The importance of progressive senescence in the biomass dynamics of giant kelp (Macrocystis pyrifera)

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The importance of progressive senescence in the biomass dynamics of giant kelp (*Macrocystis pyrifera*)

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Abstract. Temporal variation in primary producer biomass has profound effects on the structure and function of the surrounding ecological community. The giant kelp (*Macrocystis pyrifera*) exhibits strong intra-annual variation in biomass density, which is better explained by the demographic rates of fronds than by those of whole plants. To better understand the processes controlling the dynamics of giant kelp fronds we collected monthly time-series data of frond initiation and survival. These data were used to determine how frond loss and frond initiation rates were predicted by factors thought to affect the growth and survival of *Macrocystis*, including external environmental factors (i.e., wave height, day length, temperature, nutrient concentration, and neighborhood density) and intrinsic biological characteristics (i.e., frond age, plant size, and nutritional status). Our results revealed that frond dynamics were better explained by intrinsic biological processes rather than external environmental factors. A metric of frond age structure that incorporated progressive senescence was the best predictor of frond loss rate, accounting for 58% of the explained variation in frond loss. A similar analysis revealed that frond age structure was also the single best predictor of frond initiation rate, accounting for 46% of the explained variation. To further examine the importance of senescence in biomass dynamics, we used frond age-dependent mortality and frond initiation rates to predict biomass in subsequent months and found that the model explained 73% of the observed variation in biomass at our sites. Vegetation dynamics of many species including giant kelp are often considered largely in the context of external controls on resource availability and physical disturbance. Our results indicate that investigations of the processes controlling vegetation dynamics may benefit greatly from the inclusion of intrinsic biological factors such as age-dependent mortality and growth, which can outweigh the effects of external forcing in accounting for fluctuations in vegetation biomass.

Key words: demography; frond; initiation rate; life span; loss rate; macroalgae; Macrocystis pyrifera; *primary producer biomass; progressive senescence; Santa Barbara, California, USA; turnover; vegetation dynamics.*

INTRODUCTION

Temporal variation in primary producer biomass is an important feature of many communities because of its potential to greatly affect the structure and function of entire ecosystems. Changes in primary producer biomass can have cascading effects on higher trophic levels by altering the supply of food or the availability of habitat for foraging, reproduction, and rearing of offspring (Hairston et al. 1960, Ostfeld and Keesing 2000, Yang et al. 2010). The effects of changes in plant biomass extend beyond the immediate community, as they affect rates of carbon and nutrient cycling in the soil (Jackson et al. 2000) and control runoff, soil erosion, and climate across a wide range of spatial scales (Molina et al. 2007, Niyogi et al. 2009). Therefore, knowledge of the factors

underlying producer biomass dynamics is fundamental to ecology.

In many systems plant biomass fluctuates erratically in response to disturbances such as outbreaks of herbivores and diseases, fire, and severe weather conditions (White 1979, Laska 2001). These irregular changes in vegetation occur against a background of more regular fluctuations in the accrual and loss of biomass that happen in response to changes in day length, temperature, and resource availability (Chapin and Shaver 1985). While the seasonal accrual of biomass results from conditions that favor germination and growth, seasonal loss of biomass in perennial evergreen species typically reflects the demise of leaves that are continually replaced when they reach the end of their natural life span, a process termed "progressive senescence" (Leopold 1961). Progressive senescence, and the factors that influence it, may be especially important to variations in biomass, especially in the absence of severe disturbance.

1848

Progressive senescence may be regulated in plants to optimize energetic gains and resource use such that leaves with higher construction costs or lower rates of photosynthesis tend to live longer (Reich et al. 1999). Slow growing woody plants that are subjected to conditions of low nutrients and limited light have predictably longer leaf life spans than herbaceous, fast-growing plants in areas with ample nutrients and light (Tsuchiya 1991, Reich et al. 1992, 1999). An abundance of resources promotes high rates of photosynthesis and decreases the "payback time" for the construction costs of leaves, resulting in frequent leaf initiation and high leaf turnover as new leaves overgrow older ones (Kikuzawa and Ackerly 1999). Variation in the supply of resources leads to fluctuations in biomass production, leaf demography, and leaf turnover (Dennison and Alberte 1982, Aerts and de Caluwe 1995, Hikosaka 2003, 2005, Herbert and Fourqurean 2009). Despite this understanding of progressive senescence in terrestrial and aquatic plants, surprisingly little is known about this process in macroalgae, which support some of the earth's most productive ecosystems (Mann 2000). Most studies of biomass dynamics of marine macroalgae have focused on the effects of mechanical (wave) disturbance, nutrient stress, temperature, and grazing (Dayton 1985, Lobban et al. 1985, Schiel and Foster 1986). We are not aware of any studies that have examined the life spans of blades and fronds of perennial macroalgae in the context of progressive senescence and the extent to which loss of these parts contribute to seasonal biomass fluctuations.

The giant kelp *Macrocystis pyrifera* is a dominant perennial macroalga on shallow temperate reefs in the eastern Pacific and Southern Oceans. It forms extensive forests that undergo large intra- and interannual fluctuations in biomass due to disturbance from waves, grazing, nutrient starvation, and temperature stress (reviewed in Foster and Schiel 1985, North 1994, Graham et al. 2007). Much of the focus of investigations of biomass fluctuations of giant kelp has emphasized the role of these processes in removing entire individuals. However, the rates of individual plant loss and replacement cannot account for the high biomass turnover of *Macrocystis*, which has been estimated to replace its biomass six to seven times per year (Reed et al. 2008). This suggests that a significant portion of the biomass turnover in giant kelp may stem from its pattern of year-round growth coupled with progressive senescence of fronds and blades. Although the density of fronds has been shown to be a better predictor of *Macrocystis* biomass than the density of plants (Reed et al. 2009), the extent to which temporal variation in frond turnover contributes to biomass dynamics in giant kelp has yet to be examined.

Here we examined progressive senescence in giant kelp by exploring patterns and drivers of frond loss and initiation to gain a better understanding of biomass turnover. Cohorts of fronds on selected plants were followed monthly at three shallow subtidal reefs near Santa Barbara, California, USA, over a three-year period to determine their initiation rates, loss rates, and longevity. These data enabled us to examine the relative contributions of plant loss and frond loss to the biomass dynamics of giant kelp. We also examined the extent to which age-dependent mortality predicts frond cohort survivorship, and evaluated the amount of variation in loss rates and initiation rates of fronds explained by external environmental factors (temperature, nutrients, wave height, day length, density dependence, and location) and intrinsic biological processes (frond age structure and predictable life spans, nutritional status, and plant size). Finally, we used frond age-dependent mortality and frond initiation rates in a model to explain variation in biomass beyond the three-year cohort data set. Our results revealed that biomass dynamics of giant kelp are best explained by variation in the density of fronds and that intrinsic biological processes pertaining to age-dependent mortality (i.e., senescence), rather than external environmental factors, play a more important role in controlling frond dynamics.

METHODS

Focal organism and study site

The giant kelp, *Macrocystis pyrifera*, is the world's largest alga and displays some of the fastest elongation rates on record for any terrestrial or marine autotroph (Clendenning 1971). Its photosynthetic blades and gas-filled pneumatocysts are attached to rope-like stipes (collectively referred to as fronds) that extend throughout the water column from a common benthic holdfast to the sea surface where they spread out to form a dense canopy. Fronds contain ~95% of the biomass of the plant (Neushul 1963, Towle and Pearse 1973), and mature plants typically consist of tens to a hundred or more fronds. As each frond ages, it eventually forms a terminal blade and ceases to elongate; this is followed by senescence and death (Lobban 1978). Much like entire plants, fronds may succumb to wave damage, herbivory, nutrient starvation, or temperature stress before the onset of senescence (North 1994).

We collected data on *Macrocystis* biomass density, plant survivorship, and frond demographics (i.e., frond initiation, survivorship, and life span) monthly from May 2002 to May 2005 using scuba at three reefs: Mohawk (34°23′40″ N, 119°43′48″ W), Arroyo Burro (34°24′00″ N, 119°44′40″ W), and Arroyo Quemado (34°28′08″ N, 120°07′17″ W). The reefs are located near Santa Barbara, California, USA, and dimensions of their kelp forests ranged from ~300 m (Arroyo Burro and Mohawk) to ~1500 m (Arroyo Quemado) in length (alongshore dimension) and ~200 to ~300 m in width (cross-shore dimension). Sampling was done in fixed plots at 6–8 m water depth within the kelp-forested area of each reef.

Fluctuations in biomass loss from plants and fronds

During each monthly sample period we recorded frond initiations and losses on 10–15 marked plants at each site. New plants were continuously added over the study period when marked plants died or disappeared to maintain a relatively constant sample size. When a plant was selected for sampling, all the fronds >1 m in length on that plant were tagged with a color-coded nylon cable tie and tracked until they disappeared. At each subsequent monthly sampling interval, all new fronds were tagged with a color that identified them as members of the same new cohort. All previously marked fronds were scored as present or absent. Monthly estimates of biomass density, frond initiation rates, and frond loss rates for each of the three sites were treated as independent measurements in all analyses.

We evaluated the relative contribution of frond loss and plant loss to overall changes in biomass density using multiple regression in which monthly change in biomass density was the response variable and net primary production (NPP), biomass lost as fronds, and biomass lost as plants were the independent variables. Biomass density, NPP, frond loss, and plant loss were estimated using the methods of Rassweiler et al. (2008). Briefly, we estimated the biomass density of kelp based on measurements of all plants >1 m tall within plots measuring either 200 m² (Arroyo Quemado and Mohawk) or 480 m² (Arroyo Burro). Mass lost as plants and fronds was calculated based on the observed survival of individually tagged fronds and plants. Growth rate was estimated for each sample from the change in biomass over the month and the observed loss rates. NPP for each period was calculated from the biomass density at the beginning of the period, and growth and loss rates during the period. The total variation explained by the multiple regression is expected to be very high because NPP is derived from measurements of biomass density and the loss rates of fronds and plants. While the total variation explained in this case is not very informative, knowledge of the relative importance of the independent variables is instructive in understanding the processes that contribute to biomass dynamics in giant kelp.

Age structure and frond dynamics

In addition to measuring frond loss and initiation rates, tracking tagged fronds until death allowed us to construct a distribution of frond life spans, which we used to predict frond loss rates from the population age structure. Only new fronds that were tagged in the month they grew >1 m tall were used to construct the life span distribution because it was not possible to accurately age fronds already present on plants when they were first tagged. For convenience, we describe fronds as being "initiated" when they reached 1 m in length. Fronds appearing on study plants were assumed to have been initiated midway between sampling periods, and were assigned a corresponding initial age.

For the purpose of our analyses the life span of a frond was considered to be the initial age plus the number of days between its initial observation and the first date it was not observed. Only fronds that disappeared from surviving plants were used to calculate frond loss rates and the frond life span distribution.

The distribution of frond life spans was approximated using a Weibull probability density function (PDF), which is commonly used to describe survivorship in systems that show age-dependent mortality (Gurney and Nisbet 1998):

Probability of frond loss at age t

$$= f(t; \lambda, k)$$

$$= \frac{k}{\lambda} \left(\frac{t}{\lambda} \right)^{k-1} e^{(t/\lambda)^k} \quad \text{when } t \geq 0 \quad (1)$$

where k is the shape parameter and λ is the scale parameter of the Weibull distribution, and t represents time (age). The shape parameter (k) indicates the strength of age-dependent mortality in the population of fronds. If $k > 1$, then mortality rates rise with age, if $k = 1$ then mortality is age independent, and if $k < 1$ then mortality rates decline with age. The scale parameter, also known as the critical age, represents the age at which ~63% of fronds are expected to have died for all values of k.

We used maximum likelihood ("stats" package; R Development Core Team 2012) to estimate the most likely shape (k) and scale (λ) parameters of the Weibull PDF, given our data on frond life span. This approximated life-span distribution function indicates the probability of loss at each age. We used this information to predict the expected fraction of fronds in a cohort that will survive to a given date by integrating this approximated life span distribution function from zero to the age of the cohort at the date of interest. We applied this relationship to a population of fronds of mixed age, estimating the number of fronds of each cohort expected to survive to a given sampling date based on the dates those fronds were first observed and summing across the cohorts. For each sampling date, we applied this technique to predict the number of fronds expected to be present:

Predicted surviving frond count

$$= \sum_{i=0}^{n} c_i \left(1 - \int_{0}^{a_t} f(t; \lambda, k) \, dt \right) \quad (2)$$

where k and λ are the maximum likelihood shape and scale parameters, c_i is the total number of fronds initially observed in cohort i (where cohorts are indexed by the number of months since first observed from 0 to n), t is the age of a cohort at any given time, a_t is the age of cohort i at the time of interest. Predicted daily frond loss rates for each sampling interval using these predicted frond counts were calculated as follows:

$$\text{Predicted frond loss rate} = \frac{1}{d}[\ln(\hat{S}_t/\hat{S}_0)] \qquad (3)$$

where d is the number of days in the sampling interval, $\hat{S}_0$ is the number of fronds predicted to be on the plant at the beginning of the sampling interval, and $\hat{S}_t$ is the number of fronds predicted to have survived from the beginning to the end of the sampling interval.

Similarly, we calculated the observed daily frond loss rates (i.e., the proportion of fronds dying per day) for each sampling period:

$$\text{Observed frond loss rate} = \frac{1}{d}[\ln(n_t/n_0)] \qquad (4)$$

where d is the number of days in the sampling interval, n_0 is the number of fronds on the plant at the beginning of the sampling interval, and n_t is the number of fronds surviving from the beginning to the end of the sampling interval. Note that Eq. 4 is identical to Eq. 3 except that the observed frond counts are used instead of the predicted frond counts.

Daily frond initiation rate was estimated using a linear model of monthly frond increase, as opposed to the exponential decay type model used in the frond loss calculations. This is because new fronds were not expected to contribute to the creation of new fronds until at least the next month, so initiation is not compounded within a sample period:

$$\text{Daily frond initiation rate} = \frac{1}{d}\left[\frac{F_n}{F_0}\right] \qquad (5)$$

where F_n is the number of fronds initiated during the sample period, F_0 is the number of fronds present at the beginning of the sample period, and d is the number of days in the sample period. As with frond loss rate, we assumed that frond initiation rate was the same for each day of the sample period.

Relative importance of intrinsic and external factors to frond dynamics

We evaluated the role of intrinsic biological processes and external environmental factors on frond loss and initiation rates using a multiple regression approach. Intrinsic characteristics included frond age structure, nutritional status, and plant size, each of which served as independent variables in the regression models. Different measures of age structure were used to predict frond loss rate and frond initiation rate. Because we have an explicit model of how frond age affects the probability of loss, we used frond loss rate predicted from frond age structure (referred to here as age-dependent mortality) as an explanatory variable in our regression analysis of frond loss rates. By contrast, because our data do not include information on how fronds of different ages contribute to the rate at which new fronds are produced, we could not formulate a model that explicitly related frond age to initiation rates. Hence, we used mean frond age as a general metric of age structure when assessing intrinsic processes affecting frond initiation rates. The

nitrogen content of the frond (expressed as a percentage of dry mass) was used as a measure of its nutritional status. Our estimates of nitrogen content are based on composite samples of ~15 5-cm^2 disks taken from a representative sample of blades from each site on each sampling date and processed with a CE-440 CHN/O/S elemental analyzer (Exeter Analytical, Chelmsford, Massachusetts, USA). The mean number of fronds per plant, calculated across all tagged plants, was used as a measure of plant size.

The external environmental factors used as independent variables in the multiple regression model examining drivers of frond dynamics were those known or suspected to influence giant kelp, including ocean waves, water temperature, biomass density of giant kelp in the surrounding area, seawater nitrogen concentration, day length, and site. We used the maximum significant wave height that occurred between sample dates to characterize disturbance from waves. Significant wave height (H_s) represents the mean of the largest one-third of the waves recorded in a 30-min interval. Wave data were obtained from the Coastal Data Information Program Monitoring and Prediction swell predictions nearest to the sample sites (available online).[4] Bottom temperature was recorded every 10 min using loggers (Stowaway Onset tidbits, accuracy ±0.2°C; Onset Computer, Bourne, Massachusetts, USA) placed at each site. Biomass density of giant kelp at each of the three study sites was measured at each sampling date using the methods of Rassweiler et al. (2008). Nitrogen is the nutrient that is thought to most frequently limit kelp growth (Jackson 1977, Gerard 1982). The ambient concentration of dissolved inorganic nitrogen (nitrate + nitrite) was estimated at each site using the temperature–nitrogen relationships reported in McPhee-Shaw et al. (2007) for our study region (based on the temperature measurements described in this paragraph). Although dissolved inorganic nitrogen estimates and temperature were derived from the same temperature loggers, the nonlinear and saturating relationship between the two variables and different parameter estimates for the different sites means that they serve substantially different roles within the multiple regression analysis. Day length is a good correlate of daily surface and bottom irradiance, which is known to influence growth in giant kelp at our study sites (Stewart et al. 2009). Day length is also an indicator of seasonality as it can be used to distinguish between summer and winter. Mean day length for each sample period was calculated from the U.S. Naval Oceanography sunrise/sunset tables. Site was included as an independent variable to assess random effects attributed to the study site location.
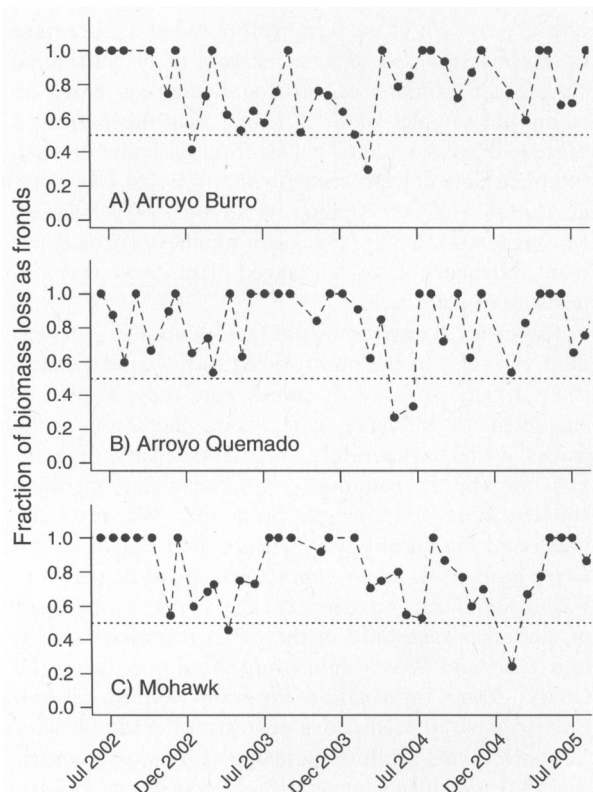
[4] http://cdip.ucsd.edu

FIG. 1. Monthly estimates of the *Macrocystis pyrifera* biomass lost as fronds from surviving plants as a fraction of the sum of biomass lost as whole plants and as fronds for the period May 2002–May 2005 at three study sites near Santa Barbara, California, USA. The dashed horizontal lines represent equal loss of biomass from fronds and plants.

Predicting biomass from age-dependent mortality and frond initiation

The age-dependent mortality relationship observed in our study suggested that kelp biomass might be explained as a function of frond initiation and programmed senescence. We tested this supposition by attempting to predict biomass density each month at our three sites from patterns of frond initiation by applying our expected age-dependent mortality relationship. We chose to evaluate this for a time period (August 2005 to April 2012) separate from that over which our age-dependent mortality relationship was calculated (May 2002 to May 2005) to avoid circularity and to extend the temporal inference of our results. We predicted the frond density for each month at each site from August 2005 to April 2012 using previous patterns of frond initiation and the age-dependent mortality. For each month, the proportion of new fronds in the sampled plants at each site was multiplied by the density of all fronds at the site (using the methods of Rassweiler et al. 2008) to estimate the density of newly initiated fronds. We applied the age-dependent mortality relationship to the density of newly initiated fronds for the previous five months to calculate the expected density of surviving

fronds in each month. Finally, we multiplied the expected density of surviving fronds by the mean dry mass of fronds (estimated in Rassweiler et al. 2008) to predict monthly biomass density. We compared these predicted values of biomass density to those that were observed to assess the importance of age-dependent mortality (i.e., senescence) on the variation in biomass over seven years at the three sites.

Statistical analyses

We used a stepwise model selection by AIC to select the most appropriate multiple regression model (Venables and Ripley 2002), from a full model containing all variables of interest for frond initiation and frond loss rates. We ranked predictor variables by importance according to the LMG method for deriving partial regression coefficients (Lindeman et al. 1980) and scaled the metrics to sum to 1 to assess the relative importance of fronds and plants to changes in biomass density and to assess the relative importance of individual intrinsic processes and external factors in frond initiation and loss. In addition to the factor's relative contribution to the final model, bivariate regressions were used to assess the independent explanatory power of each factor, and to illustrate the individual relationships between each independent variable and the response variable. Key assumptions of the multiple and bivariate regression analyses were tested and met; normality of residuals and linear relationships between explanatory and predicted variables were verified via residual analysis, and non-collinearity was verified using variance inflation factors (VIF) and tolerance values. All analyses were done using R version 2.15 (R Development Core Team 2012).

RESULTS

Biomass lost as plants and fronds

Biomass lost as fronds typically exceeded that lost as whole plants (Fig. 1). With the exception of a few relatively large spikes in plant loss that coincided with large wave events (3.64 m maximum H_s in November 2002 and 4.94 m maximum H_s in January 2004), biomass lost as plants was low; in many months it was zero. By contrast, at least some fronds were lost in all but one month of the study period (the lone exception was at Arroyo Burro in summer 2004 when total standing biomass was near zero), and total biomass lost as fronds was four times higher than that lost as plants when averaged over all sites and months (5.6 ± 0.57 vs. 1.3 ± 0.23 g dry mass·m^{-2}·d^{-1} for fronds and plants, respectively, mean ± SE, Wilcoxon signed rank test, W = 8692, P < 0.0001). Results from the multiple regression showed frond loss accounted for 53% of the explained variation in biomass density, NPP accounted for 27%, and plant loss 20% (model R^2 = 0.91). Collectively these results show that frond loss was the single best predictor of biomass dynamics of giant kelp at our sites.

Age structure and frond dynamics

Frond life span data show that loss did not occur randomly across age classes (Fig. 2A). Most fronds were lost three to four months after they reached a height of 1 m (frond age at death was 106 ± 0.60 d, mean ± SE, median age, 103 d). The pattern of frond cohort survivorship was consistent with age-dependent per capita mortality. Frond survivorship was relatively high for the first 75 d in most cohorts before dropping precipitously, with few fronds surviving more than 150 d (Fig. 2B). The maximum likelihood estimate of the critical age λ was 115.5 ± 0.56 d. The maximum likelihood estimate of the Weibull shape coefficient k (all sites pooled) was 3.12 ± 0.04, indicating survival dropped sharply as fronds approached the critical age λ. The fitted value $k = 3.12$ means that 23% of the fronds are expected to die within 10% of the critical age (103–127 d), compared to only 7% mortality during the same interval assuming age-independent mortality ($k = 1$). Within a site, the number of fronds predicted to survive to a given date based on the initiation history of fronds predicted 88% of the observed variation in the number of surviving fronds ($F_{1, 101} = 647.6$, $P < 0.0001$; Fig. 2C).

Relative importance of intrinsic and external factors to frond dynamics

Results of multiple regression analysis revealed that age-dependent mortality, maximum significant wave height, and random variation associated with site were the best predictors of frond loss rates. Collectively these three variables explained 47% of the observed variation in frond loss rates and formed the best regression model in terms of simplicity and explanatory power. Age-dependent mortality contributed 58% of the variation explained by the best-fit regression model (Fig. 3A) and accounted for 28% of the variation observed in frond loss rates when examined alone (Fig. 3B). Frond loss rate was positively related to maximum significant wave height (Fig. 3C) and accounted for 30% of the explained variation in the best-fit regression model. External factors relating to temperature, nutrient availability, day length, change in day length, and local biomass density did not explain any of the observed variation in frond loss rates, nor did intrinsic processes relating to plant size and nutritional status.

Results obtained for frond initiation rates were similar to those obtained for frond loss rates in that frond age structure was the single most important variable in accounting for the observed variation. Frond age, day length, wave height, biomass density, plant size, and temperature formed the best-fit regression model for predicting frond initiation rates and together explained 52% of the observed variation (Fig. 4A). Intrinsic biological factors associated with frond age structure (as determined by mean frond age), and plant size (as determined by the number of fronds) combined to account for 46% of the variation explained by the best-fit model (Fig. 4A) and 29% and 7% of the observed
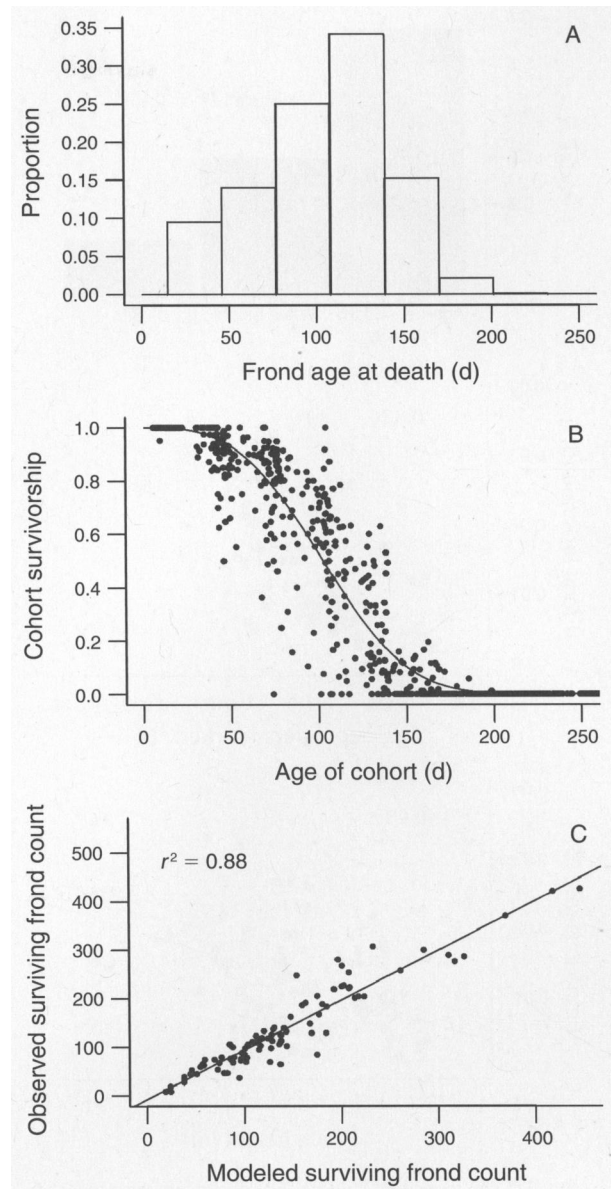

Fig. 2. Demographic data for *Macrocystis pyrifera* fronds near Santa Barbara, California, USA, collected from May 2002 to May 2005. (A) Histogram of frond life spans ($N = 4628$ fronds) binned by 31-day intervals (approximately monthly). (B) Survivorship of *Macrocystis pyrifera* frond cohorts by age with fitted Weibull cumulative density function. Note that each cohort appears in the graph several times as it ages ($N = 93$ cohorts). (C) Observed surviving fronds vs. predicted surviving fronds for each sample period. Modeled frond counts are based on age-dependent mortality derived from panel (B) and frond age structure.

variation in frond initiation rate, respectively, when evaluated independently (Fig. 4B, F). External environmental factors associated with day length, waves, biomass density, and temperature collectively accounted for the remainder of the variation explained by the best-fit model, and 21%, 9%, 12%, and 4% of the observed
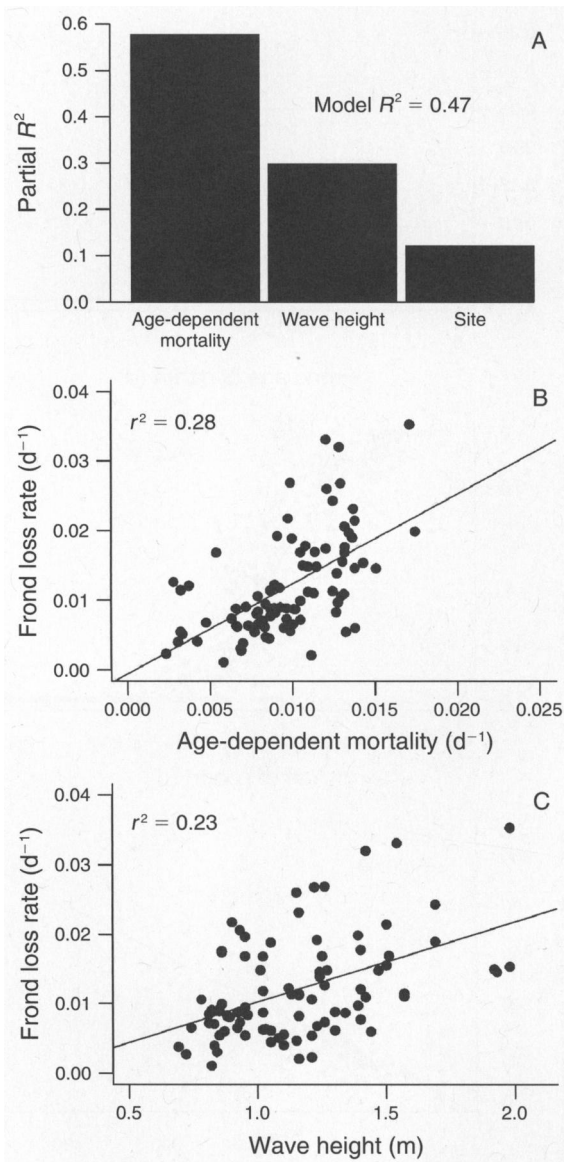
FIG. 3. (A) Partial R^2 values of the dependent variables that entered into the best-fit regression model for frond loss rates. The partial R^2 values sum to 1. (B, C) The bivariate relationships for (B) frond loss rate and frond age-dependent mortality and (C) frond loss rate and maximum significant wave height.

variation in frond initiation rates, respectively, when evaluated separately (Fig. 4C–E, G).

Predicting biomass from age-dependent mortality and frond initiation

Biomass density predicted from the age-dependent mortality relationship, frond initiation history, and mean frond mass explained over 73% of the observed variation in monthly biomass density at the three sites from 2005 to 2012 (Fig. 5). Further, the slope of the relationship between predicted biomass and observed biomass was near unity (slope = 1.23). This near one-to-

one relationship coupled with its high explanatory power corroborates the role of progressive senescence as a major determinant of biomass dynamics in giant kelp at our sites.

DISCUSSION

Most of the biomass lost by *Macrocystis* was lost as fronds from surviving plants and reductions in biomass were better explained by losses of fronds rather than entire plants. This pattern of high foliage turnover and plant persistence is not unique to kelp forests as it is the norm for perennial vascular plant systems, ranging from grasslands (Aerts and de Caluwe 1995), forests (Liski et al. 2006), and seagrass meadows (Duarte et al. 2006). However, the forces seaweeds must endure relative to many of their terrestrial counterparts set them apart as they routinely experience wave forces that are many times stronger than hurricane winds (Denny and Gaylord 2002). Given these large forces it is not surprising that the majority of studies pertaining to biomass declines in seaweeds have focused on the loss of entire plants by wave disturbance (Gaylord et al. 1994, Graham et al. 1997). We found that despite substantial losses of entire plants during periodic large wave events, most of the biomass loss in *Macrocystis* was attributed to the senescence and subsequent loss of fronds on surviving plants. This result and other recent work (Reed et al. 2008) illustrate the importance of investigating both fronds and whole plants when exploring patterns and controls of biomass dynamics in giant kelp.

Understanding the role of fronds in the biomass dynamics of giant kelp requires information on the turnover of fronds, which includes processes of frond initiation, senescence, and death. Like the leaves of many perennial evergreen species, *Macrocystis* fronds undergo progressive senescence; they are initiated continuously throughout the year as older fronds are shed when they approach a terminal age (Gerard 1976, van Tüssenbroek 1993; see *Results*). The rate of foliage turnover in vascular plants is thought to be related to leaf construction costs and resource availability (Reich et al. 1999, Hikosaka 2005). Vascular plants that have high foliage turnover and short leaf life spans typically have low construction costs and live in resource-rich environments (Reich et al. 1997, Herbert and Fourqurean 2009, van Ommen Kloeke et al. 2012). The values for life span that we observed for *Macrocystis* fronds are similar to those observed for shoots of fast-growing seagrasses in temperate regions (Duarte et al. 2006), perhaps due to similarities in construction costs and resource availability. Both giant kelp and seagrasses lack woody support structures so potentially have lower whole-plant construction costs, and both grow in aquatic environments where water is not limiting and nutrients are delivered in solution. Further study is required to assess construction costs and resource availability of seaweeds and seagrasses to determine whether leaf life span theory developed for terrestrial
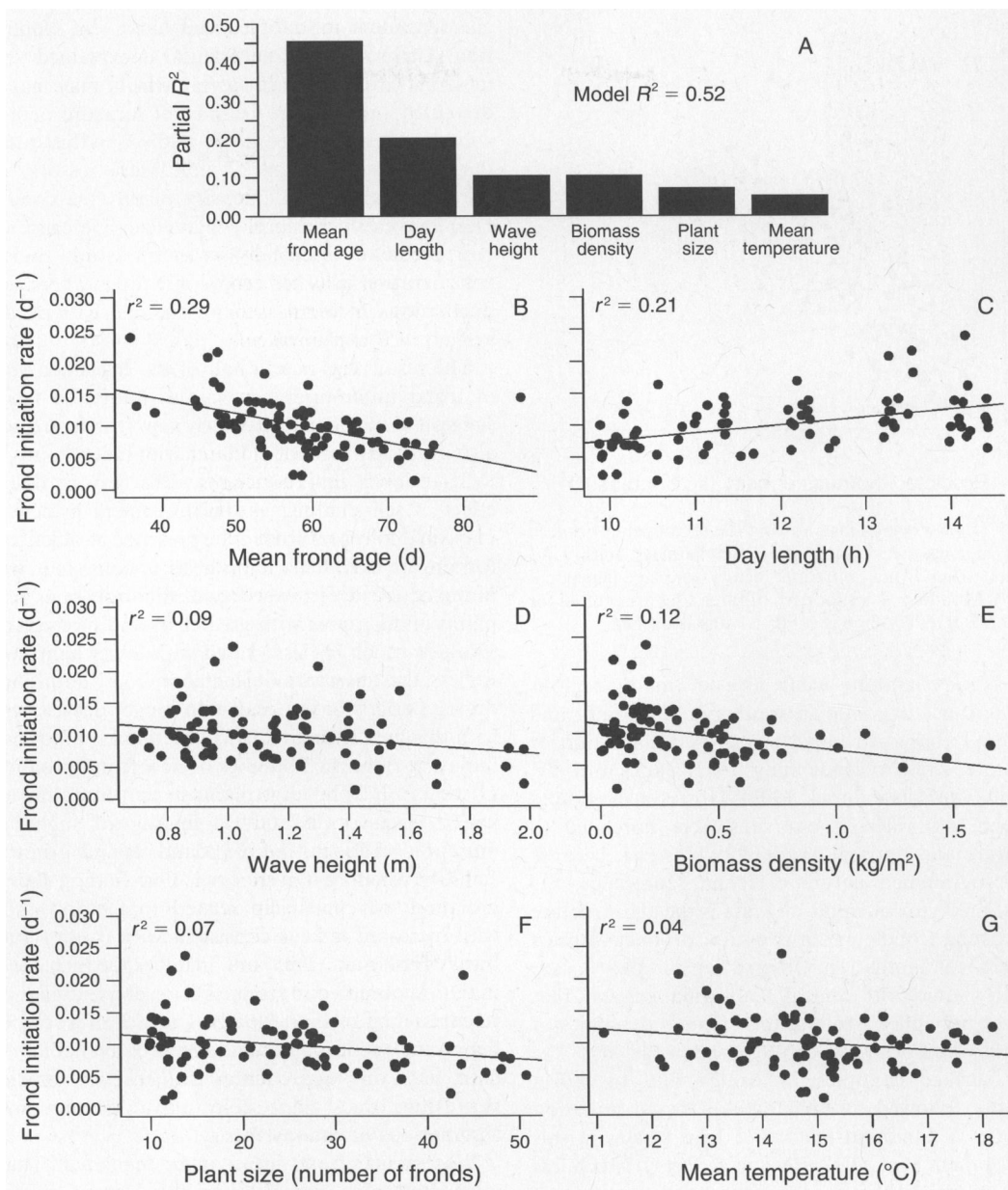
FIG. 4. (A) Partial R^2 values of the dependent variables that entered into the best-fit regression model for frond initiation rates. The partial R^2 values sum to 1. (B–G) The bivariate relationships between frond initiation rate and (B) mean frond age, (C) day length, (D) wave height, (E) biomass density, (F) plant size, and (G) temperature.

plants can be used to predict foliage turnover rates in marine systems.

A model of age-dependent mortality in which mortality rate rose with age fit our data remarkably well, suggesting that internal mechanisms, in addition to random or stochastic external events control frond loss in *Macrocystis*. We found that fronds age and die in a predictable fashion, and that age structure explained more variation in frond loss rates than did environmental factors associated with wave disturbance, temperature stress, seasonality, and the availability of light and nutrients. These environmental factors vary greatly in

magnitude across the broad geographic range of the species, which spans 120° latitude (Graham et al. 2007). *Macrocystis* is known to display a capacity for morphological and physiological adaption to local environmental conditions throughout its range (Gerard and Kirkmann 1984, Kopczak et al. 1991, Hurd et al. 1997, Graham et al. 2007), and the extent to which age-dependent mortality and senescence account for frond loss in *Macrocystis* in other regions may vary from that observed in our study.

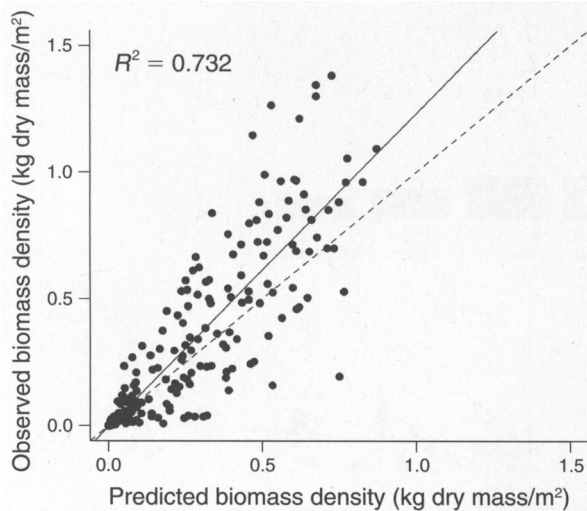A reduction in the surface canopy of *Macrocystis* during summer and autumn before the onset of winter

FIG. 5. Linear regression showing the relationship between observed biomass density and predicted biomass density (as determined from frond initiation history and age-dependent mortality). Monthly values for each of three sites are plotted for 2005–2012. Regression line is solid; 1:1 line is dashed.

storms is a common occurrence in many regions (including our study sites in southern California), and has generally been attributed to nitrogen starvation or temperature stress (Clendenning 1971, Jackson 1977, Hay 1990, van Tüssenbroek 1993). However, we found that frond loss rates at our sites were unrelated to temperature and nutrient availability. Instead, because of the programmed nature of frond senescence, the strongest predictor of frond loss rate is the age structure of the existing fronds, which is itself a product of prior patterns in frond initiation. Observations of *Macrocystis* canopy dynamics off central California suggest that senescence may play a role in the biomass dynamics of *Macrocystis* in more wave-exposed regions as well. The loss of surface canopies in winter due to storm disturbance followed by high rates of frond initiation in spring is a dominant feature of kelp forests in this region (Graham et al. 1997, Reed et al. 2011). Much less noted in central California, but nonetheless common, is the decline of the canopy in summer and autumn (Reed and Foster 1984, Donnellan 2004), despite relatively high levels of nutrients and low disturbance from waves and grazing during this time of year (Reed et al. 2011). Interestingly, the peak in frond loss that was attributed to low nutrients observed by van Tüssenbroek (1993) at the Falkland Islands, coincidently occurred approximately four months after the peak in frond initiation. Such declines are consistent with seasonal surges in frond initiation in spring that result in high frond loss rates in summer and autumn, if cohorts mature and senesce predictably.

Perhaps our strongest evidence for the importance of progressive senescence in the biomass dynamics of *Macrocystis* was our ability to predict 73% of the observed variation in biomass density at our sites from

age-dependent mortality and a history of frond initiation. There remained substantial unexplained variation in frond loss rates, however, which may have been driven by factors that we did not measure or by more complex effects than could be resolved in this study (e.g., the synergistic effects of multiple stressors, or the duration rather than intensity of adverse conditions). Despite these limitations, progressive senescence was the best predictor of frond loss in our study and merits consideration in other geographic areas where seasonal fluctuations in biomass (e.g., summer canopy decline) are not well explained.

The result that nearly half of the explained variation in frond initiation rates was attributed to frond age suggests that the rate at which new fronds are added is also internally regulated. Plants with older fronds tended to have lower initiation rates. This may be due to the effect of self-shading, as the investment in new fronds may yield lower returns in the presence of older, canopy-forming fronds. This hypothesis is consistent with the observed trend of lower frond initiation rates in larger plants and in areas with greater overall biomass density (both of which are associated with lower light levels) as well as the observation of higher frond initiation rates during periods of the year with longer days. Consistent with this are Gerard's (1976) observation of lower frond initiation rates (i.e., number of new frond produced per existing fronds) by large plants in central California and van Tuessenbroek's (1993) finding of higher frond initiation rates in the Falkland Islands during the summer when days were long. Our finding that frond initiation was positively related to factors associated with increased light is consistent with canopy turnover theory (Hikosaka 2005) and matches the increase in leaf initiation observed in seagrass in response to higher light (Dennison and Alberte 1982). The lack of a relationship between frond loss rates and resource availability in our data, however, runs counter to theoretical predictions, suggesting that giant kelp may violate some key assumptions of canopy theory.

Why should frond life span be regulated? The plant must somehow benefit from the loss of the energy already invested in the frond. It is likely that the cost of maintaining a frond increases as the frond ages. To retain a leaf or frond, a plant must continually invest resources to defend against herbivory, drag, fouling, and other environmental stresses. Even if these costs do not increase as the frond ages, studies on vascular plants show declining photosynthesis with leaf age in many species (Chabot and Hicks 1982, Kitajima et al. 1997), a phenomenon that also occurs in *Macrocystis* (Wheeler 1980). At some "optimal age," the marginal benefit of maintaining an existing frond is exceeded by the marginal benefit of producing a new frond.

Alternatively, fronds may be turned over to maximize photosynthetic gains in the canopy, as suggested by Kikuzawa (1991). Harper (1989) argued that earlier carbon gain by leaves may be favored over later gain

because early carbon gain can be reinvested quickly into new leaves, resulting in compounding returns. Higher construction costs, usually manifested as increased structural or chemical defense, decrease the production rate of leaf area (Coley et al. 1985), and result in predictably longer life spans (Reich et al. 1999, Hikosaka 2005).

Despite the importance of this iconic species, studies on the mechanisms regulating frond dynamics in *Macrocystis* have been lacking. Although the existence of senescence in giant kelp fronds has been widely recognized (Lobban 1978, North 1994, Graham et al. 2007), the high degree to which frond loss rates and biomass dynamics are a function of frond age structure has been generally underappreciated. Studies on terrestrial plants show that leaf life spans are predictable and consistent patterns in plant function exist across a broad diversity of species and biomes (Reich et al. 1997). Future studies on marine macroalgae may benefit from evaluating the applicability of theory derived from vascular plants and drawing on the wealth of research that has been done on them.

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