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# Geographical variability in the controls of giant kelp biomass dynamics

Tom W. Bell<sup>1\*</sup>, Kyle C. Cavanaugh<sup>2</sup>, Daniel C. Reed<sup>3</sup> and David A. Siegel<sup>4</sup>

<sup>1</sup>Earth Research Institute, University of California, Santa Barbara, Santa Barbara, CA 93106-3060, USA, <sup>2</sup>Department of Geography, University of California, Los Angeles, Los Angeles, CA 90095, USA, <sup>3</sup>Marine Science Institute, University of California, Santa Barbara, Santa Barbara, CA 93106-3060, USA, <sup>4</sup>Earth Research Institute and Department of Geography, University of California, Santa Barbara, Santa Barbara, CA 93106-3060, USA

## ABSTRACT

**Aim** Coastal marine environments experience a wide range of biotic and abiotic forces that can limit and punctuate the geographical range and abundance of species through time. Determining the relative strengths and nonlinear effects of these processes is vital to understanding the biogeographical structures of species. There has been an ongoing discussion concerning the relative importance of these processes in controlling the dynamics of giant kelp, *Macrocystis pyrifera*, an important structure-forming species on shallow reefs in the eastern Pacific. We used novel spatial time-series that span nearly three decades to determine the dominant drivers of giant kelp canopy biomass and the temporal and spatial scales over which they operate across the dominant range of the giant kelp in North America.

**Location** Near-shore areas from Año Nuevo, California, to the USA/Mexico border.

**Methods** We employed empirical orthogonal functions to elucidate the primary drivers of giant kelp canopy biomass across space and time and then fit generalized additive and linear models to determine the nonlinear effect and relative importance of each of these potential drivers along the c. 1500-km study region over a 25-year period.

**Results** Wave disturbance, nitrate availability and the state of the North Pacific Gyre Oscillation were the most important environmental predictors of giant kelp canopy biomass, explaining 24.5%, 12.7% and 6.1% of the variance, respectively. Environmental drivers of canopy biomass exhibited profound spatial differences in relative effect sizes. Nonlinear effect shapes of each potential biomass driver were determined, which explained these spatial differences.

**Main conclusions** These large-scale analyses help to reconcile the local-scale conclusions of canopy biomass dynamics across the California coastline and show that these dynamics differ predictably in space and time in accordance with local and regional differences in environmental drivers. By characterizing the nonlinear effects of these drivers, we identified spatio-temporal patterns of processes that cannot be detected by remote sensing.

## Keywords

Biomass dynamics, bottom-up, disturbance, empirical orthogonal function, generalized additive model, *Macrocystis pyrifera*, spatial scales of variability, top-down, USA.

\*Correspondence: Tom W. Bell, Earth Research Institute, University of California, Santa Barbara, Santa Barbara, CA 93106-3060, USA. E-mail: thomas.bell@lifesci.ucsb.edu

## INTRODUCTION

The spatial distributions of organisms are driven by a combination of abiotic and biotic forces. Abiotic forces include climate, physical features of the environment and resource availability, whereas biotic forces involve the physiological performance of individuals as well as interactions within and between species. The influence of these processes may change in direction and magnitude across a wide range of spatial and temporal scales (Menge, 1976). This variability has led to seemingly contradictory conclusions about the primary drivers of population abundance in a number of systems (reviewed in Power, 1992).

Marine coastal environments experience a wide range of forces that can limit and punctuate the geographical range of an organism through time. For example, the distributions of two species of mussel (*Mytilus edulis* and *Mytilus trossulus*) in the north-eastern Atlantic can be partly attributed to physiological stress caused by aerial exposure, whereas inter-annual variations in ice floes can interrupt the density trends along the mussels' range (Tam & Scrosati, 2011). Coastal environments also experience large-scale changes in ocean climate, which can fundamentally alter the distribution of a species. The northward range expansion of Kelle's whelk (*Kelletia kelletii*; Herrlinger, 1981) has been attributed to either warming sea-surface temperatures (SST), ocean circulation changes, or some combination of the two, across a biogeographical boundary, probably linked to El Niño events (Zacherl *et al.*, 2003). The complexity of the coastal environment may further complicate the mixture of drivers on a species through time.

The coastline of California, USA, spans four shallow marine biogeographical regions (Hall, 1964; Valentine, 1966; Abbott & Hollenberg, 1976; Blanchette *et al.*, 2008), which are marked by differences in oceanographical environments: the Mendocinian, Montereyan, Southern Californian and Ensenadian regions. Winter storms in the North Pacific create large swell waves (> 4 m height) propagating from the north-west, whereas summer months see a mixture of smaller significant wave heights (< 3 m) from the south and north-west (O'Reilly & Guza, 1993). The central coast of California (Año Nuevo to Point Conception) is more exposed to westerly and north-westerly swells as a result of its orientation, whereas the southern California mainland coast (Point Conception to the USA/Mexico border) has a range of wave exposures as a result of variable coastline orientations as well as the presence of the Californian Channel Islands. Coastal upwelling brings cold, nutrient-rich waters to the coastal shelf, and is strongest in the spring along the central coast, where nutrient-replete conditions persist for the entire year; upwelling is less intense and more intermittent in southern California, with low nutrient levels during the summer (Huyer, 1983; McPhee-Shaw *et al.*, 2007; Reed *et al.*, 2011). Large-scale low-frequency climate cycles, such as the Pacific Decadal Oscillation and El Niño–Southern Oscillation (ENSO), affect conditions on interannual

time-scales and can have large impacts on the biogeography and structure of marine communities (Dayton *et al.*, 1999; Parnell *et al.*, 2010).

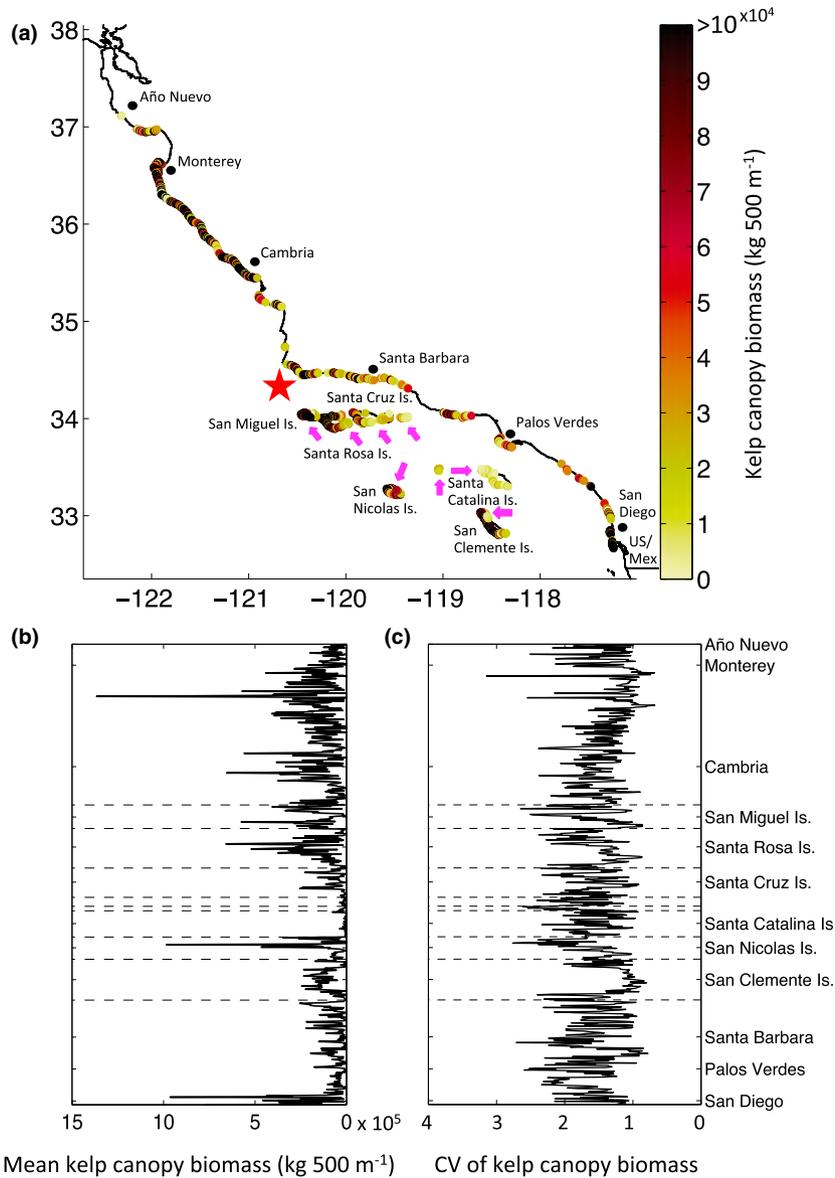
The giant kelp, *Macrocystis pyrifera* (L.) C. Agardh, is a canopy-forming macroalga that is widely distributed along the coast of California and serves as the foundation species to a productive ecosystem (Graham *et al.*, 2007). Giant kelp abundance in California is extremely dynamic. It is highly susceptible to removal by ocean waves and it is not uncommon for entire forests to be destroyed during a single storm (Seymour *et al.*, 1989; Graham *et al.*, 1997; Edwards & Estes, 2006); populations are, however, highly resilient, and recovery to a full canopy often occurs within 1–2 years after local extinction (Reed *et al.*, 2006). Individuals routinely attain lengths over 20 m and under ideal conditions can elongate at rates of 50 cm per day (Clendenning, 1971), which implies an important role for nutrient supply to support these extreme growth rates (Jackson, 1977; Gerard, 1982; Zimmerman & Kremer, 1984; Stewart *et al.*, 2009). Large areas of kelp forest can be destroyed by grazing activities, primarily by sea urchins, which can denude large areas (Harrold & Reed, 1985), and the removal of the surface canopy by mechanized harvesters causes additional reductions in kelp biomass (Kimura & Foster, 1984; Foster & Schiel, 2010). Importantly, the processes thought to dominate the regulation of giant kelp forests can vary with location and time (e.g. Jackson, 1977; Dayton *et al.*, 1992, 1999; Graham *et al.*, 1997; Edwards, 2004; Lafferty & Behrens, 2005; Parnell *et al.*, 2010; Cavanaugh *et al.*, 2011; Reed *et al.*, 2011). This suggests that the interplay between regulating forces may be understood by studying the spatial distribution of this species through time.

Recent advances in satellite image analyses allow for frequent (monthly to seasonal), long-term (25 years and continuing), high-resolution (30 m), large-scale (continental) observations of giant kelp canopy biomass (Cavanaugh *et al.*, 2011). These kelp data can be combined with spatially explicit time-series of potential drivers to quantify the effects of these drivers on giant kelp biomass across a wide geographical region. Here, we used these data to explore how nutrients, wave disturbance, low-frequency oceanographical cycles, human harvest and herbivory by sea urchins structure the spatial distribution of giant kelp biomass through time, across the species' region of dominance on the rocky reefs of California, USA. Our research focused on answering the following questions. (1) What are the dominant drivers of kelp canopy biomass dynamics? (2) How does the relative importance of these drivers vary across temporal scales of seasons to decades and spatial scales of 500 m to 1500 km?

## MATERIALS AND METHODS

### Giant kelp canopy biomass data

We studied giant kelp over its range of dominance along the coast of California, USA, encompassing the area between Año Nuevo, California, and the USA/Mexico border



**Figure 1** (a) Mean giant kelp canopy biomass at every 500-m coastline segment across every measured season, from 1986 to 2011, along the coast of California, USA. The star shows the approximate location of the Harvest platform and buoy, Point Arguello buoy, and Point Conception (plate carrée projection). (b) Mean kelp canopy biomass plotted as lines running from south to north, including the Channel Islands inside the horizontal dashed lines. Site locations for each island start at the location of the arrow and proceed clockwise around the island. (c) The coefficient of variation (CV) of kelp canopy biomass at each coastline segment across all seasons and years.

(c. 1500 km of coastline; Fig. 1). Giant kelp canopy biomass was estimated at 30-m resolution from January 1986 to January 2011 using multispectral Landsat 5 Thematic Mapper (TM) satellite imagery following procedures developed by Cavanaugh *et al.* (2011). Briefly, each Landsat 5 TM image was atmospherically corrected to standardize the radiometric signals using 50 temporally stable ground control points (Furby & Campbell, 2001). Multiple-end-member spectral mixing analysis (Roberts *et al.*, 1998) was applied to estimate the fractional cover of two end-members: one static kelp end-member, and one of 30 seawater end-members unique to each image. Kelp canopy biomass was estimated using the observed relationship between diver-estimated kelp canopy biomass and Landsat pixel kelp fraction. Cloud-free imagery allowed kelp biomass to be estimated every 1–2 months. Canopy biomass determinations were binned into 500 m segments and interpolated onto a 3-month time interval using piecewise cubic interpolation. The segment length of

500 m was chosen to avoid spatial autocorrelation, because synchrony among canopy biomass observations declines dramatically in the first 200 m of spatial separation (Cavanaugh *et al.*, 2013). Each segment was scaled as a proportion of the maximum (top 3%) canopy biomass observed across the entire time-series to account for differences in the amount of kelp (referred to here as ‘proportional kelp biomass’). Coastline segments with zero canopy biomass in more than 75% of seasons were removed from analysis, for a total of 723 coastal segments.

### Physical, biological and harvest datasets

Spatio-temporal data were compiled for variables that are anticipated to describe processes affecting giant kelp canopy biomass. Observations of significant wave height ( $H_s$ ) were assessed using the National Buoy Data Center’s (NBDC; <http://www.ndbc.noaa.gov/>) Harvest platform and Harvest

buoy, located *c.* 30 km offshore from Point Conception (Fig. 1a). The Harvest platform collected hourly observations of  $H_s$  and period from January 1987 to April 1999, and the Harvest buoy collected  $H_s$ , period and direction from March 1998 to present. Records from the platform and buoy were combined to form a single  $H_s$  time-series at the Harvest platform. Data from the Coastal Data Information Program's (CDIP; <http://cdip.ucsd.edu/>) nowcast wave-propagation model were used to assess spatial variations in  $H_s$ . CDIP provided hourly estimates of  $H_s$  at a depth of 10 m from June 1998 to November 2011 for the entire domain at 800-m spatial resolution. Each coastline segment was assigned a seasonal maximum  $H_s$  from the closest CDIP wave-model pixel. To complete the record,  $H_s$  values were statistically modelled using a generalized additive model from observations of  $H_s$  and dominant period from the Harvest platform, and a probability distribution of swell direction (see Appendix S1 in Supporting Information).

Surface nitrate concentrations were estimated using sea-surface temperature (SST) records and the observed relationship between ocean temperature and nitrate concentration following Zimmerman & Kremer (1984). A continuous time series of SST is available near the centre of the domain from the NBDC Point Arguello buoy (hourly from 1986 to 2011) located *c.* 20 km offshore from Point Arguello, and at each site from the Advanced Very High Resolution Radiometer (AVHRR; <http://www.ncdc.noaa.gov/sst/>) satellite images from 1987 to 2011. Seasonal mean nitrate values were determined for each coastline segment.

Three oceanographical climate indices were also used in this study: the North Pacific Gyre Oscillation (NPGO; <http://www.o3d.org/npgo>), Pacific Decadal Oscillation (PDO; <http://jisao.washington.edu/pdo>), and the Multivariate ENSO index (MEI; <http://www.esrl.noaa.gov/psd/enso/mei>). These climate oscillations fluctuate over interannual to decadal time-scales and are known to have large effects on the California Current system in general and on giant kelp populations in particular (Dayton & Tegner, 1984; Di Lorenzo *et al.*, 2008; Parnell *et al.*, 2010). Positive values in the NPGO index correspond with stronger wind-driven upwelling, which leads to greater nutrient concentrations along the California coast, whereas positive MEI values are associated with El Niño conditions, with decreases in wind-driven upwelling, warmer surface waters and nutrient-poor conditions. Positive PDO values indicate warmer SST, and nutrient-poor conditions along the western coast of the contiguous United States. All environmental variables were lagged by one season, because wave disturbance and changes in nutrient concentrations were expected to affect giant kelp canopy biomass over relatively short time-scales.

Kelp canopy harvest records for every California Department of Fish and Wildlife administrative bed harvested by ISP Alginates were available from 1991 until harvesting ended in 2006 (Reed, 2010). In order to calculate the amount of harvest effort in each coastline segment, the harvested kelp was apportioned to each segment based on

the proportion of total kelp canopy biomass of the segment within the administrative bed. The amount of kelp harvested was then divided by the total segment kelp canopy biomass in the season prior to obtain a measure of harvest effort, ranging from zero (no harvest) to one (complete harvest of the kelp canopy).

Densities of purple and red sea urchins (*Strongylocentrotus purpuratus* and *Mesocentrotus franciscanus*, respectively) were measured at a small fraction of the sites (Kenner *et al.*, 2013; Kushner *et al.*, 2013; Reed, 2013). Annual sea urchin density surveys started between 1982 and 2001 for the 45 sites with records long enough to be included in the analyses (see Appendix S1).

### Empirical orthogonal function analysis

Dominant drivers of kelp canopy biomass were identified using an empirical orthogonal function (EOF) analysis (Lorenz, 1956). EOF analysis compresses a set of correlated time-series into a ranked set of uncorrelated ones, each with a spatial map illustrating the loadings for that mode. EOF modes were ordered by the fraction of variance explained. Here, we decomposed the space–time distribution of kelp canopy biomass into a ranked set of orthogonal spatial loadings and temporal amplitude functions. Each EOF mode described a known fraction of the total variance in kelp canopy biomass and collectively accounted for the covariability of the space–time biomass distribution. A physical interpretation for each mode was made by examining the relationships between the EOF spatial loadings and temporal amplitude functions with the different environmental parameters. Pearson product-moment correlation coefficients between environmental variables and the EOF temporal amplitude function indicate how closely the variable matched the changes in direction and magnitude of the amplitude function through time, whereas correlations with the EOF spatial loadings indicate how closely the variable matched the magnitude of the loadings in space. Significance between EOF outputs and environmental variables was tested using permutation tests with 1000 permutations.

### Generalized additive model analysis

A generalized additive model (GAM) was applied to each coastline segment in the study domain in order to determine the dynamic relationships between kelp canopy biomass and the environmental drivers. The general concept of GAMs is that a response variable (e.g. kelp biomass) can be modelled as the sum of nonlinear functions of different predictor variables (Hastie & Tibshirani, 1990). The underlying relationship between each predictor variable and kelp canopy biomass was determined using thin-plate penalized regression splines, which adds penalties to wiggly functions to avoid overfitting (Wood & Augustin, 2002). The weight of these penalties was optimized using generalized cross-validation, which minimizes the root mean square error between the fit

**Table 1** Correlation coefficients between empirical orthogonal function temporal mode amplitude functions/spatial loadings and physical and oceanographical variables. Mean nitrate concentrations estimated from sea-surface temperature. Bold values are significant at  $P < 0.05$ .

Temporal amplitude function	Proportion of variance (%)	Max. significant wave height ( $H_s$ )	Mean nitrate	North Pacific Gyre Oscillation index	Pacific Decadal Oscillation index	Multivariate ENSO index	Southern Oscillation index
1	24.5	<b>0.592</b>	<b>0.358</b>	0.089	-0.188	0.025	-0.018
2	12.7	0.105	<b>0.490</b>	0.013	-0.021	-0.142	0.187
3	6.1	-0.066	-0.115	<b>0.436</b>	-0.028	<b>-0.354</b>	-0.025

Spatial loadings	Spatial max. $H_s$	Spatial mean nitrate	% < 1 $\mu\text{mol L}^{-1}$ nitrate
1	<b>-0.687</b>	<b>-0.762</b>	<b>0.725</b>
2	<b>-0.648</b>	<b>-0.727</b>	<b>0.655</b>
3	0.088	<b>-0.244</b>	<b>0.391</b>

and data points. Optimal model form was selected by minimizing the Akaike information criterion, which helps balance the complexity of the model versus the goodness of fit. We used the R package *MGCv* 1.8-6 to implement all GAMs with  $\alpha = 0.05$  (Wood, 2006). Standardized coefficients of each significant predictor were estimated at each coastline segment by using a multiple linear regression to fit each z-score scaled (mean, 0; variance, 1) variable to scaled proportional kelp canopy biomass.

The environmental correlates identified in the EOF analysis – maximum significant wave height, mean nitrate concentration and the value of the NPGO – were used as predictors in local GAMs for each coastline segment all lagged in time by one season (log link function; Gaussian error structure). Harvest effort was also added as a predictor to the model for the known harvested coastline segments, and a kelp occupancy term (the proportion of kelp canopy biomass in the previous season) allowed kelp canopy biomass to respond according to prior occupancy at each segment. Sea urchin density was added to the predictors already included in the GAM at sites with urchin observations (see Appendix S1 for details of the GAM method and predictions).

## RESULTS

### Spatio-temporal variability in kelp biomass

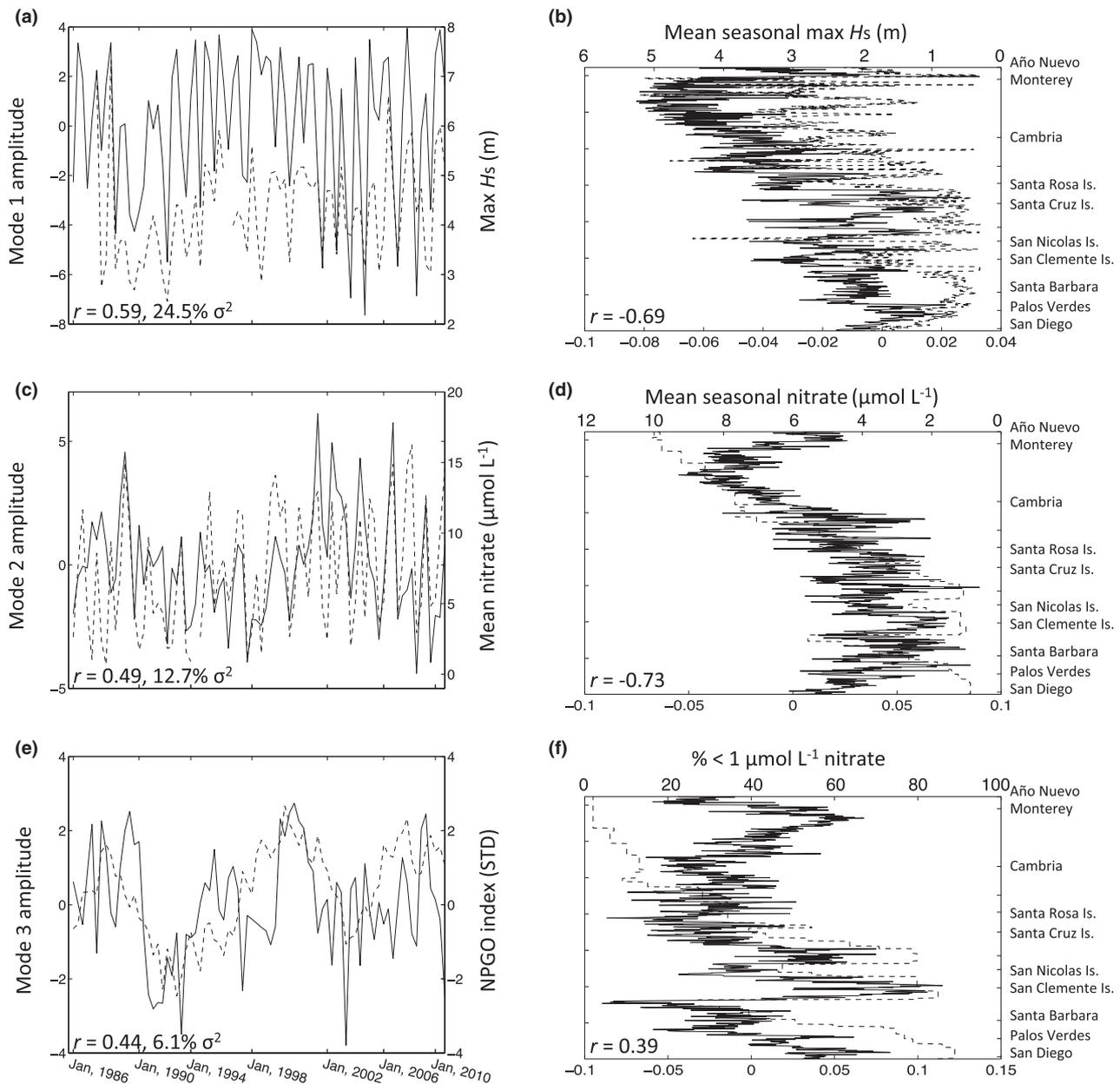
Giant kelp canopy biomass was variable throughout the study area with mean seasonal biomass per 500 m coastline segment ranging between 1000 and  $1.37 \times 10^6$  kg wet mass (Fig. 1a,b). The mean coefficient of variation (CV) averaged across all measured seasons was 1.4 for the entire study region and rarely dropped below 1 in any 500-m coastline segment, demonstrating the high variability of giant kelp canopy biomass during the 25-year study period (Fig. 1c). Marked spatial differences in CV were found between different sides of islands and between protected and exposed areas on the mainland. The study region supported a mean kelp canopy biomass of  $1.39 \times 10^8$  kg, which ranged from a maximum of  $4.14 \times 10^8$  kg in the autumn of 2005 to a

minimum of  $4.74 \times 10^6$  kg in the spring of 1998, following winter storms during a large El Niño episode.

### Diagnosing correlates of kelp biomass dynamics

EOF spatial loadings and temporal amplitude functions were linearly correlated with environmental variables, revealing the dominant environmental processes that drive variations in giant kelp biomass (Table 1). The first mode explained 24.5% of the variance and its temporal variations displayed a clear seasonal pattern, with positive values in the winter and spring and negative values in the summer and autumn. This amplitude time-series was significantly correlated with maximum  $H_s$  during the previous season from the Harvest buoy ( $r = 0.59$ ;  $P < 0.001$ ; Fig. 2a). The spatial loadings of the first mode revealed large negative values for the central coast and values near zero throughout much of southern California with exceptions on the exposed sides of the Channel Islands (Fig. 2b). Mean seasonal maximum  $H_s$  along the California coast from the CDIP  $H_s$  model was strongly correlated with the spatial loadings ( $r = -0.69$ ;  $P < 0.001$ ), implying that swells have a large negative effect on kelp biomass throughout the central coast and much less of an impact in southern California, except for exposed sites. The loadings were significantly correlated with site-specific maximum  $H_s$  in both time and space; the overwhelmingly negative spatial loadings across the study area were indicative of negative effects on kelp biomass during winter and spring, the seasons in which the temporal amplitude function of the first EOF was positive.

The second EOF mode explained 12.7% of the biomass variance and its temporal amplitude function also displayed a strong seasonal pattern (Fig. 2c). This amplitude time-series was significantly correlated with mean nitrate concentrations in the surface waters during the previous season from the Point Arguello buoy ( $r = 0.49$ ;  $P < 0.001$ ), with positive amplitude during winter and spring periods of high nitrate, and negative mode amplitudes during summer and autumn periods of low nitrate. The second mode spatial loadings displayed positive values in southern California and values near or below zero along the central coast (Fig. 2d). These

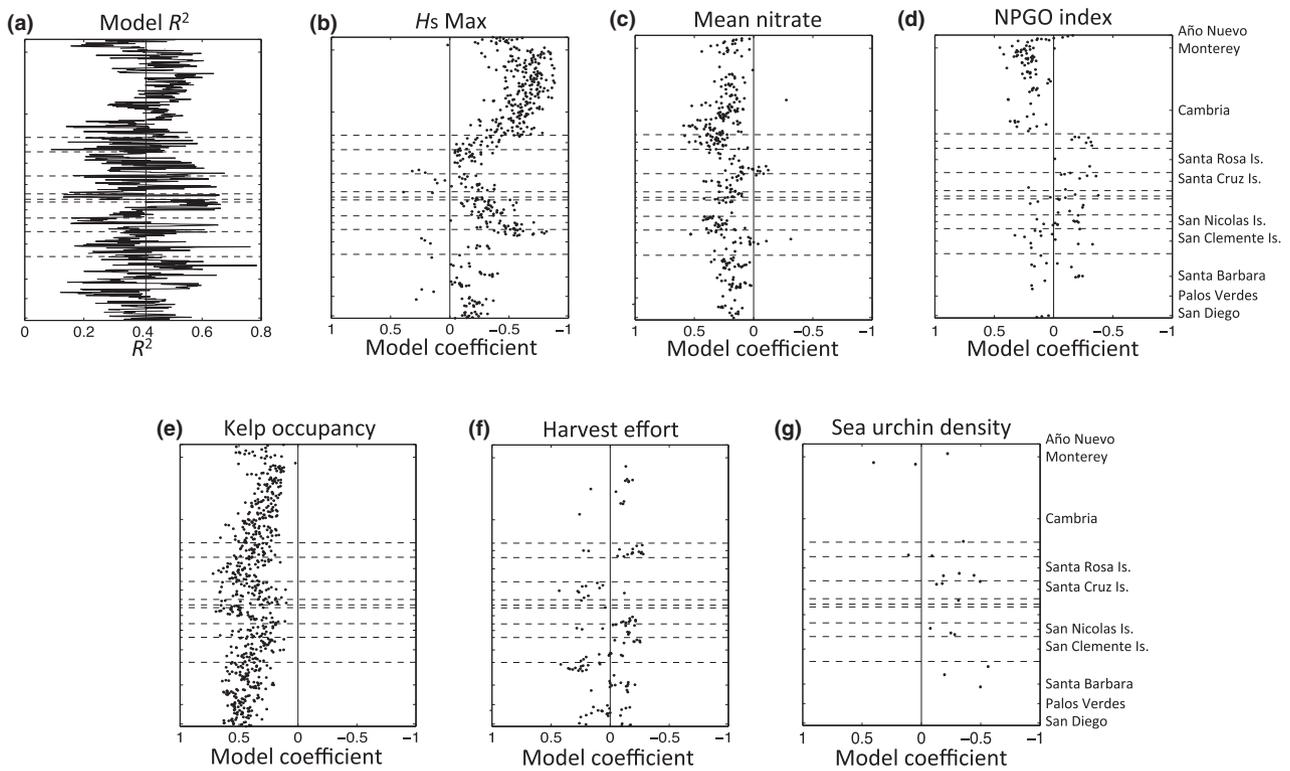


**Figure 2** First (a), second (c) and third (e) temporal amplitude functions from the empirical orthogonal function analysis of giant kelp canopy biomass dynamics along the coast of California, USA. Spatial time series as solid lines and temporally correlated physical and oceanographical variables as dashed lines, (a) maximum significant wave height ( $H_s$ ), (c) mean nitrate, and (e) North Pacific Gyre Oscillation index. Mean nitrate concentrations estimated from sea-surface temperature. These three modes explain 24.5%, 12.7% and 6.1% of the total variance, respectively. First (b), second (d), and third (f) spatial loadings as solid lines with spatially correlated environmental variables as dashed lines, (b) mean seasonal maximum  $H_s$ , (d) mean nitrate, and (f) percentage of seasons where mean nitrate  $< 1 \mu\text{mol L}^{-1}$ . All correlations shown are significant at  $P < 0.001$ .

loadings were significantly correlated with all of the spatial variables ( $P < 0.001$ ), but only mean seasonal nitrate along the California coast was consistent with the positive spatial loadings throughout most of the study area ( $r = -0.73$ ;  $P < 0.001$ ). This correlation suggests that higher nitrate concentrations correspond to positive kelp biomass levels in areas with lower mean nitrate (e.g. southern California).

The third mode explained 6.1% of the biomass variance and the temporal amplitude function displayed interannual

changes that were significantly correlated with the NPGO index during the previous season ( $r = 0.44$ ;  $P < 0.001$ ; Fig. 2e). The third mode spatial loadings showed the highest positive values along the south-eastern corner of southern California, San Clemente and Santa Catalina Islands, which are the most oligotrophic regions of the study region, and the northern half of the central coast (Fig. 2f). Positive values of NPGO are related to periods of high nitrate availability (Di Lorenzo *et al.*, 2008). The spatial loadings were significantly



**Figure 3** (a) Variance of giant kelp canopy biomass explained by a generalized additive model at each site, along the coast of California, USA. Vertical line is the ensemble mean  $R^2$ . (b–g) z-score standardized coefficient of each significant ( $\alpha = 0.05$ ) predictor (maximum significant wave height ( $H_s$ ), mean nitrate, North Pacific Gyre Oscillation index (NPGO), kelp occupancy, harvest effort, and sea urchin density) at each site. Mean nitrate concentrations estimated from sea-surface temperature. Sea urchin density observations were available from 45 of the 723 sites. Areas inside dashed lines represent the offshore Channel Islands.

correlated with the percentage of seasons with a mean surface nitrate concentration below  $1 \mu\text{mol L}^{-1}$  ( $r = 0.39$ ;  $P < 0.001$ ), the minimum threshold concentration needed to sustain kelp growth (Zimmerman & Kremer, 1984).

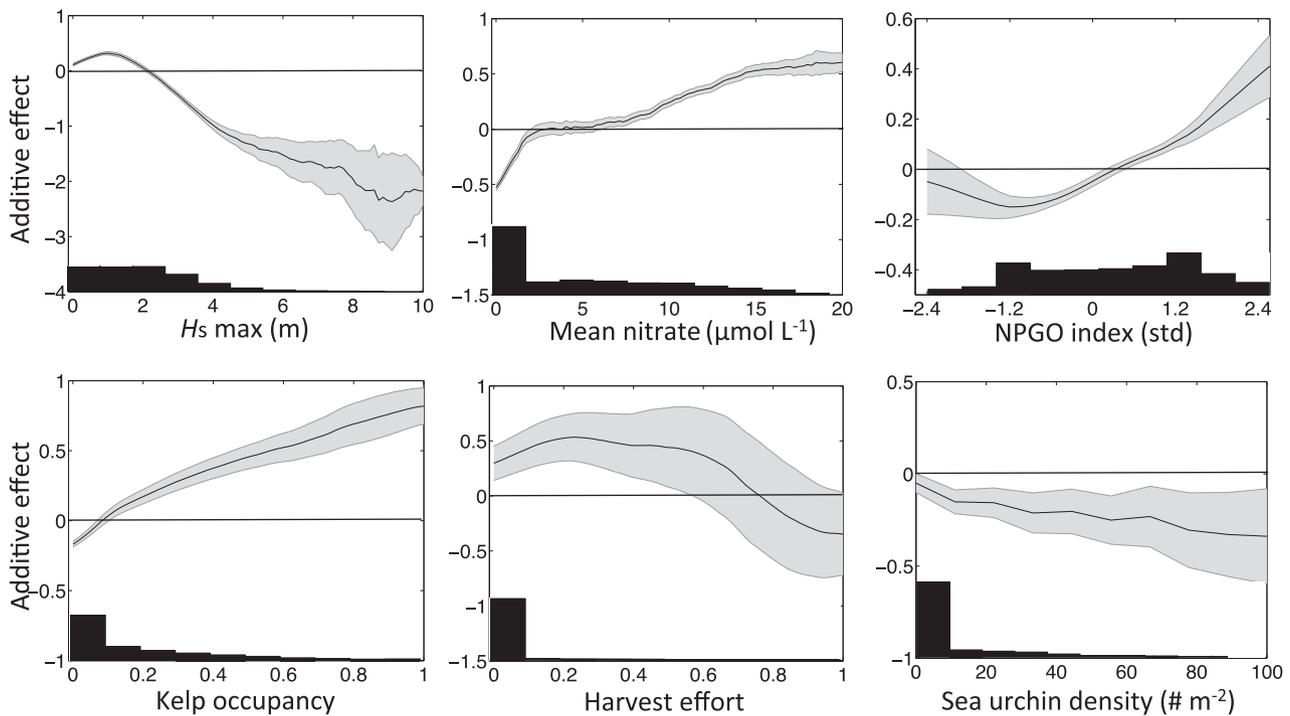
### Modelling drivers of biomass dynamics

A total of 723 coastline segments (500 m each) were analysed using individual GAMs. The  $R^2$  of the individual segment models ranged from 0.09 to 0.79 (Fig. 3a), with an ensemble mean  $R^2$  equal to 0.41. Standardized coefficients of each significant predictor were estimated for each coastline segment using a linear model to fit each variable to proportional kelp biomass (Fig. 3b–g; Table 2). At the 470 southern California coastline segments, maximum  $H_s$  was the best predictor at 36.8%, mean nitrate at 28.9%, NPGO at 5.3%, kelp harvest at 9.2%, and no significant predictor at 19.8% of the sites. Of the 253 central California segments, maximum  $H_s$  was the best predictor at 91.7%, mean nitrate at 5.5%, no significant predictor at 1.6%, and NPGO at 1.2% of the sites. Sea urchin density had the greatest magnitude-standardized coefficient at 9 of the 36 southern California sites and none of the central California sites, although southern California segments where sea urchin density was measured had lower median winter wave heights (0.94 m) than southern California as a whole (1.23 m;  $P < 0.001$ ; Wilcoxon rank-sum test).

**Table 2** Mean z-score standardized coefficient, for each tested environmental predictor of giant kelp canopy biomass, across all significant coastline segments as well as the percentage of coastline segments where the predictor was significant at  $\alpha = 0.05$ . Mean nitrate concentrations estimated from sea-surface temperature. Sea urchin density was investigated at 45 of the 723 sites.

Predictor	Mean model coefficient	Proportion significant (%)
Max. significant wave height	-0.421	67.1
Mean nitrate	0.223	49.0
North Pacific Gyre Oscillation index	0.085	21.7
Kelp occupancy	0.384	88.7
Harvest effort	-0.003	18.3
Sea urchin density	-0.212	42.2

The mean additive effect of each predictor variable on proportional kelp biomass was found by averaging the individual effect relationships of each predictor from all coastal segments where the predictor was statistically significant (Fig. 4). These plots show the mean direction and magnitude of each predictor on kelp biomass. The mean relationship with seasonal maximum  $H_s$  was nonlinear and negative and showed the largest magnitude of effect, with larger swell having a negative effect at



**Figure 4** Additive effect of each environmental predictor variable on the site-specific generalized additive giant kelp canopy biomass model over the measured range of each predictor along the coast of California, USA (maximum significant wave height ( $H_s$ ), mean nitrate, North Pacific Gyre Oscillation index (NPGO), kelp occupancy, harvest effort, and sea urchin density). The solid line is the mean effect of the predictor and the shaded regions show the 95% confidence intervals across all sites where the predictor was significant at  $\alpha = 0.05$ . The frequency of each variable through space and time is shown by the histogram at the bottom of each effect plot. Mean nitrate concentrations estimated from sea-surface temperature. Sea urchin density observations were available from 45 of the 723 sites.

maximum  $H_s > 2.5$  m. The mean relationship with nitrate showed a negative effect between values of 0 and  $2 \mu\text{mol L}^{-1}$  and positive effects at concentrations above about  $6 \mu\text{mol L}^{-1}$ . The NPGO index displayed a nonlinear effect relationship with biomass, with larger positive index values showing an increasing positive effect. Kelp occupancy showed a positive mean relationship with biomass, with greater biomass in the previous season showing positive effects at values greater than 0.1 proportional biomass. Kelp harvesting showed a small positive effect at values below 0.8 harvest effort, whereas increases in harvesting effort beyond this point had a negative effect. Sea urchin density showed negative, but diminishing, additive effects on kelp biomass as urchin density increased.

## DISCUSSION

### Spatial heterogeneity in drivers of canopy biomass dynamics

Understanding how consumer pressure, resource availability and disturbance control the dynamics of plant and algal populations is challenging, because the roles of these processes can vary in space and time (Estes & Palmisano, 1974; Menge, 1976; Hunter & Price, 1992; Reed *et al.*, 2011). Here, we have used EOF analysis and nonlinear additive modelling to identify and quantify the relative strengths of these

population drivers. For the California coastline as a whole, wave disturbance was the dominant correlate of kelp canopy biomass, followed by nitrate availability and the state of the NPGO. However, the relative importance of these factors varied spatially. Studies that focus on one or a few sites may identify how these factors relate to one another locally, but will miss how these relative effects vary spatially. By examining hundreds of local coastline segments across many hundreds of kilometres and over many generations, a comprehensive understanding of how these factors contribute to the canopy dynamics of giant kelp can be achieved.

Wave disturbance events are larger and more frequent along the central coast than the more protected southern California coastline, and thus represent a greater and more consistent driver of biomass along wave-exposed coastline (Reed *et al.*, 2011). Wave disturbance showed an increasingly negative effect on kelp biomass at  $H_s > 2.5$  m (Fig. 4). We saw a clear increase in the magnitude of the surface wave disturbance coefficient north of Point Conception, where the mean maximum winter  $H_s$  among all central coast sites was 3.3 m. Wave disturbance can also have a large effect on kelp biomass throughout southern California, such as the large storm events associated with El Niño episodes (Dayton & Tegner, 1984), although large wave events are less frequent in southern California (7.7 seasonal maximum events above 2.5 m per coastline segment in southern California, versus 39.7 in central California during

the period of study) and thus explained a smaller amount of variation in kelp dynamics in southern California.

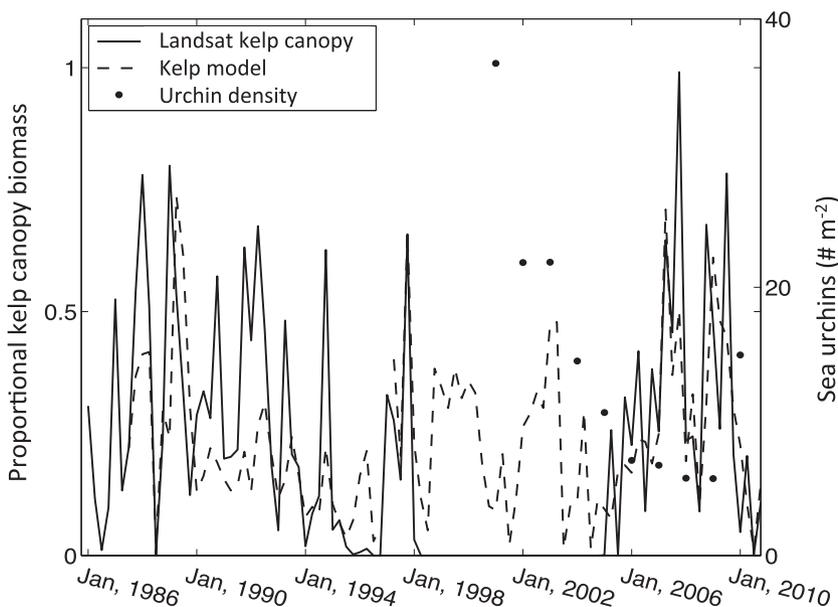
The frond elongation rate is reduced at low nitrate concentrations, and surface water nitrate concentrations (as estimated from SST) showed a significant positive relationship with canopy biomass at 49% of the sites across the entire study region (Zimmerman & Kremer, 1984). It was, however, the dominant correlate only at protected sites along the central coast or in southern California, where wave disturbance is reduced. Mean nitrate displayed negative effects on biomass at low concentrations and positive effects at high concentrations, with little effect at intermediate levels (2–6  $\mu\text{mol L}^{-1}$ ; Fig. 4). Although canopy persistence depends on many factors (Rodríguez *et al.*, 2013), in the absence of periodic removal by disturbance, kelp forests can maintain a canopy throughout the year and may be primarily influenced by interannual cycles of nutrient availability (Parnell *et al.*, 2010). Periods of high nutrient concentrations have been associated with increased kelp growth (Gerard, 1982; Zimmerman & Kremer, 1984; Stewart *et al.*, 2009), and the shoaling of high-density, nutrient-rich waters over the inner shelf explains much of the interannual variation in kelp plant density in the southern end of the study area (Parnell *et al.*, 2010). Interannual variation in nutrient concentrations is associated with changes in the state of the NPGO, which operates over interannual time-scales and is characterized by increased upwelling and horizontal advection of cool waters from the north, extending to the southern Channel Islands (Di Lorenzo *et al.*, 2008). These increased incursions of cold, nutrient-rich waters into the Southern California Bight may be partly responsible for the episodic dynamics of kelp forests in regions that are usually defined by oligotrophic conditions, such as San Clemente and Santa Catalina islands and the lower portion of the southern California mainland coast (Kopczak *et al.*, 1991; Di Lorenzo *et al.*, 2008). Positive values of the NPGO index display positive effects on kelp

biomass, with values above 1.4 having increased positive effects (Fig. 4). Although El Niño variations were not primarily correlated with any of the kelp biomass EOFs, the wave disturbance and nutrient conditions typical of these events may have been partly explained within the first three EOF temporal amplitude functions, where interannual variation in the strength of each seasonal cycle is evident, especially during strong El Niño episodes.

Top-down effects by grazing sea urchins have been hypothesized to have increased in the past two centuries as a result of human-induced alteration of kelp forest food webs. This resulted from the extirpation of sea otters by hunting and overfishing of predatory species of fish and invertebrates, and may have led to increased abundances of sea urchins and other kelp grazers (Estes & Palmisano, 1974). Our results show that higher sea urchin densities were associated with decreases in kelp canopy biomass and sea urchin density was the dominant correlate at 25% of the sites with long-term sea urchin records in southern California. For central-coast segments where urchin observations were available, sea urchin density was 20 times lower than in southern California. At two of the three central coast segments where the sea urchin density was significantly correlated with kelp biomass, a positive relationship was observed, indicating that increased kelp may be supporting greater numbers of sea urchins. This reinforces the notion that the top-down grazing by sea urchins is an important local-scale driver of kelp biomass in southern California, but not in central California in areas where sea otters are prevalent (VanBlaricom & Estes, 1988; Reed *et al.*, 2011).

### Addressing unknown drivers

The modelling of the biogeographical structure of a species requires an understanding of the relative importance of the causative environmental drivers (Fenberg *et al.*, 2014).



**Figure 5** Giant kelp canopy biomass (solid line) at the Carpinteria kelp forest site, near Santa Barbara, California, compared with the model predictions (dashed line) based on relationships with wave disturbance, nitrate concentrations, North Pacific Gyre Oscillation index, and kelp occupancy. Annual sea urchin density is shown as black dots (Reed, 2013).

Remotely sensed and modelled datasets can provide insight into the mechanisms that cause populations to fluctuate at different spatial and temporal scales. Data for some potentially important covariates, such as sea urchin density, require time-consuming diver surveys, however, which limits their spatial and temporal extent. Furthermore, records for some predictor variables, such as kelp harvest, may not extend throughout the entire time-series. The lack of comprehensive data on such drivers limits our ability to fully understand the processes that control the dynamics and distribution of the species we study.

Here, we use observations from a time-series of giant kelp canopy biomass and its major environmental drivers (e.g. wave heights, nitrate concentrations and oceanographical conditions) to model kelp biomass dynamics across a 1500-km stretch of the California coast. Sustained departures between these model predictions and observations may indicate the occurrence of unknown processes that have a significant impact on kelp biomass. An example can be seen at the Carpinteria kelp forest near Santa Barbara, California, where the time-series of sea urchin density was not included in the model (Fig. 5). From 1998 to 2005, kelp canopy was completely absent from the Carpinteria coastline segment, but the model predicted multiple cycles of kelp growth and removal during this absence. Sea urchin abundance was especially high during this absence of kelp canopy, suggesting that top-down grazing pressure overwhelmed the effects of wave disturbance and nutrient availability during this period.

The detection of model mismatch throughout the time-series may provide a path for the elucidation of unknown or poorly-known environmental drivers. By relating the degree and duration of model–data mismatches to predictors measured at local-scale sites, one can infer where and when additional forces are likely to be dominant. This can lead to directed sampling efforts or the inference of the progression of drivers through time and space, providing additional insights into the importance of unknown factors in controlling populations.

Understanding the spatial heterogeneity of processes that exert control over populations remains a major focus for landscape ecology and biogeography (Turner, 1989). Our results demonstrate the importance of multiscale analyses of ecosystem dynamics. A variety of known and unknown environmental and biotic forces interact to structure these systems, which vary not only through time, but also in space. This spatial variability has the potential to lead to conflicting conclusions concerning the relative importance of different factors, as many studies investigating biomass and population dynamics are conducted in relatively small plots, in a small portion of a species' geographical range. Large-scale, long-term, persistently sampled datasets allow for a comprehensive characterization of spatial and temporal variability and the factors that influence this variability. Results from such studies inform not only what has happened in the past, but allow one to infer how future changes in drivers may disproportionately affect certain locations or regions.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Supplementary methods.

## DATA ACCESSIBILITY

All giant kelp canopy biomass data are available as annual text files from the Santa Barbara Coastal Long Term Ecological Research Project database: <http://metacat.lternet.edu/knb/metacat/knb-lter-sbc.54.6/lter>.

## BIOSKETCH

**Tom Bell** is a PhD candidate in the Interdepartmental Graduate Program in Marine Science at the University of California, Santa Barbara. His research interests focus on examining the spatial patterns of population dynamics and primary production.

Author contributions: T.W.B., K.C.C., D.C.R. and D.A.S. conceived the study; T.W.B. and K.C.C. led the image analysis; T.W.B. led the data analysis; T.W.B. led the writing with contributions from K.C.C., D.C.R. and D.A.S.

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