UNIVERSITY OF CALIFORNIA

Santa Barbara

Turnover dynamics of the giant kelp, *Macrocystis pyrifera*

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Ecology, Evolution and Marine Biology

by

Gabriel Eduardo Rodriguez

Committee in charge:
Professor Sally Holbrook, Chair
Professor Roger Nisbet
Dr. Daniel C. Reed

December 2014

The dissertation of Gabriel Eduardo Rodriguez is approved.

Daniel C. Reed

Roger Nisbet

Sally Holbrook, Committee Chair

June 2014

VITA OF GABRIEL EDUARDO RODRIGUEZ
June 2014

EDUCATION

Bachelor of Science, California State University Monterey Bay, June 2008 (cum laude with distinction)
Master of Arts in Ecology Evolution and Marine Biology, University of California, Santa Barbara, December 2012
Doctor of Philosophy in Ecology Evolution and Marine Biology, University of California, Santa Barbara, June 2014 (expected)

PROFESSIONAL EMPLOYMENT

2008-2014: Graduate Student Researcher, Santa Barbara Coastal Long Term Ecological Research
2010-2013: University of California Santa Barbara Associated Students Coastal Fund Research Grant Principal Investigator
2008-2014: Teaching Assistant, Department of Ecology Evolution and Marine Biology, University of California, Santa Barbara

PUBLICATIONS and PRESENTATIONS

Rodriguez, G. E., Rassweiler, A., Reed, D. C., & Holbrook, S. J. (2013). The importance of progressive senescence in the biomass dynamics of giant kelp (*Macrocystis pyrifera*). Ecology.

Rodriguez, G. E. Theory and experimentation on giant kelp frond lifetimes. ASLO Ocean Science Meeting, 2012, Salt Lake City, UT (Poster Presentation)

Rodriguez, G. E., Rassweiler, A., Reed, D. C., Holbrook, S. J Internal drivers of frond dynamics control the variability in the biomass of the giant kelp (*Macrocystis pyrifera*). ASLO Aquatic Science Meeting, 2011, San Juan, PR (Poster Presentation)

Rodriguez G.E. Patterns of birth and loss: What explains the biomass dynamics of the world's largest marine alga. Western Society of Naturalists Annual Meeting, 2010, San Deigo, CA (oral presentation)

Rodriguez, G. E., Rassweiler, A., Reed, D. C., Holbrook, S. J. Environmental drivers as sources of variation in the canopy biomass of *Macrocystis pyerifera*. ASLO Ocean Science Meeting, 2010, Portland, OR (Oral Presentation)

Rodriguez, G. E., Lonhart S I. GROWTH AND REPRODUCTION OF INVASIVE KELP SPOROPHYTES (UNDARIA PINNATIFIDA), MONTEREY HARBOR. ASLO Ocean Science Meeting, 2008, Orlando, FL (Oral Presentation)

Rodriguez G.E., Lonhart S. I. UNDARIA PINNATIFIDA GROWTH RATES AND DISTURBANCE RECOVERY IN MONTEREY HARBOR. Western Society of Naturalists Annual Meeting, 2007, Ventura, CA (oral presentation)

Rodriguez, G E ; Sulkin, S D. MANIPULATING NUTRITIONAL VALUE OF CRAB LARVAE (CANCER MAGISTER) PREY, THE ROTIFER (BRACHIONUS PLICATILIS) ASLO Aquatic Sciences Meeting 2007, Santa Fe, NM (Poster Presentation)

AWARDS

UCSB Coastal Fund Research Grant, 2010, 2012, 2013
American Society of Limnology and Oceanography, Multicultural Participation (ASLOMP) Travel Scholarships 2006, 2008, 2009, 2010, 2012
NSF Graduate Research Fellowship, 2008-2011
NOAA Hollings Scholarship, 2007-2008
McNair Scholarship, 2007-2008
Multicultural Students at Sea Together (MAST) Scholarship, 2006
Multicultural Initiative in Marine Science, Undergraduate Participation (MIMSUP) Scholarship, 2006
National Hispanic Environmental Council (NHEC) Traveling Scholarship, 2006
Louis Stokes Alliance for Minority Participation Scholar, 2004-2005

FIELDS OF STUDY

Major Field: Marine Ecology

Studies in Phytoplankton and Mesograzer Ecology with Professors Brian Bingham and Stephen Sulkin, Western Washington University

Studies in Subtidal Ecolgy with Professors Michael Graham and Diana Steller, Moss Landing Marine Labs

Studies in Invasive Species Biology with Dr. Steve Lonhart, NOAA

Studies in Theoretical Ecology with Professor Roger Nisbet

Studies in Kelp Forest Ecology with Dr. Daniel Reed and Professor Sally Holbrook

ABSTRACT

Turnover dynamics of the giant kelp, *Macrocystis pyrifera*

by

Gabriel Eduardo Rodriguez

Energy fixed by primary producers supports the vast majority of life on earth. The giant kelp *Macrocystis pyrifera* is the largest marine alga in the world and supports one of the most productive ecosystems on earth. Carbon fixed by *Macrocystis pyerifera* on temparate rocky reefs not only provides essential habitat for an entire community of associated species, but also provides carbon subsidies to nearby ecological communities. Net primary productivity (NPP) is often used to quantify energy fixation by autotrophs, and researchers often measure NPP by summing the incremental increases in biomass and foliar losses. While the processes governing incremental increases in biomass have been well studied, the processes that drive the loss of foliar biomass are poorly understood.

The main theme of my research is the investigation of the drivers that regulate the lifespan of foliar biomass of giant kelp beds near Santa Barbara, California, USA. Tissue lifepspan in marine macroalgae has not received much attention from either plant ecologists or algal ecologists, despite its potential importance to the dynamics of primary productivity. *Macrocystis* is an ideal species for investigations on tissue lifespan in macroalgae for two main reasons. First, it is well studied and much of its biology is already known, and second, *Macrocystis* is locally abundant, grows fast and turns over frequently. In addition, due to

relatively benign environmental conditions for *Macrocystis* growth, the coastal margin along the Santa Barbara Channel is an ideal location to study intrinsic properties in the absence of extreme environmental forcing (such as frequent temperature spikes and severe storm events) that could overwhelm potentially important patterns.

I investigated drivers that regulate frond and blade lifespan in *Macrocystis*, and the consequences of limited frond and blade lifespans. The first chapter is a long-term, multi-site analysis of frond lifespans and exploration of internal and external drivers that could affect frond lifespans. This study provides broad spatial and temporal scope and identifies progressive senescence as an important driver of *Macrocystis* biomass dynamics. The second chapter employs a more focused field study to investigate whether spatial variability in light within a kelp forests affects lifespan, size, thickness, nitrogen content and pigment content of *Macrocystis pyrifera* blades in ways that are predicted by theory developed to predict leaf traits of vascular plants. The last chapter is a mathematical model of the system, which I parameterized with field data, to explicitly quantify the loss of blade tissue via erosion and quantify the amount of biomass not captured in traditional surveys of net primary productivity.

I found that the natural course of progressive senescence in fronds can explain much of the variability in frond loss throughout a typical year in a Santa Barbara kelp bed, that kelp blades that have more access to light have shorter lifespans (as predicted by leaf lifespan theory), and that ignoring the sub-lethal blade area losses can result in significant underestimates of net primary productivity. I believe that internal regulation of tissue turnover is an important mechanism by which giant kelp maximizes carbon gain in a changing environment and that adaptations that increase photosynthetic efficiency may be an important factor in the widespread success and dominance of *Macrocystis*.

Chapter 1

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

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 developed an age-dependent model of frond mortality from individual frond lifespan data. We evaluated how variation in frond death rates was 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., mean frond age, plant size and nutritional status). The most appropriate multiple regression models selected by AIC explained 47% of the observed variation in frond death rates and 52% of the observed variation in frond initiation rates. Frond age structure was the best predictor of frond death 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.

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, regular 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 lifespan, a process termed "progressive senescence" (Leopold 1961).

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 lifespans than herbaceous, fast growing plants in areas with ample nutrients and light (Reich et al. 1992, Reich et al. 1999, Tsuchiya 1991). 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 Caluwe 1995, Herbert and Fourqurean 2009, Hikosaka 2003, 2005).

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). Very few studies have examined the lifespans of blades and fronds of perennial macroalgae in the context of progressive senescence and the extent to which their dynamics contribute to seasonal biomass fluctuations.

The giant kelp *Macrocystis pyrifera* is a dominant perennial macroalga on shallow temperate reefs in the Pacific and Southern Oceans. It forms extensive forests that undergo large intra- and inter-annual 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 6-7 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, CA over a 3-year period to determine their initiation rates, death 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 death 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 lifespans, 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 3-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 m to ~300 m in width (cross shore dimension). Sampling was done in fixed plots at 6 to 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 deaths on 10 to15 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 greater than 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 death 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). 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 death and initiation rates, tracking tagged fronds until death allowed us to construct a distribution of frond lifespans, which we used to predict frond death 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 lifespan 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 lifespan 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 lifespan distribution.

The distribution of frond lifespans 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 death at age $f(t;\lambda,k) = \frac{k}{\lambda}\left(\frac{t}{\lambda}\right)^{k-1} e^{-\left(t/\lambda\right)^{k}}$ t=(when t ≥ 0) (Eqn. 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 lifespan. This approximated lifespan distribution function indicates the probability of death 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 lifespan 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:

$$\text{Predicted surviving frond count} \quad = \sum_{i=0}^{n} c_i \left(1 - \int_0^{a_t} f(t;\lambda,k)\,dt\right) \qquad \text{(Eqn. 2)}$$

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-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 death rates for each sampling interval using these predicted frond counts were calculated as:

$$\text{Predicted frond death rate} \quad = \frac{1}{d}\left[\ln\left(\hat{S}_t \big/ \hat{S}_o\right)\right] \qquad \text{(Eqn. 3)}$$

where d is the number of days in the sampling interval, $\hat{S}_o$ 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 death rates (i.e., the proportion of fronds dying per day) for each sampling period:

$$\text{Observed frond death rate:} \quad = \frac{1}{d}\left[\ln\left({}^{n_t}\!/\!{}_{n_0}\right)\right] \qquad \text{(Eqn. 4)}$$

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 equation 4 is identical to equation 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 death calculations. This is because new fronds were not expected to contribute to the creation of new fronds until at least the next month, and initiation is not compounded within a sample period.

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

where F_n is the number of fronds initiated during the sample period, F_o 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 death 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 death 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 death rate and frond initiation rate. Because we have an explicit model of how frond age affects the probability of death, we used frond death rate predicted from frond age structure (referred to here as age-dependent mortality) as an explanatory variable in our regression analysis of frond death 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 approximately fifteen 5 cm2 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. 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 (Hs) 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 (http://cdip.ucsd.edu) swell predictions nearest to the sample sites. Bottom temperature was recorded every 10 min using loggers (Stowaway Onset tidbits, accuracy ±0.2°C) 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 above). Although dissolved inorganic nitrogen estimates and temperature were derived from the same temperature loggers, the non-linear 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.

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 (Figure 1). With the exception of a few relatively large spikes in plant loss that coincided with large wave events (3.64 m max Hs in November 2002 and 4.94 m max Hs 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 g dry mass m-2 day-1 ± 0.57 SE vs. 1.3 g dry mass m-2 day-1 ± 0.23 SE for fronds and plants respectively, 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 R2 = 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 lifespan data show that death did not occur randomly across age classes (Figure 2a). Most fronds died three to four months after they reached a height of 1 m (mean frond age at death was 106 days ± 0.60 SE, median age = 103 days). The pattern of frond cohort survivorship was consistent with age-dependent per capita mortality. Frond survivorship was relatively high for the first 75 days in most cohorts before dropping precipitously, with few fronds surviving more than 150 days (Figure 2b). The maximum likelihood estimate of the critical age λ was 115.5 days ± 0.56 (SE). The maximum likelihood estimate of the Weibull shape coefficient k (all sites pooled) was 3.12 ± 0.04 (SE), 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 to 127 days), 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 ($F1,101 = 647.6$, $P < 0.0001$, Figure 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 death rate. Collectively these three variables explained 47% of the observed variation in frond death 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 (Figure 3a) and accounted for 28% of the variation observed in frond death rates when examined alone (Figure 3b). Frond death rate was positively related to maximum significant wave height (Figure 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 death 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 death 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 (Figure 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 (Figure 4a) and 29% and 7% of the observed variation in frond initiation rate, respectively, when evaluated independently (Figures 4b and 4f). 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 variation in frond initiation rates, respectively, when evaluated separately (Figures 4c, 4d, 4e and 4g).

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 2005-2012 (Figure 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 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, this study). 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 lifespans typically have low construction costs and live in resource-rich environments (Reich et al. 1997, Herbert and Fourqueran 2009, van Ommen Kloeke et al. 2012). The values for lifespan 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 lifespan theory developed for terrestrial 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 death 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 (Kopczak et al. 1991, Gerard and Kirkmann 1984, 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 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 death 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 rates was 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 observed by van Tüssenbroek (1993) at the Falkland

Islands attributed to low nutrients, 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 death 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 death 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 lifespan 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 re-invested 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 lifespans (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 under-appreciated. Studies on terrestrial plants show that leaf lifespans 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.

Literature Cited

Aerts, R., and H. de Caluwe. 1995. Interspecific and intraspecific differences in shoot and leaf lifespan of four *Carex* species which differ in maximum dry matter production. Oecologia 102: 467-477.

Chabot, B. F., and D. J. Hicks. 1982. The ecology of leaf life spans. Annual Review of Ecology and Systematics 13: 229-259.

Chapin, F. S., and G. R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology 66: 564-576.

Clendenning, K. A. 1971. Photosynthesis and general development. Pages 169–190 in W. J. North, editor. The biology of giant kelp beds (*Macrocystis*) in California. Beihefte Zur Nova Hedwigia, Verlag Von J. Cramer, Lehre, Germany.

Coley, P. D., J. P. Bryant, and F. S. Chapin. 1985. Resource availability and plant antiherbivore defense. Science 230: 895-899.

Dayton, P. K. 1985. Ecology of kelp communities. Annual Review of Ecology and Systematics 16: 215–245.

Dennison, W. C., and R. S. Alberte. 1982. Photosynthetic responses of *Zostera marina* L. (eelgrass) to in situ manipulations of light intensity. Oecologia 55: 137-144.

Denny, M., and B. Gaylord. 2002. The mechanics of wave-swept algae. The Journal of Experimental Biology 205: 1355-1362.

Donnellan, M. D. 2004. Spatial and temporal variability of kelp forest canopies in central California. Dissertation. Department of Marine Science, San Jose State University, California, USA.

Duarte, C., J. W. Forqurean, K. J. Dorte, and B. Olesen. 2006. Dynamics of seagrass stability and change. Pages 271-294 in A.W.D. Larkum et al., editors. Seagrasses: Biology, Ecology, and Conservation. Springer, the Netherlands.

Foster, M. S., and D. R. Schiel. 1985. The ecology of giant kelp forests in California: a community profile. U.S. Fish and Wildlife Service Biological Report 85, Washington, D.C.

Gaylord, B. G., C. A. Blanchette, and M. W. Denny. 1994. Mechanical consequences of size in wave-swept algae. Ecological Monographs 64: 287-313.

Gerard, V. A. 1976. Some aspects of material dynamics and energy flow in a kelp forest in Monterey Bay, California. Dissertation. University of California, Santa Cruz, California, USA

Gerard, V. A. 1982. Growth and utilization of internal nitrogen reserves by the giant kelp *Macrocystis pyrifera* in a low-nitrogen environment. Marine Biology 66: 27-35.

Gerard, V.A., and H. Kirkmann. 1984. Ecological observations on a branched, loose-lying form of *Macrocystis pyrifera* (L) C. Agardh in New Zealand. Botanica Marina 27: 105–109.

Graham, M.H., C. Harrold, S. Lisin, K. Light, J. M. Watanabe, and M. S. Foster. 1997. Population dynamics of giant kelp *Macrocystis pyrifera* along a wave exposure gradient. Marine Ecology Progress Series 148, 269–279.

Graham, M. H., J. A. Vasquez, and A. H. Buschmann. 2007. Global ecology of the giant kelp *Macrocystis*: from ecotypes to ecosystems. Oceanography and Marine Biology: an Annual Review 45: 39-88.

Gurney, W. S. C., and R. M. Nisbet. 1998. Ecological Dynamics. Oxford University Press, New York.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. The American Naturalist 94: 421-425.

Harper, J. L. 1989. The value of a leaf. Oecologia 80: 53-58.

Hay, C.H. 1990. The distribution of *Macrocystis* (Phaeophyta: Laminariales) as a biological indicator of cool sea surface temperature, with special reference to New Zealand waters. Journal of the Royal Society of New Zealand, 20: 313-336.

Herbert, D. A., and J. W. Fourqurean. 2009. Phosphorus availability and salinity control productivity and demography of the seagrass *Thalassia testudinium* in Florida Bay. Estuaries and Coasts 32: 188-201.

Hikosaka, K. 2003. A model of dynamics of leaves and nitrogen in a plant canopy: an integration of canopy photosynthesis, leaf life span, and nitrogen use efficiency. The American Naturalist 162: 149-164.

Hikosaka, K. 2005. Leaf canopy as a dynamic system: Ecophysiology and optimality in leaf turnover. Annals of Botany 95: 521-533.

Hurd, C. L., C. L. Stevens, B. E. Laval, G. A. Lawrence, and P. J. Harrison. 1997. Visualization of seawater flow around morphologically distinct forms of the giant kelp

Macrocystis integrifolia from wave-sheltered and exposed sites. Limnology and Oceanography 42: 156-163.

Jackson, G. A. 1977. Nutrients and production of giant kelp, *Macrocystis pyrifera*, off southern California. Limnology and Oceanography 22: 979-995.

Jackson, R. B., H. J. Schenk, E. G. Jobbágy, J. Canadell, G. D. Colello, R. E. Dickinson, C. B. Field, P. Friedlingstein, M. Heimann, K. Hibbard, D. W. Kicklighter, A. Kleidon, R. P. Neilson, W. J. Parton, O. E. Sala, and M. T. Sykes. 2000. Belowground consequences of vegetation change and their treatment in models. Ecological Applications 10: 470-483.

Kikuzawa, K. 1991. A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. American Naturalist 138: 1250-1263.

Kikuzawa, K., and D. Ackerly. 1999. Significance of leaf longevity in plants. Plant Species Biology 14: 39-45.

Kitajima, K., S. S. Mulkey, and S. J. Wright. 1997. Decline of photosynthetic capacity with leaf age in relation to leaf longevities for five tropical canopy tree species. American Journal of Botany 84: 702–708.

Kopczak, C. D., R. C. Zimmerman, and J. N. Kremer. 1991. Variation in nitrogen physiology and growth among geographically isolated populations of the giant kelp, *Macrocystis pyrifera* (Phaeophyta). Journal of Phycology 27:149-158.

Laska, G. 2001. The disturbance and vegetation dynamics: a review and an alternative framework. Plant Ecology 157: 77-99.

Leopold, A. C. 1961. Senescence in plant development. The death of plants or plant parts may be of positive ecological or physiological value. Science 134: 1727-1732.

Lindeman, R. H., P. F. Merenda, and R. Z. Gold. 1980. Introduction to bivariate and multivariate analysis. Glenview IL: Scott, Foresman. 444 pp.

Liski, J., A. Lehtonen, T. Palosuo, M. Peltoniemi, T. Eggers, P. Muukkonen, and R. Mäkipää. 2006. Carbon accumulation in Finland's forests 1922–2004 – an estimate obtained by combination of forest inventory data with modelling of biomass, litter and soil. Annals of Forest Science 63: 687-697.

Lobban, C. S. 1978. The growth and death of the *Macrocystis* sporophyte (Phaeophyceae, Laminariales). Phycologia 17: 196-212.

Lobban, C. S., P. J. Harrison, and M. J. Duncan. 1985. The physiological ecology of seaweeds. Cambridge University Press, New York, New York, USA. 366 pp.

Mann, K. H. 2000. Ecology of coastal waters: with implications for management, 2nd edition. Blackwell Science, Malden, Massachusetts, USA. 406 pp.

McPhee-Shaw, E. E., D. A. Siegel, L. Washburn, M. A. Brzezinski, J. L. Jones, A. Leydecker, and J. Melack. 2007. Mechanisms for nutrient delivery to the inner shelf: observations from the Santa Barbara Channel. Limnology and Oceanography 52: 1748–1766.

Molina, A., G. Govers, V. Vanacker, J. Poesen, E. Zeelmaekers, and F. Cisneros. 2007. Runoff generation in a degraded Andean ecosystem: Interaction of vegetation cover and land use. Catena 71: 357-370.

Neushul, M. 1963. Studies on the giant kelp, Macrocystis. II. Reproduction. American Journal of Botany 50: 354-359.

Niyogi, D., K. Alapaty, S. Raman, and F. Chen. 2009. Development and evaluation of a coupled photosynthesis-based gas exchange evapotranspiration model (GEM) for mesoscale weather forecasting applications. Journal of Applied Meteorology and Climatology 48: 349-368.

North, W. J. 1994. Review of *Macrocystis* biology. Pages 447-527 in I. Akatsuka, editor. Biology of Economic Algae. SPB Academic Publishing, The Hague, The Netherlands.

Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution 15: 232-237.

R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rassweiler, A., K. K. Arkema, D. C. Reed, R. C. Zimmerman, and M. A. Brzezinski. 2008. Net primary production, growth, and standing crop of *Macrocystis pyrifera* in southern California. Ecology 89: 2068–2068.

Reed, D. C., and M. S. Foster. 1984. The effects of canopy shadings on algal recruitment and growth in a giant kelp forest. Ecology 65: 937-948.

Reed, D. C., A. Rassweiler, and K. K. Arkema. 2008. Biomass rather than growth rate determines variation in net primary production by giant kelp. Ecology 89: 2493-2505.

Reed, D. C., A. Rassweiler, and K. K. Arkema. 2009. Density derived estimates of standing crop and net primary production in the giant kelp *Macrocystis pyrifera*. Marine Biology 156: 2077-2083.

Reed, D. C., A. Rassweiler, M. H. Carr, K. C. Cavanaugh, D. P. Malone, and D. A. Siegel. 2011. Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. Ecology 92:2108-2116.

Reich, P. B., M. B. Walter, and D. S. Ellsworth. 1992. Leaf life-span in relation to leaf plant and stand characteristics among diverse ecosystems. Ecological Monographs 62: 365-392.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: Global convergence in plant functioning. Proceedings of the National Academy of Sciences of the United States of America 94: 13730-13734.

Reich, P. B., D. S. Ellsworth, M. B. Walters, J. M. Vose, C. Gresham, J. C. Volin, and W. D. Bowman. 1999. Generality of leaf trait relationships: a test across six biomes. Ecology 80: 1955-1969.

Schiel, D. R., and M. S. Foster. 1986. The structure of subtidal algal stands in temperate waters. Oceanography and Marine Biology Annual Review 24: 265–307.

Stewart, H. L., J. P. Fram, D. C. Reed, S. L. Williams, M. A. Brzezinski, S. MacIntyre, and B. Gaylord. 2009. Differences in growth, morphology and tissue carbon and nitrogen of *Macrocystis pyrifera* within and at the outer edge of a giant kelp forest in California, USA. Marine Ecology Progress Series 375: 101-112.

Towle, D. W., and J. S. Pearse. 1973. Production of the giant kelp, *Macrocystis*, estimated by in situ incorporation of 14C in polyethylene bags. Limnology and Oceanography 18: 155-159.

Tsuchiya, T. 1991. Leaf life span of floating-leaved plants. Vegetatio 97: 149-160.

van Ommen Kloeke, A. E. E., J. C. Douma, J. C. Ordoñez, P. B. Reich, and P. M. van Bodegom. 2012. Global quantification of contrasting leaf life span strategies for deciduous and evergreen species in response to environmental conditions. Global Ecology and Biogeography 21: 224-235.

van Tüssenbroek, B. I. 1993. Plant and frond dynamics of the giant kelp, Ma*crocystis pyrifera*, forming a fringing zone in the Falkland Islands. European Journal of Phycology 28: 161–165.

Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York, New York, USA. 495 pp.

Wheeler, W. N. 1980. Pigment content and photosynthetic rates of the fronds of *Macrocystis pyrifera*. Marine Biology 56: 97-102.

White, P. S. 1979. Pattern, process and natural disturbance in vegetation. The Botanical Review 45: 229-299.

Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A.N. Wright, and K.O. Spence. 2010. A meta-analysis of resource pulse-consumer interactions. Ecological Monographs 801: 125-151.

FIGURE LEGENDS

Figure 1. Monthly estimates of the fraction of *Macrocystis pyrifera* biomass lost as fronds from surviving plants for the period May 2002 to May 2005 for three study sites near Santa Barbara, CA, USA.

Figure 2. Demographic data for *Macrocystis pyrifera* fronds near Santa Barbara, CA, USA collected from May 2002 to May 2005. (A) Histogram of frond lifespans (N = 4628 fronds) binned by 31 day intervals (approximately monthly). (B) Survivorship of *Macrocystis pyrifera* frond cohorts by age with fitted Weibull CDF. 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 2B and frond age structure.

Figure 3. (A) Partial R2 values of the dependent variables that entered into the best fit regression model for frond death rates. The partial R2 values sum to 1. The bivariate relationships for (B) frond death rate and frond age-dependent mortality, and (C) frond death rate and maximum significant wave height.

Figure 4. (A) Partial R2 values of the dependent variables that entered into the best fit regression model for frond initiation rates. The partial R2 values sum to 1. The bivariate relationships between frond initiation rate and (B) mean frond age, (C) day length, (D) waves, (E) biomass density, (F) plant size and (G) temperature.

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

Figure 1.

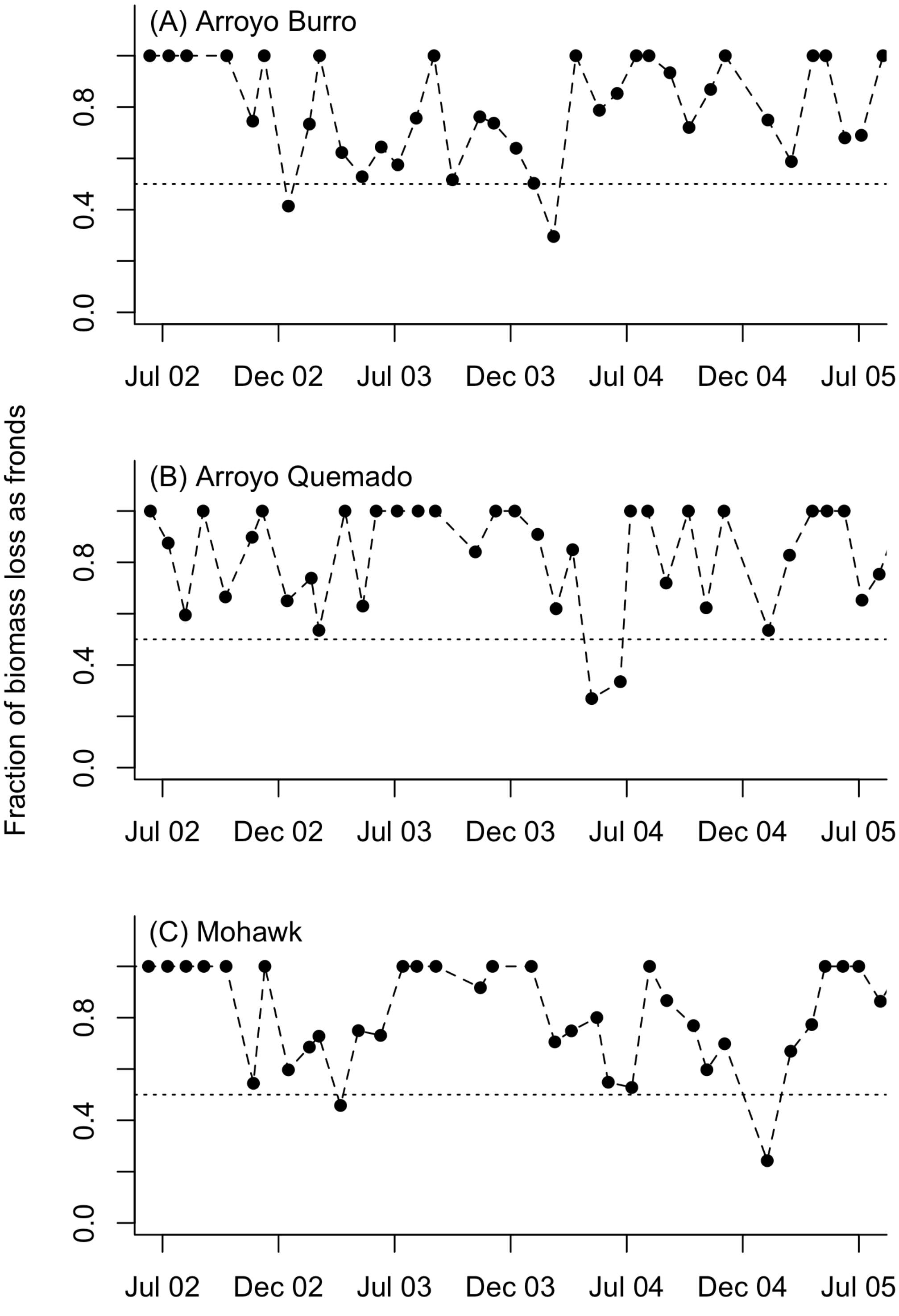

(A) Arroyo Burro
(B) Arroyo Quemado
(C) Mohawk
Fraction of biomass loss as fronds
0.0
0.4
0.8
Jul 02
Dec 02
Jul 03
Dec 03
Jul 04
Dec 04
Jul 05

Figure 2.

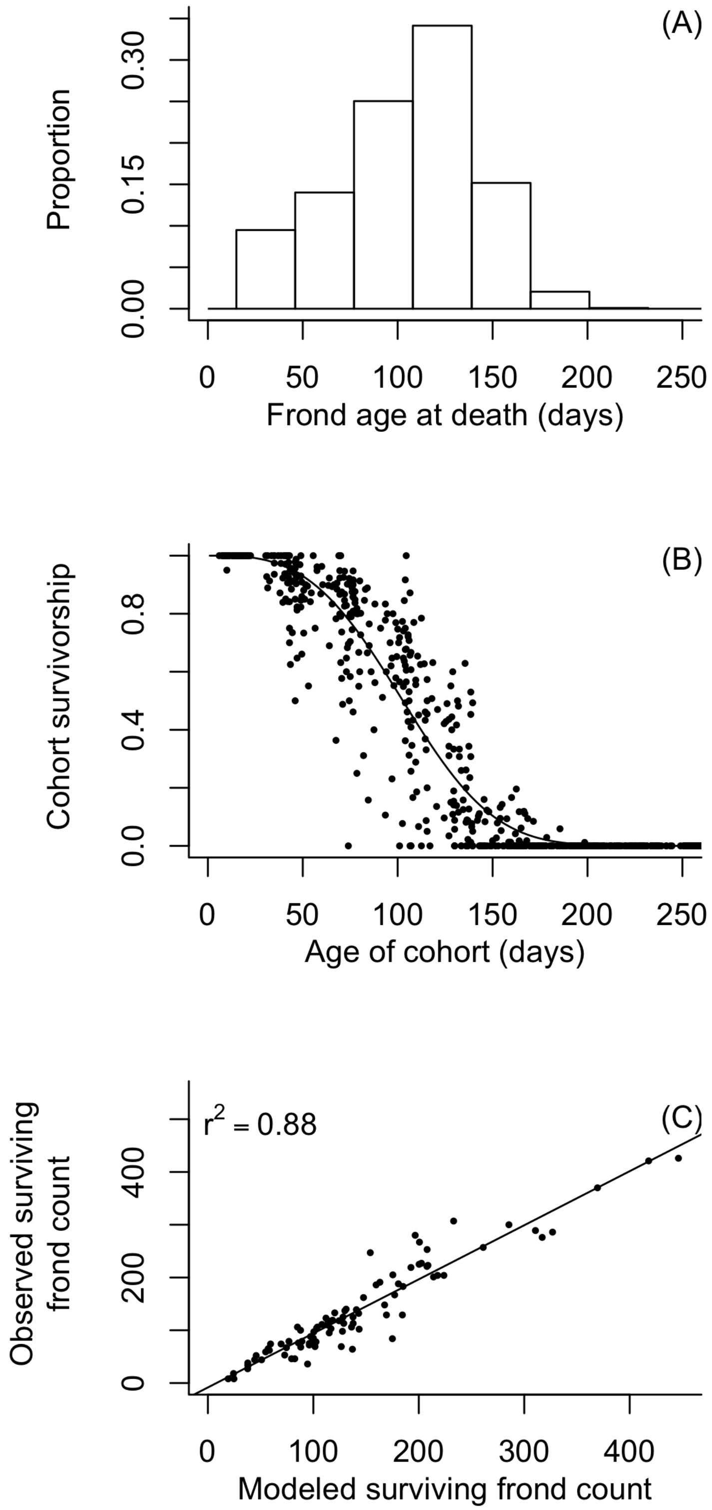

(A)
Proportion
0.00
0.15
0.30
0
50
100
150
200
250
Frond age at death (days)
(B)
Cohort survivorship
0.0
0.4
0.8
0
50
100
150
200
250
Age of cohort (days)
(C)
$r^2 = 0.88$
Observed surviving frond count
0
200
400
0
100
200
300
400
Modeled surviving frond count

Figure 3.

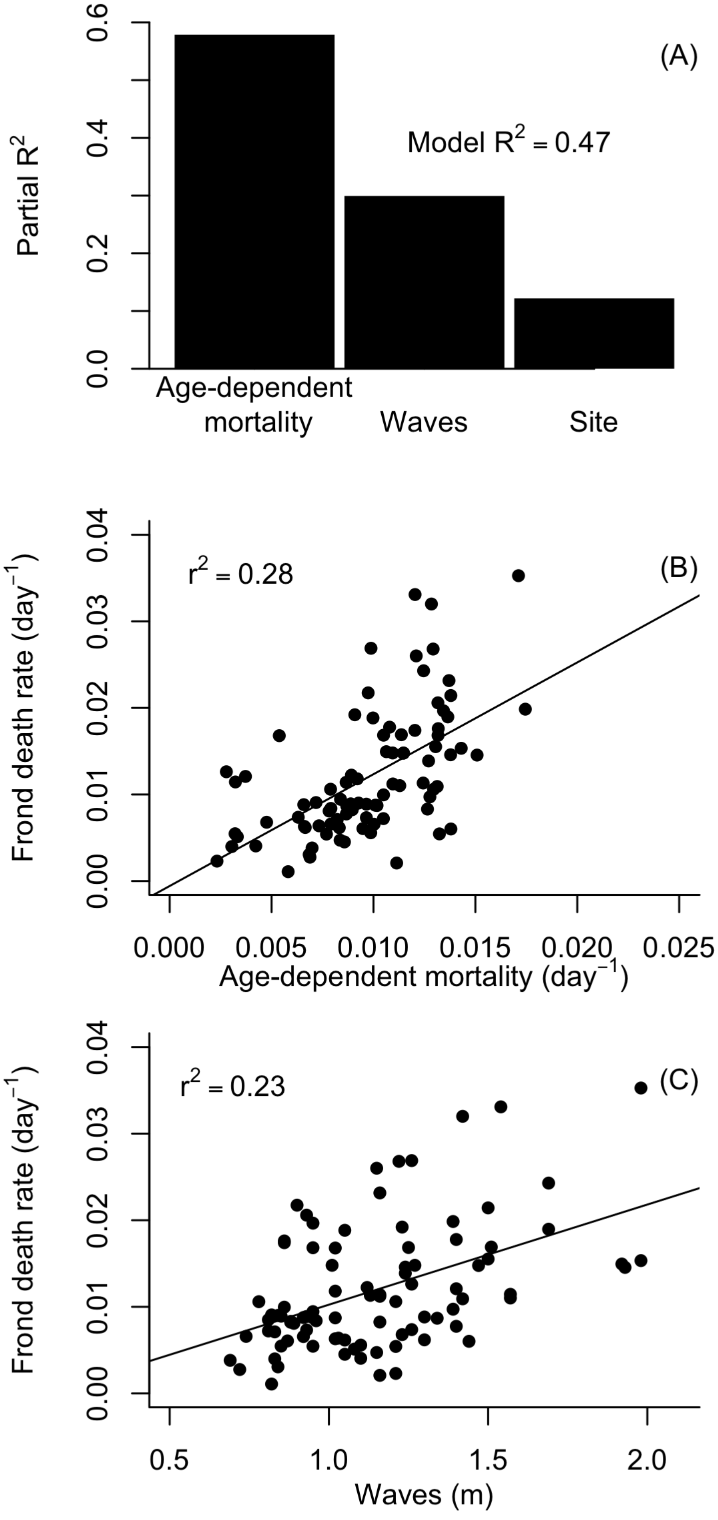
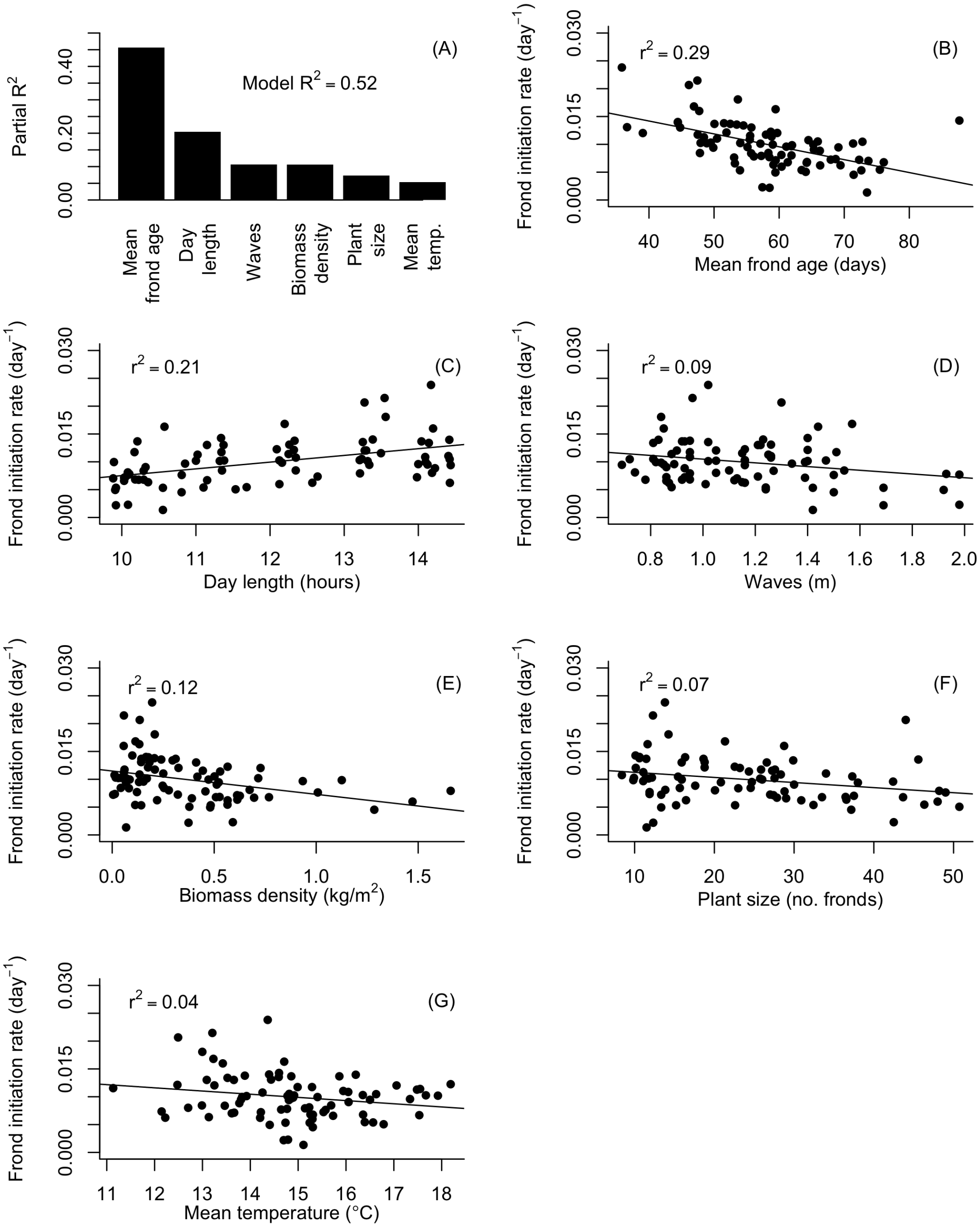
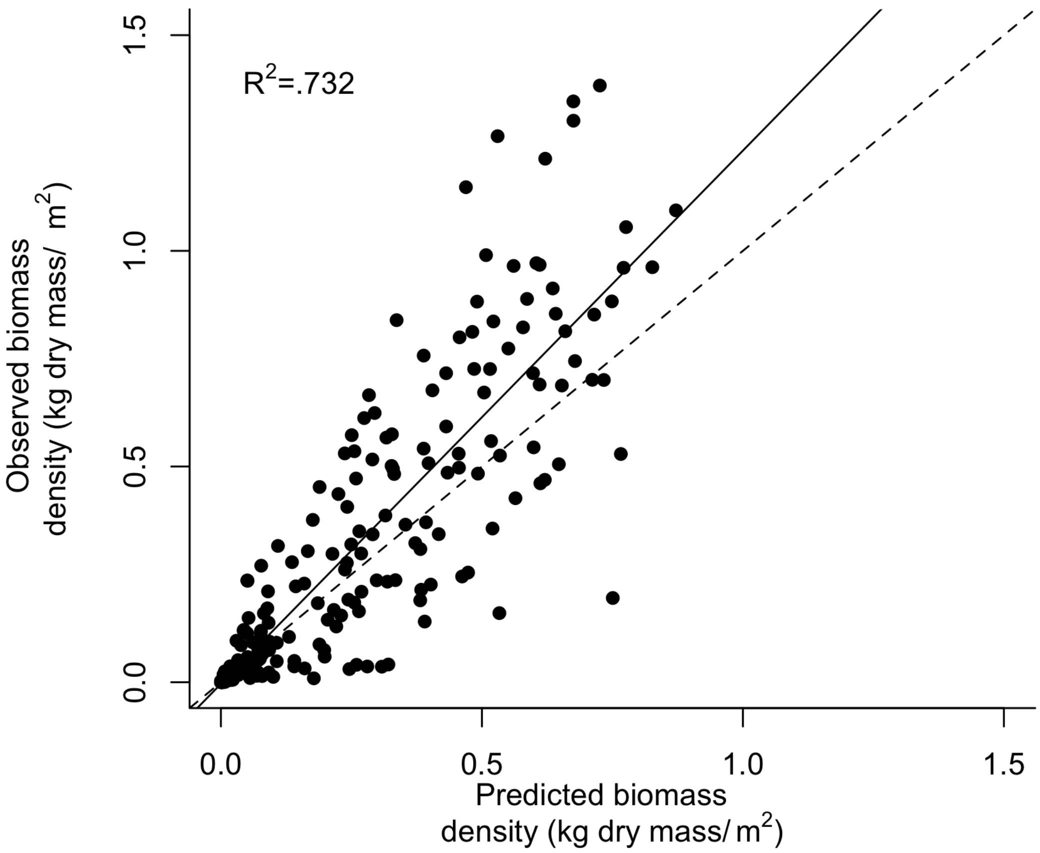

0.6
0.4
0.2
0.0
Partial R^2
(A)
Model R^2 = 0.47
Age-dependent mortality
Waves
Site
0.04
0.03
0.02
0.01
0.00
Frond death rate (day^{-1})
r^2 = 0.28
(B)
0.000
0.005
0.010
0.015
0.020
0.025
Age-dependent mortality (day^{-1})
0.04
0.03
0.02
0.01
0.00
Frond death rate (day^{-1})
r^2 = 0.23
(C)
0.5
1.0
1.5
2.0
Waves (m)

Figure 4.



(A)
Partial R^2
0.00
0.20
0.40
Model R^2 = 0.52
Mean frond age
Day length
Waves
Biomass density
Plant size
Mean temp.
(B)
r^2 = 0.29
Frond initiation rate (day^{-1})
0.000
0.015
0.030
40
50
60
70
80
Mean frond age (days)
(C)
r^2 = 0.21
Frond initiation rate (day^{-1})
0.000
0.015
0.030
10
11
12
13
14
Day length (hours)
(D)
r^2 = 0.09
Frond initiation rate (day^{-1})
0.000
0.015
0.030
0.8
1.0
1.2
1.4
1.6
1.8
2.0
Waves (m)
(E)
r^2 = 0.12
Frond initiation rate (day^{-1})
0.000
0.015
0.030
0.0
0.5
1.0
1.5
Biomass density (kg/m^2)
(F)
r^2 = 0.07
Frond initiation rate (day^{-1})
0.000
0.015
0.030
10
20
30
40
50
Plant size (no. fronds)
(G)
r^2 = 0.04
Frond initiation rate (day^{-1})
0.000
0.015
0.030
11
12
13
14
15
16
17
18
Mean temperature (°C)

Figure 5.


R^2=.732
Observed biomass density (kg dry mass/ m^2)
Predicted biomass density (kg dry mass/ m^2)
0.0
0.5
1.0
1.5
0.0
0.5
1.0
1.5

Chapter 2

Blade lifespan, structural investment, and nutrient allocation in giant kelp

Abstract

Vegetative biomass turnover is an important theme in ecology, and is a key component in qualifying the amount of energy flowing through an ecosystem. Leaf lifespan theory helps explain patterns of leaf turnover in relation to resource availability, but the predictions of this theory have not been tested for marine algae. I measured blade lifespan, size, thickness, nitrogen content, pigment content, and maximum rate of photosynthesis (P_{max}) in the subtidal marine macroalga, *Macrocystis pyrifera*, along a strong resource (light) gradient in a kelp forest near Santa Barbara, CA, USA, to test some predictions of leaf lifespan theory. I found that shorter blade lifespans and larger blade areas were associated with increased light availability. I also found that nitrogen and P_{max} decreased with blade age, and that the decrease in nitrogen content was greater in shorter-lived blades. These observations generally are consistent with patterns observed for higher plants based on leaf lifespan theory. In contrast, variation observed in pigments was inconsistent with that predicted by leaf lifespan theory. This suggests that the marine environment may place demands on resource acquisition and allocation that have not been previously considered with respect to leaf lifespan optimization.

Introduction

The turnover of plant biomass is a key component in quantifying the amount of energy flowing through an ecosystem. Turnover of plant biomass is intimately linked to leaf lifespan and factors that influence leaf lifespan have been extensively studied in many systems (Reich et al. 1997, 1999). While leaf lifespan can be affected by disturbances, such as fire, herbivory and severe weather, the natural course of cellular degeneration that accompanies aging eventually takes its toll on leaves and limits lifespans, even in the absence of disturbance.

A cost-benefit analysis approach has been widely used to predict variation in leaf lifespan as a function of resource availability (Chabot & Hicks 1982, Kikuzawa 1991, Kikuzawa & Ackerly 1999). Predictions of the cost-benefit approach are consistent with differences in leaf traits observed in plant communities through a wide range of resource availabilities and environmental conditions (Reich et al. 1999), as well as among leaves of the same individual (Dennison & Alberte 1982, Vincent 2005). This approach considers leaf lifespan to be a result of maximizing lifetime leaf carbon gain given the leaf's maintenance and construction costs as well as decreases in photosynthetic capacity (P_{max}) as the leaf ages (Chabot & Hicks 1982, Kikuzawa 1991).

Generally, increased structural investment in a leaf results in a longer lifespan, but reduces resources that can be allocated to plant growth (Coley et al. 1985, Herms & Mattson 1992). For example, thicker leaves are correlated with longer leaf lifespans, but tend to have lower P_{max} per unit leaf mass (Reich et al. 1997, Terashima et al. 2005). Thicker leaves are usually found in low resource conditions, as the plant must defend the investment made in its leaves because they are not easily replaced (Coley et al. 1985). Thinner leaves serve to maximize carbon gains, but are more susceptible to damage from herbivory and physical disturbance.

Similarly, patterns of pigment and nitrogen allocation within a canopy can depend on light gradients (Terashima et al. 2005). Studies of resource allocation within leaf canopies suggest that the optimal use of light and nutrient resources would be achieved from an inverse relationship between pigment and light so that all levels of the canopy are simultaneously saturated with light (Terashima et al. 2005). In contrast, optimization models predict that more nitrogen will be found in sun leaves than shade leaves, maximizing the rate of photosynthesis (Dietz & Heber 1984, Raines 2003). Optimization models also predict more nitrogen will be found in younger leaves, and faster decreases with age in nitrogen will be observed in shorter lived leaves (Escudero & Mediavilla 2003, Hikosaka 2005, 2010).

Despite significant progress made with respect to terrestrial plants, and the generality of the theory used to explain leaf lifespan, little work has been done on applying this theory to other phototrophs. In particular, the extent that blade lifespan in marine macroalgae is correlated to other traits predicted by leaf lifespan theory has not been examined, even though macroalgae support some of the most productive ecosystems in the world (Mann 2000). Key similarities between plants and macroalgae suggest that the applicability of leaf lifespan theory may extend to macroalgae. The limitation of resources and the costs and benefits of allocating resources to growth vs. longevity of photosynthetic tissue apply to macroalgae as well as plants. It is likely that, much like terrestrial plants, macroalgae also allocate resources to maximize performance.

The giant kelp *Macrocystis pyrifera* is an ideal macroalga to investigate the effects of light availability on the allocation of internal resources to tissue growth vs. longevity because individuals experience a strong light gradient with depth and location in the kelp forest. About 20% of surface irradiance reaches a depth of 8 m on southern California reefs in the absence of kelp, compared to 1% or less in the presence of a developed canopy (Gerard 1984). Fronds in the interior of the kelp forest are often light limited (Stewart 2006), and are exposed to a very wide range of irradiances as they grow. In contrast, fronds on the forest edge will be exposed to a smaller range of irradiances. Blades (analogues to leaves) are formed from an apical meristem on an individual frond (analogue to a branch) that grows upwards toward the surface, leaving blades behind as it grows. *Macrocystis* fronds live only a few months (Rodriguez et al. 2013) and grow rapidly through an extremely spatially heterogeneous light environment that varies with location in the kelp forest, allowing investigation of the effects of this heterogeneous light environment on performance of individual blades.

The goal of this study was to investigate whether spatial variability in light within a kelp forest affects the lifespan, size, thickness, nitrogen and chlorophyll content of *Macrocystis pyrifera* blades. If leaf lifespan theory applies to *Macrocystis*, then blades growing in higher light conditions (e.g., near the surface and at the forest edge) should have shorter lifespans, less structural investment (lower blade thickness), less pigmentation, but higher percent tissue nitrogen content than blades in lower light conditions (near the bottom and in the interior of the forest). I also expect that if blade lifespan is internally regulated, indicators of photosynthetic performance (P_{max}, blade nitrogen content) will decrease with increasing blade age, and this decrease will be more rapid in shorter-lived blades. If blades are more commonly lost via disturbance (such as wave motion or herbivory), then performance indicators related to blade lifespan should be less pronounced. I used the natural variability in light that occurs from the sea surface to the sea floor as well as the effect of intraspecific shading to evaluate the response of *Macrocystis* blades to different light environments and to separate the effects of depth and age on blade lifespan from other traits.

Methods

Overview

Frond growth in *Macrocystis pyrifera* occurs primarily from its apical meristem, and to a lesser extent through internodal elongation (North 1971, Lobban 1978). The effect of internodal elongation on blade depth is typically on the order of 1m or less (North 1971), and most blades stay near the depth in which they were formed, except when elongation moves a blade into the canopy from just below the sea surface. After separation from the apical meristem, a blade increases in surface area for about 25 days. Upon reaching its maximum size it begins to senesce from the distal end until it erodes completely. I investigated the effect of spatial variation in light on lifespan and other traits of *M. pyrifera* blades in the Isla Vista kelp forest near Goleta, CA (34°24’18”N, 119°52’05”W). The study site was located on nearly level sandstone platform at 7 m depth (± 50 cm). Two primary sources of spatial variation in light exist in a kelp forest; light extinction through the water column, and shading by the kelp canopy. To separate the effects of depth and shading, I sampled blades from midwater and in the canopy at the edge of the forest (where canopy shading is much reduced), and in the interior of the forest (where canopy shading is substantial).

I used two methods to quantify changes in blade properties that occur with age and variation in the light environment. First, I tracked intact individual blades over time *in situ* to measure changes in blade area and lifespan. To do this I measured changes in blade area and blade lifespan on the 2nd and 6th blades from the base of the frond (hereafter referred to as midwater blades), and on the 40th blade from the base of the frond (hereafter referred to as canopy blades) on multiple fronds growing at the interior and edge of the forest. This convention was chosen to account for internodal elongation and to ensure that the blades spent their entire lifetime in either the midwater or surface canopy. I also randomly collected blades of different age classes for laboratory analyses of thickness, pigment and nitrogen content, and photosynthetic performance. Since these blades were collected at the same time, blades of all ages were acclimated to the same conditions, eliminating variation in traits that can occur with changing ambient conditions.

Blade size and lifespan

Changes in blade size and blade lifespan were measured from June to October 2012. Two midwater blades and one canopy blade from each of twenty mature plants consisting of 10-50 fronds were haphazardly chosen along a transect running along the offshore edge of the kelp forest (hereafter referred to as the forest edge). Likewise, two midwater blades and one canopy blade each from another 20 mature plants were chosen from a parallel transect 10 m inshore of the edge of the forest in an area with dense kelp cover (hereafter referred to as the forest interior). A single frond from each of the 40 plants measuring ~75 cm in total length was chosen to observe changes in blade area and lifespan. All 120 blades (60 interior and 60 edge) were measured every seven days from this initial observation (or from the time of separation from the apical meristem in the case of canopy blades) until the blades had senesced to less than 10% of the maximum length, until the frond had senesced to less than 50% of maximum length, or until the frond was lost from the holdfast.

I measured the length as the maximum distance along the primary axis of the blade and blade width as the greatest distance perpendicular to the primary axis. Blade area was calculated from length and width assuming the shape was elliptical. The lifespan of the blade was defined as the time from when the blade reached 80% of maximum area to when it senesced to less than 10% of this maximum. If the frond was lost before the blades had senesced to less than 10% of the maximum length, the data for that sample blade were excluded from the analysis. Fifteen of the 120 blades were excluded from the analysis because of frond loss and no group suffered severely disproportional sample loss.

Physical and chemical properties of blades

I analyzed pigment and dry mass density (a measure of blade thickness) from 46 mature blades, and nitrogen from 46 mature and 61 senescent blades collected from haphazardly chosen plants at the edge and in the interior of the kelp forest. These blades were collected in April 2013 from the same study site as blade size and lifespan surveys. Mature midwater (N=35) blades were collected from young 3-4 m long fronds, senescent midwater blades (N=47) and mature canopy blades (N=11) were collected from fronds 5-7 m in length and senescent canopy blades (N=14) were selected from fronds > 8 m in length that had stopped elongating. Dry mass density and chlorophyll *a* (Chl *a*) mass per unit blade area for mature blades and nitrogen as a percentage of dry mass for mature and senescent blades were estimated from six 1 cm diameter cores taken from the centerline of the blade, approximately 5 cm from the base of the blade. Nitrogen content was estimated using a CE-440 CHN/O/S elemental analyzer (Exeter Analytical, Chelmsford, Massachusetts, USA).

Chl *a* was extracted using a dimethyl sulfoxide/acetone solvent and analyzed using a Shimadzu UV 2401PC spectrometer (Shimadzu Scientific Instruments, Kyoto, Japan) following the methods of Seely et al. (1972).

Photosynthetic performance

Fourteen midwater blades of known ages were collected at the conclusion of blade and lifespan surveys (October 2012) to test the hypothesis that P_{max} decreases with blade age. Blades collected for P_{max} measurements were obtained from the same plants used to evaluate blade area and lifespan, but from different fronds than those monitored for senescence. Eight blades came from plants on the forest edge, 6 blades were from the forest interior. Upon collection, blades were placed in dark sealed containers until P_{max} was measured following the methods of Miller et al. (2012). Blades were incubated in nitrogen-purged, sealed aquaria and oxygen evolution was measured using a self-contained D-Opto dissolved oxygen logger (Zebra-Tech, Nelson, New Zealand). Blades were exposed to varying levels of photosynthetically active radiation ranging from complete darkness to 700 $\mu E*m^{-2}*s^{-1}$, measured using spherical MkV/L Light Intensity Recorders manufactured by Alec Electronics Corporation (Kobe, Japan).

Light measurements

To characterize the reduction in light due to canopy shading and extinction with depth, I measured photosynthetically active radiation using spherical light sensors placed just above the canopy (surface measurement) and at 4 m depth (midwater measurement) near the start of each transect. Light sensors were deployed for 3 consecutive days during collection of the blade tissue samples from about 10:30h to 13:30h and were positioned to intercept the light falling on representative midwater and canopy blades. Light sensors recorded PAR measurements every 2 minutes; these measurements were averaged into the 3 daily replicates.

Statistical analysis

All data were analyzed using R statistical computing software version 3.0 (R Development Core Team 2013). The effects of location within the forest (interior vs. edge) and depth (canopy vs. midwater) on blade lifespan, maximum area, mass density, nitrogen and Chl *a* were analyzed in separate two-way fixed factor ANOVAs with corrections for unequal sample sizes when appropriate. The effect of age class and depth on nitrogen content was also tested with a similar two-way fixed factor ANOVA. Because there was little difference in irradiance between 4 m and 6 m depths, the blades followed at these two depths were pooled into a single midwater group resulting in the midwater group having a sample size that was approximately double that of the canopy. Response variables were examined for homoscedasticity via graphical analysis of residuals. Maximum blade area was found to be heteroscedastic and was log transformed to homogenize the variances. Tukey HSD tests were used to determine significance of pair-wise comparisons between all four treatments, and reported as letter groupings in Figure 1.

A nonlinear least squares method was used to fit a hyperbolic tangent function to the oxygen evolution rates at each light intensity to estimate P_{max} (Miller et al. 2012)**.** Linear regression was used to assess the explanatory power of age (measured in days) on photosynthetic performance (P_{max}). Conformity to the homoscedasticity assumption of the linear regression was verified by graphical examination of the residuals.

Results

Characterization of the light environment

Midwater irradiance values for the interior of the forest were very low during the 3 days sampled, averaging 3.5 (± 0.52 SE) $\mu E*m^{-2}*s^{-1}$ (Figure 1A). Light reaching the surface canopy was about 500 times higher than that in the midwater of the interior of the forest and about 3 fold higher than that in the midwater at the edge of the forest (Figure 1a). Midwater measurements taken at the edge averaged 471 (± 39.3 SE) $\mu E*m^{-2}*s^{-1}$ (Figure 1A). Measurements of incident light reaching the canopy averaged 1449 (± 83.0 SE) $\mu E*m^{-2}*s^{-1}$ (Figure 1A).

Characteristics of mature blades from different light environments

The effects of depth on blade lifespan varied with location in the forest ($F_{1,100}$=8.16, p=0.005 for depth*location). In the interior of the forest the average lifespan of midwater blades was about 40 days longer than canopy blades, whereas at the edge of the forest the average life span of midwater blades was about 24 days longer. This corresponds well to the observation that differences in irradiance between the canopy and midwater were greatest in the interior of the forest (Figure 1A). In the canopy where light was consistently high, blades growing at the edge of the forest had similar lifespans to those in the interior, averaging 56.5 days (±3.29 SE). In contrast, lifespans of midwater blades were about 8 days longer in the interior of the forest compared to the edge of the forest, averaging 92.8 (±2.25 SE) days and 84.2 (±2.31 SE) days, respectively, consistent with the lower irradiance observed in the midwater compared to the canopy.

Surface area of mature blades increased with increasing light availability (Figure 1A vs. 1C). The maximum size of blades growing in the canopy averaged about four times that of blades growing in the midwater ($F_{1,100=}$225.0, p<0.001) while the maximum size of blades at the edge of the forest averaged twice that of blades in the interior of the forest ($F_{1,100=}$20.3, p<0.001, Figure 1C). The effects of depth and location relative to the edge of the forest on maximum blade area were additive ($F_{1,100}$=1.75, p=0.189 for depth*location).

Blade mass density (Figure 1D) and nitrogen content of mature blades (Figure 1E) did not differ significantly with depth ($F_{1,42=}$0.98, p<0.212, $F_{1,42=}$0.01, p<0.917, for mass density and nitrogen respectively) or distance from the edge of the forest ($F_{1,42=}$3.56, p<0.066, $F_{1,42=}$0.86, p<0.358, for mass density and nitrogen respectively). Blade mass density averaged 4.4mg/cm^2 (±1.6x10^{-4} SE) across depths and locations in the forest (Figure 1D) while blade nitrogen averaged 2.73% ±.065 (Figure 1E).

Depth had no effect on Chl *a* content of blades growing at the edge of the forest, but had a significant negative effect on this characteristic for blades growing in the interior of the forest. Contrary to expectations, Chl *a* content of blades from the darkest portion of the forest (interior midwater) was significantly lower than that of blades from other areas of the forest (Figure 1F; $F_{1,42}$=19.6, p<0.001, depth*location).

Changes in blade characteristics with age

P_{max} decreased with blade age, which is consistent with internal regulation of leaf and blade lifespans, (r^2=0.418, p=0.49, Figure 2). Similarly, nitrogen content of blades was lower in senescent blades compared to mature blades, and this differential was larger for the shorter-lived canopy blades (Figure 3). Nitrogen content in mature blades did not differ between depths (aggregate mean = 2.66% ±0.09 SE), while the nitrogen content of senescent blades was ~40% lower (2.62% vs 1.88%) in the canopy compared to the midwater (Figure 3, $F_{1,99}=4.03$, $p=0.047$ depth*age).

Discussion

Leaf lifespan theory predicts that kelp blades growing in higher light (e.g., near the surface and at the forest edge) should have shorter lifespans, thinner blades, less pigmentation, but higher nitrogen content than blades in areas that receive less light (near the bottom and in the interior of the forest). The shortest-lived blades were found in the canopy, both on interior plants and edge plants. This is consistent with the predictions of leaf lifespan theory, since these are the blades that were exposed to the most light. However, I was unable to detect a significant difference in the lifespan of canopy blades at the edge vs. interior of the forest, likely due to the similarity of light regimes in both canopy areas. I also found that blade lifespan was not related to blade thickness. Increased wave disturbance has been shown to induce kelps to form thicker thalli to reduce breakage in wave exposed areas (Fowler-Walker et al. 2005). However, differences in wave disturbance probably did not contribute significantly to differences in blade thickness or life span, since the study was conducted during benign conditions (i.e., waves never exceeded 1.5 m in height, unpublished data). Instead, blades eroded at the distal ends at a relatively consistent rate, which is more consistent with loss due to senescence than episodic disturbance.

The decreases in tissue nitrogen and P_{max} with age also suggest internal processes, rather than disturbance, control blade lifespan. The decrease in photosynthetic performance of a leaf as it ages is an essential component of leaf lifespan optimization models: without such a decrease, leaves are predicted to have infinite lifespan (Kikuzawa 1991). Additionally, greater decreases with age in leaf nitrogen are associated with shorter leaf lifespans (Hikosaka 2003, 2005, 2010). I found the decrease in nitrogen concentration from mature blades to senescent blades was greater in the canopy (74% decrease) than in the midwater (48% decrease), a pattern consistent with predictions of leaf lifespan theory.

One assumption of leaf lifespan theory is that all leaves contribute to net carbon gain, or else they are removed from the canopy. Giant kelp blades found under a dense canopy may not contribute directly to net carbon gain and this might explain why patterns of pigment allocation were not consistent with leaf lifespan theory. Light measurements taken under the dense canopy were frequently at or below the compensation irradiance for *Macrocystis* of 10 $\mu E * m^{-2} * s^{-1}$ reported in Gerard (1976). This suggests that blades that occupy areas under a dense canopy are net carbon sinks. The lower concentration of Chl *a* of interior midwater blades where light is lowest is not consistent with strategic resource allocation to maximize photosynthesis (Terashima et al. 2005). If these blades do not receive enough light to meet their metabolic demands, adding more pigments might be a waste of valuable resources. These blades, however, had the longest lifespans recorded in this study. Optimization of carbon gain cannot explain the longer lifespan of blades, if these blades consistently run a carbon deficit.

It has been suggested that bottom and midwater blades in the interior of the kelp forest may be important in nutrient uptake. *Macrocystis* may be supplied with nutrients at depth during times of nutrient limitation, even when nutrient levels at the surface cannot support growth (Zimmerman & Robertson 1985). Colombo-Pallotta et al. (2006) showed that basal blades had high respiration compared to canopy blades. Since respiration was expected to be lower in light limited conditions, Colombo-Pallotta et al. (2006) attributed this result to the enhancement of nutrient uptake systems. Bottom and midwater blades may be retained even when there is no net positive carbon gain if the increased surface area is needed to supply nutrients to the rest of the plant.

This is the first study to explicitly test predictions of leaf lifespan theory in macroalgae. Shorter blade lifespan in areas of higher light, decrease of P_{max} with age and the greater decrease in nitrogen of shorter-lived blades were consistent with leaf lifespan theory. However, other blade properties (such as low pigment concentrations in heavily shaded blades) are inconsistent with general predictions of leaf lifespan theory. Observations that kelp blades in the interior of a kelp forest have long lifespans, despite having much lower pigment levels than predicted and living in a severely light limited environment suggest that carbon fixation may not be the primary function of these blades. Data gathered during this study and others (Zimmerman & Robertson 1985, Colombo-Pallotta et al. 2006) suggest that midwater blades in the interior of a kelp forest may actually function in nutrient absorption, rather than carbon gain. While leaf lifespan theory provides a robust theoretical framework from which to base investigation of foliar turnover, special consideration should be given to the unique demands of the fluid environment in which *Macrocystis pyrifera* lives, and the opportunities and constraints that result.

Literature Cited

Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. Annu Rev Ecol Syst 13:229–259

Coley P, Bryant J, Chapin FI (1985) Resource availability and plant antiherbivore defense. Science 230:895–899

Colombo-Pallotta M, Garcia-Mendoza E, Ladah L (2006) Photosynthetic performance, light absorption, and pigment composition of *Macrocystis pyrifera* (Laminariales, Phaeophyceae) blades from different depths. J Phycol 42:1225–1234

Dennison WC, Alberte RS (1982) Photosynthetic responses of *Zostera marina* to in situ manipulations of light intensity. Oecologia 55:137–144

Dietz K, Heber U (1984) Rate-limiting factors in leaf photosynthesis. I. Carbon fluxes in the calvin cycle. Biochim Biophys Acta 767:432–443

Fowler-Walker MJ, Wernberg T, Connell SD (2005) Differences in kelp morphology between wave sheltered and exposed localities: morphologically plastic or fixed traits? Mar Biol 148:755–767

Escudero A, Mediavilla S (2003) Decline in photosynthetic nitrogen use efficiency with leaf age and nitrogen resorption as determinants of leaf life span. J Ecol 91:880–889

Gerard V (1976) Some aspects of material dynamics and energy flow in a kelp forest in Monterey Bay, California. PhD Dissertation, University of California. Ann Arbor: PrQuest/UMI 77-16,792

Gerard V (1984) The light environment in a giant kelp forest: influence of *Macrocystis pyrifera* on spatial and temporal variability. Mar Biol 84:189–195

Herms D, Mattson W (1992) The dilemma of plants: to grow or defend. Q Rev Biol 67:283–335

Hikosaka K (2003) A model of dynamics of leaves and nitrogen in a plant canopy: an integration of canopy photosynthesis, leaf life span, and nitrogen use efficiency. Am Nat 162:149–164

Hikosaka K (2005) Leaf canopy as a dynamic system: ecophysiology and optimality in leaf turnover. Ann Bot 95:521–33

Hikosaka K (2010) Mechanisms underlying interspecific variation in photosynthetic capacity across wild plant species. 229:223–229

Kikuzawa K (1991) A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. Am Nat 138:1250–1263

Kikuzawa K, Ackerly D (1999) Significance of leaf longevity in plants. Plant Species Biol 14:39–45

Lobban C (1978) Growth of *Macrocystis integrifolia* in Barkley Sound, Vancouver Island, B.C. Can J Bot 56:2607–2711

Mann K (2000) Ecology of coastal waters: with implications for management. Blackwell Science, Malden, Massachusetts

Miller RJ, Harrer S, Reed DC (2012) Addition of species abundance and performance predicts community primary production of macroalgae. Oecologia 168:797–806

North W (1971) The biology of giant kelp beds (*Macrocystis*) in California: introduction and background. Nova Hedwigia 32:1–68

Raines C (2003) The Calvin cycle revisited. Photosynth Res 75:1–10

Reich P, Ellsworth D, Walters M, Vose J, Gresham C, Volin J, Brown W (1999) Generality of leaf trait relationships: a test across six biomes. Ecology 80:1955–1969

Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. Proc Natl Acad Sci USA 94:13730–13734

Rodriguez G, Rassweiler A, Reed D, Holbrook S (2013) The importance of progressive senescence in the biomass dynamics of giant kelp (*Macrocystis pyrifera*). Ecology 94:1848–1858

Seely G, Duncan M, Vidaver W (1972) Preparative and analytical extraction of pigments from brown algae with dimethyl sulfoxide. Mar Biol 12:184–188

Stewart HL (2006) Ontogenetic changes in buoyancy, breaking strength, extensibility, and reproductive investment in a drifting macroalga *Turbinaria ornata* (Phaeophyta). J Phycol 42:43–50

Terashima I, Araya T, Miyazawa S-I, Sone K, Yano S (2005) Construction and maintenance of the optimal photosynthetic systems of the leaf, herbaceous plant and tree: an eco-developmental treatise. Ann Bot 95:507–519

Vincent G (2005) Leaf life span plasticity in tropical seedlings grown under contrasting light regimes. Ann Bot 97:245–55

Zimmerman R, Robertson D (1985) Effects of El Niño on local hydrography and growth of the giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island, California. Limnol Oceanogr 30:1298–1302

Figure Legends

Figure 1. Irradiance and *Macrocystis* blade properties by location in the kelp forest. A) Irradiance (N=3), B) blade lifetimes (N=104), C) maximum blade area (N=104), D) blade mass per unit area (N=46), E) blade nitrogen content (N=46), and E) blade chlorophyll *a* content (N=46). All measurements given are means ± standard errors; lower case letter groupings are given to summarize the results of a Tukey HSD post-hoc test.

Figure 2. The relationship between *Macrocystis* blade photosynthetic capacity at saturating irradiance (P_{max}) and age of the blade ($r^2=0.418$, $p=0.49$). All blades are midwater blades from a representative sample of plants from the kelp forest near Isla Vista, CA.

Figure 3. Mean ($\pm$ 1 SE) blade nitrogen content for mature and senescent blades in the canopy and midwater. N=35 for mature midwater blades, N=47 for senescent midwater blades, N=11 for mature canopy blades, and N=14 for senescent canopy blades.

Figure 1

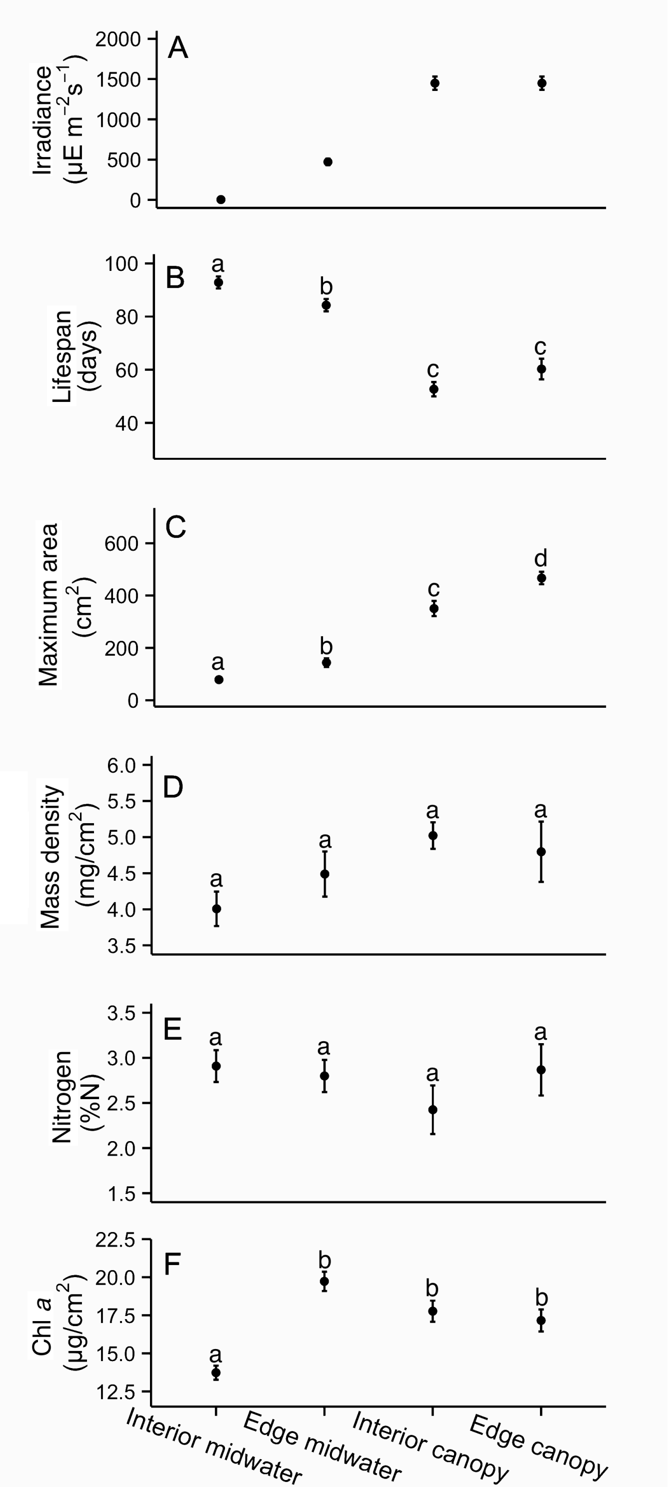

A
Irradiance
(μE m^{-2}s^{-1})
2000
1500
1000
500
0
B
Lifespan
(days)
100
80
60
40
a
b
c
c
C
Maximum area
(cm^{2})
600
400
200
0
a
b
c
d
D
Mass density
(mg/cm^{2})
6.0
5.5
5.0
4.5
4.0
3.5
a
a
a
a
E
Nitrogen
(%N)
3.5
3.0
2.5
2.0
1.5
a
a
a
a
F
Chl *a*
(μg/cm^{2})
22.5
20.0
17.5
15.0
12.5
a
b
b
b
Interior midwater
Edge midwater
Interior canopy
Edge canopy

Figure 2

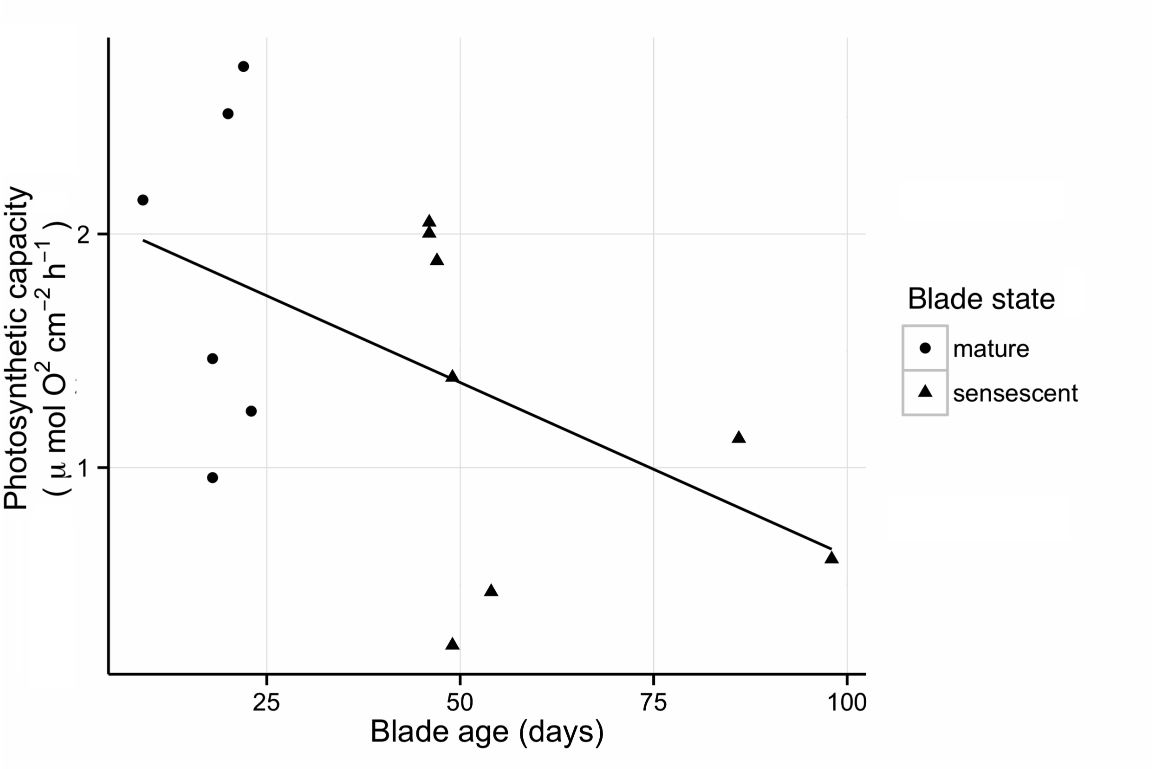
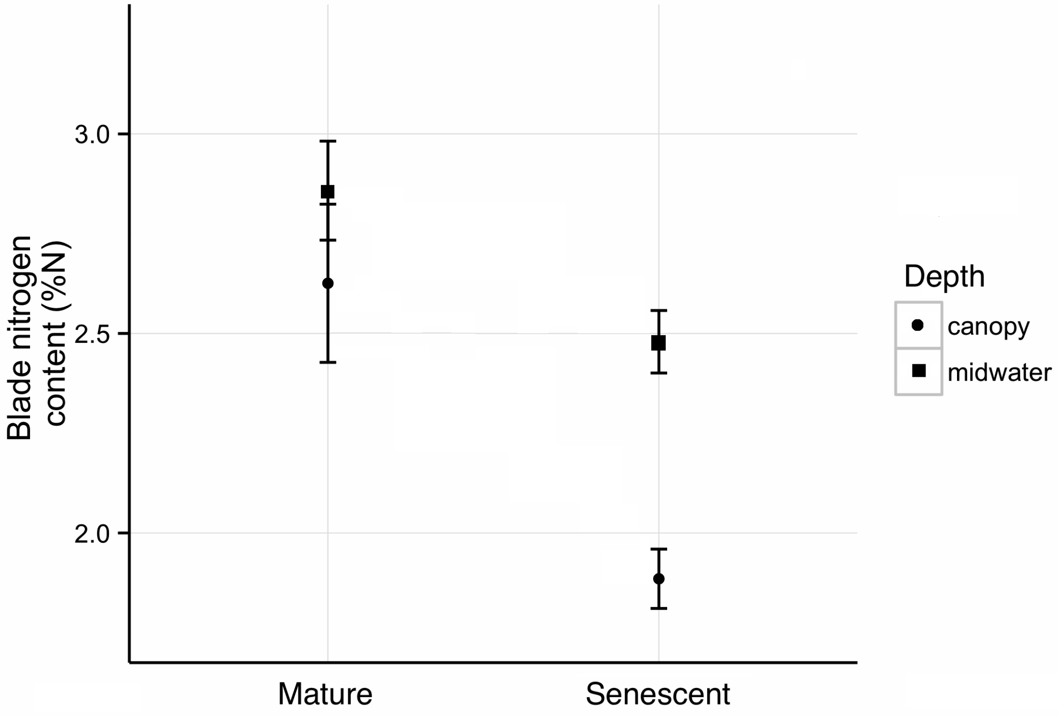


Figure 3


Blade nitrogen content (%N)
3.0
2.5
2.0
Mature
Senescent
Depth
● canopy
■ midwater

Chapter 3

Resource availability and blade senescence in the giant kelp (*Macrocystis pyrifera*)

Abstract

Rapid growth and high turnover of foliar biomass in the giant kelp *Macrocystis pyrifera* account for its extraordinarily high net primary productivity (NPP). Current methods of quantifying turnover in *Macrocystis* that focus on dynamics of whole fronds may result in underestimates of NPP because blade matter is sloughed continuously during the lifespan of a frond, before it can be measured. Here I constructed a model of frond growth and senescence to investigate the relative and absolute magnitude of blade senescence in a kelp forest, and to examine how these losses were affected by light availability. I found that fronds with greater access to light (near forest edges) lose more absolute blade biomass than fronds in the interior of the forest because they tend to be more massive, and consequently have more mass to loose. Fronds in the interior of the forest where light is much reduced were predicted to show greater proportional blade loss than fronds on the edge of the forest. The model predicts that blade senescence accounts for about 10.1% ± of edge and 11.6% of interior blade biomass produced by a frond that is not accounted for when NPP is based on measurements of whole fronds, indicating that estimates of NPP that ignore blade senescence are undervalued.

Introduction

Rapid growth and high turnover of foliar biomass in the giant kelp *Macrocystis pyrifera* are responsible for the high values of net primary productivity (NPP) observed in giant kelp forests (Reed et al. 2008). In addition to supporting local food-web diversity (Graham 2000, Byrnes et al. 2011), the high productivity of a giant kelp forest provides significant subsidies to nearby systems with low *in situ* primary productivity, such as sandy beaches (Dugan et al. 2011) and deep ocean habitats (Harrold et al. 1998, Vetter and Dayton 1999). Growth in *Macrocystis* has been well studied (reviewed in Graham et al. 2007), as has the loss of foliar biomass due to herbivory and wave disturbance (Seymour et al. 1989, Dayton et al. 1992, Graham 1997, Steneck et al. 2002, Davenport and Anderson 2007). By contrast, relatively few studies have examined the extent to which biomass turnover is governed by internal processes such as senescence. The little work that has been done indicates that age dependent mortality of individual fronds accounts for a significant fraction of biomass loss in the absence of severe grazing and disturbance (Rodriguez et al. 2013). Understanding the causes and consequences of internally controlled biomass loss in *Macrocystis* is essential for a complete understanding of the dynamics of productivity in this iconic species.

Over the lifetime of a *Macrocystis* frond, a portion of the biomass on the frond is lost before the frond itself dies, and quantification of this sloughed material may be necessary for accurate productivity estimates. Leaf litter collections are widely used to estimate foliar biomass loss and productivity in terrestrial systems (Martinez-Yrizar et al. 1996, Kristensen et al. 2008), but such techniques are difficult to employ in marine systems where water motion makes litter collection with traditional litter traps impractical or ineffective (Ross et al. 2001). Typically, when foliar losses in higher plants are difficult to observe, estimates of leaf loss are derived from leaf turnover rates (Ross et al. 2001). While this works well for plants that abruptly lose foliage as whole leaves, macroalgae may lose biomass through sloughing of senescent tissue before the blade itself dies (Rassweiler et al. 2008). These losses are very difficult to observe and quantify in large, fast growing species such as

Macrocystis. To date, efforts aimed at estimating blade sloughing in *Macrocystis* have been based on short-term incubations in the laboratory and field (Yorke et al. 2013), or on the number of missing blades on a subset of randomly sampled fronds (Gerard 1976). The logistical difficulties of scaling up such techniques to obtain forest wide estimates of blade senescence over the long-term has led others to ignore this source of biomass loss in time series estimates of net primary productivity (NPP) by *Macrocystis* (Rassweiler et al. 2008), which may result in underestimates of NPP.

Macrocystis fronds are consistently turned over throughout the year as long as ambient conditions are conducive to growth and survival (Reed et al. 2008, Rodriguez et al. 2013). Fronds begin as "frond initials" when they first separate from the basal meristem and may grow slowly until they reach ~75cm total length (Lobban 1978). Once a frond reaches about ~75cm, it grows quickly for 2 or 3 months before forming a terminal blade, which signals a slowing of growth, the onset of senescence and, ultimately, death (Lobban 1978). As a frond grows toward the surface, new blades are added near the apical meristem, where most of the elongation occurs. Senescence in *Macrocystis* blades may occur over the course of several weeks, as they erode from the distal margins of the blade, contrasting sharply with the process of abscission and abrupt shedding of whole leaves in higher plants. Additionally, all blades on a frond do not senesce simultaneously, since blades near the basal meristem are the oldest, and the lifespans of individual blades may vary with light availability (Chapter2).

In addition to the effect of light availability on blade lifespan (Chapter 2), light availability alters blade morphology (Stewart et al. 2009), and may also affect the rate of blade senescence. Blades growing in areas receiving more light (in the canopy and near the edges of the forest) tend to be larger and have shorter lifespans than blades in areas receiving less light (below the canopy and in the interior of the forest, Chapter 2). Plants growing in the interior of the kelp forest under a dense canopy receive less light than plants at the edge resulting in smaller blades and increased spacing between blades (Stewart et al. 2009). It is likely that light availability affects the rate of blade senescence and quantifying the rates of senescence could improve the accuracy of NPP estimates that ignore these losses.

Here I constructed a model of frond growth and senescence for *Macrocystis* parameterized with field data on individual blade growth and senescence. I used the natural differences in light at three different depths in the water column and at two different locations in the kelp forest (edge and interior) to observe light associated differences in blade and frond characteristics. I compared model predictions of standing blade biomass with laboratory dissections of fronds from the field to assess model credibility. The model was then used to investigate how light availability alters the relative and absolute magnitude of blade senescence in a kelp forest. I found that plants under higher light conditions lose more biomass to blade senescence, but this loss is proportional to the increase in blade biomass related to the higher light environment. The model predicts that about 10.1% of edge and 11.6% of interior blade biomass produced by a frond is lost via blade senescence before the frond as a whole is lost from the plant, and that NPP is underestimated if blade senescence is ignored.

Methods

Field observations of blade growth and senescence

I tracked changes in blade length (maximum distance along the primary axis) and width (greatest distance perpendicular to the primary axis) from 3 depths within the Isla Vista kelp forest near Goleta, CA (34.4137165^o N, 119.9221^o W): canopy blades (0 m depth), midwater blades (3 m depth) and bottom blades (6 m depth). A total of 120 blades were sampled from 20 plants near the edge of the forest and 20 plants in the interior. I also tracked the change in length and the total number of blades on fronds from which blades were sampled. Blade area was calculated from length and width assuming blade shape was elliptical. Each blade was measured approximately every 7 days from the time it was first observed after separation from the meristem until it measured 10% or less of its maximum length. Growth was observed in all blades after the first observation, and I was able to capture the entire progression of blade senescence for all blades in the study. Grazing by small herbivores can account for significant partial blade loss in a kelp forest characteristically leaving holes in healthy portions of the blade (Davenport and Anderson 2007). Since nearly all blade material in this study was lost at the distal margins, I did not distinguish between losses from grazers and losses due to sloughing.

Model overview

I used a logistic decay function to model the loss of area that occurs with blade age. This loss function was applied to each of the blades on a frond, with explicit consideration of differences in individual blade ages and changes in blade count as the frond elongates. By subtracting the blade area lost from the maximum blade area, I was also able to keep track of the expected remaining blade area for the frond as it elongated. Variability (error) in the data used to parameterize the model was propagated through the model using a resampling approach, and used to generate confidence intervals for hypothesis testing and estimation of variability. Finally, I applied the loss model over the lifespans of a population of fronds to arrive at an estimate of the total percentage of biomass lost via blade senescence before the frond as a whole is lost from the plant. Table 1 contains a list of variables and functions used in this model and the source of data used to estimate the variables, where appropriate.

Prediction of total blade biomass loss and blade senescence

I used field observations of changes in blade area over time to predict the standing blade mass and the loss of blade mass from fronds at the interior or edge of a forest.

The total standing blade mass of a frond of length *x* is given by the following summation:

$$c\sum_{i=1}^{n} f_p(g_i(h(x))) \qquad \text{Equation 1}$$

and total blade loss via senescence on a frond is:

$$c\sum_{i=1}^{n} f_l(g_i(h(x))) \qquad \text{Equation 2}$$

The logistic growth function f_p and the logistic decay function f_l are applied to the blades with ages $g_1, g_2, g_3 \ldots g_n$. Blade ages are themselves a function of the frond age $h(x)$, which can be estimated from the frond length x. The index i represents the blade number, where i=1 is the first blade to emerge on the frond, and i=n represents the last or terminal blade to emerge from the frond. The area to mass conversion c of 4.4mg/cm^2 used here was estimated in Chapter 2.

The logistic growth function f_p describes the estimated blade area remaining after g_i days of blade lifetime.

$$f_p(g_i(h(x))) = \frac{k}{1+e^{-b(g_i(h(x))-m)}} \qquad \text{Equation 3}$$

Similarly, f_l represents the blade area expected to be lost via senescence after g_i days of blade lifetime:

$$f_l(g_i(h(x))) = k - \frac{k}{1+e^{-b(g_i(h(x))-m)}} \qquad \text{Equation 4}$$

where k is the maximum blade area, b (which has a negative value) characterizes the rate of decay, m is the age at which 50% of the blade area has decayed (critical age), and g_i is blade age as a function of frond age ($h(x)$) and position of the blade on the frond (blade index i). Parameters k, b, and m were estimated from blade tracking surveys, and the relationship between blade age, frond age and frond length was estimated from frond tracking surveys (Chapter 2). Separate parameters were estimated for the 6 blade locations in the forest: bottom interior, midwater interior, canopy interior, bottom edge, midwater edge, canopy edge. Since there can be more than 200 blades on a mature frond, I used a linear interpolation to estimate blade loss parameters for sub-surface blades between the sampled depths, and all blades on the surface were given the same parameter values.

The total number of blades (n) on a frond of length x used in Equations 1 and 2 was modeled as a stepwise function of frond length:

$$n = \begin{cases} s(x)+u, & \text{if } x < t \\ s(t)+u, & \text{if } x \geq t \end{cases} \qquad \text{Equation 5}$$

where s is the mean change in blade number per unit change in frond length, u is the initial number of blades present on a frond when it is first identifiable as a viable frond (~75cm length), and t is the mean length at which a terminal blade is formed, all estimated from field observations. The stepwise function simulates the emergence of a terminal blade on the frond at length t, which marks the end of new blade production, although the frond may continue to elongate. The parameter s was estimated from the frond length- blade number data by calculating the regression slope separately for the interior and edge data. The parameter r was estimated from the frond length-frond age data using a linear regression with frond location (interior and edge) as a covariate.

New blades are produced at the apex of a frond at regular intervals as the frond grows so individual blade ages (g_i) for use in Equations 1 - 4 can be estimated from frond length:

$$g_i(h(x)) = h(x) - h(x - d_i) - a \qquad \text{Equation 6}$$

Where $h(x)$ is the estimated age of a frond of length x, $h(x\text{-}d_i)$ is the estimated frond age at length $x\text{-}d_i$, d_i is the distance from blade i to the holdfast, and a is the time for a blade to reach maximum area after separation from the apical meristem. Blades that have not reached maximum area have negative ages, and only blades with positive ages were included in the analysis. The distance of an individual blade from the holdfast was estimated from the total blade count of an individual frond and the corresponding frond length, assuming all the blades on the frond were equally spaced on the frond.

The age of a frond of length x was estimated from the field data using a linear function:

$$h(x) = r(x) + 0 \qquad \text{Equation 7}$$

where r is the estimated slope parameter of a linear regression between frond age and frond length. The equation above was given an intercept of zero, as fronds of zero length must necessarily have zero age. The parameter r was estimated from the frond length-frond age data by calculating the regression slope separately for the interior and edge data.

Error propagation and confidence intervals

To simulate natural variability in field estimates of blade parameters (Table 1) and subsequent predictions of blade mass (blade biomass lost and standing blade biomass on the frond), I resampled observed data 1000 times (with replacement), estimated the relevant parameters, and predicted standing blade mass and blade mass lost for each 1 m increment of frond length. Covariance between frond age and frond length, blade count and frond length, and the blade decay parameters was preserved by selecting entire fronds at random, and estimating all relevant parameters used in the prediction of standing blade mass and senescence from a simulated sample of 40 fronds. I report the bootstrapped 84% confidence intervals for the parameters to achieve a false positive rate of 5% or less (Payton et al. 2003) when comparing parameters among blade groupings.

Model validation

Because the senescence of every blade on a frond is not easily measured, it is very difficult to verify the model predictions of blade senescence with empirical data without collecting detailed measurements of the 200+ blades that may be present on a frond. In contrast, standing blade biomass of a frond is easily measured by removing and collectively weighing all the blades present on a frond. Thus, I compared model predictions of standing blade mass of fronds with analogous laboratory measurements of blade mass to validate the model.

I compared standing blade mass of fronds from seven plants to predicted 95% confidence intervals of standing blade mass. One whole *Macrocystis* plant from Arroyo Burro (34.400275° N , 119.7445915° W), Arroyo Quemado (34.46774988°N, 120.11905° W), Mohawk (34.3940708° N, 119.72957° W), and Carpinteria (34.3916319° N, 119.5416933° W) reefs, and 3 plants from Goleta Bay (34.4137165° N, 119.9221° W) were collected and returned to the laboratory. The plants were irrigated with seawater and kept in a covered container while en-route to the laboratory to minimize desiccation. Frond lengths and total blade wet mass of a total of ninety-seven fronds from the seven plants were measured and compared to model predictions.

To construct the 95% confidence intervals of predicted standing blade mass for comparison with observed standing blade mass, I dropped the most extreme 2.5% bootstrapped predictions. Both observed and predicted standing blade mass values were grouped into 1m frond length bins from 1m to 16m (16 frond length bins total). Predictions of standing blade mass assume an equal number of edge and interior fronds. I also report blade mass lost using 95% confidence intervals constructed using the same method. Blade mass lost is reported as absolute cumulative blade loss as well as proportional blade loss. Proportional loss is calculated as the (cumulative blade loss)/(cumulative blade loss + standing blade biomass).

To estimate the total percentage of biomass lost as sloughed material before the frond as a whole is lost from the plant, I summed the blade loss predictions for the maximum frond lengths for all the fronds that I tracked in the field. Distribution of maximum frond lengths is used here as a measure of the size distribution at death for the population of fronds I studied. Applying the blade loss model to the size distribution of fronds at death results in an estimate of how much blade biomass was lost as sloughed tissue that could not be accounted for by tracking frond mass over discrete time intervals. Total blade loss over the lifespan of a frond was reported as a percentage of the total blade biomass produced by the fronds over their lifetime.

Results

Blade parameter estimation from field data

Maximum blade area (k) decreased with depth, and was higher near the edges of the kelp forest (Figure 1A), suggesting that blades were larger where light was more abundant (Chapter 2). Maximum areas for blades varied by about an order of magnitude from a mean of ~50cm^2 for the "bottom interior" blades to a mean of ~440 cm^2 for "edge canopy" blades (Figure 1A). In contrast, the rate of blade decay (b) was highest (i.e. more negative) in canopy blades, indicating a slower rate of blade mass loss for deeper blades (Figure 1B). Estimated critical age values (50% of blade senesced) were similar across all locations surveyed; mean m parameter value for all groups was 52.2 days ±2.0SE (Figure 1C).

Frond age and blade number

The regression estimates for the change in blade number per unit change in frond length (r) indicate that edge fronds had slightly more blades than interior fronds of equal length

($F_{1,379}$=4.73, p=0.0297 frond length*location). Edge fronds produced an average of 13.5 blades per meter, while interior fronds produced about 13 blades per meter (Figure 2A). Similarly, The regression estimates for the change in blade age per change in frond length (*s*) indicate that edge fronds of a given length were younger than interior fronds of the same length ($F_{1,379}$=11.6, p<0.001 frond length*location). Edge fronds aged about 11 days per meter of elongation, while interior fronds aged 13 days for each meter of elongation (Figure 2B)

Total blade mass and frond length

Field observations of standing blade biomass were within the predicted 95% confidence intervals of standing blade biomass for 10 of the 12 frond length bins below 12 m in length (Figure 3). Measured blade biomass for fronds greater than 12 m was consistently higher than the predicted blade biomass, although only 9 out of the 188 fronds measured were longer than 12 m and only 4 fronds measured longer than 13 m. Standing blade mass is predicted to increase to a maximum, then decrease as the frond continues to elongate. This maximum approximately corresponds with the formation of the terminal blade, and marks the onset of frond senescence. While the model explicitly considers the formation of a terminal blade, the model does not include a parameter for frond death, and model fronds can continue to age and loose blade mass indefinitely. Fronds in the field do not survive long after the formation of the terminal blade, but rather senesce and die soon after. Since the longest frond observed in the plant dissections was 16 m, I limited the model output to fronds < 16 m in length.

Blade biomass loss

The model predicted that cumulative absolute blade biomass lost from a frond would increase as a function of frond length (Figure 4). The amount of blade biomass lost was low for fronds with a total length of less than 8 m, with increasing biomass loss as the fronds increased in length. Fronds at the edge of a kelp forest were predicted to lose more blade mass than fronds in the interior (~34% higher for fronds 16 m long, Figure 4), but interior fronds were predicted to show greater proportional loss for fronds < 8 m (5% average proportional loss for edge fronds, compared to 15% proportion of blade loss for interior fronds, Figure 5). Proportional frond loss was predicted to be particularly high in small fronds in the interior of the forest in a few of the bootstrapped samples, resulting in high variability for these small interior fronds. This may have been caused primarily from the resampling of one or more of the stunted fronds, which aged and senesced without elongating. All fronds were included in the final analysis so the model could provide as realistic representation of natural variability as possible.

Application of the blade loss model to the size distribution of blades (Figure 6) at the time of frond death suggests that an average of 10.1% ± (.0036 SE) of edge and 11.6% ± (.048 SE) of interior blade biomass produced is lost as sloughed material before the frond dies. This seems to contradict the prediction that large fronds may have lost as much as 50% of the total biomass produced when they reach total lengths greater than 12 m (Figure 5). However, since most of the fronds in the study were lost before they reached lengths greater than 12m, the estimate of blade biomass lost before the frond dies is weighted heavily toward shorter fronds.

Discussion

The purpose of the model of giant kelp growth was to investigate the relative and absolute magnitude of blade senescence in a kelp forest, and to estimate how much productivity is ignored by using discrete changes in observed mass to calculate NPP. Previous efforts of modeling *Macrocystis* growth have focused on estimating harvest yield (Jackson 1987), estimating survival probabilities and rates of reproduction of whole individuals (Burgman and Gerard 1990), and estimating stable age distribution and transition probabilities of a population of fronds in discrete stages (Nyman et al. 1990). This is the first model of *Macrocystis* growth to explicitly quantify the loss of blade tissue via erosion.

There was generally good agreement between model predictions and field estimates of standing blade biomass. Most of the measured estimates of mean standing blade mass were within the predicted 95% confidence interval of the corresponding frond length bin. Very few fronds reached lengths greater than 12 m, but fronds that did reach these lengths had greater blade biomass than was predicted by the model. One possible explanation could be differences in individual frond growth rates that result in increasingly different frond lengths as fronds age. Since frond lifespan is most often an internally controlled, age-dependent process (Rodriguez et al. 2013), the formation of a terminal blade may also be a function of age, rather than length, as is assumed by the model. Fronds that grow more slowly may form a terminal blade at shorter lengths than fronds that grow faster, since different length fronds may be the same age if they grew at different rates. Thus, a frond that grows quickly may develop more blade mass (in the form of large canopy blades) before it forms a terminal blade and begins to senesce. This would result in observations of fronds that are unusually massive compared to the model that assumes that terminal blades are formed at a given length, rather than a given age.

Patterns of frond growth and elongation in my study were similar to those reported in previous studies (Brown et al. 1997, Stewart et al. 2009). Fronds with access to more light at the edge of the forest showed greater elongation rates and more blades per meter than fronds that were in the interior of the kelp forest. Blades on the outside edge of the forest were larger at all depths, and blades nearest to the surface were larger than deeper blades. Differences in the accumulation of blade mass on modeled fronds were a product of faster elongation, greater blade density and larger blades of fronds on the edges compared to the interior of the kelp forest. Additionally, I found that blades near the surface had the fastest decay rates, consistent with the observation that these blades also have the shortest lifespans (Chapter 2).

Absolute biomass loss was greater at the edge of the forest relative to the interior because fronds at the edge were larger. Mean proportional biomass loss was higher in interior fronds, especially in fronds < 10 m long, primarily because of a greater proportion of stunted fronds. These stunted fronds, which never grew longer than 3-5 m, exhibited large proportional biomass loss since the few blades they did produce senesced and few new blades were formed to replace them. However, these fronds had a small effect on absolute blade loss due to their low total biomass and relatively infrequent occurrence, compared to other fronds in the population.

The model predicts that fronds longer than 13 m (both interior and edge) will have lost more than 50% of their total blade mass produced, and this proportional loss continues to increase as the frond elongates (ages). While blade losses to senescence continue to increase as long as there is blade material to loose, the formation of a terminal blade prevents new blades from being formed. This results in the prediction that cumulative blade losses will eventually exceed standing blade biomass, if the frond is not lost from the plant. The ratio of standing blade biomass to cumulative blade losses may influence the formation of the terminal blade and the onset of senescence. If the lifespan of a frond is internally controlled as a function of lifetime carbon gain (Kikuzawa 1991), then fronds may stop elongating (and begin senescing) when whole frond carbon loss exceeds carbon gain. This is supported by my observation that very few fronds that I measured in the field reached lengths longer than 12 m.

The estimate of 10.1% of edge and 11.6% of interior blade mass lost over the lifespan of a frond reflects the fact that most fronds did not survive long enough to suffer substantial proportional biomass loss from decaying blades. The actual magnitude of the NPP underestimate that results from ignoring senescence must not only consider changing blade demography, but variation in turnover rates of those blades as well. However, a prediction of the NPP underestimate that assumes a steady state of frond length (age) distribution and constant frond turnover rates is a good starting point. While reef-scale estimates of detrital production suggest that the material sloughed by *Macrocystis* may not be a significant food source for benthic suspension feeders (Yorke et al. 2013), the importance of sloughed blade tissue may extend beyond its importance to primary consumers and filter feeders.

The gradual sloughing of blade tissue, rather than abrupt abscission of whole blades, may affect the performance of the kelp forest canopy. Leaf lifespan models predict that leaves are abscised when the cost of retaining the leaf exceeds the leaf's net benefit in terms of carbon gain (Kikuzawa 1991, Hikosaka 2005). Decreases in photosynthetic performance with age have been documented in *Macrocystis* blades (Chapter 2), suggesting a decrease in blade level carbon gain and net blade benefit as blades age. These decreases in performance may not be uniform along the entire blade, since the oldest tissue is found along the distal margins of the blade. Therefore, this gradual senescence may help to optimize photosynthetic efficiency of individual blades, allowing portions of blades that fall below a performance threshold to be sloughed, while retaining parts that still provide the plant with net carbon gain. Adaptations that increase photosynthetic efficiency may increase net growth and productivity and may be an important factor in the widespread success and dominance of *Macrocystis*.

Figure Legends

Figure 1. Means (points) and bootstrapped 84% confidence intervals (grey bars) of parameter estimates for (A) blade maximum area (*k* parameter), (B) blade senescence rate (*b* parameter), and (C) critical age (*m* parameter). Blades from which the parameters were estimated were sampled from the edge of the kelp forest near the bottom (EB), the interior of the kelp forest near the bottom (IB), the edge of the kelp forest in midwater (EM), the interior of the kelp forest in midwater (IM), the edge of the kelp forest in the canopy (EC), and the interior of the kelp forest in the canopy (IC). All bootstrapped confidence intervals were constructed from a distribution of 1000 sample means of 3 blades (bottom, midwater and canopy) from 40 randomly selected fronds (20 interior and 20 edge).

Figure 2. Total frond blade count (A) and frond age (B) plotted against frond length. The grey triangles and regression lines represent data from fronds in the interior of the kelp forest, the dark circles and regression lines represent data from fronds near the edge of the kelp forest. Both plots show multiple measurements from the same sample of 20 interior and 20 edge fronds.

Figure 3. Means (points) and standard errors (vertical lines) of blade biomass estimates from *Macrocystis* plant dissections by frond length. Blade biomass estimates are from a field sample of 188 interior and edge fronds. Grey bars are 95% confidence intervals from 1000 bootstrapped estimates of predicted standing biomass.

Figure 4. Predicted cumulative absolute biomass loss by frond length for (A) edge and (B) interior fronds. Points are mean estimated values, grey bars are the 95% confidence intervals from 1000 bootstrapped estimates of predicted absolute blade loss.

Figure 5. Predicted proportional biomass loss by frond length for (A) edge and (B) interior fronds. Points are mean estimated values, each grey bar is the 95% confidence interval from 1000 bootstrapped estimates of predicted proportional blade loss.

Figure 6. Histogram of frond length at death, used to estimate total blade biomass lost as sloughed tissue. Frond lengths in 1m bins.

Figure 1

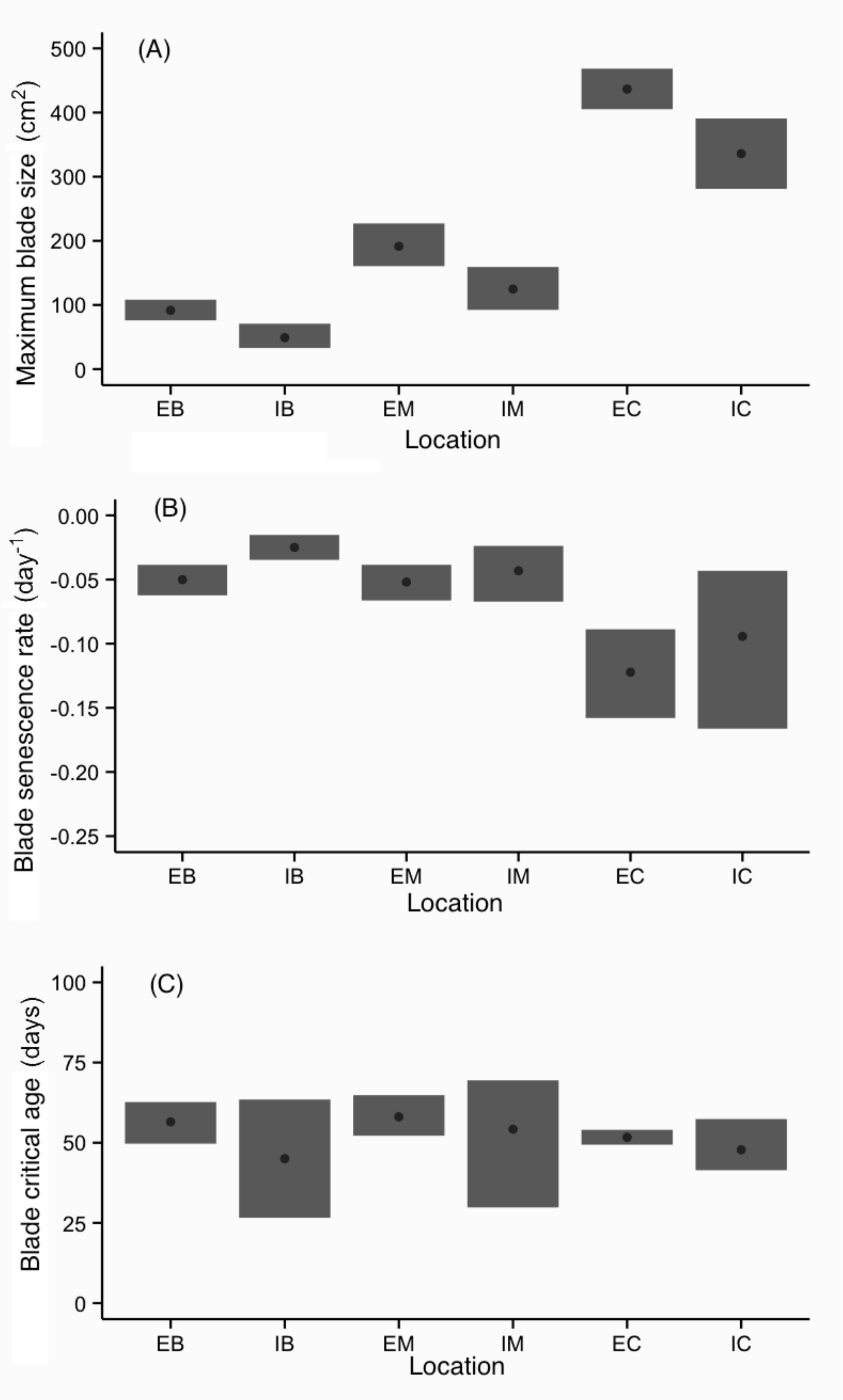

(A)
Maximum blade size (cm²)
500
400
300
200
100
0
EB
IB
EM
IM
EC
IC
Location
(B)
Blade senescence rate (day⁻¹)
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
EB
IB
EM
IM
EC
IC
Location
(C)
Blade critical age (days)
100
75
50
25
0
EB
IB
EM
IM
EC
IC
Location

Figure 2

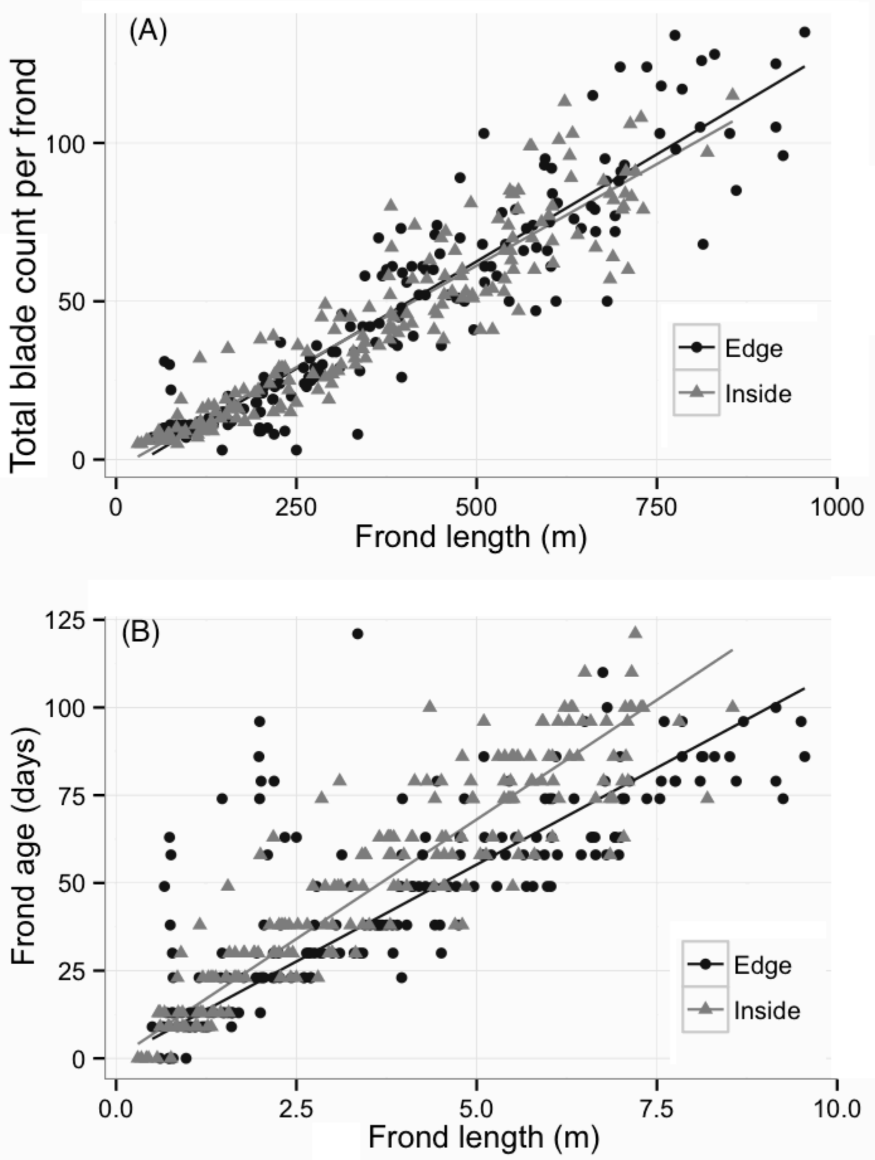
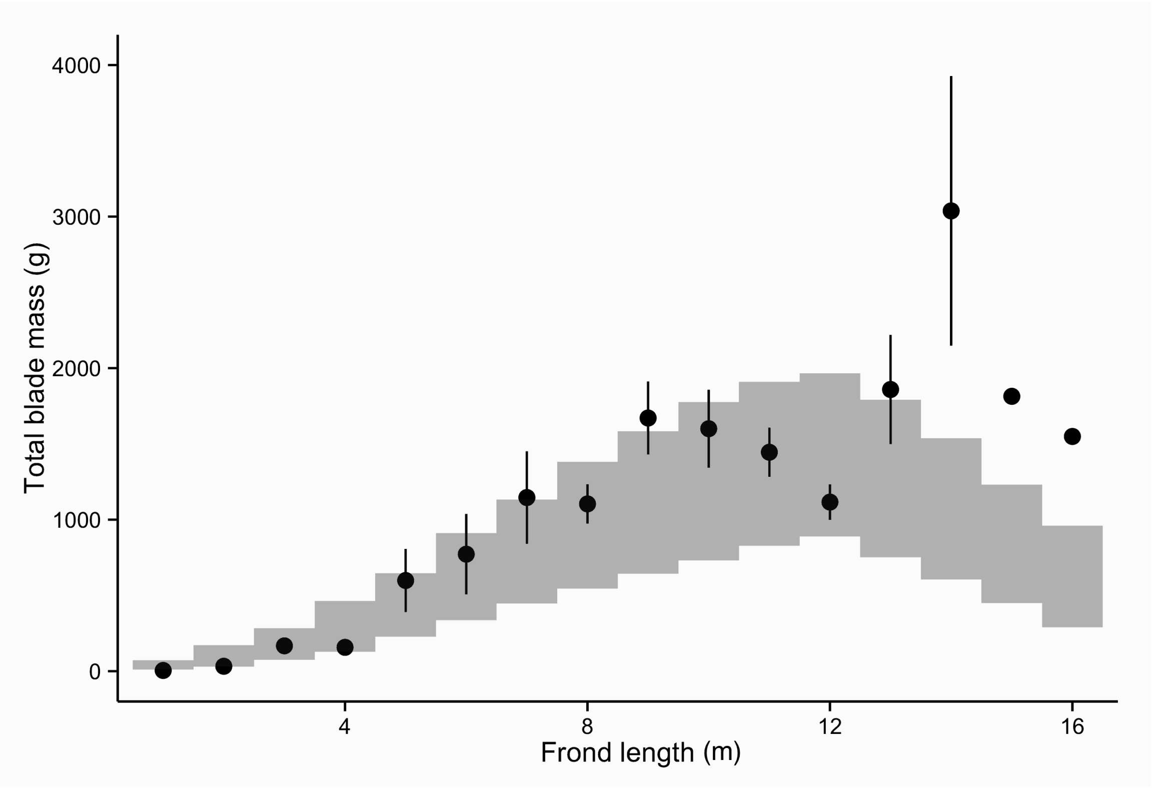

(A)
Total blade count per frond
0
50
100
0
250
500
750
1000
Frond length (m)
Edge
Inside
(B)
Frond age (days)
0
25
50
75
100
125
0.0
2.5
5.0
7.5
10.0
Frond length (m)
Edge
Inside

Figure 3



Total blade mass (g)
0
1000
2000
3000
4000
4
8
12
16
Frond length (m)

Figure 4

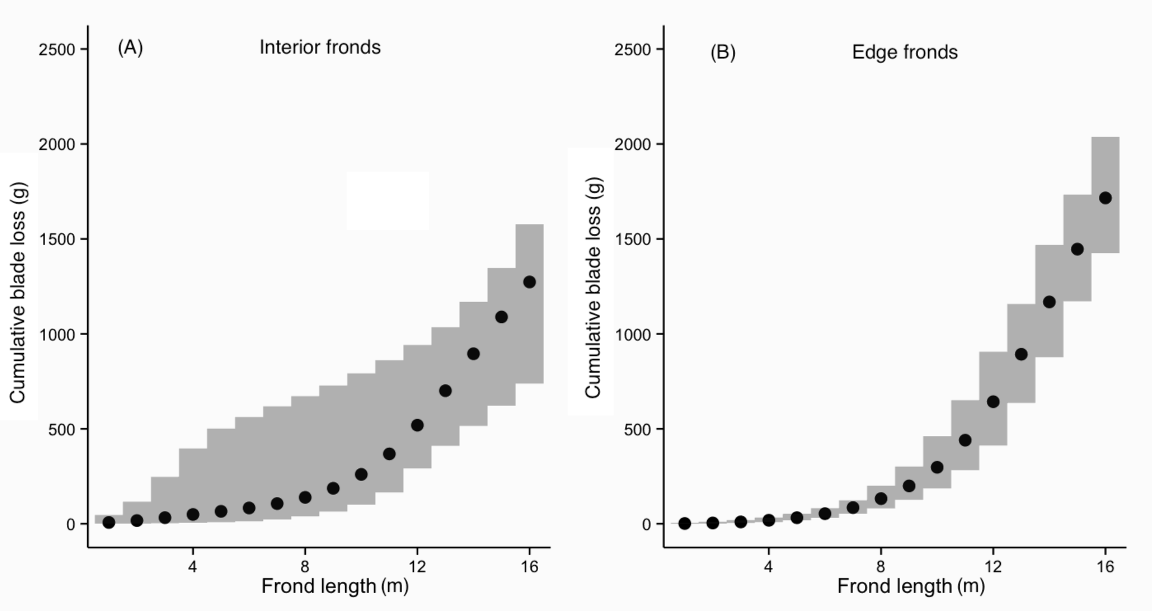


Figure 5

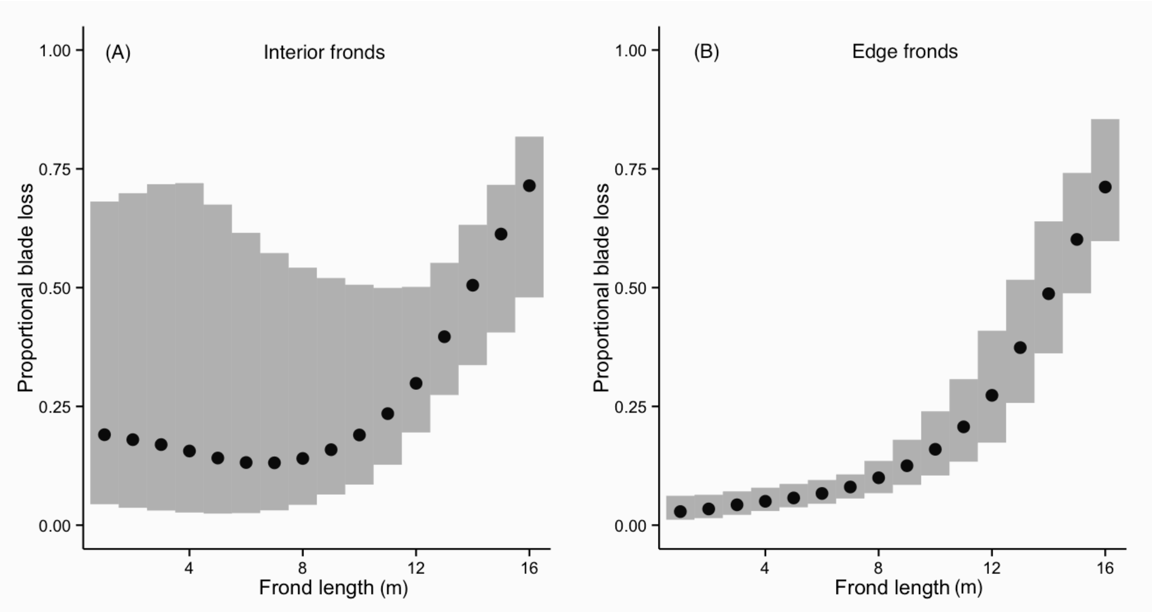


Figure 6

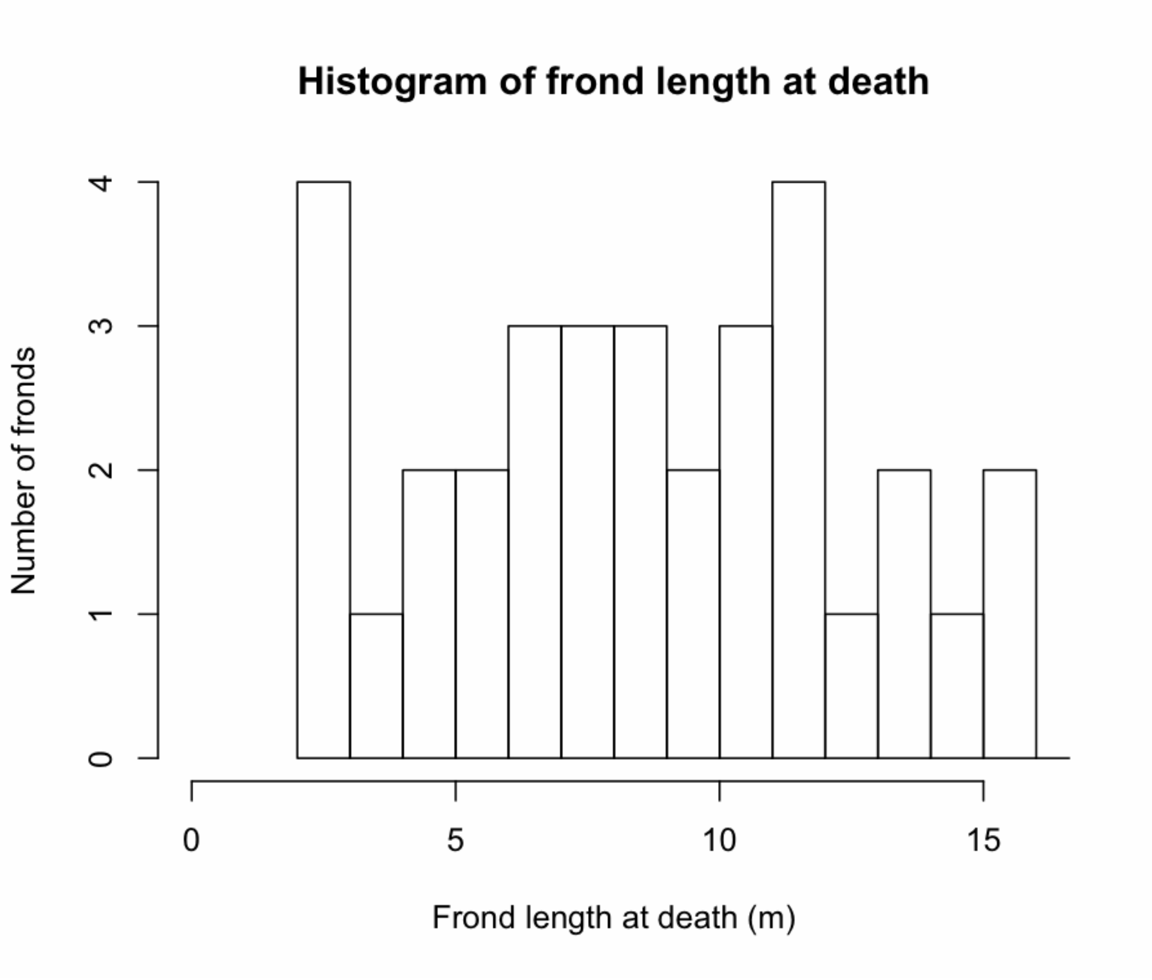

Histogram of frond length at death
Number of fronds
0
1
2
3
4
0
5
10
15
Frond length at death (m)

Table 1. List of variables and functions used in the blade growth and loss model.

Variable	**Definition**	**Source of estimate**
x	Frond length	measured or given
d_i	Distance of blade i from holdfast	estimated from blade tracking data
c	Blade area to mass conversion	estimated in Ch. 2
k	Maximum blade area	estimated from blade tracking data
b	Rate of blade area decay	estimated from blade tracking data
m	Age at which 50% of the blade area is lost (critical age)	estimated from blade tracking data
n	Number of blades on the current frond	estimated from frond tracking data
s	Change in blade number per unit change in frond length	estimated from frond tracking data
u	Initial number of blades present on a nascent frond	estimated from frond tracking data
a	The time for blade i to reach maximum area after separation from the apical meristem	estimated from blade tracking data
r	Change in frond age per unit change in frond length	estimated from frond tracking data
t	Frond length at which terminal blade is formed	estimated from frond tracking data
Function	**Definition**	
$g_i(x)$	Age of blade i, since complete formation	
$h(x)$	Age of a frond of length x	
$f_p(g_i)$	Blade area remaining after g_i days since complete formation	
$f_l(g_i)$	Blade area lost after g_i days since complete formation	

Literature Cited

Brown MT, Nyman MA, Keogh JA, Chin NKM (1997) Seasonal growth of the giant kelp *Macrocystis pyrifera* in New Zealand. Mar Biol 129:417–424

Burgman MA, Gerard VA (1990) A stage-structured, stochastic population model for the giant kelp *Macrocystis pyrifera*. Mar Biol 105:15–23

Byrnes JE, Reed DC, Cardinale BJ, Cavanaugh KC, Holbrook SJ, Schmitt RJ (2011) Climate-driven increases in storm frequency simplify kelp forest food webs. Glob Chang Biol 17:2513–2524

Davenport AC, Anderson TW (2007) Positive indirect effects of reef fishes on kelp performance: the importance of mesograzers. Ecology 88:1548–1561

Dayton P, Tegner MJ, Parnell PE, Edwards PB (1992) Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecol Monogr 62:421–445

Dugan JE, Hubbard DM, Page HM, Schimel JP (2011) Marine macrophyte wrack inputs and dissolved nutrients in beach sands. Estuaries and Coasts 34:839–850

Gerard VA (1976) Some aspects of material dynamics and energy flow in a kelp forest in Monterey Bay, California. Dissertation. University of California, Santa Cruz, California, USA.

Graham MH (1997) Factors determining the upper limit of giant kelp, *Macrocystis pyrifera* Agardh, along the Monterey Peninsula, central California, USA. J Exp Mar Bio Ecol 218:127–149

Graham MH (2004) Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. Ecosystems 7:341–357

Graham MH, Vasquez JA, Buschmann AH (2007) Global ecology of the giant kelp *Macrocystis*: from ecotypes to ecosystems. Oceanogr Mar Biol 45:39–88

Harrold C, Light K, Lisin S (1998) Organic enrichment of submarine-canyon and continental-shelf benthic communities by macroalgal drift imported from nearshore kelp forests. Limnol Oceanogr 43:669–678

Hikosaka K (2005) Leaf canopy as a dynamic system: ecophysiology and optimality in leaf turnover. Ann Bot 95:521–33

Jackson GA (1987) Modeling the growth and harvest yield of the giant kelp *Macrocystis pyrifera*. Mar Biol 95:611–624

Kikuzawa K (1991) A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. Am Nat 138:1250–1263

Kristensen E, Bouillon S, Dittmar T, Marchand C (2008) Organic carbon dynamics in mangrove ecosystems: A review. Aquat Bot 89:201–219

Lobban CS (1978) Growth of *Macrocystis integrifolia* in Barkley Sound, Vancouver Island, B.C. Can J Bot 56:2607–2711

Martinez-Yrizar A, Maass JM, Perez-Jimenez LA, Sarukhan J (1996) Net primary productivity of a tropical deciduous forest ecosystem in western Mexico. J Trop Ecol 12:169–175

Nyman MA, Brown MT, Neushul M, Keogh JA (1990) *Macrocystis pyrifera* in New Zealand: testing two mathematical models for whole plant growth. J Appl Phycol 2:249–257

Payton ME, Greenstone MH, Schenker N (2003) Overlapping confidence intervals or standard error intervals: what do they mean in terms of statistical significance? J Insect Sci 3:1–6

Rassweiler A, Arkema KK, Reed DC, Zimmerman RC, Brzezinski MA (2008) Net primary production, growth, and standing crop of *Macrocystis pyrifera* in southern California. Ecol Arch 89:2068

Reed DC, Rassweiler A, Arkema KK (2008) Biomass rather than growth rate determines variation in net primary production by giant kelp. Ecology 89:2493–2505

Rodriguez GE, Rassweiler A, Reed DC, Holbrook SJ (2013) The importance of progressive senescence in the biomass dynamics of giant kelp (*Macrocystis pyrifera*). Ecology 94:1848–1858

Ross MS, Ruiz PL, Telesnicki GJ, Meeder JF (2001) Estimating above-ground biomass and production in mangrove communities of Biscayne National Park, Florida (USA). Wetl Ecol Manag 9:27–37

Seymour RJ, Parnell IE, Dayton PK (1989) Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in Southern California. 28:277–292

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ Conserv 29:436–459

Stewart HL, Fram JP, Reed DC, Williams SL, Brzezinski MA, MacIntyre S, Gaylord B (2009) Differences in growth, morphology and tissue carbon and nitrogen of *Macrocystis pyrifera* within and at the outer edge of a giant kelp forest in California, USA. Mar Ecol Prog Ser 375:101–112

Vetter EW, Dayton PK (1999) Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons. Mar Ecol Prog Ser 186:137–148

Yorke CE, Miller RJ, Page HM, Reed DC (2013) Importance of kelp detritus as a component of suspended particulate organic matter in giant kelp *Macrocystis pyrifera* forests. Mar Ecol Prog Ser 493:113–125