

## Improved estimates of net primary production, growth, and standing crop of *Macrocystis pyrifera* in Southern California

ANDREW RASSWEILER,<sup>1,3</sup> DANIEL C. REED,<sup>2</sup> SHANNON L. HARRER,<sup>2</sup> AND J. CLINT NELSON<sup>2</sup>

<sup>1</sup>*Department of Biological Science, Florida State University, Tallahassee, Florida 32306 USA*

<sup>2</sup>*Marine Science Institute, University of California, Santa Barbara, California 93106 USA*

**Abstract.** The giant kelp *Macrocystis pyrifera* forms subtidal forests on shallow reefs in temperate regions of the world. It is one of the fastest-growing multicellular autotrophs on Earth and its high productivity supports diverse marine food webs. In 2008, we published a method for estimating biomass and net primary production (NPP) of giant kelp along with five years of data, to provide a more integrated measure of NPP than those yielded by previous methods. Our method combines monthly field measurements of standing crop and loss rates with a model of kelp biomass dynamics to estimate instantaneous mass-specific growth rates and NPP for each season of each year. We have since improved our approach to account for several previously unresolved sources of biomass loss. These improvements have led to a near doubling of our prior estimates of growth and NPP. At our site with the most persistent stand of giant kelp, NPP averages  $\sim 5.2$  kg dry mass·m<sup>-2</sup>·yr<sup>-1</sup> and results from the rapid growth ( $\sim 3.5\%$  per d) of a relatively small standing biomass ( $\sim 0.4$  kg dry mass/m<sup>2</sup> on average) that turns over  $\sim 12$  times annually. Here we provide revised estimates of seasonal biomass, growth, and NPP for the five years covered by our previous publication (2002–2006), along with more than a decade of additional data (2007–2017). We also present updated relationships for predicting giant kelp biomass and NPP from much more easily obtained measurements of frond density. These data can be used to understand the mechanisms that drive variation in giant kelp NPP at a wide range of temporal scales. No copyright or proprietary restrictions are associated with the use of this data set other than citation of this Data Paper.

**Key words:** *giant kelp; growth rate; Macrocystis pyrifera; net primary production; marine algae; standing crop.*

The complete data set is available as Supporting Information at <https://onlinelibrary.wiley.com/doi/10.1002/ecy.2440/supinfo>

IMPROVED ESTIMATES OF NET PRIMARY PRODUCTION, GROWTH AND STANDING CROP OF  
*MACROSYSTIS PRYIFERA* IN SOUTHERN CALIFORNIA

ANDREW RASSWEILER, DANIEL C. REED, SHANNON L. HARRER, AND J. CLINT NELSON

*ECOLOGY*. DATA PAPER. 2018

INTRODUCTION

Patterns and causes of spatial and temporal variation in net primary production (NPP) have been extensively documented for plants in a wide range of terrestrial habitats (Leith and Whittaker 1975, Webb *et al* 1983, Knapp and Smith 2001) and for phytoplankton in many aquatic systems (Goldman *et al* 1989, Dodson *et al* 2000, Kudela and Dugdale 2000, Yunev *et al* 2007). By comparison, there are relatively few data sets of spatial and temporal patterns in NPP by marine macroalgae, whose assemblages are believed to be among the most productive systems in the world (Mann 1973). The bulk of information on NPP for marine macroalgae has come from short-term studies done over small spatial scales using a wide variety of methods that frequently measure different attributes (e.g., dissolved oxygen production, carbon assimilation, growth, standing biomass; reviewed in Tait and Schiel 2011, Foster *et al.* 2013, Schiel and Foster 2015). Consequently, there is a limited understanding of patterns and sources of variation in NPP of this important group of primary producers.

Giant kelp, *Macrocystis pyrifera*, is the world's largest marine alga. Aggregations form dense underwater forests that extend throughout the water column on shallow rocky reefs in temperate seas around the world (Graham *et al* 2007). Individuals vary in size, and may consist of as few as one or as many as several hundred fronds. Fronds can exceed 25 m in length and grow as much as 0.5 m d<sup>-1</sup>, making giant kelp one of the fastest growing multicellular autotrophs on Earth (Clendenning 1971). These characteristics present logistical challenges for measuring giant kelp NPP; the plants' large size mean that they cannot be enclosed without substantial disruption and their rapid growth mean that they must be sampled many times per year. Furthermore, its rapid turnover rates (Rodriguez *et al.* 2013), coupled with high loss rates due to episodic disturbance necessitate frequent sampling. Large waves and grazing by dense aggregations of sea urchins tend to be the strongest forms of disturbance leading to massive kelp loss (Dayton 1985, Reed *et al.* 2011, Bell 2015), but other grazers (fishes, gastropods and small crustaceans) and adverse growing conditions caused by low nutrients, low salinity or high temperatures can also lead to reductions in the standing biomass of giant kelp (reviewed in Vasquez and Buschmann 1997, Buschmann *et al.* 2004, Graham *et al.* 2007, Schiel and Foster 2015). Numerous estimates of primary production by giant kelp have come from relatively short-term studies (hours to 18 months) using a multitude of techniques (e.g., O<sub>2</sub> evolution, C<sub>14</sub> fixation, harvest

methods, allometric measurements; reviewed in Coon 1982) or from physiological models (Jackson 1987). The result is a variety of measurements that are difficult to compare and are inadequate for evaluating inter-annual patterns across sites.

In the early 2000's, as part of the Santa Barbara Coastal Long Term Ecological Research program (SBC LTER) we developed a method for estimating reef-scale biomass and net primary production for giant kelp over timescales from seasons up through decades. Our method involves monthly field measurements of standing crop and loss rates that we combine in a simple model of kelp biomass dynamics to estimate instantaneous mass-specific growth rates and NPP for each season of each year. Our approach follows that commonly used in terrestrial studies, calculating NPP by measuring accumulation and loss of biomass, and solving for the implied production and growth rates. In 2008 we published a detailed description of our methods along with five years of data collected monthly at three kelp forests (Rassweiler *et al.* 2008), documenting strong seasonal cycles in growth and standing crop as well as substantial differences in *M. pyrifera* NPP among sites and years.

Over the past decade we have continued our monthly measurements and have added both models and direct measurements of several processes that had not been accounted for in our previous approach. Chief among these processes were additional loss terms that account for the biomass lost to blade senescence and the exudation of dissolved matter. The inclusion of these processes has led to a near doubling of our prior estimates of giant kelp NPP (revised = 1.95 \* previous,  $r^2 = 0.85$ ,  $n = 53$  seasonal estimates of NPP collected at three sites during the period 2002-2006). Here we present a new data set with revised estimates of biomass and NPP for the five years covered by our previous paper (2002-2006; Rassweiler *et al.* 2008) along with an additional eleven years (2007-2017) of previously unpublished data. The metadata contain updated methods describing the measurements made and models used to calculate standing crop, mass-specific growth and NPP. The collection of these data is ongoing by the SBC LTER and we anticipate posting updated versions on an annual basis (Rassweiler *et al.* 2018).

Because this work represents some of the most intensive measurements of giant kelp biomass and primary production to date, the relationships generated by these data have been used to calibrate and interpret a range of other data including remote sensing estimates of kelp biomass (Cavanaugh *et al.* 2010, 2011, 2013, Bell *et al.* 2015a, Castorani 2015, 2017, Young *et al.* 2016). In particular, the relationship between frond density (which is commonly measured in the field) and both standing crop and NPP (which are very rarely measured) has been applied in a number of studies (Reed *et al.* 2011, 2015b, 2016, Miller 2011). Here we present a table of those updated relationships (*Relationships between frond density, standing crop and net primary production*) that are intended to replace and supersede those based on Rassweiler *et al.* (2008) which were reported in Reed *et al.* (2009). We acknowledge, however, that the relationships we document here are based on intensive measurements of plants at three sites spread along

~20 km of coastline. While we found plant morphology was quite consistent at our sites, the species shows great variation globally (Demes et al 2009), and caution should be used when applying these relationships in new geographies.

Our measurements reveal that relationships among dry mass, carbon mass and nitrogen mass of giant kelp vary through time, which complicates the conversion of NPP from one measure of mass to another. For instance, the percentage of the dry mass of *M. pyrifera* that is carbon may vary from 20 to 40%, in part because of high variability in the mineral content of the tissue. Our data suggest that studies that ignore temporal variation in the relationships between different units of mass may not capture the true variability in NPP by *M. pyrifera*. Therefore, we present our data in terms of dry mass, carbon mass and nitrogen mass (using conversion factors derived for each sampling date) to facilitate comparisons with previous studies of *M. pyrifera* and measurements of NPP in other ecosystems.

## CLASS I. DATA SET DESCRIPTORS

### A. Data set identity

- 1) *M. pyrifera* net primary production and growth.
- 2) *M. pyrifera* standing crop, plant density and loss rates.
- 3) Census of fronds on marked plants.
- 4) *M. pyrifera* blade water, carbon, and nitrogen content.
- 5) Regression parameters to estimate biomass and production from frond density.

### B. Data set identification code link to data file

### C. Data set description

**Principal investigator:** Daniel C. Reed, Marine Science Institute, University of California, Santa Barbara, CA 93106.

**Abstract:** The giant kelp *Macrocystis pyrifera* forms subtidal forests on shallow reefs in temperate regions of the world. It is one of the fastest-growing multicellular autotrophs on Earth and its high productivity supports diverse marine food webs. In 2008, we published a method for estimating biomass and net primary production (NPP) of giant kelp along with five years of data, to provide a more integrated measure of NPP than those yielded by previous methods. Our method combines monthly field measurements of standing crop and loss rates with a model of kelp biomass dynamics to estimate instantaneous mass-specific growth rates and NPP for each season of each year. We have since improved our approach to account for several previously unresolved sources of biomass loss. These improvements have led to a near doubling of our prior estimates of growth and NPP. At our site with the most persistent stand of giant kelp, NPP averages ~5.2 kg dry mass m<sup>-2</sup> y<sup>-1</sup> and results from the rapid growth (~3.5% per day) of a relatively

small standing biomass ( $\sim 0.4$  kg dry mass  $m^{-2}$  on average) that turns over  $\sim 12$  times annually. Here we provide revised estimates of seasonal biomass, growth and NPP for the five years covered by our previous publication (2002-2006), along with more than a decade of additional data (2007-2017). We also present updated relationships for predicting giant kelp biomass and NPP from much more easily obtained measurements of frond density. These data can be used to understand the mechanisms that drive variation in giant kelp NPP at a wide range of temporal scales. No copyright or proprietary restrictions are associated with the use of this data set other than citation of this Data Paper.

**Key words:** *giant kelp*, *growth rate*, *Macrocystis pyrifera*, *net primary production*, *marine algae*, *standing crop*

## CLASS II. RESEARCH ORIGIN DESCRIPTORS

### A. Overall project description

**Identity:** Net primary production, growth and standing crop of the giant kelp, *Macrocystis pyrifera* in the Santa Barbara Channel.

**Originator:** Daniel C. Reed, Marine Science Institute, University of California, Santa Barbara, CA 93106.

**Period of Study:** 2002-2017 (ongoing).

**Objectives:** To quantify the magnitude and variability in net primary production, growth rate and standing crop of *Macrocystis pyrifera* at relevant spatial and temporal scales.

**Abstract:** Same as above.

**Sources of funding:** The collection of all data was done by the Santa Barbara Coastal Long Term Ecological Research program which is funded by the National Science Foundation (awards OCE-9982105, OCE-0620276, OCE-1232779).

### B. Specific subproject description

**Species description:** The giant kelp, *Macrocystis pyrifera*, is a brown alga in the order Laminariales. It forms dense forests on shallow rocky reefs along the Pacific coasts of North and South America, and along the coasts of New Zealand, southern Australia, South Africa, and the subantarctic islands (Wormersley 1954). *M. pyrifera* is the world's largest alga. An adult sporophyte (hereafter referred to as a plant as per Bolton 2016) consists of a bundle of fronds (often totaling more than 100) anchored by a common

holdfast. Each frond consists of a rope-like stipe and many regularly spaced lanceolate blades, each buoyed by a small gas bladder. New fronds originate in the basal foliage just above the holdfast and grow vertically in the water column. Upon reaching the sea surface, the fronds (sometimes exceeding 30 m in length) spread out to form a dense canopy.

*Macrocystis pyrifera* exhibits relatively consistent growth form at shallow reefs along the Santa Barbara coast. But globally it has shown remarkable morphological variation. Recent syntheses have concluded that *Macrocystis* around the world are all the same species, despite wide variation in blade morphology, holdfast architecture and overall size (Demes et al 2009). Because our data represent intensive sampling at three sites from a 20 km stretch of coast, attempts to extrapolate beyond this geography must be done with caution and consideration of the wide variation in this species.

**Site description:** Data are collected at three kelp forests in the Santa Barbara Channel, California, USA: Arroyo Quemado (34° 28.127' N, 120° 07.285' W), Arroyo Burro (34° 24.007' N, 119° 44.663' W), and Mohawk (34° 23.660' N, 119° 43.800' W). At these sites, *M. pyrifera* grows on rocky substrates at depths of 4 to 15 m within 700 m of shore.

**Site type:** Temperate reef in the shallow subtidal zone.

**Geography:** Santa Barbara, CA; southwestern coast of USA, northeastern Pacific Ocean.

**Habitat:** Rocky reefs on gently sloping shelf in the shallow subtidal zone. Reefs are seasonally exposed to moderate swells, sand movement and freshwater runoff from land.

**Site history:** The mainland coast of the Santa Barbara Channel has long been subjected to commercial and recreational fishing. Red sea urchins and spiny lobster are the major commercial fisheries in giant kelp forests in this region at present. *M. pyrifera* has been commercially harvested in the Santa Barbara Channel since the early 1900s. Harvesting consists of trimming the entire surface canopy down to a depth of ~1.3 m. No commercial harvesting of giant kelp from the study sites occurred during the period that these data were collected.

**Climate:** The Santa Barbara region has a Mediterranean climate characterized by relatively calm and dry conditions in summer and autumn, prevailing northwesterly winds in the spring and episodic rain storms in the winter. This environmental setting creates strong seasonality in the supply of nutrients from upwelling, terrestrial runoff, internal waves, and in physical disturbance from storm-generated surface waves.

## Research approach/methods:

### *Calculating net primary production*

We investigate spatial and temporal variation in NPP of *M. pyrifera* by combining field measurements with a simple model of kelp dynamics. We calculate NPP by *M. pyrifera* as the total amount of biomass produced during the period between each sampling date (approximately one month) that explains the observed change in the foliar standing crop (FSC = total mass excluding the holdfast and sporophylls) given the loss rate of biomass during the period. Our model is based on the assumption that within a sampling period kelp grows at a constant mass-specific rate ( $g$ ), such that new biomass is produced in proportion to existing FSC ( $S$ ). The model also assumes that biomass is lost at a constant mass specific rate ( $l$ ), which is equivalent to biomass having a constant probability of loss during the period. Thus, the instantaneous rate of change in FSC is equivalent to the FSC multiplied by the difference between the mass-specific growth rate and loss rate.

Equation 1: 
$$\frac{dS}{dt} = S(g - l)$$

We apply this model to each sampling interval of the study, combining it with field measurements of FSC and independent estimates of loss rates to calculate the growth rate and NPP of *M. pyrifera*. At each site, we sample *M. pyrifera* plants monthly in a permanent plot between 200 m<sup>2</sup> and 480 m<sup>2</sup> in area (see **Sample design/field methods**). We use allometric equations and conversion factors generated from extensive measurements of plants collected from our study sites to convert *in situ* length measurements of each plant into estimates of FSC in terms of dry mass, carbon mass and nitrogen mass per unit area of ocean bottom (see **Sample design/field methods**). For each monthly sampling period we also independently measure the biomass loss rate ( $l$ ) as the sum of the losses of: (1) whole plants, (2) whole fronds from surviving plants, (3) partial fronds from surviving plants due to boat propeller damage, (4) senescing blade material from surviving fronds, and (5) dissolved material released from blades and stipes on surviving plants.

Our field measurements of FSC and loss rates enable us to calculate the average mass specific growth rate of *M. pyrifera* on monthly time scales, but our estimates are much more reliable on seasonal and annual scales because a measurement error (for example an over-count of fronds in one month) tends to produce an overestimate of NPP in one month and an underestimate in the next, which offset when the measurements are aggregated on multi-month timescales. The model we use to describe kelp growth within the sampling period is based on explicit assumptions about how growth occurs. We tested alternative forms of the growth model (e.g., linear, exponential, logistic), and found that our calculations of NPP and growth rate are robust to the choice of growth

model (see *Testing the robustness of assumptions of kelp growth*). All results presented here were calculated using the exponential model, because it makes the simplest assumptions about growth and loss (both occur as a constant proportion of FSC):

To determine NPP for the period between any two sampling dates, we use our measurements of FSC and loss rate to calculate the average mass specific growth rate of *M. pyrifera* during the sampling interval ( $T$  days) that explains the change in FSC:

Equation 2: 
$$g = \frac{1}{T} \ln\left(\frac{S_t}{S_0}\right) + l$$

Returning to Eq.1, we see that the instantaneous rate of NPP at time ( $t$ ) is the product of the growth rate ( $g$ ) and the foliar standing crop ( $S_t$ ), so we calculate the total production over a sampling interval from 0 to  $T$ , as the integral of this product:

Equation 3: 
$$NPP = \int_0^T g S_t dt$$

We assume that  $g$  is constant over the sampling interval and account for the fact that biomass is changing by expressing  $S_t$  at any time  $t$  as a function of FSC at the beginning of the sampling interval ( $S_0$ ):  $S_t = S_0 e^{(g-l)t}$ . Mean daily NPP is obtained by integrating instantaneous NPP over each sampling interval and dividing by  $T$ :

Equation 4: 
$$NPP = \frac{\int_0^T g S_0 e^{(g-l)t} dt}{T}$$

Solving the integral gives:

Equation 5: 
$$NPP = \frac{g S_0}{g-l} (e^{(g-l)T} - 1)$$

We have used this approach to calculate NPP and specific growth rate seasonally at the three sites since spring 2002. Mean daily NPP and growth rate of *M. pyrifera* for each season are calculated as the average NPP and growth rate for all days in the season (seasons are: winter, spring, summer, and autumn as defined by the winter solstice, spring equinox, summer solstice, and autumnal equinox).



### *Testing the robustness of assumptions of kelp growth*

Our calculations of NPP are based on the assumption that the rate of production of kelp biomass at each site is proportional to FSC (i.e. production at any time is the growth rate multiplied by the standing stock). This assumption implies an exponential growth form, from which equations 1 through 5 are derived. To explore whether this assumption about kelp growth influenced our results, we performed all calculations using an alternative set of equations derived from the assumption that growth is not proportional to FSC (i.e. the rate of production is constant over the period, implying linear growth of biomass). NPP and mass specific growth rate are almost identical when calculated using the two growth forms (exponential versus linear;  $r^2 > 0.99$ , slope = 1.0 for both growth and NPP).

We also evaluated the robustness of our calculations using hypothetical datasets produced by an individual-based mathematical model of a kelp forest. We calculated NPP for each hypothetical dataset using the approach outline above (Eq. 1 through 5) and compared the model output to the true NPP of the simulated forest. This approach allowed us to determine if equations 1 through 5, which assume exponential growth, break down when kelp does not grow exponentially. In particular, we explored the accuracy of our calculations when kelp grows logistically, as has been assumed in other studies (reviewed in North 1994). Regardless of whether our simulated kelp forest grew linearly, exponentially, or logistically, our calculated values of NPP (using Eq. 1 through 5) matched the true NPP (i.e., the amount of production that occurred during the individual based simulation;  $r^2 > 0.90$ ). Thus, our results are robust to the form of the growth model used.

### *Special cases – when there is no biomass*

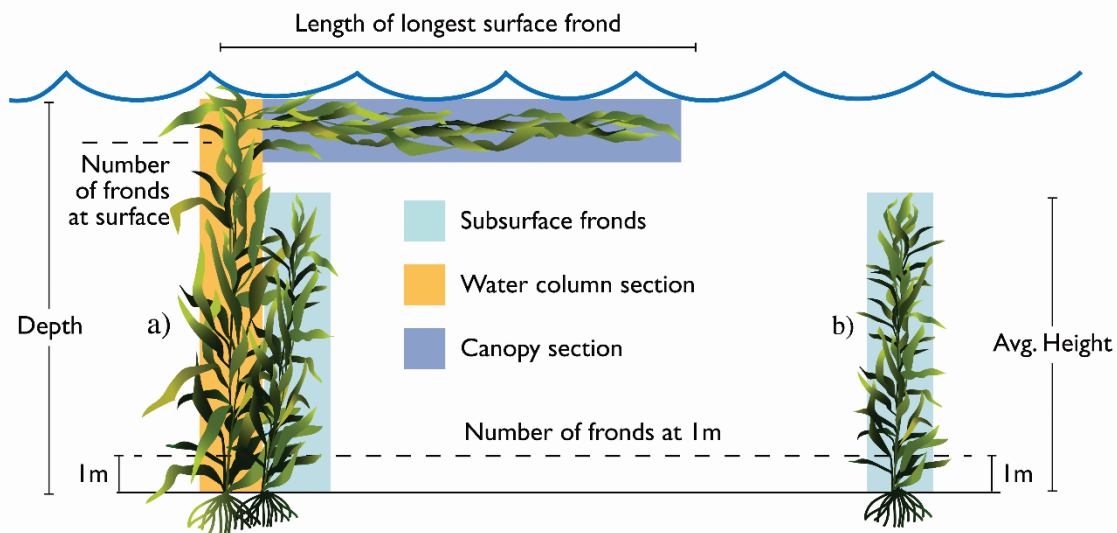
The three sites were chosen because they historically supported kelp forests. Indeed at least some giant kelp was present in over 93% of our 559 sampling events (between 2002 and 2017). However, occasionally giant kelp disappears entirely from our sampled plots. This presents an obstacle for a method of estimating growth and NPP that is based on an exponential growth model. For this reason, we apply special rules for the following categories of events: 1) If FSC is present at the beginning of a period but not at the end of the period we assign NPP a value of zero ( $n = 5$  events). 2) Similarly, we assign NPP to zero if there is no FSC at either the beginning or the end of a period ( $n = 28$  events). 3) If FSC is absent at the beginning of a period and present at the end of the period we calculate NPP based on a simple linear model. In these cases, we divide the amount of FSC present on the latter sampling date by the number of days elapsed since the previous sampling date to yield mass accumulation rate on a per day basis ( $n = 5$  events). In all three cases the mass specific growth rate is undefined and is set to missing in the dataset. If loss rates are known, for example if tagged plants are still being monitored adjacent to, but outside of our sampling plots, then those loss rates are reported

for these time periods. Note that these special cases represent a small number of events (38 out of 522) and a vanishingly small amount of potential NPP given the small amount of giant kelp present.

### Sampling design/field methods:

#### *Measuring standing crop*

On each sampling date (approximately once a month) we measure *M. pyrifera* FSC in permanent plots at the three sites using SCUBA. Plots are either 200 m<sup>2</sup> (Arroyo Quemado and Mohawk; made up of an array of ten 20 m x 1 m transects) or 480 m<sup>2</sup> (Arroyo Burro; made up of three transects: 60 m x 2 m, 40 m x 2 m and 20 m x 2 m, respectively). We calculate FSC based on measurements of all *M. pyrifera* plants in the plot with at least 1 frond > 1 m in length. We characterize each plant using three distinct plant sections (Figure 1). The “sub-surface” section consists of fronds that do not reach the surface, typically recently initiated fronds with small blades (Figure 1a, fronds shaded in light blue; Figure 1b). Fronds that do reach the surface are treated as having two sections: the “water column” section is the portion of these fronds that is underwater, stretching from the holdfast to the sea surface (Figure 1a, frond parts shaded in orange). This section usually has mature and senescent blades sparsely distributed along the stipe. The “canopy” section is the portion of these fronds that floats at the sea surface, typically consisting of mature blades spaced closely along the stipe (Figure 1a, frond parts shaded in dark blue).



**Figure 1: Diagram illustrating the measurements taken on each kelp plant. The different colored shading indicates which fronds (and frond portions) are included in each plant “section”.**

For each plant within the sampling area we count the number of fronds 1 m above the holdfast ( $N_{1m}$ ), the number of fronds at the surface ( $N_{surface}$ ), measure the water depth

in meters at the top of the holdfast ( $D$ , equivalent to the length of the water column section of the fronds reaching the surface) and measure the length of the canopy portion of the longest frond in meters ( $MAX$ ). We use these data to calculate the length of each plant section, according to the following equations:

Equation 6a:            Length of subsurface section =  $(N_{1m} - N_{surface}) (1 + \frac{1}{2} [D - 1])$

Equation 6b:            Length of water column section =  $(N_{surface})(D)$

Equation 6c:            Length of canopy section =  $(N_{surface})(\frac{1}{2} MAX)$

The accuracy of equations 6a, b and c in estimating the length of each plant section in the field was tested by comparing estimates of length obtained using equations 6a, b and c to actual lengths. This was done by collecting a subset of plants measured in the field using the methods described above and transporting them to the laboratory where we measured the maximum frond length of each plant and the total length of the three frond sections relative to the depth where the plant was collected. Total frond length estimated using equations 6a, b and c explained 99% of the variation in the cumulative length of all fronds above the holdfast, when all fronds were measured individually ( $N = 55$  plants,  $r^2 = 0.99$ , slope = 1.02). Similarly, we estimated total frond length of 147 plants in the field using equations 6a, b and c and found that those estimates agreed closely with more detailed field measurements of those plants, in which the length of each frond was measured to the nearest meter *in situ* ( $N = 147$ ,  $r^2 = 0.99$ , slope = 0.99).

While plants reaching the surface account for more than 92% of kelp biomass in our data, young plants may have one or more fronds longer than 1 m, but no fronds reaching the surface (Figure 1b). For these plants, we measure  $N_{1m}$  (which is usually  $< 4$  m) and estimate the average length of fronds on the plant in meters ( $AVG$ ). The cumulative length of these fronds is calculated as  $N_{1m} * AVG$ , and these fronds are treated the same as water column fronds when their mass and elemental composition are calculated (see *Conversion from length to weight of dry mass, carbon, and nitrogen*).

#### *Treatment of missing measurements*

In approximately 1% of plants, the fronds become tangled with those of neighboring plants and prevent divers from obtaining reliable measurements of  $N_{surface}$  and  $MAX$ . In these cases, the length of each section of the plant is estimated using only the number of fronds 1 m above the holdfast. The estimate is based on the relationship between fronds at 1 m and the length of each section for all plants successfully sampled at the given site within a three month window centered on the month in which missing data occurred (a moving average is used to smooth out month-to-month variation in the estimates). Using relationships matched by month accounts for systematic seasonal

variation in length per frond at 1 m above the holdfast, while using relationships matched by site accounts for variation from site to site including variation in depth. These relationships were estimated using linear regression with a Y intercept fixed at zero (although a simple calculation of average length per frond at 1 meter yields identical relationships). The regressions excluded cut and partial plants (see *Plants at the edge of the sampling plots* and *Loss of partial fronds due to propeller damage*). In rare cases where depth was not recorded (0.3% of observations) depth was estimated using the average depth of all other plants sampled at that site.

#### *Plants at the edge of the sampling plots*

A small proportion of plants (6.3%) occurred on the edge of the transect such that only a portion of them was present in the sampled area. Before 2005, a plant was sampled if more than 50% of the plant was found within the transect. This approach was unbiased with respect to average plant density and biomass, but created high variance in biomass from month to month, especially when a large plant was located near the edge of the transect and was sampled in some months and not in others depending on small deviations in how the transect tape was laid out. We changed the sampling protocol in 2005 so that when a plant was located partially within the transect, only the fronds occurring within that transect are sampled (and those fronds are noted as representing a “partial plant”). Counting fronds at the surface and estimating frond lengths of these “partial plants” is often not possible, and the length of each section of these plants is estimated from fronds at 1 m as described above in *Treatment of missing measurements*. In cases where divers are able to obtain all measurements without disturbing the plants, the normal allometric relationships are applied.

#### *Conversion from length to weight of dry mass, carbon, and nitrogen*

Standing crop is estimated by converting the total length (in meters) of each plant into the total wet mass (in kilograms). The length to wet mass conversion is based on 55 plants collected from the three sites during monthly surveys in 2003. These plants were transported to the laboratory where we first separated the fronds from each plant into the three sections (canopy, water column, and subsurface) and measured their length and weight. We then used linear regression to determine the relationship between weight and length of the fronds from each section for each plant. We apply the mean slope of the regression lines obtained for the 55 plants to the field data to convert the total length of *M. pyrifera* to FSC. The ratio of frond wet mass (kg) to frond length (m) was 0.117 for the subsurface section, 0.105 for the water column section, and 0.259 for the canopy section.

Ratios used to convert wet mass to dry mass, dry mass to carbon mass, and dry mass to nitrogen mass are derived from *M. pyrifera* tissue samples obtained from mature blades collected at each site on each sampling date. Blades are collected from 15

different plants, approximately 2 m from the growing tip of a frond reaching the surface, or from the longest fronds available at the site (in cases when no canopy is present). Blades are transported to the laboratory in opaque insulated containers where they are cleaned of epiphytes, rinsed in a dilute acid solution and patted dry with a paper towel. A 5 cm<sup>2</sup> disk is excised from the central portion of each blade and weighed (using a Mettler AE 200 Analytical balance), dried in an oven for 2 to 5 days at 60°C, and reweighed. The samples are ground to a powder using a mortar and pestle and the powdered samples from all 15 blades are combined to form a composite sample for each site on each sampling date. Because conversion from wet to dry mass was relatively consistent both across space and time, a single average ratio (0.094) calculated across all samples collected through 2016 (n = 1055) is used to convert wet mass to dry mass. The same ratio was used to convert wet stipe mass to dry mass, as dry:wet weight ratios were statistically indistinguishable for portions of blades (N=112) and stipes (N=114) sampled over the first 12 months of the project.

The carbon and nitrogen content of each composite sample is measured using an elemental analyzer (Carlo-Erba Flash EA 1112 series, Thermo-Finnigan Italia, Milano, Italy). The percent carbon and nitrogen of the composite sample from each sampling event (site\*year\*month) is used to convert dry mass of FSC on that sampling date to mass of carbon and nitrogen. In the event that kelp is present but kelp tissue data are not available (2 observations), we use an average value specific for that site and month calculated from our time series through 2016. Following the same logic by which missing plant measurements are estimated, we use the mean percent nitrogen and carbon for the given site in the given month averaged over all years. This approach accounts for systematic seasonal variation and inherent site differences that may contribute to variability in tissue carbon and nitrogen content.

Because we sample blades from the canopy only, we developed a conversion factor for each element that allows us to calculate the carbon and nitrogen composition of FSC as a whole. The conversion factors are based on tissue samples taken from each section of the 55 plants referenced above. The carbon and nitrogen content of subsurface, water column and canopy blades of these 55 plants were similar (differences are less than 5% of the mean), so we apply the canopy blade values to all blade mass. However, carbon mass was 12% lower and nitrogen mass was 44% lower in stipes than in blades. FSC is converted to units of carbon ( $C_{mass}$ ) adjusting for the ratio of blades to stipes as follows:

$$\text{Equation 7: } C_{mass} = SC_{composite} \frac{C_{blades} m_{blades} + C_{stipe} m_{stipe}}{C_{blades}}$$

where  $S$  is FSC,  $C_{composite}$  is the percent carbon in the composite sample,  $C_{blades}$  and  $C_{stipe}$  are average percent carbon in the blades and stipes of the 55 plants, and  $m_{blades}$  and  $m_{stipe}$  are the fraction of the mass of the 55 plants consisting of blades and stipes, respectively. Substituting nitrogen for carbon in Equation 7 yields an estimate of FSC in units of nitrogen.

We found that length to weight relationships and wet weight to dry weight conversion factors were consistent across space and time and so we apply the same factors to all three of our sites. However, considering the wide range of morphological variation found in this species around the globe, we caution that these relationships should be validated before applying our model to populations in other regions. We found carbon and nitrogen content to be relatively similar on blades from different sections of an individual plant, but this may not hold in other geographic or environmental contexts. Moreover, because carbon and nitrogen content varied substantially within our sites and across time, they are likely to vary across larger geographic and temporal scales.

#### *Measuring loss rates*

Our calculations of NPP incorporate five sources of biomass lost during the interval between sampling periods: (1) the loss of entire plants ( $p$ ), (2) the loss of fronds from surviving plants ( $f$ ), (3) the loss of partial fronds from surviving plants due to boat propeller damage ( $c$ ), (4) the loss of blades or parts of blades from surviving fronds due to senescence ( $b$ ), and (5) the loss of dissolved material released from blades and stipes on surviving plants due to exudation and senescence ( $d$ ). So total loss rate ( $l$ ), is the sum of the component loss rates ( $p$ ,  $f$ ,  $c$ ,  $b$  and  $d$ ). Methods for estimating each rate are described below.

FronD loss, blade deterioration, and dissolved losses occur throughout the year; with plants continuously losing biomass through these processes. Losses of whole plants are usually caused by water motion associated with large waves that rip plants off the bottom and are concentrated in winter months, while losses of partial fronds from propellers are similarly sporadic and mainly occur during the first few months of lobster season (chiefly October and November) when fishing boats are concentrated in the kelp forest. Our approach focuses on the average probability of loss, treating loss as a process that is distributed across the month in which it occurs.

#### *Loss of whole fronds and whole plants*

We use the change in the density of tagged fronds and tagged plants to calculate instantaneous per capita mortality rates (sensu Gurney and Nisbet 1998). Assuming that lost fronds and plants are of average size, these mortality rates are equivalent to mass-specific loss rates of FSC. We measure the loss of fronds on approximately 15 focal plants per site during each sampling interval. We count all fronds on each focal plant at the beginning of each sampling interval, and marked all counted fronds with zipties.

Prior to 2006, each frond was individually marked. Since then, the counted fronds have been collectively surrounded with a loose zip tie collar (as a bundle) to minimize contact between zip ties and the fronds. We rarely observed any frond mortality or damage associated with the zipties.

At the end of the sampling interval, we count the number of tagged fronds that remain from the previous sample. We also count the number of new fronds that grew to 1 m in size during the sampling interval and tag these fronds to prepare for the next sampling event. The loss rate of fronds from a single plant ( $f_k$ ) is estimated based on the number of fronds at the beginning ( $F_0$ ) and end ( $F_T$ ) of the sampling interval:

Equation 8: 
$$f_k = -\frac{1}{T} \ln\left(1 - \frac{F_T}{F_0}\right)$$

We average  $f_k$  among the 10 to 15 surviving focal plants to calculate a frond loss rate ( $f$ ) for each site during each period. Note that our decision to calculate a loss rate for each plant and then average across plants leads loss rates on small plants to have a higher weighting on a per-frond basis. But the alternative of summing all fronds and then calculating loss rate of the aggregated population of fronds could lead to loss rates on the largest plant to dominate the calculation.

The loss rate of plants ( $p$ ) is estimated similarly, using the same 15 plants that were tagged to estimate frond loss. Each plant is tagged with a unique ID fastened to its holdfast. We also map the location of each tagged plant so it can be easily re-identified if the tag is lost. In months where plants are lost, new plants are tagged to maintain a sample size of approximately 15 plants. We estimate the loss rate of plants ( $p$ ) from the number of tagged plants at the beginning ( $P_0$ ) and end ( $P_T$ ) of each monthly sampling interval:

Equation 9: 
$$p = -\frac{1}{T} \ln\left(1 - \frac{P_T}{P_0}\right)$$

Equations 8 and 9 are not defined for cases in which all tagged fronds or all tagged plants are lost. In these cases we perform the calculations as though  $\frac{1}{2}$  of a frond or  $\frac{1}{2}$  of a plant remained at the end of the sampling. If no tagged plants or fronds were present at the beginning of the sampling period, loss rates from these processes are not estimated for that period, and NPP is set to undefined unless there is no biomass present at the end of the sampling period in which case it is set to zero as described in *Special cases – when there is no biomass* section above.

### *Loss of partial fronds due to propeller damage*

The estimates of frond loss rate described above are based on counts of fronds at 1 m above the holdfast, and do not account for cases where part of the frond breaks off above that height while the bottom of the frond remains. Although this happens occasionally, it accounts for a small proportion of fronds under most conditions; fronds that break are typically undergoing senescence and the whole frond is lost quite rapidly. Across the 2,123 fronds counted on the 55 plants (see *Conversion from length to weight of dry mass, carbon, and nitrogen*), fewer than 7 percent were observed to be senescent and longer than 1 m, representing 2.9 percent of the biomass. A notable exception to this pattern occurs when the propellers of boats driving through the kelp forest cut fronds near the surface. Plants cut by propellers are readily recognized by divers when sampling because they appear as healthy plants with a large fraction of fronds that have been cleanly severed near the surface. Although cut plants make up a small proportion in the dataset as a whole, they are relatively common in October and November at the beginning of lobster season when commercial fishing boats actively set and retrieve lobster traps in kelp forests. The occurrence of cut plants (defined as plants for which more than 50% of the fronds have been sliced off near the surface) in October and November can be as high as 47.2%, and averaged 7.2% during these months across all sites and years. Thus there is a potential to substantially understate NPP in these months if losses of biomass arising from fronds being cut by boat propellers are not accounted for.

To account for this form of loss, divers record plants with > 50% of fronds abruptly severed within 1 meter of the surface as being “cut”. By comparing the average size of cut plants to that of uncut plants with a similar number of fronds at 1 m from that site on the same date we estimate that on average a cut plant has 81% of the mass of a similar-sized uncut plant. Comparisons were made by grouping plants into 10-frond size classes based on the number of fronds at 1 m above the holdfast and comparing cut to uncut plants within each group. From this observation we assume that for each plant marked as cut, missing biomass equivalent to 19% of the observed biomass had been lost. When cut plants are observed, we sum cut biomass across the whole site and calculate a per day loss rate ( $c$ ), based on biomass at the beginning ( $S_0$ ) and end ( $S_T$ ) of the period, total biomass lost through propeller cuts ( $S_C$ ), and the number of days elapsed between sampling dates:

Equation 10: 
$$c = -\frac{1}{T} \ln\left(\frac{S_T}{S_0}\right) - \frac{1}{T} \ln\left(\frac{S_T + S_C}{S_0}\right)$$

### *Loss of mass due to blade senescence*

Blades often undergo senescence and breakage before the frond to which they are attached is lost. We estimated the rate of biomass lost to blade senescence using data



from a collaborative study in which we measured blade area in a cohort of tagged blades on a weekly basis that yielded size trajectories of 120 blades (Rodriguez *et al.* 2016). Using these data we developed a model simulating a population of blades of mixed ages, assuming blades grew and deteriorated according to those observed trajectories (Rassweiler *et al.* 2017). This model yielded daily deterioration rates for subsurface blades ( $b_{sub}$ ), water column blades ( $b_{wc}$ ), and canopy blades ( $b_{can}$ ). Constant losses due to deterioration can account for a substantial fraction of NPP, but our estimates are somewhat conservatively low (and thus potentially lead to underestimates of NPP) given that our analyses assume a loss rate of zero during blade growing phases when growth rates exceed losses. We estimate the daily loss rate of blades due to deterioration ( $b$ ) as the summation of the daily deterioration rate for subsurface ( $b_{sub}$ ), water column ( $b_{wc}$ ), and canopy blades ( $b_{can}$ ) multiplied by the average fraction of biomass ( $fracBld$ ) comprised of that tissue over the period:

$$\text{Equation 11: } b = b_{sub}fracBld_{sub} + b_{wc}fracBld_{wc} + b_{can}fracBld_{can}$$

#### *Loss of dissolved mass*

Our initial calculations of NPP (Rassweiler *et al.* 2008) did not include losses of dissolved organic matter (DOM) resulting from exudation and senescence. Recently, we quantified the release of DOM by giant kelp at our Mohawk study site and found that it was substantial and varied as a function of irradiance and tissue type (Reed *et al.* 2015a). Specifically, our results showed that blade mass released DOM at 2.5 times the rate of stipe mass, and both released DOM faster under high light conditions than in low light. To account for these losses, we combined our estimates of blade and stipe biomass with ongoing measurements of average daily surface and bottom irradiance collected since 2008 (Reed 2017). Based on Reed *et al.* (2015a), the mass specific dissolved loss rate of blade biomass ( $d_{blade}$ ) is:

$$\text{Equation 12: } d_{blade} = 4.90 \times 10^{-4} + 1.66 \times 10^{-5} \times PAR$$

Where  $PAR$  is the mean daily irradiance ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) averaged over a 24 hour cycle. Mass specific dissolved loss rates of stipe biomass were calculated based on the same equation, but discounted to 39% of the rates used for blades.

The daily irradiance used to calculate dissolved loss rates ( $PAR$ ) differed for mass in the canopy section (exposed to relatively direct sunlight) and in the water column and subsurface sections (for which irradiance is reduced both by shading from the canopy and attenuation in the water column). For biomass in the canopy section we based  $PAR$  on the mean daily irradiance, measured at the surface over the sampling period. For blade biomass in the subsurface and water column sections, we based  $PAR$  on the depth-

integrated irradiance calculated from measured mean daily irradiance at the surface and mean daily irradiance measured at 7 m depth, and assuming exponential attenuation of light with depth. This calculation assumes that attenuation was consistent with depth below the canopy section. Of course, the details of light attenuation likely vary from site to site and moment to moment due to environmental conditions such as water quality, current and canopy density. Daily irradiance prior to 2008 was not measured directly, so we estimate it using the average site-specific attenuation value for each day of the year based on surface and bottom irradiance data collected from 2008 – 2016. Mean daily mass specific dissolved loss rate for FSC as a whole ( $d$ ) is calculated as a weighted average of the loss rates for blade and stipe mass from each plant section, where weighting factors are based on the fraction of the total FSC made up by each tissue type, averaged across the period.

### **Quantification of uncertainty/error estimation:**

Our estimates of NPP, FSC, and loss rates are each based on a lengthy set of calculations described above, and rely on a suite of periodically measured variables, along with some fixed parameters (such as conversion factors), each of which is estimated from a focused, shorter term set of measurements. Each of these measurements and parameters are imperfectly known, and the uncertainty/error in the measurements and parameters results in uncertainty around our estimates of each variable. Because an error in a measurement or an estimated parameter can propagate through the calculations in complex ways, we use Monte Carlo methods to propagate the uncertainty in these measurements (Harmon *et al.* 2007).

The general approach of the Monte Carlo method is to repeat the process of calculating NPP 1000 times, in which each replicate iteration represents an alternative possible dataset and set of parameters. Because the data and parameters used in each iteration are slightly different, each iteration yields a different calculated NPP value. We use the standard deviation of these values, which are distributed normally, as the standard error in our estimate of NPP. This Monte Carlo approach also yields distribution in the estimates of FSC, growth rate, loss rates, and other variables, which are used to calculate the associated standard errors around our best estimates.

Each replicate iteration is based on the actual measurements and on our best parameter estimates, but within each iteration each data point is drawn from a distribution centered on the actual measurement. The shape and variability in that distribution is based on independent measurements of observer errors in some cases, or is estimated based on variation within the dataset. The errors we include in our calculations are summarized in Table 1.

The “spatio-temporal scale” column in Table 1 indicates the spatial and temporal scale at which random values are chosen within each Monte Carlo iteration. For example, errors in the “Count of plants” are applied on the “transect\*period” scale, which means in each iteration we draw a different error value to modify the plant count observed on each transect in each sampling period (typically a month). Within any given period one transect might be assigned a positive error while another might get a negative error. By contrast, the error in the “Ratio of blade mass to stipe mass” is assigned at the “iteration” scale, so a single error value is applied to each iteration of the Monte Carlo (the same error is applied to all sites in all periods for the run).

Table 1. A summary of the errors included in the uncertainty analysis

<b>Variable to which error is applied</b>	<b>Spatio-temporal scale</b>	<b>Source of error estimate</b>
Count of plants	transect * period	Repeated sampling of the same transect by different investigators
Count of fronds	transect * period	Repeated sampling of the same transect by different investigators (0.63 correlation with error in “count of plants”)
estimate of total length of all fronds	transect * period	Repeated sampling of the same transect by different investigators (0.83 correlation with error in “count of fronds”)
Parameters converting length to weight	transect * period * plant	Regression errors from measurements of plant sections sampled in the laboratory
Parameters converting wet mass to dry mass	replicate iteration	Regression error based on replicate samples of plant tissue that were weighed dried and reweighted
Ratio of blade mass to stipe mass	replicate iteration	Regression errors from measurements of plant sections sampled in the laboratory
% Nitrogen	site * period	Replicate composite samples of blade tissue collected from the same site*period
% Carbon	site * period	Replicate composite samples of blade tissue collected from the same site*period
Loss rate of whole plants	site * period	Draw from binomial defined by observed plant loss rate and number of tagged plants

Loss rate of fronds from surviving plants	site * period * plant	Site-specific variation in frond loss rates from different plants during a sampling interval (uncertainty is larger for plants with fewer tagged fronds)
Loss rate of blade mass from surviving fronds	Site * period	Variation in simulated population of blades (see Rassweiler <i>et al</i> 2017)
Loss rate of dissolved material through exudation	site * period	Observed variation in exudation among replicate blades and stipes measured on the same day

**Taxonomy and systematics:** *Fucus pyriferus* Linnaeus 1771: 311. *Macrocystis pyrifera* (L) C. Agardh 1820: 47; Setchell and Gardner 1925:627; Smith 1944:144. Abbott and Hollenberg 1976.

**Permit history:** Collections are made under permits from the State of California Department of Fish and Game.

**Legal/organizational requirements:** None.

**Project personnel:** The authors are responsible for sampling design, model development and data analyses. Data collection and management have been supervised by the authors with assistance from Mike Anghera, Bryn Evans and Brent Mardian.

### CLASS III. DATA SET STATUS AND ACCESSIBILITY

#### A. Status

**Latest update:** The data set currently spans the period from June 2002 to December 2017. Data collection is ongoing. Data will be added as collected and verified.

**Latest Archive date:** December 2017.

**Metadata status:** The metadata are complete and up to date.

**Data verification:** In the field, data are immediately checked for outliers and recording errors. After initial entry into Excel, all entries are checked by two people. Automated routines in SAS and R check data for inconsistencies and outliers in measurements of

plant morphology, counts of fronds, plant density and other measurements. SAS codes also check for missing values. Outliers are flagged and rechecked for accuracy.

## **B. Accessibility**

**Storage location and medium:** Original data file exists on the Santa Barbara Coastal Long Term Ecological Research project's data server and are backed up on magnetic tape at the Marine Science Institute, University of California, Santa Barbara.

**Contact person:** Andrew R. Rassweiler, e-mail: rassweiler@bio.fsu.edu. Tel. 850 644 1555, Department of Biological Science, Florida State University, Tallahassee, Florida, 32306 4295, USA.

**Copyright restrictions:** None.

**Propriety restrictions:** None.

**Costs:** None.

## **CLASS IV. DATA STRUCTURAL DESCRIPTORS**

### **A. Data Set File**

#### **Identity:**

- 1) *M. pyrifera* net primary production and growth
- 2) *M. pyrifera* standing crop, plant density, and loss rates
- 3) Census of fronds on marked plants
- 4) *M. pyrifera* blade water, carbon, and nitrogen content
- 5) Regression parameters to estimate biomass and production from frond density

#### **Size:**

- 1) *M. pyrifera* net primary production and growth = 29 kb
- 2) *M. pyrifera* standing crop, plant density, and loss rates = 199 kb
- 3) Census of fronds on marked plants = 180 kb
- 4) *M. pyrifera* blade water, carbon, and nitrogen content = 37 kb

5) Regression parameters to estimate biomass and production from frond density = 7 kb

**Format and storage mode:** ASCII text, comma delimited. No compression scheme was used.

**Header information:** See variable names in Section B.

**Alphanumeric attributes:** Mixed.

**Special characters/fields:** None.

**Authentication procedures:** Sums of numeric columns are provided for each dataset.

1) *M. pyrifera* net primary production and growth: Year = 373812, NPP\_dry = 1.60647, NPP\_carbon = 0.46831, NPP\_nitrogen = 0.02853, Growth\_rate\_dry = 6.39557, Growth\_rate\_carbon = 6.40304, Growth\_rate\_nitrogen = 6.41831, SE\_NPP\_dry = 0.19165, SE\_NPP\_carbon = 0.05979, SE\_NPP\_nitrogen = 0.00458, SE\_growth\_rate\_dry = 0.76696, SE\_growth\_rate\_carbon = 0.78117, SE\_growth\_rate\_nitrogen = 0.84850.

2) *M. pyrifera* standing crop, plant density, and loss rates: FSC\_dry = 155.50522, FSC\_carbon = 45.44702, FSC\_nitrogen = 2.83047, FSC\_fraction\_canopy = 142.77821, Frond\_density = 2026.59583, Plant\_density = 199.82833, Surface\_Irradiance = 380781.14303, Bottom\_Irradiance = 16329.15201, Subsurface\_Irradiance = 85319.12831, Plant\_loss\_rate = 3.31000, Frond\_loss\_rate = 9.61688, Cut\_fron\_loss\_rate = 0.09285, Blade\_loss\_rate = 4.846156, Dissolved\_loss\_rate = 1.29000, Carbon\_lost\_as\_plants = 0.15001, Carbon\_lost\_as\_fronds = 0.69050, Carbon\_lost\_as\_cut\_fronds = 0.00983, Carbon\_lost\_as\_blades = 0.46257, Carbon\_lost\_as\_dissolved = 0.12052, SE\_FSC\_dry = 16.93813, SE\_FSC\_carbon = 5.89261, SE\_FSC\_nitrogen = 0.55795, SE\_FSC\_fraction\_canopy = 9.98502, SE\_fron\_density = 164.04413, SE\_plant\_density = 10.0031, SE\_plant\_loss\_rate = 1.73772, SE\_fron\_loss\_rate = 2.70650, SE\_cut\_fron\_loss\_rate = 0.01253, SE\_blade\_loss\_rate = 0.34718, SE\_dissolved\_loss\_rate = 0.10331, SE\_carbon\_lost\_as\_plants = 0.09778, SE\_carbon\_lost\_as\_fronds = 0.19374, SE\_carbon\_lost\_as\_cut\_fronds = 0.00153, SE\_carbon\_lost\_as\_blades = 0.05590, SE\_carbon\_lost\_as\_dissolved = 0.01221.

3) Census of fronds on marked plants: Total\_fronds = 166075, New\_fronds = 40722.

4) *M. pyrifera* blade water, carbon, and nitrogen content: Replicate = 1693, Dry\_to\_wet\_ratio = 98.6, Percent\_carbon = 34696.91, Percent\_nitrogen = 2391.19.

5) Regression parameters to estimate biomass and production from frond density: Model = 336, Slope = 1.99495, Intercept = 0.04047, rsquare = 67.02, N = 3794.

## **B. Variable information, variable definitions**

**Dataset 1:** *Macrocystis pyrifera* net primary production and growth

**Site:** The name of the kelp forest sampled, ABUR = Arroyo Burro, AQUE = Arroyo Quemado, MOHK = Mohawk Reef. See Section I.B for more details.

**Year:** Sampling year. Format is YYYY.

**Season:** Season (winter, spring, summer, and autumn as defined by the winter solstice, spring equinox, summer solstice, and autumnal equinox) in which the site is sampled.

**NPP\_dry:** The mean daily production of *M. pyrifera* dry mass ( $\text{kg m}^{-2} \text{d}^{-1}$ ) for each season of each year. These data are calculated by integrating the instantaneous rate of production during each period and dividing by the number of days (see Section I.B Equation 2). Production for all days in each season is averaged.

**NPP\_carbon:** The mean daily production of *M. pyrifera* carbon mass ( $\text{kg m}^{-2} \text{d}^{-1}$ ) in each season of each year. These data are calculated by integrating the instantaneous rate of production during each period and dividing by the number of days (see Section I.B Equation 2). Production for all days in each season is averaged.

**NPP\_nitrogen:** The mean daily production of *M. pyrifera* nitrogen mass ( $\text{kg m}^{-2} \text{d}^{-1}$ ) in each season of each year. These data are calculated by integrating the instantaneous rate of production during each period and dividing by the number of days (see Section I.B Equation 2). Production for all days in each season is averaged.

**Growth\_rate\_dry:** The mean instantaneous growth rate of *M. pyrifera* dry mass ( $\text{d}^{-1}$ ) for each season of each year. These data are calculated as the growth rate necessary to explain the observed change in biomass during each period, given the initial biomass and the independently measured loss rates (see Section I.B Equation 1). Growth rates for all days in each season are averaged.

**Growth\_rate\_carbon:** The mean instantaneous growth rate of *M. pyrifera* carbon mass ( $\text{d}^{-1}$ ) for each season of each year. These data are calculated as the rate necessary to explain the observed change in biomass during each period, given the initial biomass and the independently measured loss rates (see Section I.B Equation 1). Growth rates for all days in each season are averaged.

**Growth\_rate\_nitrogen:** The mean instantaneous growth rate of *M. pyrifera* nitrogen mass ( $d^{-1}$ ) for each season of each year. These data are calculated as the growth rate necessary to explain the observed change in biomass during each period, given the initial biomass and the independently measured loss rates (see Section I.B *Equation 1*). Growth rates for all days in each season are averaged.

**SE\_NPP\_dry:** The standard error of NPP\_dry. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and it incorporates error in our estimates of biomass, plant loss, frond loss, cut loss, blade loss, and dissolved loss rates.

**SE\_NPP\_carbon:** The standard error of NPP\_carbon. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and it incorporates errors in our estimates of biomass, plant loss, frond loss, cut loss, blade loss, and dissolved loss rates.

**SE\_NPP\_nitrogen:** The standard error of NPP\_nitrogen. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and it incorporates errors in our estimates of biomass, plant loss, frond loss, cut loss, blade loss, and dissolved loss rates.

**SE\_growth\_rate\_dry:** The standard error of Growth\_rate\_dry. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and it incorporates errors in our estimates of biomass, plant loss, frond loss, cut loss, blade loss, and dissolved loss rates.

**SE\_growth\_rate\_carbon:** The standard error of Growth\_rate\_carbon. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and it incorporates errors in our estimates of biomass, plant loss, frond loss, cut loss, blade loss, and dissolved loss rates.

**SE\_growth\_rate\_nitrogen:** The standard error of Growth\_rate\_nitrogen. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and it incorporates errors in our estimates of biomass, plant loss, frond loss, cut loss, blade loss, and dissolved loss rates.

**Table 2.** *Macrocystis pyrifera* net primary production and growth

Variable name	Variable definition	Units	Storage Type	Numeric range	Missing values
Site	Site	N/A	Character	N/A	N/A



Year	Sampling year	N/A	Numeric	2002-2017	N/A
Season	Sampling season	N/A	Character	N/A	N/A
NPP_dry	Seasonal production of <i>M. pyrifera</i> dry mass	kg m <sup>-2</sup> d <sup>-1</sup>	Numeric	0 – 0.0470	
NPP_carbon	Seasonal production of <i>M. pyrifera</i> carbon mass	kg m <sup>-2</sup> d <sup>-1</sup>	Numeric	0 – 0.01289	
NPP_nitrogen	Seasonal production of <i>M. pyrifera</i> nitrogen mass	kg m <sup>-2</sup> d <sup>-1</sup>	Numeric	0 – 0.00091	
Growth_rate_dry	Instantaneous growth rate of <i>M. pyrifera</i> dry mass	d <sup>-1</sup>	Numeric	0 – 0.10861	
Growth_rate_carbon	Instantaneous growth rate of <i>M. pyrifera</i> carbon mass	d <sup>-1</sup>	Numeric	0 – 0.11170	
Growth_rate_nitrogen	Instantaneous growth rate of <i>M. pyrifera</i> nitrogen mass	d <sup>-1</sup>	Numeric	0 – 0.10451	
SE_NPP_dry	Standard error of NPP_dry	kg m <sup>-2</sup> d <sup>-1</sup>	Numeric	0 – 0.00454	
SE_NPP_carbon	Standard error of NPP_carbon	kg m <sup>-2</sup> d <sup>-1</sup>	Numeric	0 – 0.00133	
SE_NPP_nitrogen	Standard error of NPP_nitrogen	kg m <sup>-2</sup> d <sup>-1</sup>	Numeric	0 – 0.00013	
SE_growth_rate_dry	Standard error of Growth_rate_dry	d <sup>-1</sup>	Numeric	0 – 0.03047	
SE_growth_rate_carbon	Standard error of Growth_rate_carbon	d <sup>-1</sup>	Numeric	0 – 0.03060	
SE_growth_rate_nitrogen	Standard error of Growth_rate_nitrogen	d <sup>-1</sup>	Numeric	0 – 0.03203	

**Dataset 2:** *Macrocystis pyrifera* standing crop, plant density and loss rates

**Site:** The name of the kelp forest sampled, ABUR = Arroyo Burro, AQUE = Arroyo Quemado, MOHK = Mohawk Reef. See Section I.B for more details.

**Date:** Date on which the site was sampled. Format is MM/DD/YYYY.

**FSC\_dry:** The dry mass of the foliar standing crop of *M. pyrifera* ( $\text{kg m}^{-2}$ , excluding sporophylls and holdfast). These data are obtained by calculating the dry mass of each plant (see Section I.B *Measuring standing crop*) and dividing the total dry mass of all plants in the plot by the area of the plot. Plants without at least one frond longer than 1m are excluded.

**FSC\_carbon:** The carbon mass of the foliar standing crop of *M. pyrifera* ( $\text{kg m}^{-2}$ , excluding sporophylls and holdfast). These data are obtained by calculating the carbon mass of each plant (see Section I.B *Measuring standing crop*) and dividing the total carbon mass of all plants in the plot by the area of the plot. Plants without at least one frond longer than 1m are excluded.

**FSC\_nitrogen:** The nitrogen mass of the foliar standing crop of *M. pyrifera* ( $\text{kg m}^{-2}$ , excluding sporophylls and holdfast). These data are obtained by calculating the nitrogen mass of each plant (see Section I.B *Measuring standing crop*) and dividing the total nitrogen mass of all plants in the plot by the area of the plot. Plants without at least one frond longer than 1m are excluded.

**FSC\_fraction\_canopy:** The fraction of total foliar standing crop observed in the canopy section. This fraction is obtained by calculating the subsurface, water column, and canopy mass of each plant (see Section I.B *Measuring standing crop*) and dividing the canopy mass by the total (canopy mass + water column mass + subsurface mass).

**Frond\_density:** The density of *M. pyrifera* fronds (number  $\text{m}^{-2}$  longer than 1 m).

**Plant\_density:** The density of *M. pyrifera* plants (number  $\text{m}^{-2}$ ). Plants without at least one frond longer than 1m are excluded.

**Surface\_irradiance:** Mean daily instantaneous irradiance ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) measured by PAR irradiance loggers. This mean is based on each 24-hour day over the course of the sampling interval.

**Bottom\_irradiance:** Mean daily instantaneous irradiance ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) measured by PAR irradiance loggers mounted on the seafloor. This mean is based on each 24-hour day over the course of the sampling interval.

**Subsurface\_irradiance:** Mean daily instantaneous irradiance ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) calculated for the water column. Subsurface irradiance is calculated by integrating average surface and bottom irradiance over the water column depth (bottom irradiance is measured by PAR sensors mounted on the seafloor at Mohawk and Arroyo Quemado). This mean is based on each 24-hour day over the course of the sampling period.

**Plant\_loss\_rate:** The loss rate of *M. pyrifera* plants during the sampling interval (fraction of plants lost  $\text{d}^{-1}$ ). These data are based on losses of approximately 15 tagged plants (see Section I.B *Measuring loss rates*).

**Fronde\_loss\_rate:** The mean loss rate of fronds during the sampling interval (fraction of fronds lost  $\text{plant}^{-1} \text{d}^{-1}$ ). This value is based on the mean proportional frond loss averaged among tagged plants that survived to the end of the sampling interval; losses of fronds on plants that did not survive to the end of the sampling interval are accounted for in the plant loss rate (see Section I.B *Measuring loss rates*).

**Cut\_fronde\_loss\_rate:** The loss rate of tissue cut by boat propellers (fraction of mass lost  $\text{d}^{-1}$ ) during the sampling interval (see Section I.B *Measuring loss rates*).

**Blade\_loss\_rate:** The loss rate of deteriorating tissue (fraction of mass lost  $\text{d}^{-1}$ ) due to blade senescence during the sample interval (see Section I.B *Measuring loss rates*).

**Dissolved\_loss\_rate:** The loss rate of dissolved organic matter (fraction of mass lost  $\text{d}^{-1}$ ) from blades and stipes during the sampling interval (see Section I.B *Measuring loss rates*).

**Carbon\_lost\_as\_plants:** The rate of carbon mass lost in the form of plants ( $\text{kg m}^{-2} \text{d}^{-1}$ ). This value is obtained by calculating the total carbon mass of plants lost during the sampling interval and dividing by the number of days in the sampling interval.

**Carbon\_lost\_as\_fronde:** The rate of carbon mass lost in the form of fronds ( $\text{kg m}^{-2} \text{d}^{-1}$ ). These data are obtained by calculating the total carbon mass of fronds lost during the sampling interval and dividing by the number of days in the sampling interval.

**Carbon\_lost\_as\_cut\_fronde:** The rate of carbon mass lost in the form of fronds cut by a propeller near the surface ( $\text{kg m}^{-2} \text{d}^{-1}$ ). These data are obtained by calculating the total carbon mass of cut fronds lost during the sampling interval and dividing by the number of days in the sampling interval.

**Carbon\_lost\_as\_blades:** The rate of carbon mass lost in the form of deteriorating blades due to senescence ( $\text{kg m}^{-2} \text{d}^{-1}$ ). These data are obtained by calculating the total carbon mass of senescing blades lost during the sampling interval and dividing by the number of days in the sampling interval.

**Carbon\_lost\_as\_dissolved:** The rate of carbon mass lost in the form of dissolved organic matter ( $\text{kg m}^{-2} \text{d}^{-1}$ ). These data are obtained by calculating the total carbon mass of dissolved matter lost during the sampling interval and dividing by the number of days

in the sampling interval. These data are equivalent to production and release of dissolved carbon by *M. pyrifera*.

**SE\_FSC\_dry:** The standard error of FSC\_dry. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and includes observer and regression error. Observer error consists of errors made in the number of plants sampled and in the measurement of their size. Regression errors include variability in the allometric relationships used to calculate the size of the three plant sections, as well as uncertainty in the length:wet-mass and wet-mass:dry-mass conversion ratios.

**SE\_FSC\_carbon:** The standard error of FSC\_carbon. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and includes observer and regression error. Observer error consists of errors made in the number of plants sampled and in the measurement of their size. Regression errors include variability in the allometric relationships used to calculate the size of the three plant sections, as well as uncertainty in the length:wet-mass, wet-mass:dry-mass and dry-mass:carbon-mass conversion ratios.

**SE\_FSC\_nitrogen:** The standard error of FSC\_nitrogen. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) includes observer and regression error. Observer error consists of errors made in the number of plants sampled and in the measurement of their size. Regression errors include variability in the allometric relationships used to calculate the size of the three plant sections, as well as uncertainty in the length:wet-mass, wet-mass:dry-mass and dry mass:nitrogen-mass conversion ratios.

**SE\_FSC\_fraction\_canopy:** The standard error of FSC\_fraction\_canopy. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and includes observer and regression error. Observer error consists of errors made in the number of plants sampled and in the measurement of their size. Regression errors include variability in the allometric relationships used to calculate the size of the three plant sections, as well as uncertainty in the length:wet-mass and wet-mass:dry-mass and conversion ratios.

**SE\_plant\_density:** The standard error of Plant\_density. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and reflects variation in the total number of plants counted in a transect. This estimate is produced by comparing density estimates of the same transect obtained by different observers on the same day.

**SE\_fronD\_density:** The standard error of FronD\_density. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and reflects variation in

the total number of fronds counted in a transect. This estimate is produced by comparing density estimates of the same transect obtained by different observers on the same day.

**SE\_plant\_loss\_rate:** The standard error of Plant\_loss\_rate. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and includes sampling error associated with calculating a mean loss rate for the entire plot based on approximately 15 tagged plants.

**SE\_fronn\_loss\_rate:** The standard error of Fronn\_loss\_rate. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and includes sampling error associated with calculating a mean loss rate for the entire plot based on approximately 15 tagged plants.

**SE\_cut\_fronn\_loss\_rate:** The standard error of Cut\_fronn\_loss\_rate. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and is propagated from uncertainty in other more directly measured variables.

**SE\_blade\_loss\_rate:** The standard error of Blade\_loss\_rate. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and is derived from simulations of a population of blades being initiated and deteriorating. It includes uncertainty related to sampling error of blades and uncertainty in plant and fronn loss rates.

**SE\_dissolved\_loss\_rate:** The standard error of Dissolved\_loss\_rate. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and includes uncertainty in estimates of tissue-specific exudation rates, and uncertainty in the ratio of blade exudation : stipe exudation.

**SE\_carbon\_lost\_as\_plants:** The standard error of Carbon\_lost\_as\_plants. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and is propagated from uncertainty in other more directly measured variables.

**SE\_carbon\_lost\_as\_fronns:** The standard error of Carbon\_lost\_as\_fronns. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and is propagated from uncertainty in other more directly measured variables.

**SE\_Carbon\_lost\_as\_fronns:** The standard error of Carbon\_lost\_as\_fronns. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and is propagated from uncertainty in other more directly measured variables.

**SE\_carbon\_lost\_as\_cut\_fronns:** The standard error of Carbon\_lost\_as\_cut\_fronns. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying*

*Uncertainty*) and is propagated from uncertainty in other more directly measured variables.

**SE\_carbon\_lost\_as\_blades:** The standard error of Carbon\_lost\_as\_blades. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and is propagated from uncertainty in other more directly measured variables.

**SE\_carbon\_lost\_as\_dissolved:** The standard error of Carbon\_lost\_as\_dissolved. This error is calculated using Monte Carlo methods (see Section I.B *Quantifying Uncertainty*) and is propagated from uncertainty in other more directly measured variables.

**Table 3.** *Macrocystis pyrifera* standing crop, plant density and loss rates

Variable name	Variable definition	Units	Storage Type	Numeric range	Missing values
Site	Site	N/A	Character	N/A	N/A
Date	Sampling date	N/A	Character	N/A	N/A
FSC_dry	Dry foliar standing crop	kg m <sup>-2</sup>	Numeric	0 -2.3828	
FSC_carbon	Carbon foliar standing crop	kg m <sup>-2</sup>	Numeric	0 - 0.70244	
FSC_nitrogen	Nitrogen foliar standing crop	kg m <sup>-2</sup>	Numeric	0 – 0.05506	
FSC_fraction_canopy	Fraction of foliar standing crop observed in the canopy section	NA	Numeric	0 – 0.63940	
FronD density	Density of fronds	no. m <sup>-2</sup>	Numeric	0 – 21.105	
Plant_density	Density of plants	no. m <sup>-2</sup>	Numeric	0 – 2.33	
Surface_Irradiance	Mean daily irradiance measured at the surface	μmol m <sup>-2</sup> s <sup>-1</sup>	Numeric	403.66 – 1025.85	
Bottom_Irradiance	Mean daily irradiance measured on the seafloor	μmol m <sup>-2</sup> s <sup>-1</sup>	Numeric	5.90 – 172.9472	

Subsurface_Irradiance	Meane daily irradiance integrated from surface to seafloor	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Numeric	68.80 – 291.21	
Plant_loss_rate	Instantaneous loss rate of plants	$\text{d}^{-1}$	Numeric	0 – 0.09091	
Fronnd_loss_rate	Instantaneous loss rate of fronds	$\text{d}^{-1}$	Numeric	0 – 0.10515	
Cut_fronnd_loss_rate	Instantaneous loss rate of fronds cut by propellers	$\text{d}^{-1}$	Numeric	0 – 0.00370	
Blade_loss_rate	Instantaneous loss rate of deteriorating blades	$\text{d}^{-1}$	Numeric	0.00382 – 0.01291	
Dissolved_loss_rate	Instantaneous loss rate of dissolved organic matter	$\text{d}^{-1}$	Numeric	0.0012– 0.00437	
Carbon_lost_as_plants	Rate of carbon mass lost in the form of plants	$\text{kg m}^{-2} \text{d}^{-1}$	Numeric	0 – 0.00454	
Carbon_lost_as_fronnds	Rate of carbon mass lost in the form of fronds	$\text{kg m}^{-2} \text{d}^{-1}$	Numeric	0 – 0.00912	
Carbon_lost_as_cut_fronnds	Rate of carbon mass lost in the form of fronds cut by a propeller	$\text{kg m}^{-2} \text{d}^{-1}$	Numeric	0 – 0.00086	
Carbon_lost_as_blades	Rate of carbon mass lost in the form of deteriorating blades	$\text{kg m}^{-2} \text{d}^{-1}$	Numeric	0 – 0.00591	
Carbon_lost_as_dissolved	Rate of carbon mass lost in the form of dissolved organic matter	$\text{kg m}^{-2} \text{d}^{-1}$	Numeric	0 – 0.00187	
SE_FSC_dry	Standard error of FSC_dry	$\text{kg m}^{-2}$	Numeric	0 – 0.26798	

SE_FSC_carbon	Standard error of FSC_carbon	kg m <sup>-2</sup>	Numeric	0 – 0.09345	
SE_FSC_nitrogen	Standard error of FSC_nitrogen	kg m <sup>-2</sup>	Numeric	0 – 0.01097	
SE_fraction_canopy	Standard error of fraction_canopy	NA	Numeric	0 – 0.06807	
SE_fron_d_density	Standard error of Fron_d_density	no. m <sup>-2</sup>	Numeric	0 – 1.99263	
SE_plant_density	Standard error of Plant_density	no. m <sup>-2</sup>	Numeric	0 – 0.13674	
SE_plant_loss_rate	Standard error of Plant_loss_rate	d <sup>-1</sup>	Numeric	0 – 0.01841	
SE_fron_d_loss_rate	Standard error of Fron_d_loss_rate	d <sup>-1</sup>	Numeric	0 – 0.04518	
SE_cut_fron_d_loss_rate	Standard error of Cut_fron_d_loss_rate	d <sup>-1</sup>	Numeric	0 – 0.00056	
SE_blade_loss_rate	Standard error of Blade_loss_rate	d <sup>-1</sup>	Numeric	0.00034 – 0.0011	
SE_dissolved_loss_rate	Standard error of Dissolved_loss_rate	d <sup>-1</sup>	Numeric	0.00010 – 0.00033	
SE_carbon_lost_as_plants	Standard error of Carbon_lost_as_plants	kg m <sup>-2</sup> d <sup>-1</sup>	Numeric	0 – 0.00256	
SE_carbon_lost_as_fron_d	Standard error of Carbon_lost_as_fron_d	kg m <sup>-2</sup> d <sup>-1</sup>	Numeric	0 – 0.00238	
SE_carbon_lost_as_cut	Standard error of Carbon_lost_as_cut	kg m <sup>-2</sup> d <sup>-1</sup>	Numeric	0 – 0.00010	
SE_carbon_lost_as_blades	Standard error of Carbon_lost_as_blades	kg m <sup>-2</sup> d <sup>-1</sup>	Numeric	0 – 0.00088	
Carbon_lost_as_dissolved	Standard error of Carbon_lost_as_dissolved	kg m <sup>-2</sup> d <sup>-1</sup>	Numeric	0 – 0.00022	



**Dataset 3:** *Census of fronds on marked plants*

**Site:** The name of the kelp forest sampled, ABUR = Arroyo Burro, AQUE = Arroyo Quemado, MOHK = Mohawk Reef. See Section I.B for more details.

**Plant\_ID:** A unique identification label for each plant sampled. The lettered prefix indicates the site where the plant is located; the number identifies the plant.

**Date:** Date the site is sampled. Format is MM/DD/YYYY.

**Total\_fronds:** The total number of fronds > 1 m in length on the plant at the time of sampling. These data include tagged fronds remaining from previous sampling dates and any new fronds.

**New\_fronds:** The number of untagged fronds > 1 m in length on the plant. These fronds were initiated during the sampling interval, or were not yet 1m long on the previous sampling date. Zeros represent periods in which no new fronds were counted. Missing data indicates plants that were sampled for the first time, where new fronds could not be distinguished from old fronds.

**Table 4.** *Census of fronds on tagged plants*

Variable name	Variable definition	Units	Storage Type	Numeric range	Missing values
Site	Site	N/A	Character	N/A	N/A
Plant_ID	Identification label for each tagged plant	N/A	Character	N/A	N/A
Date	Sampling date	N/A	Character	N/A	N/A
Total_fronds	Number of fronds on the plant	no. fronds	Numeric	0-247	
New_fronds	Number of new fronds on the plant since the last sampling date	no. fronds	Numeric	0-41	

**Dataset 4:** *M. pyrifera* blade water, carbon, and nitrogen content

**Site:** The name of the kelp forest sampled, ABUR = Arroyo Burro, AQUE = Arroyo Quemado, MOHK = Mohawk Reef. See Section I.B for more details.

**Date:** Date the site is sampled. Format is MM/DD/YYYY.

**Replicate:** Identification label for replicate analytical sample from a composite of 15 kelp blades collected at a particular site on a given month.

**Dry\_to\_wet\_ratio:** The ratio of dry to wet mass of a composite sample of 15 kelp blades collected at a particular site on a given month.

**Percent\_carbon:** The percentage of blade mass comprised of carbon in a composite sample of 15 kelp blades collected at a particular site on a given month.

**Percent\_nitrogen:** The percentage of blade mass comprised of nitrogen in a composite sample of 15 kelp blades collected at a particular site on a given month.

**Table 5.** *M. pyrifera* blade water, carbon, and nitrogen content

Variable name	Variable definition	Units	Storage Type	Numeric range	Missing values
Date	Sampling date	N/A	Character	N/A	N/A
Site	Site	N/A	Character	N/A	N/A
Replicate	Identification label for replicate analytical sample	N/A	Character	N/A	N/A
Dry_to_wet_ratio	Ratio of dry mass to wet mass of blade tissue	N/A	Numeric	0.01 – 0.18	.
Percent_carbon	Percent of dry mass of blade tissue comprised of carbon	%	Numeric	20.25 – 44.52	.
Percent_nitrogen	Percent of dry mass of blade tissue comprised of nitrogen	%	Numeric	0.66 – 4.36	.

**Dataset 6:** *Regression parameters to estimate biomass and production from frond density*

**Model:** Numeric identifiers assigned to a linear regression performed between measured frond density in a specified month and calculated FSC for that month, NPP for that season, or NPP for that year.

**Independent variable:** The independent variable used in a linear regression performed between measured frond density (fronds > 1 meter tall per m<sup>2</sup>) in a specified month and calculated FSC for that month, NPP for that season, or NPP for that year. These variables represent monthly measurements of frond density collected at three sites from 2002-2017.

**Dependent variable:** The dependent variable used in a linear regression performed between frond density measured for a specified month and calculated FSC for that month, NPP for that season, or NPP for that year. “FSC dry” is dry mass of *M. pyrifera* (dry kg m<sup>-2</sup>, excluding sporophylls and holdfast) calculated for the specified month. “Canopy FSC dry” and “Water column FSC dry” are dry mass of *M. pyrifera* (dry kg m<sup>-2</sup>, excluding sporophylls and holdfast) calculated in the canopy section and water column section for the specified month, respectively. “Seasonal NPP dry” is the mean daily rate of *M. pyrifera* biomass production averaged over the season in units of dry mass (dry kg m<sup>-2</sup> d<sup>-1</sup>). “Seasonal NPP carbon” is the mean daily NPP of *M. pyrifera* averaged over the season in units of carbon mass (kg m<sup>-2</sup> d<sup>-1</sup>). Seasonal NPP estimates are calculated by integrating the instantaneous rate of production during a season and dividing by the number of days in the season. “Annual NPP dry” is the mean daily NPP of *M. pyrifera* averaged over the year in units of dry mass (kg m<sup>-2</sup> d<sup>-1</sup>). “Annual NPP carbon” is the mean NPP of *M. pyrifera* averaged over the year in units of carbon mass (kg m<sup>-2</sup> d<sup>-1</sup>). Annual NPP estimates are calculated by integrating the instantaneous rate of production during a year and dividing by the number of days in the year.

**Slope:** The slope parameter of a linear regression performed between measured frond density in a specified month and calculated FSC for that month, NPP for that season, or NPP for that year. The slopes for relationships between frond density and “FSC” are in units of dry kg m<sup>-2</sup>. The slope for relationships between frond density and “Seasonal NPP dry” and “Annual NPP dry” are in units of dry kg m<sup>-2</sup> d<sup>-1</sup>. The intercept for relationships between frond density and “Seasonal NPP carbon” and “Annual NPP carbon” are in units of carbon kg m<sup>-2</sup> d<sup>-1</sup>.

**Intercept:** The intercept parameter of a linear regression performed between measured frond density in a specified month and calculated FSC for that month, NPP for that season, or NPP for that year. Relationships estimating FSC were forced through the origin and no intercept is given. The intercept for relationships between frond density and “Seasonal NPP dry” and “Annual NPP dry” are in units of dry kg m<sup>-2</sup> d<sup>-1</sup>. The intercept for relationships between frond density and “Seasonal NPP carbon” and “Annual NPP carbon” are in units of carbon kg m<sup>-2</sup> d<sup>-1</sup>.

**pvalue:** The p-value of a linear regression performed between measured frond density in a specified month and calculated FSC for that month, NPP for that season, or NPP for that year.

**rsquare:** The coefficient of determination ( $r^2$ ) of a linear regression performed between measured frond density in a specified month and calculated FSC for that month, NPP for that season, or NPP for that year.

**N:** The sample size of a linear regression performed between measured frond density in a specified month and calculated FSC for that month, NPP for that season, or NPP for that year. The sample size for regressions predicting FSC represents all site\*months from May 2002 - December 2017. The sample size for regressions predicting seasonal NPP represent all site\*seasons from spring 2002 - autumn 2017 and the sample size for regressions predicting annual NPP represent all site\*years from 2003-2017.

**Table 6.** Regression parameters to estimate biomass and production from frond density.

Variable name	Variable definition	Units	Storage Type	Numeric range	Missing values
Model	Identifier of a linear regression performed between frond density in a specified month and FSC, seasonal NPP, or annual NPP	N/A	Numeric	1-7	N/A
Independent_variable	Independent variable of a linear regression performed between frond density in a specified month and FSC, seasonal NPP, or annual NPP	N/A	Character	N/A	N/A
Dependent_variable	Dependent variable of a linear regression performed between frond density in a specified month and FSC, seasonal NPP, or annual NPP	N/A	Character	N/A	N/A
Slope	Slope parameter of a linear regression performed between frond density in a specified month and	N/A	Numeric	0.00029 – 0.09907	.

	FSC, seasonal NPP, or annual NPP				
Intercept	Intercept parameter of a linear regression performed between frond density in a specified month and FSC, seasonal NPP, or annual NPP	N/A	Numeric	-0.00163 – 0.00371	.
pvalue	P-value of a linear regression performed between frond density in a specified month and FSC, seasonal NPP, or annual NPP	N/A	Character	NA	N/A
rsquare	Coefficient of determination ( $r^2$ ) value of a linear regression performed between frond density in a specified month and FSC, seasonal NPP, or annual NPP	N/A	Numeric	0.28 - 1	.
N	Sample size of a linear regression performed between frond density in a specified month and FSC, seasonal NPP, or annual NPP	N/A	Numeric	40 - 48	.

## CLASS V. SUPPLEMENTAL DESCRIPTORS

### A. Data acquisition

**Data forms:** XEROX “Never tear” paper.

**Location of completed forms:** Marine Science Institute, University of California, Santa Barbara, CA 93106

**Data entry/verification procedures:** Divers record data on printed datasheets made of “Never Tear” paper attached to acrylic slates. Data are entered into a database in the laboratory and double-checked. Data sheets are scanned and saved electronically. Data files and data sheets in pdf format are stored on the Santa Barbara Coastal Long Term Ecological Research project’s servers. Data sheets are held at PI’s address.

**B. Quality assurance/quality control procedures:** See comments on data verification (Class III, Section A), data entry/verification procedures (Class V, Section A), and computer programs and data processing algorithms (Class V, Section D).

**C. Related material:** Bottom temperature for each site is recorded by loggers (2002-present). Surface irradiance and bottom irradiance is recorded by loggers (2008-present).

**D. Computer programs and data processing algorithms:** SAS data validation and analysis programs are maintained on the data server at the Marine Science Institute, University of California, Santa Barbara.

**E. Archiving:** N/A

**F. Publications using the data set:** Harmon *et al.* 2007; McPhee-Shaw 2007; Fram *et al.* 2008, Rassweiler *et al.* 2008, Reed *et al.* 2008, Stewart *et al.* 2009, Reed *et al.* 2009, Reed and Brzezinski 2009, Cavanaugh *et al.* 2010, Cavanaugh *et al.* 2011, Miller *et al.* 2011, Reed *et al.* 2011, Brzezinski *et al.* 2013, Cavanaugh *et al.* 2013, Foster *et al.* 2013, Hofmann *et al.* 2013, Rodriguez *et al.* 2013, Yorke *et al.* 2013, Cavanaugh *et al.* 2014, Bell *et al.* 2015a, Bell *et al.* 2015b, Castorani *et al.* 2015, Morton *et al.* 2016, Reed *et al.* 2015a, Reed *et al.* 2015b, Reed *et al.* 2016, Castorani *et al.* 2017.

**G. Publications using the same sites:** The three sites sampled here are the focus of a range of work by the SBC-LTER which can be found on the publications page of the SBC-LTER website (<http://sbc.lternet.edu>).

**H. History of data set usage:**

**Data request history:** N/A

**Data set update history:** N/A

**Review history:** N/A

**I. Questions and comments from secondary users:** N/A

## Acknowledgments

We thank M. Anghera, B. Evans, B. Mardian, and numerous others who spent many hours underwater in cold, uncomfortable conditions assisting us in data collection. We also thank K. K. Arkema, M. A. Brzezinski and R. C. Zimmerman who were instrumental in developing the method for estimating NPP generated here and were authors on the previous version of this dataset. Our estimates of dissolved losses owe greatly to the work of C. A. Carlson and E. R. Halewood. Our estimates of losses due to blade senescence were greatly influenced by the works of R. J. Miller, G. E. Rodriguez and C. E. Yorke. We acknowledge R. Nisbet for thoughtful discussions about using models of kelp dynamics to estimate NPP and growth and P. Raimondi for advice about how to express our estimates of uncertainty. This work is based on support from the National Science Foundation to the Santa Barbara Coastal Long Term Ecological Research program under grant numbers OCE 9982105, OCE 0620276 and OCE 1232779.

## Literature Cited

- Abbott, I. A. and G. J. Hollenberg. 1976. Marine algae of California. Stanford University Press. Stanford California.
- Bell, T. W., K. C. Cavanaugh and D. A. Siegel. 2015a. Remote monitoring of giant kelp biomass and physiological condition: An evaluation of the potential for the Hyperspectral Infrared Imager (HypIRI) mission. *Remote Sensing of Environment* **167**: 218–228.
- Bell, T. W., K. C. Cavanaugh, D. C. Reed and D. A. Siegel. 2015b. Geographic variability in the controls of biomass dynamics of giant kelp. *Journal of Biogeography* **42**: 2010-2021.
- Bolton, J. J. 2016. What is aquatic botany?— And why algae are plants: The importance of non-taxonomic terms for groups of organisms. *Aquatic Botany* 132:1–4.
- Brzezinski, M. A., D. C. Reed, S. Harrer, A. Rassweiler, J. M. Melack, B. M. Goodridge, and J. E. Dugan. 2013. Multiple sources and forms of nitrogen sustain year-round kelp growth on the inner continental shelf of the Santa Barbara Channel. *Oceanography* **26**: 114-123.
- Buschmann, A.H., Vásquez, J.A., Osorio, P., Reyes, E., Filún, L., Hernández-González, M.C. and Vega, A., 2004. The effect of water movement, temperature and salinity on abundance and reproductive patterns of *Macrocystis* spp. (Phaeophyta) at different latitudes in Chile. *Marine Biology*, 145:849-862.
- Castorani, M. C., D. C. Reed, F. Alberto, T. W. Bell, R. D. Simmons, K. C. Cavanaugh, D. A. Siegel and P. T. Raimondi. 2015. Connectivity structures local population dynamics: a long-term empirical test in a large metapopulation system. *Ecology* **96**: 3141-3152.

- Castorani, M. C., D. C. Reed, P. T. Raimondi, F. Alberto, T. W. Bell, D. A. Siegel and R. D. Simons. 2017. Fluctuations in population fecundity drive demographic connectivity and structure metapopulation dynamics. *Proceedings of the Royal Society B* **284**: 20162086.
- Cavanaugh, K. C., D. A. Siegel, B. P. Kinlan, and D. C. Reed. 2010. Scaling giant kelp field measurements to regional scales using satellite observations. *Marine Ecology Progress Series* **403**: 13-27.
- Cavanaugh, K. C., D. A. Siegel, D. C. Reed and P. E. Dennison. 2011. Environmental controls of giant-kelp biomass in the Santa Barbara Channel, California. *Marine Ecology-Progress Series* **429**: 1-17.
- Cavanaugh, K. C., B. E. Kendall, D. A. Siegel, D. C. Reed, F. Alberto and J. Assis. 2013. Synchrony in dynamics of giant kelp forests is driven by both local recruitment and regional environmental controls. *Ecology* **94**: 499-509.
- Cavanaugh, K. C., D. A. Siegel, P. T. Raimondi and F. Alberto. 2014. Patch definition in metapopulation analysis: a graph theory approach to solve the mega-patch problem. *Ecology* **95**: 316–328.
- Clendenning, K. A. 1971. Photosynthesis and general development. Pages 169-190 *in* W. J. North, editor. *The biology of giant kelp beds (Macrocystis) in California*. Beihefte Zur Nova Hedwigia, Verlag Von J. Cramer, Lehre, Germany.
- Coon, D. 1982. Primary productivity of macroalgae in North Pacific America. Pages 447-454 *in* O. R. Zaborsky, editor. *CRC Handbook of biosolar resources*. CRC Press, Boca Raton, Florida, USA.
- Dayton, P.K., 1985. The structure and regulation of some South American kelp communities. *Ecological Monographs*, 55:447-468.
- Demes, K. W., M. H. Graham, and T. S. Suskiewicz. 2009. Phenotypic plasticity reconciles incongruous molecular and morphological taxonomies: The giant kelp, *macrocystis* (laminariales, phaeophyceae), is a monospecific genus. *Journal of Phycology* 45:1266–1269.
- Dodson, S. I., S.E. Arnott and K.L. Cottingham. 2000. The Relationship in Lake Communities between Primary Productivity and Species Richness. *Ecology* **81**: 2662-2679.
- Foster, M.S., Reed, D.C., Carr, M.H., Dayton, P.K., Malone, D.P. Pearse, J.S. and Rogers-Bennett, L. 2013. Kelp forests in California, p. 115-132. In: Lang, M., R. L. Marinelli, S. J. Roberts and P. R. Taylor (editors), *Research and Discoveries: The Revolution of Science Through SCUBA*. Smithsonian Contributions to the Marine Sciences No. 39, Smithsonian, Wash., D.C.
- Fram, J. P., H. L. Stewart, M. A. Brzezinski, B. P. Gaylord, D. C. Reed, S. L. Williams and S. MacIntyre. 2008. Physical pathways and utilization of nitrate supply to the giant kelp, *Macrocystis pyrifera*. *Limnology and Oceanography* **53**: 1589-1603.



- Graham, M. H., J. A. Vasquez, and A. H. Buschmann. 2007. Global ecology of the giant kelp *Macrocystis*: from ecotypes to ecosystems. *Oceanography and Marine Biology: an annual Review* **45**:39-88.
- Goldman, C. R., A. Jassby and T. Powell. 1989. Interannual Fluctuations in Primary Production: Meteorological Forcing at Two Subalpine Lakes. *Limnology and Oceanography* **34**: 310-323.
- Gurney, W. S. C. and R. M. Nisbet. 1998. *Ecological Dynamics*. Oxford University Press. New York City.
- Harmon, M. E., D. L. Phillips, J. Battles, A. Rassweiler, R. O. Hall and W. K. Lauenroth. 2007. Quantifying uncertainty in net primary production measurements. *Pages 238 – 260, in: T. J. Fahey and A. K. Knapp, editors. Principles and standards for measuring primary production*. Oxford University Press. New York.
- Hofmann, G. E., C. A. Blanchette, E. B. Rivest and L. Kapsenberg. 2013. Taking the pulse of marine ecosystems: the importance of coupling long-term physical and biological observation in the context of global change biology. *Oceanography* **26**(3): 140-148.
- Jackson, G. A. 1987. Modelling the growth and harvest yield of the giant kelp *Macrocystis pyrifera*. *Marine Biology* **95**: 611-624.
- Kudela, R., and R. C. Dugdale. 2000. Nutrient regulation of phytoplankton productivity in Monterey Bay, California. *Deep-Sea Research II* **47**:1023-1053.
- Knapp, A. K. and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* **291**: 481-484.
- Leith, H., and R. H. Whittaker. 1975. *Primary productivity of the biosphere*. Springer-Verlag, New York.
- Mann, K. H. 1973. Seaweeds: their productivity and strategy for growth. *Science* **182**: 975-981.
- McPhee-Shaw, E. E., D. A. Siegel, L. Washburn, M. A. Brzezinski, J. L. Jones, A. Leydecker, and J. Melack. 2007. Mechanisms for nutrient delivery to the inner shelf: Observations from the Santa Barbara Channel. *Limnology and Oceanography* **52**: 1748-1766.
- Miller, R. J., D. C. Reed, and M. A. Brzezinski. 2011. Partitioning of primary production among giant kelp (*Macrocystis pyrifera*), understory macroalgae, and phytoplankton on a temperate reef. *Limnology and Oceanography* **56**: 119-132.
- Morton, D. N., T. W. Bell and T. W. Anderson. 2016. Spatial synchrony of amphipods in giant kelp forests. *Marine Biology* **163**: 32.
- North, W. J. 1994. Review of *Macrocystis* biology. *Pages 447– 527 in: I. Akatsuka, editor. Biology of economic algae*. SPB Academic, The Hague, The Netherlands.
- Rassweiler, A., K. K. Arkema, D. C. Reed, M. A. Brzezinski and R. C. Zimmerman. 2008. Net primary production, growth and standing crop of *Macrocystis pyrifera* in southern California. *Ecology* **89**: 2068.

- Rassweiler A., S. Harrer, D. Reed, J. Nelson. 2018. SBC LTER: REEF: Net primary production, growth and standing crop of *Macrocystis pyrifera* in Southern California. Environmental Data Initiative.  
<http://dx.doi.org/10.6073/pasta/7c99effc9ca052b92cb5979bb3cff48e>.
- Rassweiler A., G. Rodriguez, S. Harrer, D. Reed. 2017. SBC LTER: REEF: *Macrocystis pyrifera* blade area and loss in Southern California. Environmental Data Initiative.  
<http://doi.org/10.6073/pasta/2d78cd888e92b4cef8615e60a9aab83d>.
- Reed, D. C., A. Rassweiler, and K. K. Arkema. 2008. Biomass rather than growth rate determines variation in net primary production by giant kelp. *Ecology* **89**: 2493-2505.
- Reed, D. C. and M. A. Brzezinski. 2009. Kelp forests. *in*: The management of natural coastal carbon sinks. Laffoley, D. and G. Grimsditch, eds. International Union for Conservation of Nature (IUCN).
- Reed, D. C., A. Rassweiler, and K. K. Arkema. 2009. Density derived estimates of standing crop and net primary production in the giant kelp *Macrocystis pyrifera*. *Marine Biology* **156**: 2077-2083.
- Reed, D. C., A. Rassweiler, M. H. Carr, K. C. Cavanaugh, D. P. Malone and D. A. Siegel. 2011. Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. *Ecology* **92**: 2108-2116.
- Reed, D. C., C. A. Carlson, E. R. Halewood, J. C. Nelson, S. L. Harrer, A. R. Rassweiler and R. J. Miller. 2015a. Patterns and controls of reef-scale production of dissolved organic carbon by giant kelp *Macrocystis pyrifera*. *Limnology and Oceanography* **60**: 1996-2008.
- Reed, D. C., A. R. Rassweiler, R. J. Miller and S. J. Holbrook. 2015b. The value of broad temporal and spatial perspective in understanding dynamics of kelp forest ecosystems. *Marine and Freshwater Research* **67**: 14-24.
- Reed, D. C., L. Washburn, A. Rassweiler, R. Miller, T. Bell and S. Harrer. 2016. Extreme warming challenges sentinel status of kelp forests as indicators of climate change. *Nature Communications* **7**: 13757.
- Reed D. 2017. SBC LTER: Kelp Removal Experiment: Daily photon irradiance at the surface and seafloor. Environmental Data Initiative.  
<http://dx.doi.org/10.6073/pasta/ca886073ad26a1df6d6b9b0d1750e49b>.
- Rodriguez, G. E., A. Rassweiler, D. C. Reed and S. J. Holbrook. 2013. The importance of progressive senescence in the biomass dynamics of giant kelp (*Macrocystis pyrifera*). *Ecology* **94**: 1848-1858.
- Rodriguez, G. E., D. C. Reed and S. J. Holbrook. 2016. Blade life span, structural investment, and nutrient allocation in giant kelp. *Oecologia* **182**: 397.
- Schiel, D. R., and Foster, M. S. (2015). The biology and ecology of giant kelp forests. University of California Press.
- Stewart, H. L., J. P. Fram, D. C. Reed, S. L. Williams, M. A. Brzezinski, S. MacIntyre and B. P. Gaylord. 2009. Differences in growth, morphology, tissue carbon and

- nitrogen of *Macrocystis pyrifera* within and at the outer edge of a giant kelp forest in California, USA. Marine Ecology Progress Series **375**: 101-112.
- Tait L.W, and Schiel D.R. (2011) Dynamics of productivity in naturally structured macroalgal assemblages: importance of canopy structure on light-use efficiency. Mar Ecol Prog Ser 421:97-107. <https://doi.org/10.3354/meps08909>.
- Vasquez, J.A. and Buschmann, A.H., 1997. Herbivore-kelp interactions in Chilean subtidal. Revista Chilena de Historia Natural 70:41-52.
- Webb, W. L., W. K. Lauenroth, S. R. Szarek, and R. S. Kinerson. 1983. Primary production and abiotic controls in forests, grasslands, and desert ecosystems in the United States. Ecology **64**:134-151.
- Wormersley, H. B. S. 1954. The species of *Macrocystis* with special reference to those on southern Australia coasts. University of California Publication of Botany **27**: 109-132.
- Young, M. A., K. C. Cavanaugh, T. W. Bell, P. T. Raimondi, C. A. Edwards, P. T. Drake, L. Erikson and C. Storlazzi. 2016. Environmental controls on spatial patterns in the long-term persistence of giant kelp in central California. Ecological Monographs **86**: 45-60.
- Yorke, C. E., R. J. Miller, H. M. Page and D. C. Reed. 2013. The relative importance of kelp detritus as a component of suspended particulate organic matter in giant kelp (*Macrocystis pyrifera*) forests. Marine Ecology Progress Series **493**: 113-125.
- Yunev, O.A., J. Carstensen, S. Moncheva, A. Khaliulin, G. Ærtebjerg, and S. Nixon. 2007. Nutrient and phytoplankton trends on the western Black Sea shelf in response to cultural eutrophication and climate changes. Estuarine Coastal and Shelf Science **74**: 63-76.