverse relationship that we found between FSC and growth rate is similar to that detected by Gerard (1976) for *Macrocystis* in central California and suggests light limitation (via density-dependent shading) as an important factor in determining patterns of kelp growth. Consistent with this hypothesis is the seasonal growth pattern (high in winter and spring and low in summer and autumn) that we recorded at Arroyo Quemado and to a lesser extent Mohawk, which was completely out of phase with the seasonal pattern observed in FSC (i.e., low in winter and spring and high in summer and autumn). This reduced growth

during seasons of high biomass tends to dampen within-year variation in NPP.

Light limitation via density-dependent shading cannot account for the variable growth rates observed at Arroyo Burro, where FSC remained low for most of the study. Instead, changes in the age structure of the population appeared to be the primary source of large fluctuations in an otherwise relatively constant pattern of annual growth, as younger kelp plants appeared to grow faster than older kelp plants. Differences in age structure may also have accounted for the occasional lag in growth at Mohawk relative to Arroyo Quemado (Fig. 4) as the FSC at Mohawk consisted of a greater proportion of young, fast-growing individuals due to more frequent recruitment at this site. Changes in age structure are common following a disturbance and have been shown to be an important source of interannual variation in growth and NPP in other systems (Sprugel and Bormann 1980, Li et al. 2003).

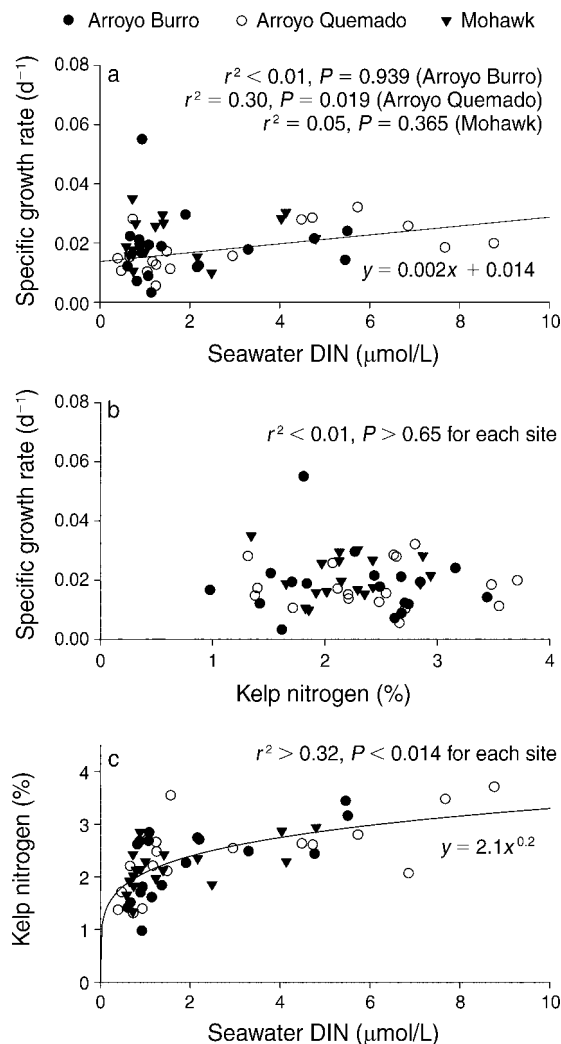


FIG. 6. The relationship between (a) specific growth rate and the ambient concentration of dissolved inorganic nitrogen (DIN) in seawater, (b) specific growth rate and nitrogen content of giant kelp (*Macrocystis pyrifera*), and (c) kelp nitrogen content and ambient DIN concentration. Data are seasonal means for Arroyo Burro (solid circles), Arroyo Quemado (open circles), and Mohawk (solid triangles) for the period June 2002 to December 2006. The regression line in (a) is for Arroyo Quemado; the regression line in (c) is for all sites combined.

The relatively high values of NPP by *Macrocystis* reported here ( $\sim 2.3 \text{ kg dry mass} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ) are nearly identical to those found by Gerard (1976) in central California (assuming a wet mass/dry mass ratio of 10) and support Mann's (2000) contention that giant kelp forests are among the most productive systems in the world. It is worth noting that our measurements of *Macrocystis* NPP underestimate total forest production because they did not account for the partial loss of kelp fronds (due to grazing, breakage, senescence) or the loss of dissolved organic exudates, nor did they account for production by understory algae and phytoplankton, which contribute additional sources of primary produc-

tion to kelp forests ecosystems. Although growth rate was a poor predictor of annual variation in *Macrocystis* NPP, it is principally responsible for giant kelp's high mean rates of NPP, which result from rapid growth of a relatively small standing crop (usually  $< 1 \text{ kg dry mass/m}^2$ ) that turns over an average of approximately seven times per year.

Our results highlight the importance of viewing net primary production by a system as a suite of biotic and abiotic factors interacting with several key attributes of primary producers. We depict these interactions in a conceptual model in which the standing crop of primary producers and their rates of growth and recruitment combine to determine NPP (Fig. 8). Disturbance acts to directly reduce the standing crop of primary producers, whereas the delivery of resources enhances their vital rates (i.e., growth and recruitment). Disturbances may also have positive or negative effects on resource supply, depending of the nature of the disturbance (e.g., fire vs. grazing) and the type of resource (e.g., light vs. nutrients). These concepts apply generally to most systems.

Although many studies have examined one or more components of our model, few if any have explored them all simultaneously. By studying giant kelp at several sites over multiple years we were able to evaluate the relative strengths of most of the interactions depicted in Fig. 8 over a relatively broad range of conditions. We found that periodic wave disturbance led to large seasonal reductions in kelp standing crop at all three sites. However, we observed significant among-site differences in standing crop dynamics as the loss of kelp biomass due to waves was much reduced at Arroyo Burro following persistent sand inundation (Fig. 1a). Our observations of reduced rates of recruitment and growth during seasons with initially high standing crops (Figs. 3b and 5a) coupled with the weak and inconsistent relationship between growth and nitrogen (Fig. 6) support the hypothesis that standing crop negatively affected recruitment and growth via density-dependent competition for light (shown by the negative effect of standing crop on recruitment, growth, and resource supply in Fig. 8). That increases in FSC always followed pulses in recruitment is in turn consistent with the positive effects of recruitment and growth on FSC depicted in the model. Our finding that loss rates and NPP accounted for nearly 80% of the observed annual variation in FSC at the beginning of the subsequent year (Table 1b) provides evidence for a positive feedback between NPP and FSC that was countered by losses in FSC due to disturbance. Lastly, our findings are consistent with the positive interactions between standing crop and NPP and between recruitment and NPP (Fig. 8), which collectively explained 84% of the variation in annual NPP of giant kelp at our sites (Table 1a). Surprisingly, the only interaction in our conceptual model of NPP that we failed to find evidence for was a positive relationship between growth rate and

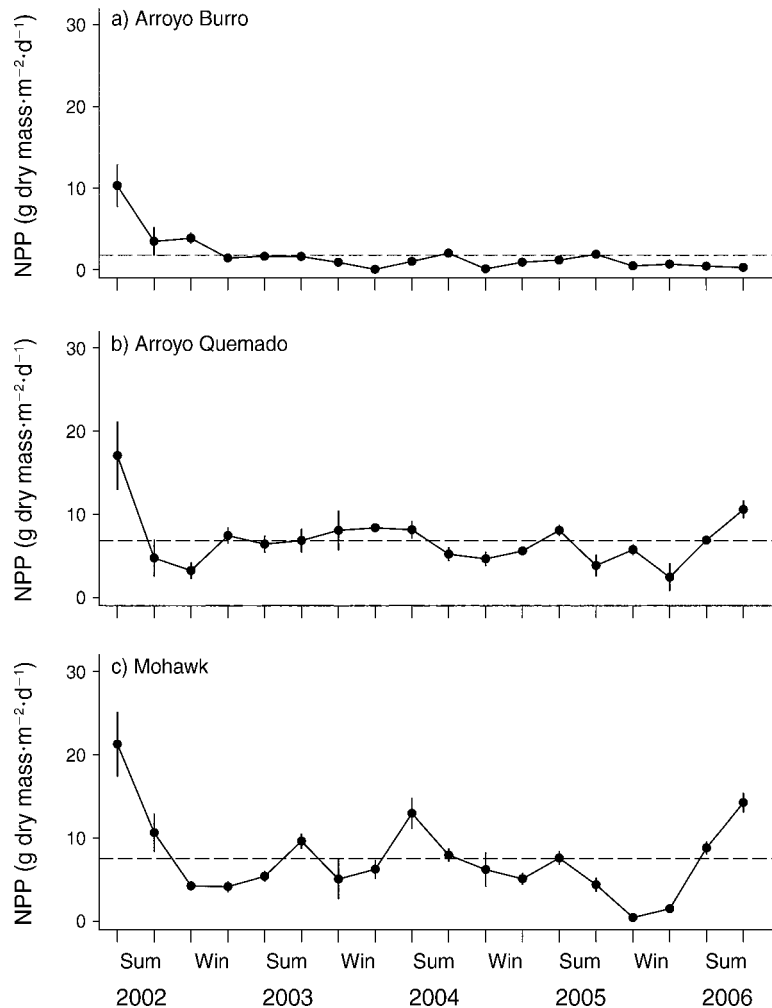


FIG. 7. Estimates ( $\pm$ SE) of net primary production (NPP) of giant kelp (*Macrocystis pyrifera*) at the three study sites by season (Sum, summer; Win, winter). Horizontal dashed lines represent the time-averaged means for each site.

TABLE 1. Results from stepwise multiple regression analyses investigating the relative contributions of (a) foliar standing crop at the start of the growing season [ $\log(\text{initial FSC})$ ] and annual recruitment density of giant kelp (*Macrocystis pyrifera*) to variation in annual net primary production (NPP), and (b) previous year's NPP and loss rate of kelp biomass in autumn of the previous year (loss) to initial FSC.

Source	df	$R^2$	F	P
a) Dependent variable: annual NPP				
Model	2	0.8418	23.94	0.0002
$\log(\text{initial FSC})$	1	0.6263	21.00	0.0013
Recruitment	1	0.2155	12.26	0.0067
Residual variation	9	0.1582		
b) Dependent variable: $\log(\text{initial FSC})$				
Model	2	0.7951	17.47	0.0008
$\log(\text{NPP})$	1	0.5774	19.73	0.0016
Loss	1	0.2177	9.56	0.0129
Residual variation	9	0.2049		

Notes: Tolerance variables were  $>0.9$ , and condition indices were  $<10$  for each analysis, indicating no significant collinearity among the independent variables in either (a) or (b). Data for this study were collected at three kelp forests located off the coast of Santa Barbara, California, USA.

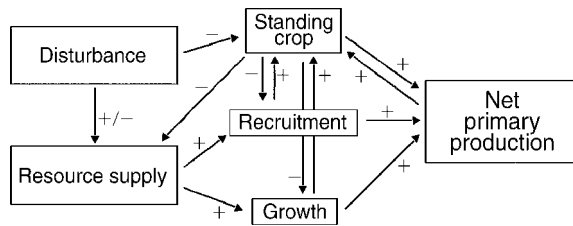


FIG. 8. Conceptual model of the factors influencing net primary production.

NPP, which we attribute to the relatively low variability observed in growth rate relative to that observed for FSC and recruitment.

The degree to which interannual variability in NPP of a system arises from disturbance-driven fluctuations in standing crop (the upper portion of Fig. 8) vs. resource-driven fluctuations in growth (the lower portion of Fig. 8) depends on the vital rates of its primary producers, environmental conditions that influence rates of disturbance and the availability of resources, and the length of time that the system is studied. The tendency to date has been to focus on resource-driven fluctuations in growth, perhaps because they are more amenable to study over the short term. However, the failure to account for disturbance-driven fluctuations in standing crop can lead to overestimates of the mean and underestimates of the variance in NPP, particularly in systems consisting of relatively long-lived or slow-growing perennials (Li et al. 2003). Systems such as giant kelp forests, which are characterized by frequent disturbance followed by rapid recovery via high rates of recruitment and growth, have the potential to provide considerable insight into the multitude of ways that biotic and abiotic factors interact with the standing crop and vital rates of primary producers to influence net primary production.

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