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NET PRIMARY PRODUCTION, GROWTH, AND STANDING CROP OF *MACROCYSTIS PYRIFERA* IN SOUTHERN CALIFORNIA

***Ecological Archives* E089-119**

Andrew Rassweiler,[1,5] Katie K. Arkema,[1] Daniel C. Reed,[2] Richard C. Zimmerman,[3] and Mark A. Brzezinski[4]

[1]*Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106 USA*
[2]*Marine Science Institute, University of California, Santa Barbara, California 93106 USA*
[3]*Department of Ocean, Earth, and Atmospheric Sciences, Old Dominion University, 4600 Elkhorn Avenue, Norfolk, Virginia 23529 USA*
[4]*Department of Ecology, Evolution, and Marine Biology, and the Marine Science Institute, University of California, Santa Barbara, California 93106 USA*

Abstract. Marine macroalgae are believed to be among the most productive autotrophs in the world. However, relatively little information exists about spatial and temporal variation in net primary production (NPP) by these organisms. The data presented here are being collected to investigate patterns and causes of variation in NPP by the giant kelp, *Macrocystis pyrifera,* which is believed to be one of the fastest growing autotrophs on earth. The standing crop and loss rates of *M. pyrifera* have been measured monthly in permanent plots at three sites in the Santa Barbara Channel, USA. Collection of these data began in June 2002 and is ongoing. Seasonal estimates of NPP and growth rate are made by combining the field data with a model of kelp dynamics. The purpose of this Data Paper is to make available a time series of *M. pyrifera* NPP, growth, and standing crop that is appropriate for examining seasonal and interannual patterns across multiple sites. Data on plant density in each plot and censuses of fronds on tagged plants at each site are also made available here. NPP, mass-specific growth rate, and standing crop are presented in four different metrics (wet mass, dry mass, carbon mass, and nitrogen mass) to facilitate comparisons with previous studies of *M. pyrifera* and with NPP measured in other ecosystems. Analyses of these data reveal seasonal cycles in growth and standing crop as well as substantial differences in *M. pyrifera* NPP among sites and years.

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

The complete data sets corresponding to abstracts published in the Data Papers section of the journal are published electronically in *Ecological Archives* at ⟨http://esapubs.org/archive⟩. (The accession number for each Data Paper is given directly beneath the title.)

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[5]E-mail: rassweil@lifesci.ucsb.edu

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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 1984, 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. 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 consist of many fronds, each of which can exceed 25 m in length and grow as much as 0.5 m/d, making giant kelp one of the fastest growing autotrophs on earth (Clendenning 1971). These characteristics present logistical challenges for measuring giant kelp NPP. Furthermore, its rapid turnover rates coupled with high loss rates due to episodic disturbance from waves and sea urchin grazing necessitate frequent sampling. Previous 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_2 evolution, C_{14} 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 inadequate for evaluating interannual patterns across sites.

Here we present a unique ongoing data set of the standing crop, mass specific growth rate, and net primary production of *M. pyrifera* for three sites in the Santa Barbara Channel, USA. Our data consist of monthly field measurements of giant kelp standing crop and loss rates. We combine these data with a simple model of kelp dynamics to estimate specific growth rates and NPP for each season of each year. These methods in part follow a conceptual approach common in terrestrial studies, calculating NPP by measuring accumulation and loss of biomass. Our measurements reveal that relationships among wet mass, 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%, largely because of high variability in the mineral content of the tissue (authors' unpublished data). These 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*. We present our data in terms of wet mass, 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.

METADATA 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.

B. Data set identification code

M_pyrifera_net_primary_production_and_growth.txt

M_pyrifera_standing_crop_plant_density_and_loss_rates.txt

Census_of_fronds_on_marked_plants.txt

C. Data set description

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

Abstract: Marine macroalgae are believed to be among the most productive autotrophs in the world. However, relatively little information exists about spatial and temporal variation in net primary production (NPP) by these organisms. The data presented here are being collected to investigate patterns and causes of variation in NPP by the giant kelp, *Macrocystis pyrifera,* which is believed to be one of the fastest growing autotrophs on earth. The standing crop and loss rates of *M. pyrifera* are measured monthly in permanent plots at three sites in the Santa Barbara Channel, USA. Collection of these data began in June 2002 and is ongoing. Seasonal estimates of NPP and growth rate are made by combining the field data with a model of kelp dynamics. The purpose of this Data Paper is to make available a time series of *M. pyrifera* NPP, growth, and standing crop that is appropriate for examining seasonal and interannual patterns across multiple sites. Data on plant density in each plot and censuses of fronds on tagged plants at each site are also made available here. NPP, mass-specific growth rate, and standing crop are presented in four different metrics (wet mass, dry mass, carbon mass, and nitrogen mass) to facilitate comparisons with previous studies of *M. pyrifera* and with NPP measured in other ecosystems. Analyses of these data reveal seasonal cycles in growth and standing crop as well as substantial differences in *M. pyrifera* NPP among sites and

years.

D. ***Key words:*** *giant kelp; growth rate;* Macrocystis pyrifera*; marine algae; net primary production; 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: 2002–2006 (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.

Source(s) of funding: The collection of all data is funded by the National Science Foundation (awards OCE-9982105, OCE-0620276).

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 individual 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.

Site description: Data are collected at three kelp forests in the Santa Barbara Channel, California, USA: Arroyo Quemado (34^{o} 28.127' N, 120^{o} 07.285' W), Arroyo Burro (34^{o} 24.007' N, 119^{o} 44.663' W), and Mohawk (34^{o} 23.660' N, 119^{o} 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: Low-relief 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 top 1.3 m from the surface canopy. 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, 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 and 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 using field measurements and a simple model of kelp dynamics. We calculate NPP of *M. pyrifera* as the total amount of biomass produced during the period between each sampling date (approximately 1 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 being 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 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^2 and 480 m^2 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 individual plant into estimates of FSC in terms of wet mass, 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 loss rate of whole plants and of fronds on surviving plants.

Our field measurements of FSC and loss rate enable us to calculate the average mass specific growth rate of *M. pyrifera* on seasonal and annual time scales; limitations of the sampling methodology render our data less appropriate for examining patterns of growth over shorter time scales. 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 not sensitive 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 S).

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:

$$\mathrm{NPP} = \int_0^T g S_t \, dt$$

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, growth rate g and loss rate l ($S_t = S_0 e^{(g-l)t}$). 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 us:

Equation 5:

$$NPP = \frac{gS_0}{g-l}\left(e^{(g-l)T} - 1\right)$$

Beginning in spring 2002 we have used this approach to calculate NPP and specific growth rate seasonally at the three sites. Mean daily NPP and growth rate of *M. pyrifera* for each seasonare calculated as the average NPP and growth rate for all days in the season, where the rates for each day are the mean rates of the sampling interval in which the day occurs (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 g multiplied by the standing stock S). 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 data sets produced by an individual-based mathematical model of a kelp forest. We calculated NPP for each hypothetical data set using the approach outline above (Eq. 1 through 5) and compared the data 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 do not depend on the form of the growth model used.

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^2 (Arroyo Quemado and Mohawk) or 480 m^2 (Arroyo Burro) in area. We calculate FSC based on measurements taken of all *M. pyrifera* plants in the plot with at least 1 frond greater than 1 m in length. We characterize each plant using three distinct plant sections (Fig.1a). The "sub-surface" section consists of fronds that do not reach the surface, typically recently initiated fronds with small blades. 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 surface. This section usually has mature and senescent blades sparsely distributed along the stipe. The "canopy" section is the portion of these fronds which floats at the sea surface, typically consisting of mature blades spaced closely along the stipe.

For each plant within the sampling area we count the number of fronds 1 m above the holdfast (F_{1m}), the number of fronds at the surface ($F_{surface}$), 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, the amount of the longest frond which is floating at the surface). We use these data to calculate the length of each plant section, according to the following equations:

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

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

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

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 and returning 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 in the laboratory 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, $r^2 = 0.993$, 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* ($N = 147$, $r^2 = 0.986$, slope = 0.99).

While plants reaching the surface account for more than 90% of kelp biomass, young plants may have one or more fronds longer then 1 m, but no fronds reaching the surface (Figure 1b). For these plants, we measure N_{1m} (which is usually <6) and the length of each frond, recording 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 subsurface fronds when their mass and elemental composition is calculated (see below).

Less than 1% of the time, $N_{surface}$ and/or MAX can not be determined for a plant because it is tangled with neighboring plants. In these cases the total length of the plant is estimated based only on the number of fronds 1 m above the holdfast, which by itself predicts almost 90% of the variation in total length ($N = 55$ plants, $r^2 = 0.86$, slope = 0.98).

We estimate standing crop 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 2003. First, we separated the fronds from each plant into the three sections (canopy, water column, and subsurface) and measured their length and weight. Then we 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 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 10 to 15 different plants, approximately 2 m from the growing tip of a frond reaching the surface. 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^2 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 powered samples from all 10 to 15 blades are combined to form a composite sample for each site on each sampling date. The percent carbon and nitrogen 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 in the composite sample is used to convert dry mass of FSC to mass of carbon and nitrogen. Because these values are based on samples of blades from the canopy only, we developed a conversion factor for each element that allows us to calculate the elemental composition of FSC as a whole. The conversion factors are based on tissue samples taken from each section of 55 plants. The elemental compositions of subsurface, water column and canopy sections of these 55 plants are similar (differences are less than 5% of the mean), but on average carbon is 12% lower and nitrogen 44% lower in stipes than in blades. FSC is converted to units of carbon (C_{mass}) as follows:

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.

Measuring loss rate

Our calculations of net primary production incorporate two sources of lost biomass: the loss of entire plants and the loss of fronds from surviving plants. Frond loss occurs throughout the year; plants continuously lose biomass as old fronds senesce. Losses of whole plants are usually caused by water motion associated with large waves that rip plants off the bottom. Although losses occur sporadically, our approach focuses on the average probability of loss, and uses 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. The total loss rate of FSC (l) is thus the sum of the loss rate of plants (p) and of fronds from surviving plants (f): $l = p + f$.

We measure the loss of fronds on 10 to15 focal plants per site. We count all fronds on each focal plant at the beginning of each sampling interval, and attach a ziptie to the base of each counted frond to identify it. 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 period and tag these fronds to prepare for the next sampling period. 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 for each site during each period.

The loss rate of plants (p) is estimated similarly, using the same 10 to 15 plants that were tagged to estimate frond loss. Each plant is tagged with a unique ID, ziptied to its holdfast. We also map the location of each tagged plant so it can be easily re-identified if the tag is torn away. 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. More generally, equations 1 through 9 do not apply if complete extinction occurs.

Our calculations of NPP do not include losses arising from dissolved organic exudates or the loss of parts of fronds due to breakage, senescence and grazing. Partial frond loss due to grazing is thought to be relatively small (Gerard 1976), whereas the loss of dissolved organic matter (DOM) may constitute a substantial fraction of NPP (based on rates of DOM loss measured in other species of kelp; Abdullah and Fredriksen 2004, Wada et al. 2007). Loss rates of DOM have not been reported for *Macrocystis pyrifera*, but preliminary measurements done at one of our sites suggest losses of DOM may be substantial in this species as well (C. Carlson, *personal communication*). Because we neglect these losses, we are underestimating NPP to some degree.

Quantification of uncertainty/error estimation:

Our calculations of NPP are based on a set of underlying measurements, such as plant density and total plant length. These measurements have errors associated with them, including sampling, observer and regression errors, many of which we are able to estimate. Because these measurements are combined in a relatively complex way to calculate NPP, we use Monte Carlo methods to propagate the uncertainty in these measurements (Harmon et al. 2007). We generate 1,000 versions of the underlying data in which each data point is drawn from a distribution centered on the actual measurement. In some cases the distribution is based on independent measurements of observer errors and in other cases it is estimated from the variability in the actual data. The 1,000 data sets yield a distribution of calculated NPP values. We use the standard deviation of these values, which are distributed normally, as the standard error in our estimate of NPP. The same Monte Carlo process is used to estimate errors in standing crop, growth rate and loss rates.

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 Mike Anghera, Bryn Evans, Shannon Harrer, Brent Mardian, and Clint Nelson.

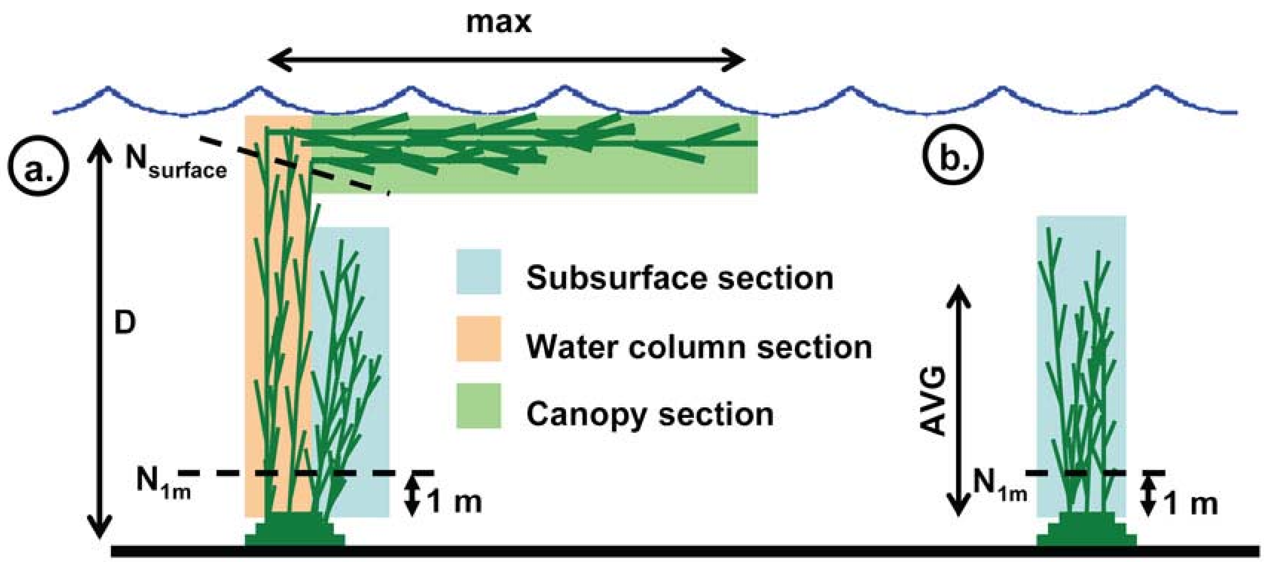

FIG. 1. Measurements taken to estimate the cumulative length of fronds in the three plant sections for: (a) kelp plants that reach the surface and (b) kelp plants that do not reach the surface.

CLASS III. DATA SET STATUS AND ACCESSIBILITY

A. Status

Latest Update: The data set currently spans the period from June 2002 to December 2006. Data collection is ongoing. Data will be added as collected and verified.

Latest Archive date: December 2006.

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 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: Daniel C. Reed, e-mail: reed@lifesci.ucsb.edu. Tel. 805 893 7047, Marine Science Institute, University of California, Santa Barbara, CA 93106 USA.

Copyright restrictions: None.

Proprietary restrictions: None.

Costs: None.

CLASS IV. DATA STRUCTURAL DESCRIPTORS

A. Data Set File

Identity:

(1) M. pyrifera net primary production and growth -- `M_pyrifera_net_primary_production_and_growth.txt`

(2) M. Pyrifera standing crop, plant density, and loss rates -- `M_pyrifera_standing_crop_plant_density_and_loss_rates.txt`

(3) Census of fronds on marked plants -- `Census_of_fronds_on_marked_plants.txt`

Size:

(1) M. pyrifera net primary production and growth -- 11 kb

(2) M. Pyrifera standing crop, plant density, and loss rates -- 27 kb

(3) Census of fronds on marked plants -- 53 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: Empty fields are denoted by -99999.

Authentication procedures: Sums of numeric columns are provided for each data set.

1) *M. pyrifera* net primary production and growth: Year = 108228, NPP_wet = 3.20891, NPP_dry = 0.29094, NPP_carbon = 0.08133, NPP_nitrogen = 0.005711, Growth_rate_wet = 1.03202, Growth_rate_dry = 1.04453, Growth_rate_carbon = 1.04916, Growth_rate_nitrogen = 1.06828, SE_NPP_wet = 0.62098, SE_NPP_dry = 0.05628, SE_NPP_carbon = 0.01677, SE_NPP_nitrogen = 0.00143, SE_growth_rate_wet = 0.18521, SE_growth_rate_dry = 0.18721, SE_growth_rate_carbon = 0.19294, SE_growth_rate_nitrogen = 0.22056.

2) *M. pyrifera* standing crop, plant density, and loss rates: FSC_wet = 586.99, FSC_dry = 53.73, FSC_carbon = 15.26, FSC_nitrogen = 1.0403, Plant_density = 66.35, Plant_loss_rate = 0.78314, Frond_loss_rate = 2.1072, SE_FSC_wet = 77.77, SE_FSC_dry = 6.8827, SE_FSC_carbon = 2.2367, SE_FSC_nitrogen = 0.22044, SE_plant_density = 6.3556, SE_plant_loss_rate = 0.473321, SE_frond_loss_rate = 0.50679.

3) Census of fronds on marked plants: Total_fronds = 45631, New_fronds = -27487431.

B. Variable information, variable definitions

Data set 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_wet: The seasonal rate of *M. pyrifera* biomass production in units of wet mass ($kg{\cdot}m^2{\cdot}d$). This variable is calculated by integrating the instantaneous rate of production during each period and dividing by the number of days (as described in Section I.B *Equation 2)*. Production for all days in each season is averaged.

NPP_dry: The seasonal rate of *M. pyrifera* biomass production in units of dry mass ($kg{\cdot}m^2{\cdot}d$). This variable is calculated by integrating the instantaneous rate of production during each period and dividing by the number of days (as described in Section I.B *Equation 2)*. Production for all days in each season is averaged.

NPP_carbon: The seasonal rate of *M. pyrifera* biomass production in units of carbon mass ($kg{\cdot}m^2{\cdot}d$). This variable is calculated by integrating the instantaneous rate of production during each period and dividing by the number of days (as described in Section I.B *Equation 2)*. Production for all days in each season is averaged.

NPP_nitrogen: The seasonal rate of *M. pyrifera* biomass production in units of nitrogen mass ($kg{\cdot}m^2{\cdot}d$). This variable is calculated by integrating the instantaneous rate of production during each period and dividing by the number of days (as described in Section I.B *Equation 2)*. Production for all days in each season is averaged.

Growth_rate_wet: The seasonal growth rate of *M. pyrifera* wet mass (d^{-1}). This variable is 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_dry: The seasonal growth rate of *M. pyrifera* dry mass (d^{-1}). This variable is 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 seasonal growth rate of *M. pyrifera* carbon mass (d^{-1}). This variable is 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_nitrogen: The seasonal growth rate of *M. pyrifera* nitrogen mass (d^{-1}). This variable is 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_wet: The standard error in our estimate of NPP in units of wet mass ($kg{\cdot}m^2{\cdot}d$). This error is produced using Monte Carlo methods, as described in Section I.B Quantifying Uncertainty. It incorporates errors in estimates of biomass, plant loss rates and frond loss rates.

SE_NPP_dry: The standard error in our estimate of NPP in units of dry mass ($kg{\cdot}m^2{\cdot}d$). This error is produced using Monte Carlo methods, as described in Section I.B Quantifying Uncertainty. It incorporates errors in our estimates of biomass, plant loss rates and frond loss rates.

SE_NPP_carbon: The standard error in our estimate of NPP in units of carbon mass ($kg{\cdot}m^2{\cdot}d$). This error is produced using Monte Carlo methods, as described in Section I.B Quantifying Uncertainty. It incorporates errors in our estimates of biomass, plant loss rates and frond loss rates.

SE_NPP_nitrogen: The standard error in our estimate of NPP in units of nitrogen mass ($kg{\cdot}m^2{\cdot}d$). This error is produced using Monte Carlo methods, as described in Section I.B Quantifying Uncertainty. It incorporates errors in our estimates of biomass, plant loss rates and frond loss rates.

SE_growth_rate_wet: The standard error in our estimate of the growth rate of wet mass (d^{-1}). These data are produced using Monte Carlo methods, as described in Section I.B Quantifying Uncertainty. The error in our estimate of growth incorporates errors in our calculations of biomass, plant loss rates and frond loss rates.

SE_growth_rate_dry: The standard error in our estimate of the growth rate of dry mass (d^{-1}). These data are produced using Monte Carlo methods, as described in Section I.B Quantifying Uncertainty. The error in our estimate of growth incorporates errors in our calculations of biomass, plant loss rates and frond loss rates.

SE_growth_rate_carbon: The standard error in our estimate of the growth rate of carbon mass (d^{-1}). These data are produced using Monte Carlo methods, as described in Section I.B Quantifying Uncertainty. The error in our estimate of growth incorporates errors in our calculations of biomass, plant loss rates and frond loss rates.

SE_growth_rate_nitrogen: The standard error in our estimate of the growth rate of nitrogen mass (d^{-1}). These data are produced using Monte Carlo methods, as described in Section I.B Quantifying Uncertainty. The error in our estimate of growth incorporates errors in our calculations of biomass, plant loss rates and frond loss rates.

Table 1. *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	2002–2006	N/A
Season	Sampling season	N/A	Character	N/A	N/A
NPP_wet	Net primary production of wet mass per m^2 per day	kg $m^{-2}d^{-1}$	Numeric	0.00033–0.25838	-99999
NPP_dry	Net primary production of dry mass per m^2 per day	kg $m^{-2}d^{-1}$	Numeric	$2.168*10^{-5}$–0.021273	-99999
NPP_carbon	Net primary production of carbon mass per m^2 per day	kg $m^{-2}d^{-1}$	Numeric	$6.19*10^{-6}$–0.006167	-99999
NPP_nitrogen	Net primary production of nitrogen mass per m^2 per day	kg $m^{-2}d^{-1}$	Numeric	$5.95*10^{-7}$–0.000384	-99999
Growth_rate_wet	Growth of new wet mass per day per wet mass of kelp	day^{-1}	Numeric	0.001693–0.04987	-99999
Growth_rate_dry	Growth of new dry mass per day per dry mass of kelp	day^{-1}	Numeric	0.00333–0.05504	-99999
Growth_rate_carbon	Growth of new carbon mass per day per carbon mass of kelp	day^{-1}	Numeric	0.00515–0.05583	-99999
Growth_rate_nitrogen	Growth of new nitrogen mass per day per nitrogen mass of kelp	day^{-1}	Numeric	0.00429–0.04841	-99999
SE_NPP_wet	Standard error in the net primary production of wet mass	kg m^{-2} d^{-1}	Numeric	$9.88*10^{-5}$–0.04818	-99999
SE_NPP_dry	Standard error in the net primary production of dry mass	kg m^{-2} d^{-1}	Numeric	$7.36*10^{-6}$–0.00416	-99999
SE_NPP_carbon	Standard error in the net primary production of carbon mass	kg m^{-2} d^{-1}	Numeric	$1.99*10^{-6}$–0.00112	-99999
SE_NPP_nitrogen	Standard error in the net primary production of nitrogen mass	kg m^{-2} d^{-1}	Numeric	$2.06*10^{-7}$–$8.74*10^{-5}$	-99999
SE_growth_rate_wet	Standard error in the growth rate of wet mass	day^{-1}	Numeric	0.00131–0.00721	-99999
SE_growth_rate_dry	Standard error in the growth rate of dry mass	day^{-1}	Numeric	0.00133–0.007198	-99999
SE_growth_rate_carbon	Standard error in the growth rate of carbon mass	day^{-1}	Numeric	0.001496–0.007164	-99999
SE_growth_rate_nitrogen	Standard error in the growth rate of nitrogen mass	day^{-1}	Numeric	0.002405–0.00748	-99999

Data set 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_wet: The wet mass of the foliar standing crop of *M. pyrifera* (kg/m^2, excluding sporophylls and holdfast). These data are obtained by first calculating the wet mass of each plant, using methods detailed in Section I.B *Measuring standing crop*, and then dividing the total wet 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_dry: The dry mass of the foliar standing crop of *M. pyrifera* (kg/m^2, excluding sporophylls and holdfast). These data are obtained by first calculating the dry mass of each plant, using methods detailed in Section I.B *Measuring standing crop*, and then 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* (kg/m^2, excluding sporophylls and holdfast). These data are obtained by first calculating the carbon mass of each plant, using methods detailed in Section I.B *Measuring standing crop*, and then 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* (kg/m^2, excluding sporophylls and holdfast). These data are obtained by first calculating the nitrogen mass of each plant, using methods detailed in Section I.B *Measuring standing crop*, and then 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.

Plant_density: The density of *M. pyrifera* plants in the plot ($no./m^2$). Plants without at least one frond longer than 1m are excluded.

Plant_loss_rate: The loss rate of *M. pyrifera* plants during the sampling interval (fraction of plants lost/day). These data are based on losses of 10 to15 tagged plants, as described in Section I.B *Measuring loss rate.*

Frond_loss_rate: The average loss rate of fronds during the sampling interval (fraction of fronds lost/day). These data are the mean loss rate of tagged fronds from 10 to15 tagged plants, as described in Section I.B *Measuring loss rate*. The mean is based on frond loss from plants that survive the period; losses of whole plants are accounted for in the plant loss rate.

SE_FSC_wet: The standard error in our estimate of foliar standing crop in units of wet mass (kg/m^2). This estimate is produced using Monte Carlo methods, as described in Section I.B Quantifying Uncertainty. The error in wet mass includes two types of 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 conversion ratio.

SE_FSC_dry: The standard error in our estimate of foliar standing crop in units of dry mass (kg/m^2). This estimate is produced using Monte Carlo methods, as described in section I.B Quantifying Uncertainty. The error in dry mass includes two types of 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 in our estimate of foliar standing crop in units of carbon mass (kg/m^2). This estimate is produced using Monte Carlo methods, as described in Section I.B Quantifying Uncertainty. The error in carbon mass includes two types of 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 in our estimate of foliar standing crop in units of nitrogen mass (kg/m^2). This estimate is produced using Monte Carlo methods, as described in Section I.B Quantifying Uncertainty. The error in nitrogen mass includes two types of 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_plant_density: The standard error in our estimate of *M. pyrifera* plant density ($no./m^2$). Error in plant density reflects variation in the total number of plants sampled in a plot. This estimate is produced by comparing repeated sampling by different observers of a single plot.

SE_plant_loss_rate: The standard error in our estimate of *M. pyrifera* plant loss (day^{-1}). This error is sampling error associated with calculating a mean loss rate for the entire plot based on 10 to15 tagged plants.

SE_frond_loss_rate: The standard error in the calculated rate of frond loss (day^{-1}**).** This error is sampling error associated with calculating a mean loss rate for the entire plot based on 10 to 15 tagged plants.

Table 2. *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_wet	Foliar standing crop in units of wet mass per m^2	kg/m^2	Numeric	0.01664–17.68	-99999

FSC_dry	Foliar standing crop in units of dry mass per m^2	kg/m^2	Numeric	0.001245–1.659	-99999
FSC_carbon	Foliar standing crop in units of carbon mass per m^2	kg/m^2	Numeric	0.00032–0.44858	-99999
FSC_nitrogen	Foliar standing crop in units of nitrogen mass per m^2	kg/m^2	Numeric	0.00002978–0.0402	-99999
Plant_density	Density of plants	$no./m^2$	Numeric	0.002083–2.285	-99999
Plant_loss_rate	Instantaneous loss rate of plants	day^{-1}	Numeric	0–0.0380	-99999
Frond_loss_rate	Instantaneous loss rate of fronds	day^{-1}	Numeric	0.002964–0.043378	-99999
SE_FSC_wet	Standard error in our estimate of foliar standing crop in units of wet mass	kg/m^2	Numeric	0.004915–2.84	-99999
SE_FSC_dry	Standard error in our estimate of foliar standing crop in units of dry mass	kg/m^2	Numeric	0.0003763–0.2432	-99999
SE_FSC_carbon	Standard error in our estimate of foliar standing crop in units of carbon mass	kg/m^2	Numeric	0.00009916–0.074383	-99999
SE_FSC_nitrogen	Standard error in our estimate of foliar standing crop in units of nitrogen mass	kg/m^2	Numeric	0.00001027–0.00844	-99999
SE_plant_density	Standard error in the density of plants	$no./m^2$	Numeric	0.0002472–0.22285	-99999
SE_plant_loss_rate	Standard error in the loss rate of plants	day^{-1}	Numeric	0–0.01570	-99999
SE_frond_loss_rate	Standard error in the loss rate of fronds	day^{-1}	Numeric	0.0005939–0.014558	-99999

Data set 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 both 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 period, or were not yet 1-m 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 3. 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	0–110	-99999
New_fronds	Number of new fronds on the plant since the last sampling date.	no. fronds	Numeric	0–51	-99999

CLASS V. SUPPLEMENTAL DESCRIPTORS

A.Data acquisition

Data forms: XEROX "Never tear" paper.

Location of completed data forms: Marine Science Institute, University of California, Santa Barbara, CA 93101

Data entry/verification procedures: Divers are supplied with slates with "Never Tear" paper to record all data in the field. Data are then entered into a computer 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: Wave data for region available from the coastal data information program (CDIP; Goleta Point buoy; station 107). Bottom temperature for each site is recorded by loggers (2002–present).

D. Computer programs and data processing algorithms: SAS data validation and analysis programs are held at Marine Science Institute, University of California, Santa Barbara.

E. Archiving: N/A

F. Publications using the data set: Harmon et al. (2007), McPhee-Shaw (*in press*), and D. C. Reed, A. Rassweiler, and K. K. Arkema. 2008. Biomass rather than growth rate determines variation in net primary production by giant kelp. *Ecology* 89:*in press*.

G. History of data set usage

H. Data set update history: N/A

Review history: N/A

Questions and comments from secondary users: N/A

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[Back to E089-119]