CLIMATE CONTROLS ON THE GIANT KELP POPULATIONS OF THE SANTA BARBARA CHANNEL, CALIFORNIA

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ABSTRACT

Synthesizing long-term observations at multiple spatial and temporal scales is vital to understanding and predicting ecosystem responses to a changing climate. Here, we
developed a novel method for measuring giant kelp (*Macrocystis pyrifera*) canopy biomass using LANDSAT 5 Thematic Mapper satellite imagery for the Santa Barbara Channel. The regional, 25-year mean giant kelp canopy biomass was estimated at 43700 metric tons and was highly variable (C.V. = 87%), illustrating the important role of disturbance in regulating regional scale giant kelp biomass. The canopy biomass determinations were compared with oceanographic and climatic data to assess the roles of environmental processes in determining regional and subregional giant kelp biomass. Seasonal losses and recoveries of regional kelp canopy biomass were correlated with surface gravity wave heights and sea surface temperature ($r^2 = 0.50$ and 0.30 respectively), the later of which is inversely related to nutrient availability. On interannual timescales, regional kelp canopy biomass lagged wave heights, sea surface temperature, and the North Pacific Gyre Oscillation (NPGO) index by 3 years, indicating potential relationships between these variables and population-level recruitment and mortality cycles. Cluster analysis demonstrated that subregions with similar temporal dynamics were largely determined by environmental conditions. The dynamics of kelp biomass in exposed subregions were related to surface wave disturbance while kelp dynamics in sheltered regions tracked sea surface temperatures more closely. This work demonstrates how long-term, high-frequency remote observations of dynamic systems such as kelp forests can be combined with physical data to better understand how physical drivers impact ecological systems in space and time.
INTRODUCTION

Climate-related changes in the oceans appear to be accelerating: oceans are becoming warmer and more acidic, nutrient distributions are changing, and, in some regions such as the Northwest Pacific, the frequency and intensity of large storms are increasing (e.g., Easterling et al. 2000, Behrenfeld et al. 2006, IPCC 2007a, Meehl et al. 2007; Doney et al. 2009). Many marine ecosystems have displayed dramatic responses to recent fluctuations in climate, and accumulating evidence suggests that coastal marine ecosystems are especially vulnerable to the effects of climate change (e.g., Harley et al. 2006, Przeslawski et al. 2008; Hoegh-Guldberg and Bruno 2010). However, our understanding of how climate changes will affect coastal marine ecosystems is limited.

Data collection in many coastal ecosystems is labor intensive and there are relatively few long-term (>20 yr) studies of change in coastal marine ecosystems as compared to terrestrial systems (Rosenzweig et al. 2008). Increasing the number of long-term, large-scale data sets on coastal ecosystems and their responses to climate changes is of critical importance.

Among coastal primary producers, forests of giant kelp (*Macrocystis pyrifera*) are particularly sensitive to climate change (Graham et al. 2007). Giant kelp is the world’s largest alga and its numerous fronds extend vertically in the water column and form a canopy at the sea surface. Giant kelp’s biomass is exceptionally dynamic; short lifespans of both fronds and entire plants (4 - 6 months and 2 - 3 years, respectively) combine with rapid growth (~ 2% d⁻¹) to produce a standing biomass that turns over 6 to 7 times per year (Reed et al. 2008). Because of such rapid turnover, the biomass dynamics of giant kelp responds quickly to changes in environmental conditions.
Giant kelp recruitment and growth are controlled by abiotic factors including substrate availability, solar radiation, water temperature, and nutrient availability as well as the biotic effects of inter- and intra-species competition for space and light and grazing (reviewed in Graham et al. 2007). In southern California, growth is fastest in winter and spring when nutrients are high, temperature is low and competition for light and space is low (due to low algal biomass) and slowest during summer when nutrients are low, temperatures are high and competition for light and space is high due to well developed algal canopies (Zimmerman and Kremer 1986, Reed et al. 2008). The relatively low capacity of giant kelp to store nutrients (~30 days, Zimmerman and Kremer 1986) causes populations to respond rapidly to fluctuations in nutrient supply. Much like growth, the recruitment of giant kelp in southern California and elsewhere responds greatly to fluctuations in nutrients, temperature, and light as determined by biotic and abiotic processes (Dayton et al. 1984, Reed and Foster 1984, Reed et al. 2008). Giant kelp produces spores throughout the year (Reed et al. 1996) and the recruitment of new plants typically occurs whenever favorable conditions of light, temperature and nutrients coincide (Deysher and Dean 1986).

Giant kelp mortality occurs in the form of senescence, trophic interactions (i.e., grazing), and surface wave-driven disturbance (Graham et al. 2007). Reed et al. (2008) found that both frond losses and plant mortality were correlated to wave heights in kelp forests near Santa Barbara, California. While correlated to waves, frond losses occurred continuously throughout the year and significant losses occurred from senescence unrelated to wave dislodgement. On the other hand, plant-level loss was episodic and occurred primarily during periods of high waves. Large-scale mortality can also result
from extreme nutrient limitation; for example, kelp populations across southern and Baja California were devastated by the warm, nutrient poor conditions of the 1983 and 1997 El Niño events (Dayton & Tegner 1984, Dayton & Tegner 1989, Dayton 1999, Edwards 2004). The regional dynamics of giant kelp reflect the interplay of these physical and biological forcings that control the mechanisms of recruitment, growth, and mortality.

The relative importance of resource availability (light/nutrients) vs. physical disturbance (waves) in controlling the biomass dynamics of giant kelp remains an open question. For example, Dayton et al. (1999) found that large-scale, low frequency changes in nutrient availability had the largest effects on kelp populations in San Diego; however, recent analyses of kelp forests in central and southern California during 2001-2009 (a period lacking any major nutrient poor El Niño conditions) showed that wave driven disturbance explained more variability in kelp biomass and production than either nutrient availability or consumer pressure (Reed et al. 2008, Reed et al. in prep). It is clear that the influence that each of these physical forcings has on kelp populations is dependent on the spatial and temporal scales of observation (Edwards et al. 2004). The vast majority of long-term kelp studies have been made at the local scale and so it has been difficult to test how their conclusions apply to larger areas. In the past, aerial and satellite imagery has been used to examine kelp forests at regional scales; however, these studies have all been either short-term pilot studies (e.g. Deysher 1993, Stekoll et al. 2006) or limited to just a few years (e.g. Donnellan 2004, Cavanaugh et al. 2010), too short a period to examine interannual to decadal variability in kelp biomass dynamics.

Here, we describe the development of a new kelp canopy biomass dataset possessing unprecedented spatial and temporal resolution and extent using multispectral
imagery from the LANDSAT 5 Thematic Mapper (TM) sensor. These observations enabled the assessment of giant kelp canopy biomass at 30 m resolution across the entire Santa Barbara Channel every 1 to 2 months for 25 years (1984 to 2009). We compare these novel observations of giant kelp forests with oceanographic and climate observations to assess resource and disturbance driven controls on kelp populations at multiple spatial and temporal scales. Our objectives were to determine (1) the relative importance of resource availability and wave disturbance in driving both seasonal and interannual cycles of regional kelp biomass in the Santa Barbara Channel and (2) the level of spatial variability in the importance of these forcing processes within the Channel. We show that kelp biomass was significantly related to significant wave heights, sea surface temperatures (SST), and climate indices at seasonal to interannual timescales. We also demonstrate that these responses were spatially partitioned into distinct subregions within the Santa Barbara Channel. A picture of a complex system emerges where large-scale climate changes drive variability in temperature, nutrient levels, and surface gravity wave energy, which in turn drives spatially variable seasonal and interannual cycles in giant kelp canopy biomass. Variability in kelp biomass has been shown to impact many other trophic levels (Graham 2004, Byrnes et al. in review), thus the ecological implications of these results are far-reaching. A more complete understanding of how giant kelp forests vary in space and time will provide insight into how they affect the vast number of ecologically and economically important species associated with them.

METHODS
Study site

We used available LANDSAT 5 TM satellite imagery to track giant kelp canopy biomass across the entire Santa Barbara Channel from 1984 to 2009. The study area included the coastline from Pismo Beach, CA to Oxnard, CA and each of the northern Channel Islands (Figure 1). Oceanographic conditions over this region are highly dynamic in space and time (Harms and Winant, 1998, Otero and Siegel, 2004); thus the region represents an ideal system in which to investigate the importance of physical controls on the spatiotemporal distributions of giant kelp populations.

The Santa Barbara Channel experiences pronounced seasonal cycles in sea surface temperature, nutrient conditions, and wave energy. During the winter, major storms move across the Northwest Pacific and send large northwesterly swells into the Santa Barbara Channel. Wave energy from these storms is a major source of giant kelp mortality in the region (Reed et al. 2008). Nutrient levels are relatively high in the winter as a deepening of the mixed layer entrains nutrients into surface waters. Spring represents a period of transition in the wave climate of the Santa Barbara Channel as the frequency of large northwesterly wave events decreases, giving way to smaller southerly swells that are characteristic of summer months (Adams et al. 2008). Nutrient levels in the nearshore regions generally reach maximums during spring months due to coastal upwelling. The role of upwelling in providing nutrients and rapid incorporation by biological processes leads to a strong negative relationship between SST and nutrient levels (McPhee-Shaw et al. 2007). During the summer and fall, vertical stratification increases creating warmer temperatures and lower nutrient levels (e.g., McPhee-Shaw et
al. 2007, Fram et al. 2008). Less intense southerly swells are common in the summer months and can affect exposed south-facing coastlines.

The seasonal cycles in resource availability and physical disturbance are superimposed on longer period cycles driven by El Niño/Southern Oscillation (SOI), Pacific Decadal Oscillation (PDO), and North Pacific Gyre Oscillation (NPGO) events. These climate cycles alter seawater temperatures, nutrient levels, and storm patterns, and can have dramatic effects on kelp populations (e.g., Dayton & Tegner 1990, Edwards 2004). El Niños generally correspond with a deepening of mixed layer, reduced upwelling, warmer surface waters, and reduced ecosystem productivity along the U.S. west coast (Barber and Chavez 1983). Strong El Niño years have also been shown to produce stronger winter storms that take more southerly tracks across the North Pacific, resulting in larger wave events along the coast of Southern California (Seymour 1998, Adams 2008). The PDO is a longer period cycle that changes state every 20-40 years (Mantua and Hare 2002); positive phases generally correspond with increased SST. Whereas the PDO represents the 1st mode of sea surface height variability in the Northeast Pacific and is the dominant signal in physical parameters such as SST, the recently identified NPGO is the 2nd mode of sea surface height variability and is better correlated with ecosystem productivity metrics such as nutrient levels, salinity, and phytoplankton chlorophyll (Di Lorenzo et al. 2008, 2009). All of the above climate cycles control large-scale, low frequency changes in physical variables important to kelp populations.

The Santa Barbara Channel also experiences a great deal of spatial variability in oceanographic conditions. The region is located at the convergence of the equatorward flowing California Current and the recirculating Southern California Eddy and Inshore
Countercurrent (Hickey 1979). Strong upwelling north of Pt. Conception creates cool, nutrient rich conditions throughout most of the year while regions in the eastern portion of the Channel experience warmer, more nutrient limited conditions during summer months (Otero and Siegel, 2004). While there is spatial variability in the SST of the Santa Barbara Channel, the vast majority of the region’s temporal variability is homogeneous across the entire channel (Otero and Siegel 2004, see below).

Even more dramatic is the spatial variability in wave exposure. Again, Point Conception represents a natural boundary: the coastline north of Pt. Conception is exposed to both powerful winter northwest swells as well as weaker summer southern swells while the coastline south of Pt. Conception is sheltered from northern swells by Pt. Conception and from southern swells by the Channel Islands (O’Reilly and Guza 1993). The Channel Islands themselves present a myriad of exposures, but in general the north sides of the islands are exposed to northwest swells and sheltered from southern swells, while the opposite is true for the south facing sides of the islands. It is important to note that while the above descriptions depict wave exposure in general, the precise spatial distribution of wave energy along the coast of our study area depends on the specific direction of a given swell (Adams et al. 2008). As with SST and nutrients, large, long-period swells affect the entire Channel, but to varying degrees due to the large amount of spatial variability in wave exposure. Clearly, subtidal ecosystems of the Santa Barbara Channel such as giant kelp experience physical conditions that vary substantially in space and time.
Satellite estimation of giant kelp canopy biomass

Giant kelp forms a dense floating surface canopy that is distinctive when viewed from above. In our study area, giant kelp is the only canopy forming macrophyte in water depths from 5 to 30 m. This greatly simplifies its quantification from satellite imagery. The spectral signature of a giant kelp canopy is similar to that of photosynthetically active terrestrial vegetation, namely a high near infrared and significantly lower visible reflectance (Jensen et al. 1980; Cavanaugh et al. 2010). Water absorbs almost all incoming near-infrared energy so kelp canopy is easily differentiated using its near-infrared reflectance signal.

The LANDSAT 5 TM sensor has acquired 30 m spatial resolution multispectral imagery nearly continuously from 1984 to the present on a 16-day repeat cycle (Markham et al. 2004). TM obtains data in 7 spectral bands: blue (450-520 nm), green (520-600 nm), red (630-690 nm), near infrared (760-900), shortwave infrared (1500-1750 and 2080-2350 nm), and longwave (thermal) infrared (10400-12500 nm) (http://landsat.gsfc.nasa.gov/about/tm.html). TM data is stored as 8-bit encoded radiance, with 256 possible “brightness values” representing the range of radiance for each band. The kelp near infrared (band 4) radiance signal, while strong compared to that of water, spans only the lowest ~40 brightness values detectable by TM. Each LANDSAT scene covers an area 170 x 180 km; the scene we used for this study included the entire study area described above (Figure 1). During preprocessing, LANDSAT images were geometrically corrected using ground control points and a digital elevation model to achieve a scene-to-scene registration accuracy < 7.3 m (Lee et al. 2004). We selected 209 relatively cloud-free images that provided us with coverage of the study area.
approximately every 2 months from April 1984 to September 2009 (http://glovis.usgs.gov/).

The following describes the automated classification process that we developed in order to consistently and efficiently transform these 209 images into maps of kelp canopy biomass. First, a single orthorectified TM image was atmospherically corrected to apparent surface reflectance using an atmospheric transmission model (MODTRAN4; Berk et al. 1998). We used this corrected image as a reference and standardized the radiometric signals from all other images to this reference using 50 targets that were assumed to be spectrally stable across the time series (i.e. airport runways, highways, sand dunes, lakes; Furby & Campbell 2001, Baugh & Groeneveld 2008). Outliers were manually removed to reduce the effects of temporal changes in some of these targets. This ‘target matching’ procedure accounted for all atmospheric, sensor, and processing differences between the scenes and created a time-series of standardized TM imagery.

We estimated kelp canopy abundance from the calibrated TM reflectance data using multiple endmember spectral mixture analysis (MESMA). Spectral mixture analysis models the fractional cover of two or more “endmembers” within a pixel. Each endmember represents a pure cover type, and endmembers are assumed to combine linearly (Adams et al., 1993). Standard spectral mixture analysis uses a uniform set of endmembers for the entire image. One challenge in the near-shore marine zone is that the “water” reflectance is influenced by sun glint, breaking surface waves, phytoplankton blooms, dissolved organic matter, sediment runoff, etc. Since water reflectance is highly variable in space and time, a single water endmember cannot be used (Figure 2A).
Roberts et al. (1998) developed MESMA to allow endmembers to vary on a per-pixel basis. By selecting from multiple endmembers for one or more cover types, MESMA can better capture the spectral variability of the cover type within an image and through time. MESMA has been extensively used for mapping terrestrial vegetation, include aridland vegetation (Okin et al., 2001), shrublands (Dennison and Roberts, 2003a), forests (Youngentob et al., in review), and salt marsh (Li et al., 2005).

We modeled pixel reflectance as the linear mixture of reflectance from two endmembers: kelp and water. Thirty water endmembers were selected from non-kelp covered areas within each TM scene using the endmember selection technique described by Dennison and Roberts (2003b). A single kelp endmember was selected by extracting kelp-covered pixel spectra from each image and finding the single spectrum that fit the entire library of kelp spectra with the lowest root mean square error (RMSE) (Dennison and Roberts, 2003b). The pixels in each TM image were then modeled as a two-endmember mixture of kelp and each of the 30 water endmembers. The final model (out of 30) chosen for each pixel was the model that minimized RMSE when fit to the spectrum of that pixel. The result of this process was a measure of the relative fraction of each pixel that was covered by kelp canopy (Figure 2B). We used a kelp fraction threshold of 0.15 to automate the identification of ‘kelp-covered’ pixels. The multiple endmember process successfully delineated kelp canopy extent under a variety of conditions. Figure 2 provides examples of how our technique retrieved kelp fractions from images that were contaminated by large amounts of sediment runoff (Feb 23, 2005) and high levels of sun glint (July 4, 2006).
The retrieved kelp fractions were then compared to giant kelp canopy biomass observations that were collected by divers at permanent plots maintained by the Santa Barbara Coastal Long Term Ecological Research (SBC LTER) project at the Arroyo Quemado and Mohawk kelp forests (Figure 1). The data and the methods used to measure giant kelp canopy biomass from diver surveys are described in detail in Rassweiler et al. (2008). Briefly, divers measured the length of all fronds along 5 transects (40 x 1 m) within a plot (40 x 40 m) and converted these lengths to biomass using validated length to weight regressions. Each plot was overlapped by four 30 m TM pixels. For each TM image, we compared the mean kelp fraction of these pixels to the diver measured canopy biomass of each plot with a linear regression.

**Regional physical and climate datasets**

Pearson correlation coefficients between the satellite-derived time series of regional kelp canopy biomass and physical and climate data that represented first order controls of growth (temperature and nutrients) and disturbance (waves) were calculated on both seasonal and interannual timescales. Kelp canopy biomass was square root transformed to meet assumptions of normality. SST was used as a proxy for ambient nitrate concentrations to investigate the effect of nutrient availability on growth and mortality. Temperature and nitrate are strongly inversely correlated in this region (McPhee-Shaw et al. 2007, Fram et al. 2008). Hourly SST measurements were collected from the National Data Buoy Center’s Pt. Arguello buoy for 1984-2009 (Figure 1). The Pt. Arguello buoy is located west of the Santa Barbara Channel and north of Pt. Conception. While generally relatively cool and nutrient rich compared to the rest of the region, this part of our study area captures the temporal variability of the entire region.
Otero and Siegel (2004) performed temporal principal components analysis on 4 years (October 1997-June 2001) of satellite-derived SST within our study area and found that 91% of the temporal variance was explained by the first mode of variability, which was positively correlated with all parts of the study area. Hence, a single point measurement of SST should be a reliable indicator of the regional temporal variability in SST and, by extension, nutrient concentrations.

Significant wave height observations were acquired from the National Data Buoy Center’s Harvest buoy and Harvest platform sites (Figure 1). The Harvest platform measured significant wave height every 3 hours from January 1987 to April 1999 and the Harvest buoy has collected data two times an hour from March 1998 to the present. We combined these datasets to create a single time series of daily mean significant wave height from 1987-2009, using the Harvest buoy data when both the buoy and platform were operational. Overlapping data from the two were nearly identical (regression slope $= 0.96$, bias $= 0.18$, $r^2 = 0.97$). Both the Harvest buoy and Harvest platform were located west of the Santa Barbara Channel in offshore locations exposed to long-period northwest and south swells. Giant kelp is predominantly affected by extreme wave events (Gaines & Denny 1993, Utter & Denny 1996) and powerful, long-period swell (> 12 seconds) is more important than short-period sea in causing kelp mortality. Since long-period swell affects the entire Channel, we accepted a point measurement as an accurate characterization of the regional wave environment with the understanding that there would be significant spatial variability in the size of breaking waves for a given swell. Currently there is no spatially explicit dataset of nearshore wave heights that matches the spatial resolution and temporal extent of our kelp data. The nearshore wave models that
do exist for the Santa Barbara Channel are parameterized using the same Harvest buoy data we used in this study (the Coastal Data Information Project’s swell model: http://cdip.ucsd.edu).

The Harvest buoy collects wave direction as well as height and period. For the period that the Harvest buoy was operational (1998-present), seasonal histograms of wave direction were calculated for all swell events with periods >= 12 seconds in order to capture the seasonal variability in swell direction. The directional data were used to identify sections of the coast that represented strong gradients in wave exposure.

The kelp time series was also compared to the indices of three climate cycles known to affect oceanographic conditions in the Santa Barbara Channel: the Southern Oscillation Index or SOI (http://www.cpc.noaa.gov/data/indices/soi), the Pacific Decadal Oscillation or PDO (http://jisao.washington.edu/pdo/), and the North Pacific Gyre Oscillation or NPGO (http://www.o3d.org/npgo/data/NPGO.txt). By convention, positive anomalies in the PDO represent warmer, nutrient poor conditions in the Santa Barbara Channel while positive anomalies in the SOI and NPGO represent increased upwelling, nutrient, and chlorophyll-a levels. We reversed the sign of the SOI and NPGO for all figures and analyses so that positive deviations in all climate indices represent warmer, nutrient poor conditions.

**Subregional dynamics**

Spatial heterogeneity in the responses of local kelp populations to regional physical forcings cannot be captured by a regional comparison. Clustering analysis was used to understand how the relationships between physical variables and kelp canopy
dynamics varied in space. First, the coastline was divided into 1 km segments and each pixel of kelp canopy was assigned to the closest coastline segment. Segments where kelp did not appear in at least 25% of the images were removed from analysis. Because the amount of kelp in each coastline segment varied from segment to segment, the 1-km segment biomass values were standardized as the proportion of that segment’s maximum biomass over the entire time series. The data were then normalized across segments by subtracting the regional mean and dividing by the regional standard deviation of each date. Each segment’s degree of wave exposure was calculated using an exposure index based on Baardseth (1970). A circle with a radius of 100 km was placed at the center of each 1 km section of coastline and divided into 40 sectors, each of which had an angle of 9°. Sectors were given a score of 0 if they intersected land and 1 if they were free of land. The exposure index is the sum of sector scores; 0 represents complete shelter and 40 represents maximum exposure.

K-means clustering was used to identify subregions with similar temporal dynamics (e.g. Huth 1996). K-means classification is an unsupervised classification technique that requires the number of clusters to be specified beforehand. The data were clustered using 2-7 clusters to examine the robustness of the results. The kelp canopy biomass of each subregion was then compared to the physical and climate data described above.

RESULTS

LANDSAT estimation of kelp canopy biomass
A strong positive linear relationship was found between the LANDSAT derived kelp fraction index and giant kelp canopy biomass ($r^2 = 0.64$, $p << 0.001$, df = 94; Figure 3). We restricted our comparisons to canopy biomass rather than total biomass because optical remote sensing only detects floating kelp. Generally canopy biomass is highly correlated to total biomass ($r^2 = 0.92$; unpublished SBC LTER data); however, the relationship between TM kelp fraction and canopy biomass was stronger than between kelp fraction and total biomass ($r^2 = 0.49$, $p << 0.001$, df = 94). This discrepancy was driven by a few data points where the ratio of canopy to total biomass was unusually low. Neither tidal nor current fluctuations had any effect on the kelp fraction/canopy biomass relationship ($p = 0.65$ and 0.25 when the residuals of the fraction-biomass relationship were compared to local tides and currents for the time of LANDSAT data collection, respectively). This result agrees with previous work showing that the relatively weak tidal fluctuations and current speeds in this area do not affect remote sensing estimates of kelp biomass as they do in other locations (Cavanaugh et al. 2010 compared to Britton-Simmons et al. 2008). The relationship between satellite derived kelp fraction and diver measured canopy biomass (Figure 3) was used to transform images of kelp fractional cover into quantitative, validated maps of giant kelp canopy biomass. These maps are available every 1 to 2 months for the past 25 years and resolve giant kelp canopy biomass on spatial scales of 30 m to regional scales, which is here defined as the extent of the LANDSAT 5 TM scene used (Figure 1).

**Regional dynamics**

The regionally averaged giant kelp canopy biomass is shown in Figure 4A. The long-term (1984-2009) mean regional giant kelp canopy biomass was 43,700 wet metric
tons but there was an extremely high amount of variability about this mean, as evidenced by a temporal coefficient of variation of 86%. Changes in regional kelp biomass were rapid and order of magnitude increases and decreases in regional mean biomass routinely occurred over a span of less than 4 months. Most years displayed a seasonal cycle with biomass minimums occurring in the winter followed by rapid growth in the spring and early summer leading to maximums in late summer or early fall; however, the amplitude and timing of this cycle varied substantially. This seasonal cycle was superimposed on a cycle with a 12-13 year period. In this longer cycle relatively low periods of canopy biomass in 1984-1990 and 1994-2003 were separated by high biomass periods in 1990-1995 and 2003-2009. The length of this cycle matches the 11-13 year period of the NPGO (Figure 4A; Di Lorenzo et al 2008). We plotted the kelp and NPGO time series together in Figure 4A to emphasize this match in periods and to facilitate the interpretation of Figures 4A & D. There were no long-term trends in the regional canopy biomass time series.

Both SST and wave height displayed the pronounced seasonal cycles characteristic of this region (Figure 4B and 4C). SST typically reached its annual minimum between February and March and its maximum between August and October. Significant wave height maximums occurred in the winter months, corresponding with the timing of increased storm activity in the North Pacific. Between 1987 and 2009 the annual maximum winter (Dec.-Feb.) wave height averaged 4.9 m while the annual maximum summer (June-Aug.) wave height averaged 3.26 m. During our study period annual mean significant wave heights increased significantly at the pace of 0.02 m yr\(^{-1}\) \((F_{1,22} = 25.9, p < 0.001)\). This positive trend in wave height agrees with other
observations of increasing wave heights in the Northeast Pacific over the last 60 years (Bromirski et al. 2003, Ruggiero et al. 2010).

The oscillations of the three climate cycles ranged from 3-7 years (SOI) to 11-13 years (NPGO) to 20-30 years (PDO) (Figure 4 A & D). All climate indices experienced both positive and negative extremes during our study period. The 1990s saw a number of positive El Niño anomalies and the 1997-1998 El Niño was one the strongest ever recorded. La Niña conditions were present in 1998-1999, 2001, and 2008. The NPGO cycled fairly consistently with positive (nutrient poor) anomalies in the early 1990s and mid 2000s separated by negative anomalies in the early 2000s. The PDO displayed mostly positive anomalies from the beginning of the time series until the early to mid 2000s when negative anomalies became more prevalent; this change may represent a shift of the PDO from the warm phase that began in the late 1970s (Mantua et al. 1997, Peterson and Schwing 2003). All climate indices were positively correlated with SST (Table 1). The NPGO was weakly negatively correlated with higher wave heights; there was no significant relationship between either SOI or PDO and waves.

Seasonal relationships to physical and climate variables

We examined the relationships between physical and climate variables and monthly variability in kelp biomass by calculating Pearson correlation coefficients between square root normalized regional kelp canopy biomass and each of the physical and climate variables. Univariate correlation analyses indicated that there were significant but weak negative relationships between kelp canopy biomass and both SST and wave height on monthly timescales (Table 1). The failure of SST and wave height to
explain much variation in kelp canopy biomass at this scale is not surprising given the high level of month-to-month variability in the kelp time series as well as the large spatial scale over which regional kelp biomass was evaluated. The PDO was the only climate index with a significant correlation to kelp biomass, however the relationship was again weak. While the SOI index was not significantly correlated with kelp biomass, strong El Niño events in the winters of 1997-1998 and 2002-2003 corresponded with massive regional kelp canopy losses (regional kelp biomass dropped to almost zero). In addition, strong La Niña events in late 1988 and 2008 marked large increases in regional kelp biomass.

We further investigated the relationship between physical forcings and seasonal kelp variability by isolating winter canopy losses and spring recoveries and comparing them to our physical forcing variables. Winter loss was defined as the percent change in regional kelp canopy biomass from the fall (Aug-Nov) maximum to the winter (Dec-March) minimum of each year; the specific time frame varied from year to year depending on the timing of kelp maximums and minimums. We compared the percent loss of kelp to the maximum wave height over the same time period and found a strong polynomial relationship between the two that appeared to saturate between wave heights of 6-7 m (Figure 5A). Only the extreme wave events appeared to control regional kelp biomass, we did not find significant relationships between waves and kelp losses for other times of the year when waves were smaller. There was no significant relationship between winter loss and nutrient levels ($r^2 = 0.00$, $p = 0.75$). Among the climate indices we found a weak but significant positive relationships between winter PDO and kelp loss.
(r² = 0.19, p = 0.03) and between winter SOI and kelp loss (r² = 0.16, p = 0.05) but no significant relationship between NPGO and kelp loss (r² = 0.05, p = 0.31).

A similar analysis was performed between spring recovery and nutrient levels. Spring recovery was defined as the increase in canopy biomass between the winter (Dec-March) minimum and the spring/summer (April-July) maximum of each year. Biomass increases were log transformed to meet assumptions of normality for the linear regression. There was a weaker (as compared to kelp loss vs. waves), but still highly significant negative linear relationship between spring/summer recovery of regional kelp biomass and mean SST (Figure 5B). There was no significant relationship between spring recovery and wave heights or any of the climate indices.

Interannual relationships to physical and climate variables

To investigate the drivers of interannual variability in kelp canopy biomass we calculated the cross correlation, at lags of 0-6 years, of annual mean canopy biomass and the annual means of SST, and the 3 climate indices, and annual maximums of significant wave height. On interannual timescales there was no direct significant relationship between annual mean kelp canopy biomass and any of the physical or climate variables (Table 1B). However, cross correlation analysis revealed strong and significant 3-year lagged relationships between kelp canopy biomass and SST, waves, and NPGO (r = -0.48, 0.48, and -0.50 respectively; Figure 6). There was no significant relationship between kelp canopy biomass and SOI or PDO at any lag.

Subregional dynamics
The clustering analysis divided the Santa Barbara Channel into subregions along wave exposure and nutrient gradients. The clustering results were robust to varying the number of clusters used in the k-means algorithm: all solutions separated the mainland coastline at Pt. Conception and separated the north and south sides of the Channel Islands. We displayed the results from the 4-group clustering in Figure 7; increasing the number of clusters simply further separated these 4 ‘major’ subregions into smaller groups. The subregions from the 4-cluster solution were labeled A to D in order of decreasing mean exposure as measured by the exposure index (Table 2). Bonferroni adjusted paired t-tests demonstrated that the mean exposures of the two ‘exposed’ subregions (A and B) were not significantly different from each other, but each was significantly different from the two ‘sheltered’ regions (C and D) (p<0.01). It is important to note that the exposure index measures potential exposure, it does not take into account the direction of swells. Because the largest swells in the Santa Barbara Channel come from the northwest (Figure 7), the index may overestimate the realized exposure of regions that are sheltered from northwest swells, but exposed to swells from other directions (i.e. subregion B).

Temporal dynamics of the four subregions were relatively similar (mean pairwise r = 0.61, Figure 8); however, upon closer inspection it was possible to identify differences that tracked wave exposure. Kelp canopy biomass dynamics of the exposed subregions were well correlated to maximum wave heights, but not SST, while the dynamics of sheltered subregions corresponded to SST, but not wave heights (Table 2). In addition, the strength of seasonal cycles increased with increasing exposure (Figure 9). As the strength of the seasonal cycle decreased with decreasing exposure, the strength of
the longer 12-13 year period cycle increased, suggesting a closer connection between the
NPGO and sheltered regions (Figure 8). For example, the extended periods of low
regional canopy biomass in 1984-1990 and 1994-2003 reflected a near complete lack of
recovery in the sheltered regions; the exposed regions maintained relatively high levels of
biomass during these years.

DISCUSSION

Remote sensing of kelp forests

Our LANDSAT 5 TM dataset represents the first high resolution, local- to
regional-scale assessment of giant kelp canopy biomass on monthly to decadal
timescales. This dataset is itself a significant accomplishment as it provides a novel view
into kelp forest dynamics across a wide range of scales. Previous studies have
demonstrated the feasibility of measuring kelp canopy cover and biomass with aerial and
satellite imagery (Jensen et al. 1980, Deysher 1993, Stekoll et al. 2006, Cavanaugh et al.
2010); however these studies have not had the extended temporal coverage that is
presented here. Recent work by Parnell et al. (2010) examined annual to decadal
variability in giant kelp cover near San Diego using aerial surveys, but they used annual
kelp maximums and so did not measure seasonal variability. While LANDSAT provides
unmatched temporal resolution and coverage, it has a coarser spatial resolution than the
sensors used in some of these previous studies (30 m as compared to ~1 m in Stekoll et
al. 2006 and 10 m in Cavanaugh et al. 2010). In addition, LANDSAT has a relatively
low radiometric resolution; this limits the ability of the sensor to differentiate small
changes in reflectance between pixels. One consequence of the reduced spatial and
radiometric resolution of LANDSAT is higher levels of uncertainty when comparing
satellite data to transect scale diver-measured biomass (the $r^2$ between LANDSAT and
diver measured canopy biomass was 0.64 compared to 0.77 for Cavanaugh et al. 2010
and 0.84 for Stekol et al. 2006). Nevertheless, the LANDSAT-canopy biomass
relationship was still strong and highly significant and provides a path for assessing
regional satellite canopy biomass variations. As the availability of imagery with higher
spatial and radiometric resolutions increases, more accurate remotely sensed time series
of kelp can be developed using techniques similar to the one we have presented here.

Regional dynamics

Recently, investigators have speculated that the global extent of kelp forests is
shrinking (i.e. Hoegh-Guldberg and Bruno 2010). We did not find a significant negative
long-term trend in the 25-year record of kelp canopy biomass of the Santa Barbara
Channel. Long-term trends in giant kelp are difficult to identify because canopy biomass
varies across orders of magnitude over short time periods. Large disturbance events (i.e.
strong El Niños) cause dramatic large-scale reductions in canopy biomass, however
recoveries can be almost as rapid. There is an upper limit on the amount of kelp that the
region can support that is based simply on the availability of suitable habitat. However, it
seems difficult to identify a regional equilibrium for giant kelp canopy due to its highly
dynamic nature. If the global extent of kelp is indeed shrinking, then it will likely be
difficult to detect in regions such as the Santa Barbara Channel that are at the center of
giant kelp’s hemispherical range. While we did not observe a long-term directional trend
in kelp canopy biomass, we did find that regional scale kelp biomass oscillated on cycles
with periods of 1 and 12-13 years. The annual cycles were related to winter storm activity and, to a lesser extent, nutrient levels (Figure 5). While physical storm driven mortality was direct and immediate, the effect of nutrients on kelp growth were likely delayed and complicated by a number of other factors including the availability of light and space, spore settlement and recruitment, etc.; hence, a weaker relationship was observed. In addition, variability in the nutrient/temperature relationship may propagate to our attempts at relating nutrient levels to biomass dynamics. While these winter losses and spring recoveries characterized the annual cycle in general there was a great deal of variability in the amplitude and timing of these cycles from year to year.

Interannual relationships between kelp canopy biomass and physical drivers were less clear. Recovery of kelp populations can be extremely rapid and so annual means and maximums can be decoupled from the previous winter’s wave disturbance. This may help explain why past studies using annual observations made in the summer or fall failed to find a relationship between waves and kelp population metrics (Tegner et al. 1996).

The longer period cycles in kelp biomass corresponded to the NPGO, waves, and nutrient levels (as inferred from SST), but lagged these variables by 3 years (Figure 6). This 3-year lag is somewhat counterintuitive in light of the rapid turnover of the fronds that create kelp canopies. We suspect that the lagged relationships are related to plant level recruitment and mortality. While losses at the frond level occur continuously throughout the year, mortality of entire plants occurs more episodically and is related to large wave events (Reed et al. 2008). Exceptionally large wave events can clear space and allow for dramatic spikes in recruitment (Graham et al. 1997). Previous work has shown that environmental conditions at the time of recruitment and juvenile growth of kelp cohorts
can have long lasting effects on population dynamics and community structure (Tegner et al. 1997, Dayton et al. 1999). For example, Tegner et al. (1997) compared succession after 2 large disturbances under contrasting oceanographic regimes and found that nutrient rich conditions led to high densities and competitive dominance of giant kelp that lasted for the life of the cohort. This result agrees with the lagged negative relationship we found between nutrient levels and kelp canopy biomass. Together, large waves and high nutrient levels in a given year allow for the recruitment and juvenile growth of a new cohort of giant kelp plants (Figure 10). This cohort matures over the next 2-3 years, developing high levels of canopy biomass in the absence of severe storms. Currently, in Southern California severe storms occur at the average frequency of 1 every 3.5 years (Graham et al. 1997), thus allowing populations to expand their areal extents until the cycle is repeated or all available habitat is utilized. In addition, LANDSAT only measures canopy changes; it takes approximately 6-8 months for a newly recruited kelp plant to reach the surface (author’s personal observations) and so there is an inherent lag in responses observed with satellite imagery.

Many studies have linked massive declines in kelp populations to severe El Niño conditions and have observed rapid recovery of kelp populations during nutrient rich La Niña events (Dayton and Tegner 1989, Dayton 1992, 1999, Edwards 2004). In addition, Parnell et al. (2010) found that the response of kelp populations to El Niño events is modulated by low frequency changes in the PDO: the importance of nutrient control in the San Diego area increased after the PDO switched to a warm phase in the late 1970s. However, the relationship between kelp and the NPGO has largely been neglected. We observed that strong El Niño events in 1987, 1997, and 2003 coincided with large
regional mortality events (Figure 4); however, the long (12-13 year) period cycles in
regional kelp biomass were better correlated with the NPGO, again at a 3 year lag. The
NPGO is driven by regional variations in wind-driven upwelling and horizontal advection
and corresponds closely with correlates of ecosystem productivity such as nutrient levels
and chlorophyll concentrations (Di Lorenzo et al. 2008). Therefore, the NPGO appears
to influence decadal variations in kelp canopy biomass though large-scale, low frequency
changes in nutrient availability that in turn affect recruitment and growth of kelp
populations.

While no long-term trends were evident in the kelp time series, we did see a
significant long-term increase in mean and maximum wave heights over our study period.
Other studies have observed similar trends in the Eastern Pacific (Bromirski et al. 2003,
Ruggiero et al. 2010) and many climate models predict that the frequency, and possibly
the intensity of large storms will continue to increase in this region (Easterling et al.
2000, Meehl et al. 2000, Meehl et al. 2007). This has the potential to increase the effects
of wave events on the more sheltered coastlines of southern California, leading to higher
annual winter losses. Reed et al (2008) found that biomass at the start of the growth year
(after winter storm disturbances) explained 63% of the observed variation in annual net
primary productivity of three kelp populations in the Santa Barbara Channel. Therefore,
increased wave losses would likely lead to decreased productivity by giant kelp in this
region. In addition, the implications of increased levels of physical disturbance span
trophic levels as repeated kelp loss due to waves has been linked to lower diversity and
complexity of kelp forest food webs (Byrnes et al. in review).

Subregional dynamics
The Santa Barbara Channel experiences a large amount of spatial variability in environmental conditions. As a result, the regional comparison of kelp biomass to physical variables may be confounded by the response of subregions that are controlled by different physical forcings. We found that subregions with similar temporal dynamics could be separated statistically and these subregions have different wave exposures and respond differently to variations in SST and presumably nutrient levels (Table 2). The dynamics of the relatively sheltered mainland coastline south of Pt. Conception (subregion D) were significantly correlated with SST, but not maximum wave height. Tegner et al. (1996) observed similar behavior in the Pt. Loma kelp forest near San Diego: a measure of canopy density was significantly correlated with SST but not wave heights. Also, in many years minimum canopy biomass levels occurred in late summer/early fall for subregion D (Figure 9). This is generally a time of relatively low wave energy and low nutrient levels, suggesting that senescence unrelated to waves is causing these annual minimums.

Our results indicate that Pt. Conception marks a major biogeographic boundary for the dynamics of giant kelp forests in California. Changes in kelp biomass along the exposed coastline north of Pt. Conception were well correlated with wave height, but not SST as high storm mortalities were observed each winter. This created a pronounced and predictable seasonal cycle with lower interannual variability than the more sheltered subregions to the south (Figure 9). The high variation in canopy biomass observed in October and November (e.g. long boxes in Figure 9A) reflect variability in the timing of the onset of the winter storm season. Relatively high nutrient conditions in this subregion likely allowed for consistent spring recovery each year (Jackson 1987). This result
agrees with a study by Donnellan (2004) that found that seasonal canopy dynamics of exposed Central Californian kelp beds were highly regular and predictable. The subregions containing the Channel Islands represented a combination of more complex exposures. Subregion B displayed dynamics similar to the exposed subregion A even though subregion B was protected from large northwest swells. This likely reflects the fact that both subregions are rarely nutrient limited and so nutrient fluctuations have less control on biomass dynamics in these regions. Like the coastline north of Point Conception, the south sides of the two westernmost Channel Islands are typically bathed in cold, nutrient-rich upwelled water (Harms and Winant 1998; Otero and Siegel, 2004).

Previous local empirical and theoretical studies have observed kelp populations fluctuating on cycles of 3-5 years and have theorized that these fluctuations are due to seasonal forcings such as wave disturbance. Graham et al. (1997) found these cycles in both exposed kelp populations of central California as well as more sheltered populations of southern California. Their work suggested that in sheltered populations recruitment occurred continuously and so the cycles were controlled by the irregularity of large storm events. In exposed populations where large storms occurred more frequently, sporadic recruitment created a lag in recovery that was dependent on the coincidence of a juvenile population and conditions suitable for juvenile growth. Such lags in recovery can cause interannual cycling. Nisbet and Bence (1989) developed a family of 2-stage kelp population models (juvenile and adults) that reproduced similar 3-5 year cycles as well as more regular annual cycles. Their models were based on the idea that population dynamics are driven by recruitment events which are in turn controlled by temperature, bottom irradiance, and unknown stochastic factors. Their models predicted that larger
seasonal fluctuations in surface irradiance and adult mortality, such as those that occur in central California, should lead to more regular annual recruitment. On a regional scale, we found that 3-5 year cycles were much more evident in sheltered subregions than in exposed regions (compare subregion A to subregion D in Figure 8). Exposed coastlines experienced regular annual cycles of winter mortality and spring recovery. The increased regularity of the annual cycles we observed compared to those observed by Graham et al. (1997) in central California may have been due to the difference in the spatial scales of our studies. In exposed regions, recovery lags that produce irregular cycles at local scales (as in Graham et al. 1997) may be averaged out at the regional scale. A regional cycle will be apparent if mortality is consistent across the entire region and enough local populations recover each year.

Long-term time series data from sensors such as LANDSAT is becoming increasingly available at little to no cost. While the benefits of increased spatial coverage have been well recognized, the temporal coverage of these datasets has been under-utilized. Given the time and costs involved in collecting field data in situ there is great potential for satellite data such as LANDSAT to provide much needed insight into the patterns and controls of dynamic systems like giant kelp forests over large spatial and long temporal scales.

Acknowledgements

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Coastal Long-Term Ecological Research site. K Cavanaugh would like to acknowledge support from the NASA Earth System Science fellowship program.
Cavanaugh et al.: Climate controls on kelp populations

LITERATURE CITED


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Figure 1. LANDSAT TM scene displaying study area, Pt. Arguello, Harvest, and Harvest Platform buoys, and LTER diver transects at the Arroyo Quemado (AQUE) and Mohawk (MOHK) kelp forests.
Figure 2. Satellite kelp fraction analysis. (A) LANDSAT false color image of giant kelp beds off Santa Barbara coast. Note variability of water reflectance resulting from sediment runoff in the Feb. 23, 2005 image and glint in the July 4, 2006 image. (B) Kelp fraction images from spectral unmixing process. Brighter pixels correspond to higher kelp fractions. The slight banding apparent in the water is noise that occurs when the detector transitions from bright land targets to dark ocean targets.
**Figure 3.** Validation of LANDSAT satellite biomass estimates. Linear regression analysis between LANDSAT kelp fractions and diver measured canopy biomass (kg/m²) measurements for Arroyo Quemado and Mohawk (n=96). The gray lines represent 95% confidence intervals for the relationship.
Figure 4. Santa Barbara Channel regional mean time series of (A) giant kelp canopy biomass and NPGO anomalies. Kelp canopy biomass was summed across the entire study area for each image date. 1 month running mean of (B) SST and (C) significant wave height from Pt. Arguello buoy, Harvest platform, and Harvest buoy data. (D) Monthly SOI and PDO anomalies. Asterisks in (A) represent strong El Niño events, with the two asterisks in 1997-1998 identifying the strongest El Niño on record, while triangles represent strong La Niña events (as classified by Smith and Sardeshmukh 2000)
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**Table 1.** Pearson correlation coefficients for regional giant kelp and climactic forcing data calculated on (A) monthly and (B) annual timescales. For the monthly comparisons regional kelp canopy biomass from each image date was correlated to the mean of the physical and climate data from 30 days before the image date. For the annual comparisons the annual mean of kelp was compared to the annual means of SST, SOI, PDO, and NPGO and the annual maximum of wave height. Bold values are significant at the 99% confidence level.
Figure 5. Regression analysis between (A) winter kelp canopy biomass losses and maximum wave height and (B) spring/summer kelp canopy biomass recovery and mean SST. Winter losses were calculated as the change in kelp canopy biomass from the fall (Sept.-Nov.) maximum to the winter/spring (Dec-May) minimum. Recovery represents change in kelp canopy biomass from the winter/spring (Dec-May) minimum to the summer (June-Aug.) maximum. Maximum wave height and mean SST for each year were calculated over the same periods.
Figure 6. Cross-correlation analysis (at lags of 0-6 years) of climate indices and physical variables on annual mean kelp canopy biomass. Annual mean kelp was compared to mean SST, SOI, PDO, and NPGO and maximum wave height for each year. Bold bars are significant at the 95% level.
Figure 7. Results from k-means cluster analysis (N=4 clusters) on monthly canopy biomass data binned into 1 km sections of coastline. Subregions are labeled A-D in order of decreasing exposure. Histograms of significant wave height ($H_s$) and direction for swells with periods larger than 12 seconds are provided for winter (Dec-Feb) and summer (June-August).
Figure 8. Timeseries of kelp canopy biomass summed across each subregion identified in Figure 7. Subregions are labeled A-D in order of decreasing exposure.
Figure 9. Box and whisker plots of the seasonal cycle in canopy biomass for each subregion. For each year between 1984-2009 the proportion of that year’s maximum biomass was calculated for each month. Boxes represent the lower quartile, median, and upper quartile of the proportion of annual maximum biomass and whiskers extend to the lower and upper extremes of the data. Longer boxes represent months with higher variability in their relative canopy biomass levels. Boxes whose notches (not whiskers) do not overlap have significantly different medians at a 95% confidence level.
Table 2. Mean exposure index and correlation to physical data for each subregion. Subregional kelp from each image date was correlated to the mean of the physical and climate data from 30 days before the image date. Bold values are significant at 99% level.

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Figure 10. Conceptual model of factors that influence regional giant kelp canopy biomass