

The response of giant kelp (*Macrocystis pyrifera*) in southern California to low-frequency climate forcing

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Abstract

The nutrient climate on the inner shelf off southern California changed markedly across the 1976–1977 North Pacific climate regime shift. With respect to giant kelp (*Macrocystis pyrifera*) canopies off southern California, the nitrate climate shifted from relatively replete conditions prior to the regime shift to depleted conditions afterward, and the dynamics of 14 giant kelp forests appeared to change as a result. The response of giant kelp to nutrient-replete years before the regime shift was dampened compared to their response afterward. The sensitivity of these kelp-forest canopies to nutrient limitation appears to have increased since the regime shift. This intensification of physical control after 1977 is evident in the strong correlation of seawater density (σ_t) and *M. pyrifera* density. The linear fit of the percent of time the 25.1 σ_t isopycnal bathes the inner shelf, accounted for ~ 71% of the variability in kelp density off Point Loma, and the median depth of this isopycnal has deepened ~ 5 m since the regime shift. The wave climate also intensified beginning in the early 1970s. The dampened kelp response prior to the regime shift was likely due to greater biological control of kelp canopies via consumer and competitive processes (i.e., biological modulation) or decreased physical control at possibly many trophic levels. Our results suggest that the response of kelp forests to El Niño Southern Oscillation events is mediated by lower frequency climate modes that may modulate the regulatory importance of biological and physical processes on giant kelp.

The term “regime shift” was first coined by John Isaacs in 1976 on the eve of perhaps the largest regime shift on record in the North Pacific (Isaacs 1976). Isaacs’ discussion was intended as a provocative re-examination of the concept of “steady state” as applied to fisheries science and ecology. Since then, profound ecological responses to changes in climatic or anthropogenic forcing have been documented in many ecosystems. Well-known examples of climate-driven marine “ecosystem regime shifts” (Bakun 2004) or “phase transitions” (Duffy-Anderson et al. 2005) include those for salmon (Mantua et al. 1997), sardines (Chavez et al. 2003), other finfishes (MacCall 1996; Hare and Mantua 2000), and copepods (Beaugrand et al. 2002). Abrupt shifts in ecological systems have also been observed as a result of endogenous biotic processes and human disturbance (Scheffer et al. 2001). The defining ecological modes (cf., phases) of regimes are at least partly stable and affect several trophic levels. Regime modes are typically binary in nature (e.g., “sardine vs. anchovy” or “kelp vs. barrens”), though some systems exhibit multiple modes (Collie et al. 2004). Isaacs (1976) argued > 30 yr ago that these biological modes could not be due to a “normal distribution of perturbations.” Rather, low-frequency climate processes must “perturb” these modes.

Most of the ocean climate variability observed in the North Pacific from the early 20th century to present is captured by the first two modes of sea surface temperature anomalies (SSTA) and height variability that are referred to

as the Pacific Decadal Oscillation (PDO; Mantua et al. 1997) and the Victoria Mode (Bond et al. 2003) or North Pacific Gyre Oscillation (Di Lorenzo et al. 2008). The dominant variability of these modes is on decadal to multidecadal time scales and, therefore, much longer than the interannual fluctuations associated with the El Niño Southern Oscillation (ENSO). On interannual time scales, ENSO dominates the extra-tropical variability both through the excitation of coastally trapped waves that propagate along the eastern boundaries (Enfield and Allen 1983) and through an atmospheric teleconnection that drives a PDO-type response in the North Pacific (Alexander 1992). Particularly dramatic is the effect of the coastally trapped waves during the positive and negative phases of ENSO, which in the California Current, modulate the depth of the thermocline and alongshore currents resulting in lower and higher, respectively, nutrient concentrations in the surface waters. On multidecadal timescales the North Pacific climate exhibited abrupt changes in the late 1970s (~ 1976–1977; Miller et al. 1994), a period that also coincided with major changes in many North Pacific ecosystems that collectively have become recognized as an unambiguous ecological regime shift or phase transition (McGowan et al. 2003). Low-frequency non-ENSO variability of SSTA shifted in 1976–1977 (Mestas-Nunez and Enfield 2001) from negative to positive, thereby increasing the amplitudes of ENSO events since that time. The effects of such enhanced ENSO band variability on coastal ecosystems are presently poorly understood. Superimposed onto the changes in decadal and ENSO climate scales has

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been a freshening and warming trend of the California Current and concomitant reductions in nutrients and zooplankton biomass that accelerated with the 1976–1977 regime shift (Roemmich and McGowan 1995).

Giant kelp forests (*Macrocystis pyrifera*) along the west coast of the U.S. occur on the extreme coastal margin of the California Current System (CCS). Their productivity and growth is limited by dissolved inorganic nitrogen (DIN; Wheeler and North 1980), mainly in the form of nitrate (Jackson 1977; Zimmerman and Kremer 1984, their fig. 9), which is the principal species of DIN that is delivered into the euphotic zone by physical processes, and has been shown to primarily limit kelp growth (Jackson 1977; Zimmerman and Kremer 1984). In the upper ocean (< 200 m), nitrate concentrations are strongly dependent on density and temperature (Kamykowski and Zentara 1986). Therefore, from a climate perspective (cf. “resource” or “bottom-up”), cool high-nutrient periods such as La Niñas are typically associated with increased levels of giant kelp productivity, growth, survival, and reproduction (Dayton et al. 1999). Yet despite the well-established relationship between temperature and nitrate (Zimmerman and Kremer 1984), temperature accounts for less than half of the variability in proxies of giant kelp abundance such as canopy area, density, or harvest within the CCS (North et al. 1993; Tegner et al. 1996). Despite this, macroalgal stands at kelp-forest scales and greater are generally considered climate (cf. resource) driven (Dayton et al. 1999). However, the relative importance of climate, consumer, and competitive processes on kelp-forest community structure remain controversial (Foster et al. 2006).

Although there is consensus that El Niños and La Niñas present poor and improved growing conditions for kelps, respectively, it is not known how kelp-forest canopies and communities respond to combinations of these events that occur at different frequencies and amplitudes over decadal and longer time scales (Dayton et al. 1999) or to climatic regime shifts such as the 1976–1977 regime shift when the amplitudes of ENSO SST anomalies increased due to lower frequency climate forcing. Here, we present evidence that *M. pyrifera* canopy cover in 14 forests in southern California exhibited a phase transition across the regime shift when kelp canopy appears to have become more climate-driven than before, and this phase persists at present. This has important implications for our understanding of kelp-forest ecosystem dynamics and management, because most of the literature is based on time series that began after the regime shift (Dayton et al. 1999).

The goal of our study was to investigate the interannual and decadal climate forcing of kelp forests at both local and regional scales. First, we investigated the nutrient climate on the inner shelf of southern California across the 1976–1977 regime shift by establishing a relationship between seawater density and nitrate concentration. We then tested whether this relationship changed across the regime shift. Next, we compared the time series of regional giant kelp canopy cover, quantified from aerial photographs, to nitrate concentrations derived from the relationship between seawater density and nitrate. Finally, we explored the strength of climate control of giant kelp

forests after the regime shift by relating seawater density directly to densities of giant kelp quantified in situ.

Methods

The types of data used in our study, their sources, and the periods they were used are listed in Table 1. These are all described below and are organized by our general approach above. All analyses were conducted using R (R Development Core Team 2005).

Giant kelp forests off southern California—Giant kelp forests off southern California are located primarily on subtidal rocky bottoms ~ 5–30 m deep along the mainland, islands, and shallow offshore banks that are nested within the complex bathymetry of the shelf. Individual kelp forests range in size from ~ 7 km² off Point Loma in San Diego County, the largest kelp forest off California, to ephemeral stands of kelp as small as a few hundred square meters at their largest extent. Kelp forests located along the mainland of San Diego and Orange Counties were included in our regional analysis. This area extends northward from the Mexican border for ~ 125 km.

Nutrient climate on the inner shelf—No adequate time series exists of nitrate within the California Current System that extends back to the 1976–1977 regime shift. For the purposes of this study, a nitrate time series is required in which nitrate was sampled regularly and frequently enough to capture seasonal variability. This issue has been addressed in other studies using modeling techniques (Di Lorenzo et al. 2008) or the use of temperature as a proxy for nitrate concentration. However, the use of nutrient models can be problematic and the results are not verifiable. Furthermore, the relationship between nitrate and temperature is more variable than the relationship between nitrate and seawater density (Kamykowski and Zentara 1986). Nitrate concentrations within the CCS vary with the relative contributions of source waters, primarily including subarctic water, upwelled undercurrent water, subtropical water, and surface runoff (Lynn and Simpson 1987). The temperature–salinity signatures of these waters are different, as are their nitrate concentrations. For these reasons, we used seawater density (σ_t) in lieu of temperature as a proxy for nitrate to develop a nutrient time series (i.e., nitrate concentrations on the inner shelf) that spanned the 1976–1977 regime shift. Specifically, we used all available nitrate, temperature, and salinity data (see Table 1) sampled at the Scripps Institution of Oceanography (SIO) Pier (temperature and salinity available from <<http://shorestation.ucsd.edu/>>) and at nearshore California Cooperative Fisheries Investigation (CalCOFI, <<http://calcofi.org/>>) stations offshore of San Diego and Orange Counties. The SIO Pier is located in San Diego County and is ~ 5 km and 20 km north of the central portions of the La Jolla and Point Loma kelp forests, respectively.

The relationship between nitrate and seawater density was established from bottle samples in which temperature, salinity, and nitrate were measured from the same bottle. These sources included near-surface and bottom (~ 5 m

Table 1. List of measured and derived data types used in study; GAM=Generalized Additive Model, PCA = Principal Components Analysis, σ_t = seawater density. Data period refers to the period that data were used in this study.

Measured	Application in study	Source	Data period	Sampling frequency
Temperature, salinity	Derive σ_t (Fig. 1) and Spice (Fig. 12)	Scripps Pier (bottom)	1926–2008*	Daily
Nitrate	Derive σ_t (Fig. 1)	CalCOFI	1949–2008	Quarterly
	Fit to σ_t using GAMs (Fig. 1)	CalCOFI	1959–2008	Quarterly†
	—	Scripps Pier	1986–2000	Semiweekly
	—	—	2003–2008	Semiweekly
Kelp canopy area (aerial)	Analyzed using PCA to develop PC1 as estimator of regional kelp canopy (Kelp PC1; Fig. 4)	MBC Applied Environmental	1967–2008	Surveys conducted 3–4 times each yr to estimate annual maximum
Kelp density (in situ)	Fit to σ_t (Figs. 6, 7)	Dayton Lab (SIO)	1983–2008	Quarterly
Sea level	Fit to Kelp PC1	Scripps Pier	1967–2008	Hourly
Derived	Application in study	Derivation method		
Seawater density (σ_t)	(1) Used to estimate daily NO_3 based on GAM fit (Fig. 1) (2) Predictor of in situ kelp density (Figs. 6, 7)	Foffonoff and Millard (1983)		
Nitrate	(1) Time series of annual NO_3 concentrations based on average of daily values (Fig. 2).	GAM (Wood 2006)		
	(2) Comparisons of daily NO_3 concentrations across the regime shift (Fig. 3)			
	(3) Annual averages of daily NO_3 estimates based on GAM fit used as predictor of Kelp PC1 (Fig. 5)			
Kelp PC1	Fit to derived nitrate and evaluated by regime (Fig. 5)	PCA (Legendre and Legendre 1998)		

* Bottom temperature and salinity data used in this study (SIO pier surface data available 1916–present).

† Nitrate sampling was sporadic prior to 1978.

deep) samples from the SIO Pier and from CalCOFI hydrocast water samples collected at discrete depths from the surface to ~ 500 m deep. Surface-water samples from SIO Pier that were analyzed for nitrate were collected semiweekly from 1986 to 2000 and from 2003 to present. Pier bottom samples were analyzed for nitrate from semiweekly samples from 1997 to 2000. CalCOFI has conducted quarterly surveys within the CCS since 1949. Hydrocasts have been conducted since then at no fewer than 66 permanent stations. Nitrate has been regularly analyzed from CalCOFI water samples since 1983. Before 1983, nitrate was analyzed only sporadically beginning in 1959. Because the relationship between nitrate and seawater density varies regionally (Kamykowski and Zentara 1986) we used CalCOFI data from stations located off San Diego and Orange Counties within ~ 25 km from shore (Sta. 90.35, 90.30, 90.28, 93.30, 93.28, and 93.26.7).

Temperature and salinity from both SIO Pier and CalCOFI were used to calculate seawater density (σ_t), which was then fit to nitrate using Generalized Additive Models (GAM; Wood 2006)—assuming normal error structure and an identity link function. Nitrate was modeled as a smooth function of seawater density, where the smooth function was represented by thin plate regression splines and the smoothing parameter was selected using generalized cross-validation (GCV; Wood 2006). GCV reduces overfitting by selecting the amount of smoothing based on the ability of models of different smoothness to predict data not used in model construction. Nitrate was fit to σ_t for all data across the regime shift (“pooled” model) and separately for each regime period (1959–1977 and 1978–2008; Fig. 1). The assumption for the pooled model was that the relationship between σ_t and

nitrate did not change across the regime shift. A complication for separate regime fits was that only 142 preregime samples were available compared to 10,084 samples after. Also, the range of σ_t before 1978 for which nitrate had also been estimated was relatively truncated (no observations < 24.337).

A time series of daily nitrate was predicted for the period 1926–2008 from the SIO Pier time series of derived σ_t (Table 1) using the fitted pooled model described above. Mean annual nitrate concentrations were computed as the average of predicted concentration values within each year. The standard error on these annual averages was computed as the square root of the sum of the variance about the average concentration (assuming the predicted concentration values were exact) and the variance associated with the GAM model predictions (conditional on the estimated smoothing parameter; Wood [2006, p. 245]). For the separate pre–regime shift and post–regime shift models, estimated annual averages were also computed from predicted daily nitrate, except that any pre–regime shift predictions < 0 were set to zero. Negative predictions of concentration for the pre–regime shift data occurred because no data on nitrate concentration at low seawater densities were available. Hence, the nonlinearity of the relationship is not well-described below $\sigma_t \sim 24.5$ for the pre–regime shift period. A value of zero was used because this gives a conservative (minimum) annual estimate for comparison to the post–regime shift period (*see* Results section).

Relationship of nitrate and seawater density across the regime shift—To test whether the relationship between nitrate and seawater density changed across the regime

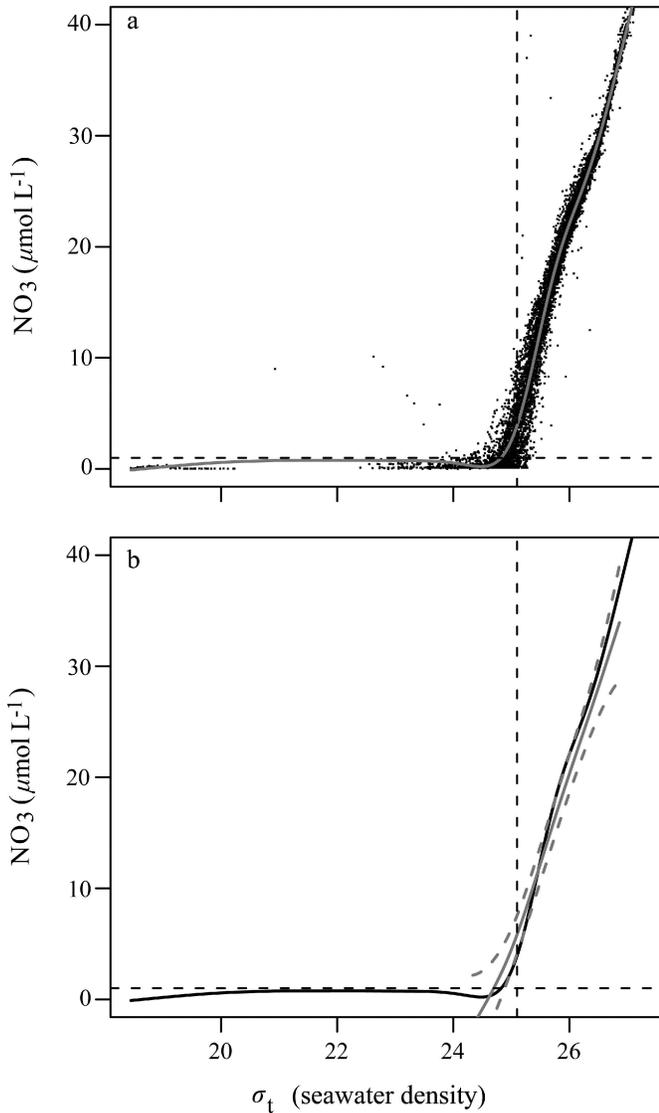


Fig. 1. Nitrate concentration as a function of seawater density (σ_t) for CalCOFI stations nearest SIO Pier and for SIO Pier (see text). Vertical dashed line in both plots indicates $\sigma_t = 25.1$, the best predictor of adult *M. pyrifera* density (see text) in Pt. Loma, horizontal dashed line in both plots indicates NO_3 growth threshold for *M. pyrifera*. (a) points represent data and gray curve indicates GAM fit for all data pooled. (b) black curve shows the GAM fit based on all data (same as in [a]), gray curve shows the GAM fit based on only the pre-regime shift data. Dashed gray curves indicate the approximate point-wise 95% confidence band for the pre-regime shift curve.

shift, another GAM was fitted to pooled pre-regime shift and post-regime shift data that were first limited to the range of seawater density values available for preregime years ($\sigma_t \sim 24.337\text{--}26.862$). This GAM had two parts: an overall smooth function representing all the data and an additional smooth function for the pre-regime shift data (i.e., an added nonlinear contribution for the pre-regime shift period). A test of the null hypothesis of no difference across the regime shift was obtained from an *F*-test of the significance of the added pre-regime shift smooth function.

Table 2. Loadings of first three principal components (see text) of kelp-forest canopy-cover time series in 14 kelp forests (from north to south) in southern California. PC1, PC2, and PC3 refer to the first, second, and third principal components. Scripps Pier is located between the La Jolla and Del Mar kelp forests.

Kelp forest	PC1	PC2	PC3
Dana Pt.	0.230	0.358	0.020
San Mateo Pt.	0.276	0.223	0.404
San Onofre	0.266	0.198	0.370
Barn Kelp	0.164	0.196	-0.661
Encina	0.322	0.070	0.162
North Carlsbad	0.326	-0.113	0.252
Carlsbad	0.212	-0.397	-0.024
Leucadia	0.265	-0.388	-0.096
Cardiff	0.346	-0.106	-0.055
Solana Beach	0.318	-0.181	-0.162
Del Mar	0.174	-0.462	0.054
La Jolla	0.289	0.321	-0.168
Pt. Loma	0.286	0.039	-0.314
Imperial Beach	0.178	0.239	-0.060
% variance	0.512	0.206	0.087
Cumulative % variance	0.512	0.717	0.804

In addition, the GCV scores of models fitted without and with the added pre-regime shift smooth function were also compared (Wood 2006). Finally, because of the imbalance in samples sizes for the pre and post-regime shift periods, a simulation was done to compare the difference in the nonlinear relationships between the two periods when the post-regime shift period was represented by the same number of observations as available for the pre-regime shift period. Data from the post-regime shift period were resampled, without replacement, to match the sample size of the preregime period. A GAM model was fit to the combined pre-regime shift and resampled post-regime shift data, with an added smooth function for the pre-regime shift period. The *p*-value associated with an *F*-test of the added smooth function for the pre-regime shift period and the difference in GCV scores for GAM models without and with the added pre-regime shift smooth function was recorded. This procedure was repeated 10,000 times, and the percentage of *F*-tests with *p*-values ≤ 0.05 , and the percentage of nonnegative differences in GCV scores (indicating improvement in model fit with the added smooth function), were calculated.

Nitrate and regional kelp canopy cover—The relationship between giant kelp and the nutrient (nitrate) climate on the inner shelf was examined using an aerial photographic record of 14 kelp forests (Table 2) off San Diego and Orange Counties. Kelp-forest canopy cover in southern California, from the Mexican border to the southern border of Los Angeles County, has been estimated annually from aerial photographs since 1967 (North et al. 1993). Aerial surveys have been conducted two to four times each year over that period, and the annual maximum coverage observed for each kelp forest was used as the annual estimate of canopy cover. This time series of giant kelp canopy is the only regional time series of giant kelp condition that we know of that spans the 1976–1977 regime shift.

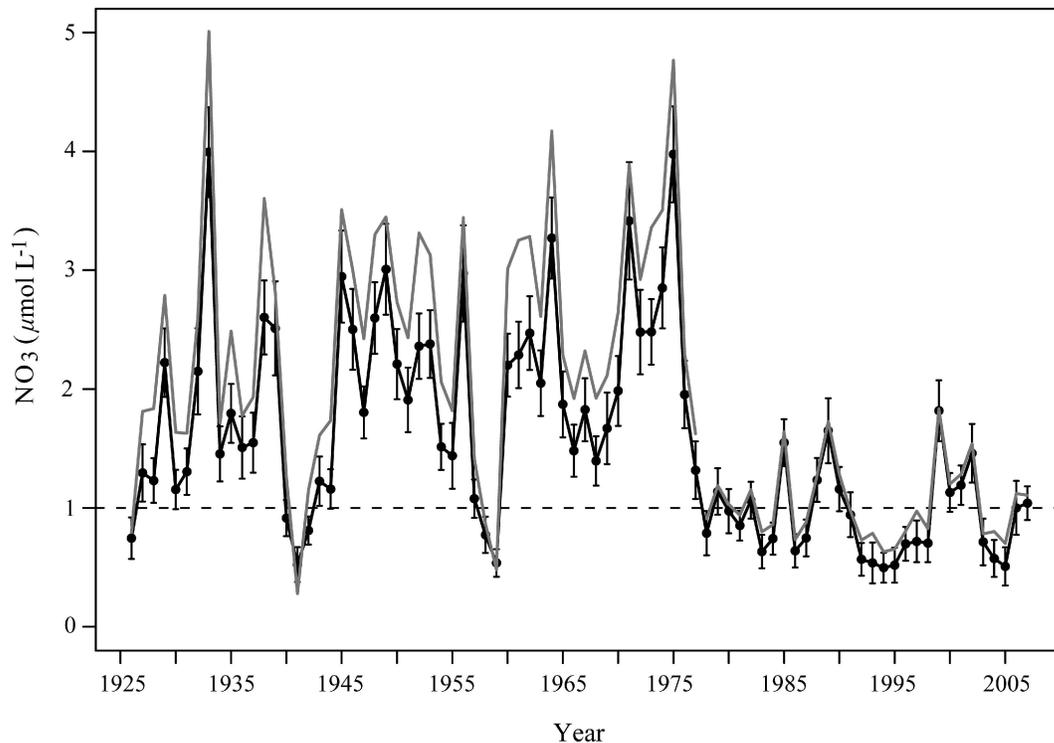


Fig. 2. Time series of estimated annual mean NO_3 concentration at the bottom of the SIO pier (depth ~ 5 m). Nitrate estimates are based on a GAM fit of NO_3 as a function of σ_t at CalCOFI stations closest to SIO (see Fig. 1). Black line and circles indicate GAM fit of data pooled across the regime shift. Gray line indicates GAM fit for separate regimes. Horizontal dashed line indicates NO_3 threshold for kelp growth (Zimmerman and Kremer 1984). Error bars indicate 95% confidence.

Kelp forests in the study region range in size from ~ 0.2 km² to 6.6 km²; therefore, principal components analysis (PCA—Legendre and Legendre 1998) was used to develop a regional index of kelp condition. This avoids skewing the index toward the condition of larger forests that would dominate the signal if canopy areas were summed. We compared the first principal component of regional annual kelp canopy (“kelp PC1”) to annual mean nitrate concentrations estimated from our GAM model fits of nitrate and σ_t . To test for differences in the response of kelp canopy to nitrate before and after the regime shift, we compared the results of fitting linear regression models to the data, with and without an added intercept and slope for the pre-regime shift period. Additionally, a simulation was done to determine how error associated with the estimates of nitrate might affect our results. An iteration of the simulation involved the following steps: (1) A data set of nitrate values was created by resampling annual concentrations from independent Gaussian distributions with means and variances per Fig. 2 (pooled model); (2) A linear regression model with these mean concentrations was fit to kelp PC1, with an added slope for the pre-regime shift period; (3) The coefficient of this added slope and its p -value were recorded. This process was repeated 10,000 times, and the range of coefficient values for the added pre-regime shift slope and the proportion of p -values ≤ 0.05 were obtained.

Sea level at the SIO Pier was also compared to kelp PC1. Hourly sea-level data were low-pass-filtered to remove

periods less than seasonal and averaged by year. The effect of sea level on kelp PC1 was tested using an analysis of covariance (ANCOVA; Zar 1984) with regime (pre and post) representing the groups.

Seawater density and kelp density—The heightened response of kelp forests after the regime shift (see Results) suggests that the relative role of climate forcing has increased. Therefore, we characterized the degree of nutrient control exhibited during this period because it represents an upper bound on the degree of climate control of kelp forests in southern California over at least the last half century.

The most sensitive method to estimate the climate (nutrient) control of giant kelp dynamics is to relate seawater density directly to *M. pyrifera* biomass or density estimated in situ. The advantage of using σ_t is that errors in the fit of nitrate on seawater density are eliminated. However, the drawback is that the nonlinear nature of the relationship is also eliminated, thus possibly masking the effects of subtle changes in seawater density on kelps near the nitrate threshold. To characterize the climate control of kelp during the postregime period we used kelp data from our ongoing quarterly time series at Pt. Loma and related them directly to σ_t estimated from daily temperature and salinity measured at the base of the SIO Pier (Table 1) using simple linear models. The predictor variable used in the model was the percent of time each year (for the period 01 Oct to 30 Sep) that seawater density was greater than a threshold value that was varied iteratively to

achieve the best fit (maximal r^2 , simple linear regression model; Zar [1984, p. 261]). The October–September calendar year was used for σ_t because it corresponds to our seasonal kelp-forest monitoring schedule—the October to December period corresponds to the growth conditions that giant kelp was exposed to just prior to our winter observations in January. Our in situ *M. pyrifera* density data are from five study sites in Point Loma located at depths ranging from 12 m to 18 m. All macroalgae within four permanent 25×4 -m band transects have been monitored at each site since 1983 (Dayton et al. 1992). The response variable used in our models was the density of adult *M. pyrifera* (defined as having achieved at least four stipes since recruitment). The models were run iteratively, varying the seawater density threshold ($\sigma_t = 24.8$ – 25.5) and time lags (up to 2 yr using weights w , where $\Sigma w = 1$) to maximize r^2 .

Results

Nitrate–seawater density relationship—The relationship between σ_t and nitrate is strongly nonlinear with an inflection point (model fit using all data) near $\sigma_t = 25$ (Fig. 1). The p -value for the smooth function (which had ~ 9 effective df) was < 0.01 . This model explained 98% of the deviance. The separate GAM fits to the pre- and post-regime shift data were also both significant (p -values both < 0.01 ; effective df of ~ 2.5 and 9, respectively), and explained 65% and 98% of the deviance, respectively. The change in the nutrient climate on the inner shelf off San Diego and Orange Counties is shown in Fig. 2. Clearly, the nitrate climate on the inner shelf decreased dramatically beginning in 1977 and appears to remain depressed as illustrated by both the pooled model and separate regime shift models of Fig. 2. The separate fit of nitrate on σ_t prior to the regime shift is conservative in this respect because the assignment of zero for fitted nitrate values < 0 tends to make the periods more equitable by decreasing the annual average nitrate concentrations pre-regime shift. The only comparable periods of decreased nitrate concentrations prior to the regime shift appear consistent with large El Niño events in the early 1940s and the late 1950s. The nonlinearity in the nitrate–seawater density relationship magnifies the warming and freshening trends in the CCS that increased with the regime shift (Bograd and Lynn 2003). Cross-regime differences in both temperature and salinity, which are typically reported (rather than seawater density) exhibit clear differences across the regime shift, but their combined effect on the post-regime shift nutrient climate is magnified by the nonlinear relationship between nitrate and seawater density. Figure 2 indicates that the annual means of nitrate concentration since 1977 have mostly been less than the threshold necessary for the growth of *M. pyrifera* ($1 \mu\text{mol L}^{-1}$ —dashed line in Fig. 2; Zimmerman and Kremer 1984). A plot of the cumulative distribution of nitrate for each regime indicates that nearshore concentrations of nitrate were $> 1 \mu\text{mol L}^{-1}$ growth threshold $\sim 40\%$ of the time prior to the regime shift and $< 25\%$ of the time after the regime shift (Fig. 3).

An obvious question is whether the relationship between nitrate and seawater density has changed over time,

particularly with regard to the regime shift. The answer is problematic because limited data are available to fit the relationship prior to the regime shift, and the available data do not contain observations at sea water densities below ~ 24.33 . By contrast, $\sim 2\%$ of the observations from the post-regime shift period correspond to values of seawater density in the range of ~ 18.45 – 24.33 . The test of differences in the seawater density–nitrate relationship across the regime shift indicated that the added smooth function for the pre-regime period was significant (approximate F -test, $p < 0.01$) but showed effectively no improvement in the GCV score, with a change from 2.77 to 2.75 with the additional preregime smooth function. Thus the evidence for a difference is weak. This is consistent with the results of the simulation, which found that only 0.51% of the p -values (at an α -level of 0.05) and 0.26% of the differences in GCV scores were consistent with a change in the relationship of seawater density to nitrate from pre-regime to post-regime shift periods. Moreover, it can be seen in Fig. 1 that the fitted curve of the pooled data model falls within the approximate point-wise 95% confidence band for the pre-regime shift curve. Thus, there is little evidence that the relationship between nitrate and density changed across the regime shift.

Aerial canopy time series and regime response of giant kelp—The first principal component of kelp canopy cover from 1967 to 2007 for kelp forests off Orange and San Diego Counties is shown in Fig. 4. Kelp PC1 accounted for $\sim 51\%$ of the PCA variance. Loadings of each kelp forest on kelp PC1 (Table 2) are positive and plots of individual forests indicate that this principal component captures the regional interannual variability of giant kelp canopy cover. Loadings of principal components beyond the first suggest that those modes capture interannual variability in kelp canopy among forests and are likely due to local processes. The second and third modes (PC2 and PC3, respectively; Table 2) accounted for $\sim 21\%$ and $\sim 8\%$ of the variance, respectively.

The time series of kelp PC1 does not exhibit any obvious cross-regime response of the kelp forests to a dramatic shift in nutrient climate (Fig. 4). Instead, the most obvious signal is its relationship to the strongest ENSO events in the Niño 3.4 and multivariate ENSO time series. These include the negative Niño 3.4 years when nutrient conditions were good for kelp growth (1988–1989, and 2002–2003) and positive events when conditions were poor (1971–1972, 1982–1983, and 1997). However, there are notable departures that do not appear directly related to ENSO, which may be due to the modulation of ENSO effects on kelp forests by decadal or lower frequency climate forcing, biological lag effects, or the varying degree of extra-tropical ENSO penetration to southern California.

The relationship of kelp PC1 and estimated annual mean nitrate concentrations at the SIO Pier indicates that response of regional kelp to nitrate changed abruptly with the regime shift (Fig. 5). Prior to the regime shift, when annual mean nitrate concentrations were typically much greater, the response of kelp canopy cover to nitrate appears dampened compared to the kelp response after the

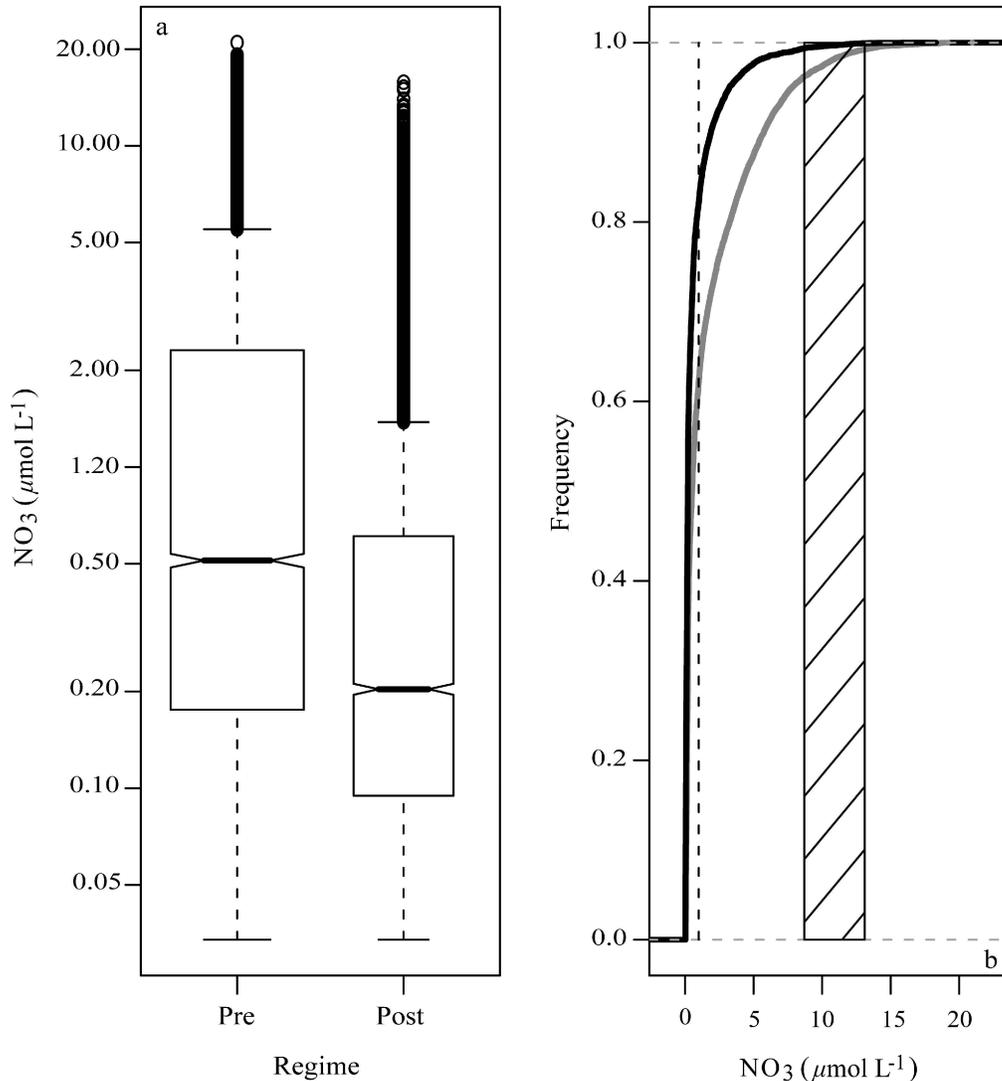


Fig. 3. (a) Box-plot of estimated daily NO_3 concentrations at the bottom of the SIO pier (depth ~ 5 m) before and after the 1977 regime shift. Nitrate concentrations were estimated from the GAM fit between nitrate and density (derived from temperature and salinity, which have been sampled continuously since 1926) for all data pooled. Horizontal dashed line indicates the threshold concentration necessary for *M. pyrifera* growth (Zimmerman and Kremer 1984), bold line = median, boxes = 25th and 75th percentiles, whiskers = 95th percentiles, circles = outliers. (b) Cumulative distribution of nitrate concentration for the same periods (preregime = gray, postregime = black). Dashed vertical line indicates the NO_3 threshold for *M. pyrifera* growth, box indicates the range of half-saturation uptake (Haines and Wheeler 1978).

regime shift when the kelp forests appear to be responding more directly to nutrients.

Based on Akaike Information Criteria (AIC) differences and AIC weights (Burnham and Anderson 2002), the best fitting linear model of kelp PC1 to estimated annual mean nitrate concentration was one with a common intercept but different slopes for the pre-regime and post-regime shift periods (see Table 3). The ratios of AIC weights of this model to the other two models with common slope (the evidence ratio) were both > 5.0 , indicating reasonable evidence in favor of a change in the relationship across the regime shift. The coefficient of the added pre-regime shift slope was -2.03 (p -value = 0.019), indicating that there was less of an increase in the kelp response to increasing nitrate before 1978 compared to the post-regime shift

period (post-regime shift slope = 3.36, $p < 0.01$). Of the 10,000 simulated tests, 86.9% had a p -value for the t -test of the added pre-regime shift slope of ≤ 0.05 (range = 0.0009–0.23), and all 10,000 added slope estimates were negative (range = -2.68 to -1.03). Thus, it appears that the error associated with our estimates of nitrate concentration does not meaningfully affect the conclusions.

The analysis of covariance of kelp PC1 as a function of annual mean sea level at the SIO Pier indicated that kelp PC1 was significantly related to sea level (slope estimate = -31.829 , SE = 13.896, adj. $r^2 \sim 0.135$, $p \sim 0.03$). The added regime effect and the interaction of sea level and regime were not significant (p -values of 0.43 and 0.15, respectively). However, a plot of kelp PC1 as a function of sea level (not shown) indicated that the overall negative

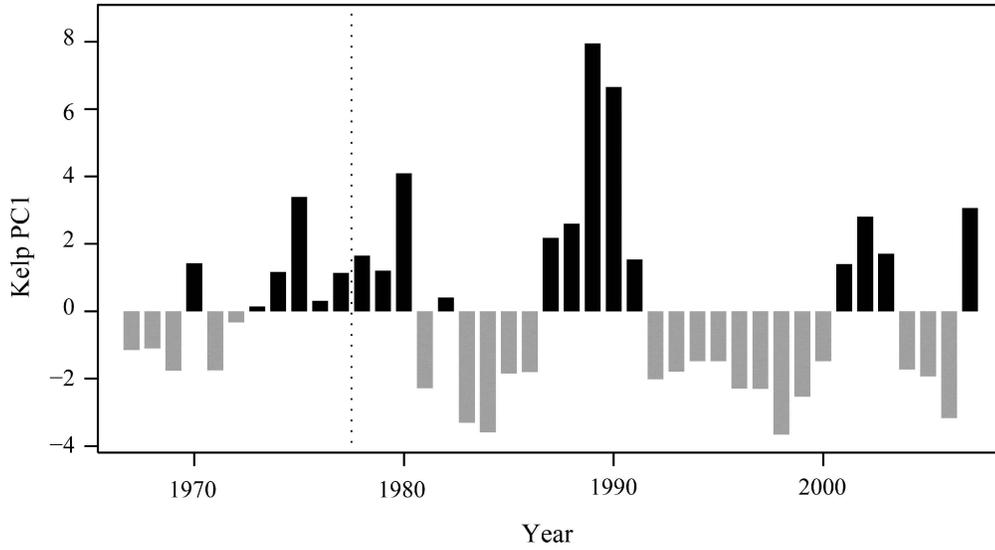


Fig. 4. Time series of the first principal component (Kelp PC1) of kelp canopy cover of 14 kelp forests in southern California. Kelp canopy cover was estimated from aerial photographs. Vertical dashed line indicates regime shift.

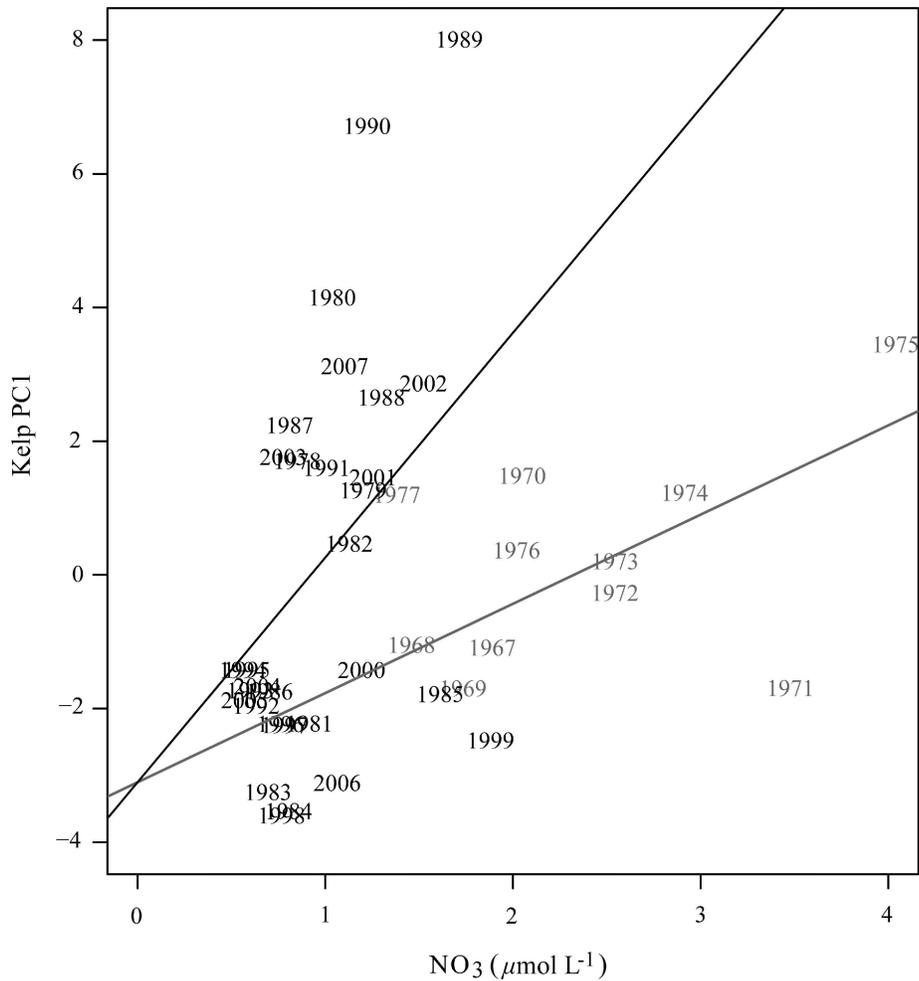


Fig. 5. First mode of regional kelp canopy area (Kelp PC1, estimated from aerial photographs) of 14 kelp forests in southern California (*see text*) as a function of estimated annual mean $[NO_3]$ at the bottom of SIO Pier (depth ~ 5 m). Lines indicate linear regression models for relationship by regime (preregime = gray, postregime = black).

Table 3. Table of Akaike Information Criteria (AIC) results of models in which regional kelp canopy response (kelp PC1) was fitted to nitrate (estimated from σ_t) by regime (Fig. 5). w_i = AIC weights (Burnham and Anderson 2002, p. 75). Δ_i = difference in AIC, relative to the “best” model (Burnham and Anderson 2002, p. 71).

Model	AIC	Δ_i	w_i
Common intercept	200.1	4.7	0.05
Common intercept, common slope	199.4	4.0	0.07
Different intercepts, common slope	198.6	3.2	0.10
Common intercept, different slope	195.4	0	0.52
Different intercepts, different slopes	196.8	1.4	0.26

slope was largely driven by the data from the post-regime period. Pearson product-moment correlation coefficients (Zar 1984) were, therefore, estimated for each period. Estimates of r were -0.106 and -0.367 for before and after respectively, corresponding to r^2 values of 0.011 ($p \sim 0.75$) and 0.136 ($p \sim 0.043$).

Postregime climate control of giant kelp—The increased importance of nutrient climate control of giant kelp after the regime shift is evident in the relationship between kelp density on the permanent band transects in Pt. Loma and seawater density (Figs. 6, 7). The linear model of kelp

density as a function of nonlagged seawater density was maximal ($r^2 \sim 0.61$) when the seawater density threshold was ≥ 25.1 (i.e., the fraction of each year that $\sigma_t \geq 25.1$). The overall best fit was achieved when kelp densities were fit using a weighted combination of the $25.1 \sigma_t$ threshold for each year with the prior year (i.e., kelp density $_y = 0.25(f\sigma_{y-1}) + 0.75(f\sigma_y)$, where y is year and $f\sigma$ is the fractional number of days per year (Oct–Sep) that the density at the base of the SIO Pier was ≥ 25.1). This linear relationship accounted for $\sim 71\%$ of the variance. Inspection of Fig. 1 indicates that the σ_t threshold at 25.1 is close to the density at which our nitrate fit intercepts the $1\text{-}\mu\text{mol L}^{-1}$ nitrate threshold for kelp growth. Previous studies have indicated that stipe density, as opposed to plant density (used in this study), is a more sensitive indicator of *M. pyrifera* biomass (Tegner et al. 1997; Reed et al. 2009), but stipe density capacities are site-specific (Tegner et al. 1997), so it was not valid to average stipe densities among different sites.

Discussion

Knowledge of decadal climate patterns in the North Pacific dates back to the 1860s when R. H. Dana (1869, p. 211) related that “... the climate has altered; that the

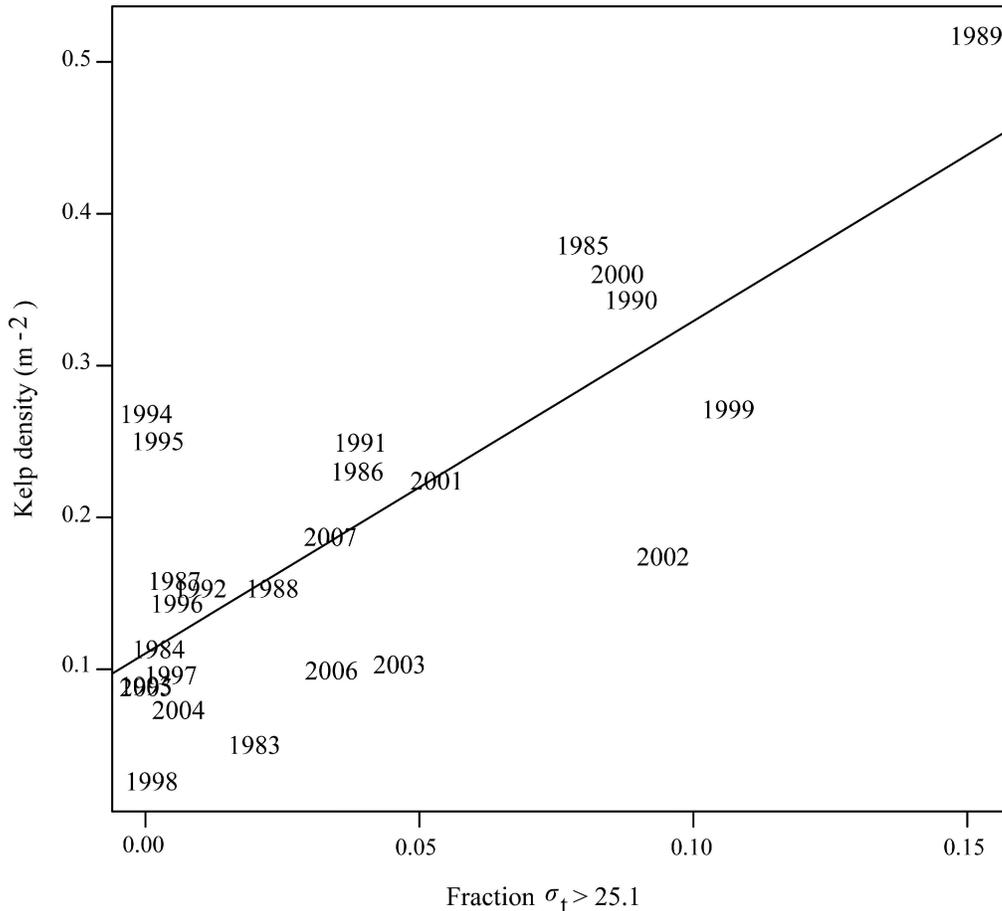


Fig. 6. Density of adult *M. pyrifera* (m^{-2}) in the Pt. Loma kelp forest plotted as a function of the fraction of the time that σ_t at the bottom of the SIO Pier was > 25.1 for each year (adjusted $r^2 = 0.61$, $p = 3.8 \times 10^{-6}$).

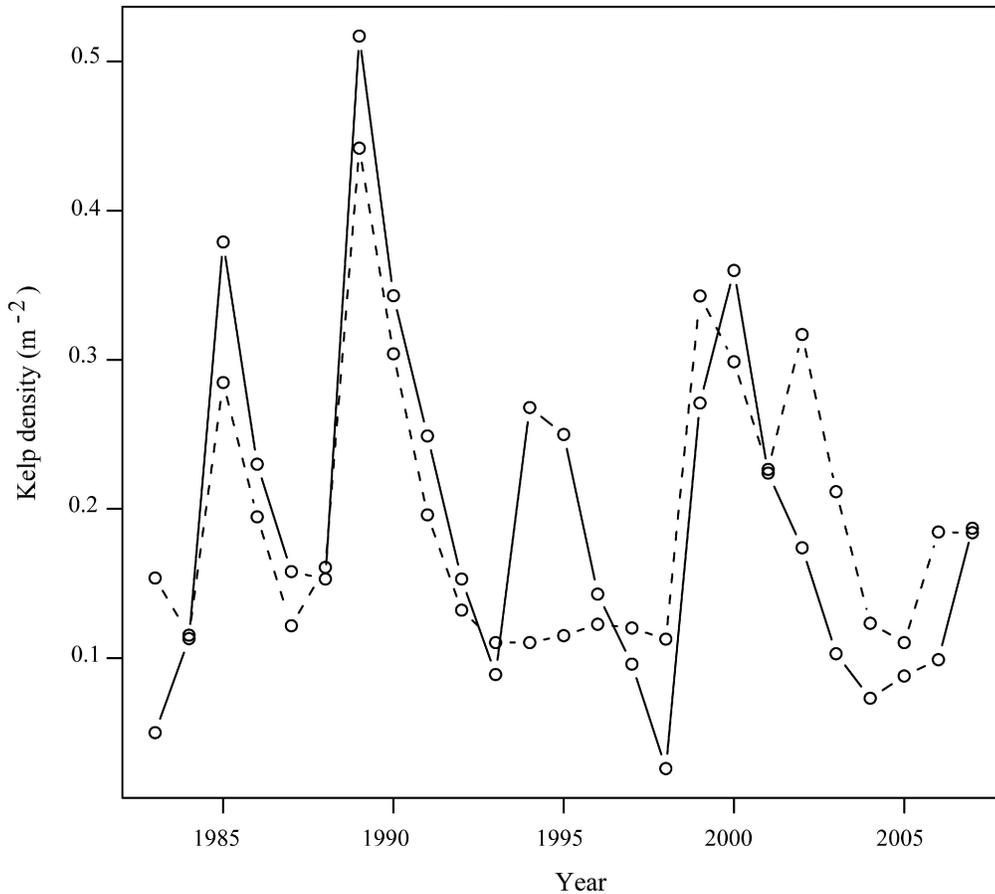


Fig. 7. Time series of adult *M. pyrifera* (m^{-2}) in the Pt. Loma kelp forest (solid line) and fitted values (dashed line) resulting from the linear fit of density on fraction of time $\sigma_t > 25.1$.

southeasters are no longer the bane of the coast they once were and that vessels now anchor inside the kelp at Santa Barbara and San Pedro all the year round.” Here, we have attempted to determine the effects of low-frequency climate on giant kelp populations in southern California, enabled by a kelp time series that spans nearly a half-century. We observed that low-frequency climate appears to regulate the response of *Macrocystis pyrifera* to interannual and ENSO scale climate.

Seawater density structure and nutrient climates—The seawater density structure in the nearshore environment off southern California changed fundamentally in 1977 (Roemmich and McGowan 1995) and our results indicate that the nonlinear relationship between σ_t and nitrate was similar before and after the regime shift. The truncated range of σ_t for which nitrate data were available prior to the regime shift was analyzed conservatively by assigning zeroes for nitrate concentrations for σ_t values below this range. Even so, the nitrate climate prior to 1977 based on daily estimates of seawater density at SIO Pier was much greater than that afterward. Together, these findings indicate that the nutrient climate of surface and near-surface waters (i.e., kelp-forest depths) shifted fundamentally in 1977 from relatively nutrient-replete conditions for giant kelp to nutrient-poor conditions (Figs. 2, 3). Prior to

the regime shift, the inner shelf was bathed by waters with densities above the threshold that best predicts giant kelp density ($\sigma_t = 25.1$, hereafter referred to as the “ σ_t threshold”) much more frequently than after (Fig. 8). In fact, annual mean nitrate conditions, as estimated from σ_t , appear to have changed across this regime shift from being greater than the σ_t threshold much of the time to a climate mainly less than this threshold (Fig. 2). It is also apparent that annual mean nutrient conditions during even the most nutrient-replete years after the regime shift never exceeded a quarter of a standard deviation above the long-term mean. Seasonal patterns of change in the σ_t threshold across the regime shift (Fig. 9) indicate that nutrient conditions during spring and summer, the most important seasons for giant kelp recruitment (Dayton et al. 1984) and growth (Dean and Jacobsen 1984), became much less favorable after the regime shift. The nonlinear relationship between nitrate and σ_t indicates that subtle yet persistent changes in the depth of the σ_t threshold (Fig. 10 in this paper, and isopycnal surfaces throughout the Southern California Bight in Bograd and Lynn [2003, their fig. 6]) can disproportionately affect the nutrient climate to which kelps on the shallow shelf are exposed. Nutrient conditions for kelp forests appear to have switched from a background of nutrient-replete conditions interrupted by large El Niño events in 1940–1942 and 1957–1959, to one below this

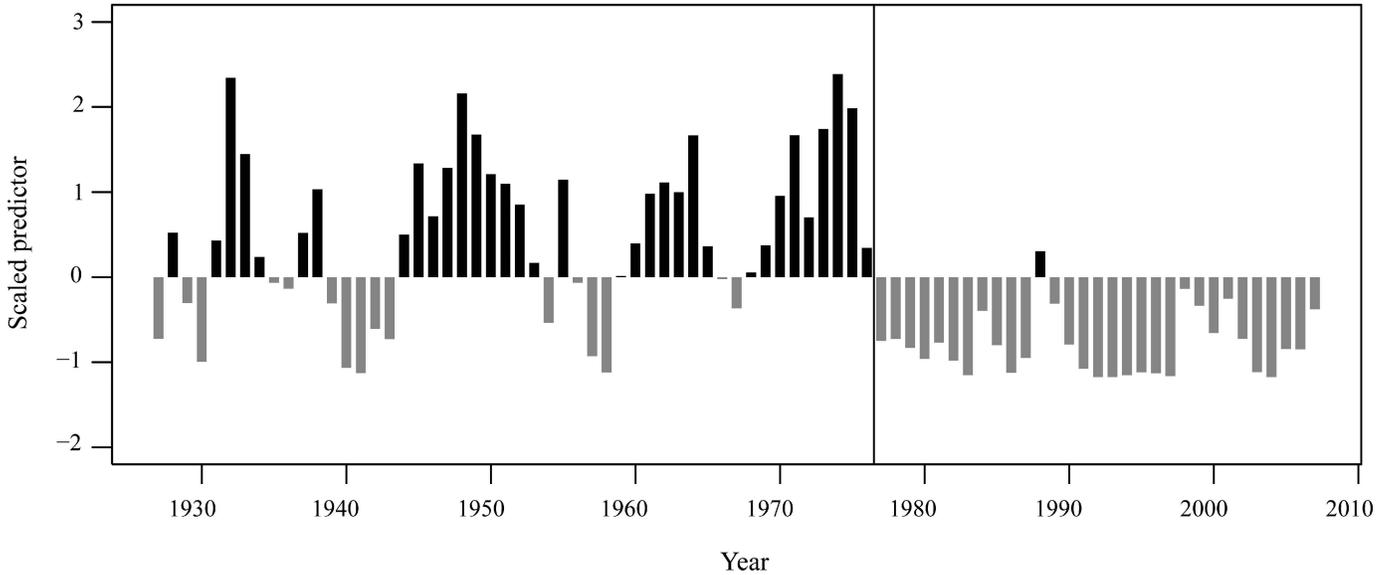


Fig. 8. Time series of the fraction each year seawater density (σ_t) was > 25.1 (σ_t threshold), the best predictor of giant kelp density. Values are scaled above and below the time series mean (~ 0.120) by the standard deviation (~ 0.103). Vertical solid line indicates 1977 regime shift.

threshold except for brief periods, most of which occurred during La Niñas (1985, 1988–1989, and 1999). This pattern persists at present, having exhibited no signs of a reversal to preregime conditions.

An obvious expectation of such a dramatic shift in the nutrient climate on giant kelp is decreased plant density and canopy area. However, the longest time series available (Fig. 11) indicates that historical highs for canopy area prior to the regime shift were less than the highs afterward. All of these kelp forests appear to have responded more strongly to high nutrient events after the regime shift than before. Their response prior to the regime shift appears dampened or nearly absent by comparison (Figs. 5, 11).

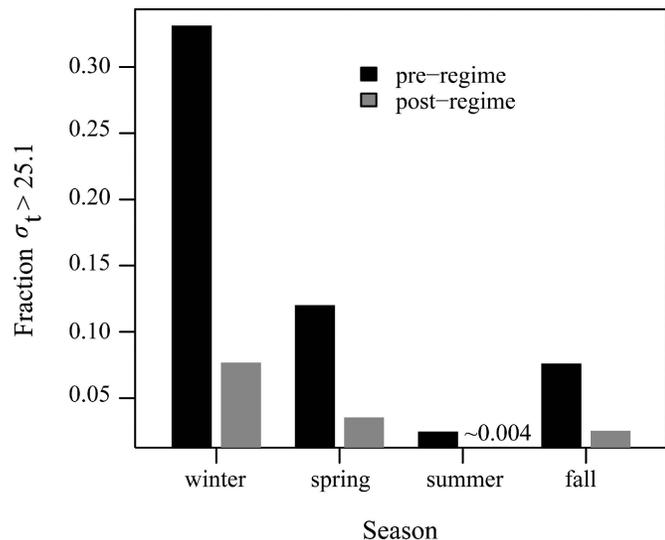


Fig. 9. Fraction of the time that σ_t , at the bottom of the SIO pier (depth ~ 5 m) was > 25.1 by season before (black bars) and after (gray bars) the regime shift.

Our findings raise several important questions. Is the kelp response to the regime shift real, and is the kelp time series long enough to support our findings? How valid is our linear predictor of giant kelp density (σ_t threshold)? What mechanisms are responsible for the observed change in kelp

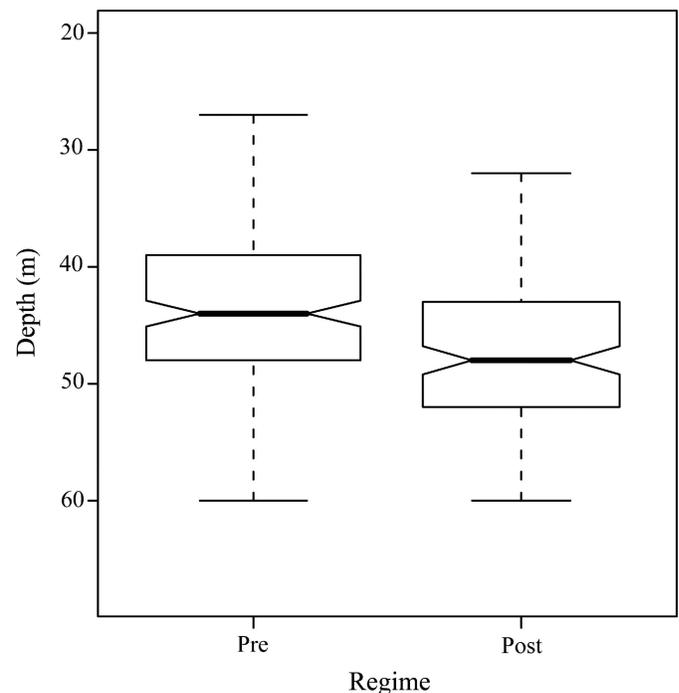


Fig. 10. Box-plot of the depth distributions of the $25.1 \sigma_t$ isopycnal from CalCOFI line 90 Sta. 37 (see text) before and after 1977 regime shift. Bold lines = medians, boxes = 25th and 75th percentiles, whiskers = 95th percentiles, outliers omitted. Width of boxes indicates relative sample size and notches approximate 95% confidence intervals for medians.

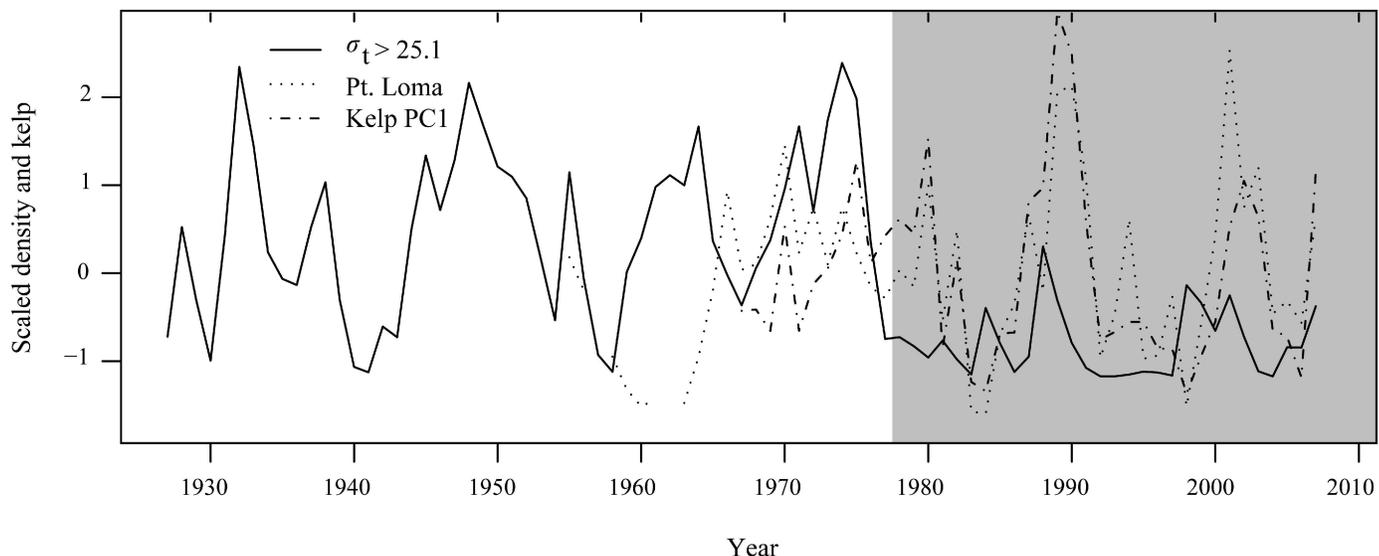


Fig. 11. Time series of the seawater density threshold predictor for giant kelp (the fraction of each year $\sigma_t \geq 25.1$ at the bottom of the SIO Pier, solid line—see Fig. 6 for relationship), canopy cover of the Pt. Loma kelp forest estimated from aerial photographs (dotted line), and the first mode of canopy cover in all kelp forests off San Diego and Orange Counties (estimated from aerial photographs—dot-dash line). Data are centered on their respective means and scaled by their standard deviations for inclusion in one plot. Gray area indicates postregime period.

response, if it is real, to nutrient-replete years across the regime shift? How have the physical conditions changed on the inner shelf off southern California, and what does this portend for the future of giant kelp given possible further warming and increased stratification? And finally, what are the implications for the management of kelp forests?

The cross-regime response of giant kelp—The response of giant kelp that we observed across the 1976–1977 regime shift is based on our use of seawater density as a proxy for nitrate across the regime shift, and the assumption that the length of our kelp canopy time series is adequate. The relationship between σ_t and nitrate concentration in the upper ocean is complex due to the interaction of atmospheric, oceanographic, and biological processes that affect each property. However, while the relationship varies spatially at regional or larger scales, little variability is observed at local scales, and most of this variability is seasonal (Kamykowski and Zentara 1986). The nitrate proxy reported in the classic kelp literature has been temperature rather than σ_t (Jackson 1977) largely because most of the density variation in upwelling ecosystems, where kelps typically thrive, is associated with temperature. However, σ_t is generally a better predictor of nitrate, especially in areas where salinity is variable (Kamykowski and Zentara 1986) and in the present case where the salinity and temperature have both changed since the regime shift. Annual means of salinity and temperature at the base of the SIO pier are plotted in spice-density space in Fig. 12. Spice (Flament 2002) is a state variable useful for discriminating water masses in density profiles. Spice increases with increasing temperature and salinity and is nearly orthogonal to isopycnals in temperature–salinity space. Figure 12 shows what is already well-known, that temperature has increased and salinity has decreased in the CCS since the regime shift,

with a concomitant decrease in density. But it also shows that density variability has been driven more by salinity since the regime shift (i.e., salinity has been more variable). These salinity variations appear decadal and are independent of large-scale climate indices, whereas temperature variability is mainly interannual and related to ENSO (Schneider et al. 2005). Therefore, σ_t is a better proxy for nitrate than temperature at decadal scales and across the regime shift.

The length of the aerial kelp time series is ~ 41 yr, 11 of which were prior to the regime shift. Is such a short biological time series adequate to define kelp response regimes? Our aerial kelp time series is similar in length to time series that have previously been characterized as displacement regime shifts (Overland et al. 2008). The concept of displacement refers to periods when biotic means are significantly displaced (“perturbed” in Isaacs [1976]) from the long-term mean, and this concept has been applied to time series shorter than 50 yr. However, the regime shift we describe for kelps in southern California does not refer to a mean condition (i.e., kelp density or canopy area), but rather the response of *M. pyrifera* in southern California to the different nutrient climates across the regime shift (Fig. 5). Canopy area, the biological response variable in this case, is not bimodal; rather, the slopes of kelp response to forcing are significantly different. The response of giant kelp to nutrient forcing prior to the regime shift is limited to 11 yr. However, aerial data for Pt. Loma extend further back in time to the mid-1950s with some gaps (Fig. 11). This longer time series at Pt. Loma indicates that the response of *M. pyrifera* canopy to nutrient forcing prior to the beginning of the regional kelp time series (1967) was also dampened. Nutrient conditions during the mid-1950s were relatively moderate to high and followed a decade-long period of elevated-nutrient conditions, yet giant kelp canopy in 1955 was less than half a

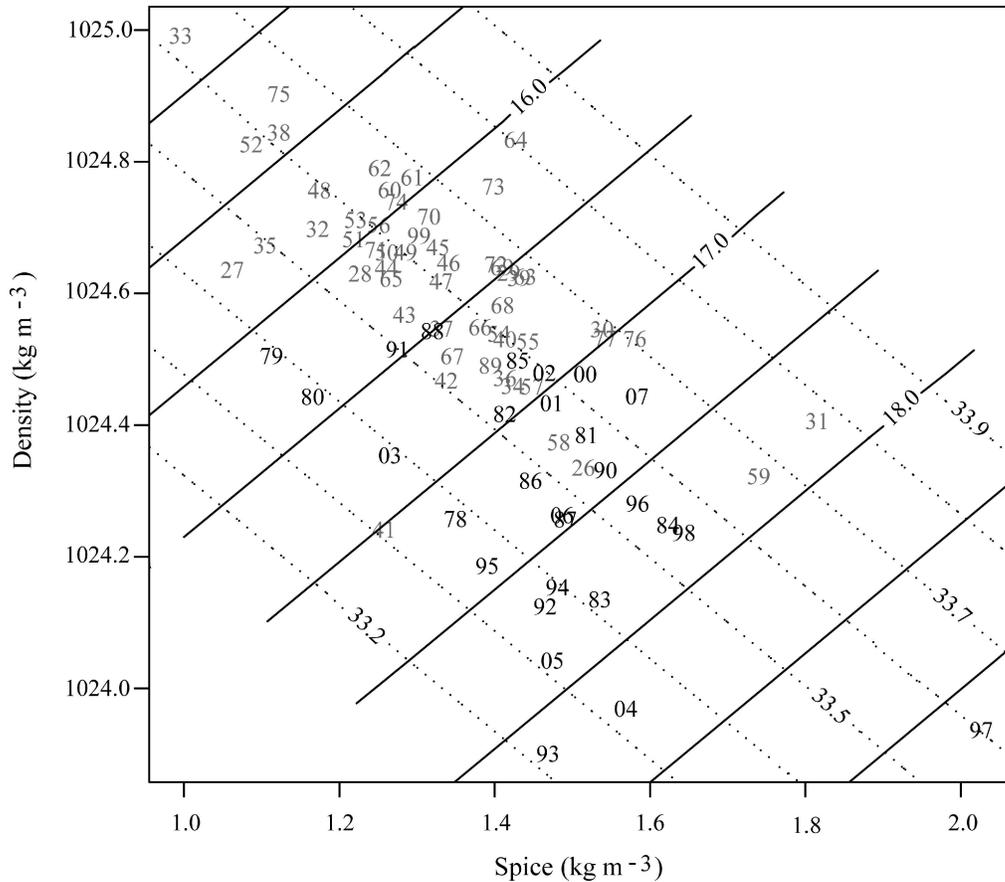


Fig. 12. Bivariate plot of annual mean seawater density and spice at the bottom of the SIO Pier (~ 5 m depth). Contour lines indicate isolines of temperature (solid) and salinity (dotted). Years prior to the 1977 regime shift are gray and postregime years are black.

standard deviation above the long term mean. This period was followed by a large El Niño event characterized by an extended period of poor nutrient conditions relative to the pre-regime shift period, in which canopy cover collapsed and failed to recover even with the onset of strong nutrient forcing in the early 1960s. The canopy area of Pt. Loma is similar to the first mode of the kelp response for all 14 forests (kelp PC1) so it is likely that Pt. Loma also reflects the regional kelp condition prior to 1967. Occasional earlier observations of other kelp forests in the region using similar methodologies (Neushul 1981) support this generalization. Thus, the record of dampened kelp response to nutrient forcing extends at least to 1955, which lengthens our pre-regime record to ~ 22 yr, and the total time series to > 50 yr.

Seawater density threshold—The importance of the σ_t threshold for giant kelp in southern California is supported by two independent lines of evidence: (1) The GAM fits of nitrate on σ_t intersect the nitrate threshold for *M. pyrifera* growth ($1 \mu\text{mol L}^{-1}$) near $\sigma_t = 25.1$ (Fig. 1); (2) The predictive skill of the σ_t threshold, which accounted for ~ 71% of the variability in kelp density at Pt. Loma. Previous work investigating the importance of nutrient control of giant kelp used temperature, which accounted for no > 46% to 24% of the variance (North et al. 1993;

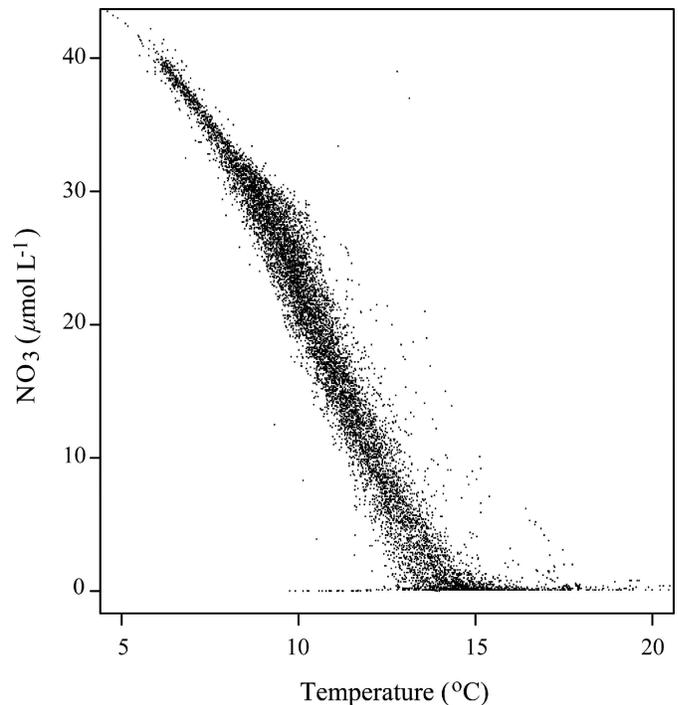


Fig. 13. Nitrate concentration as a function of temperature for the same CalCOFI stations and SIO pier data as Fig. 1.

Tegner et al. 1996) for three possible reasons: (1) Density is a better predictor of nitrate than temperature (Fig. 13). The deviance explained by the GAM fit of density was $\sim 98\%$ (GCV = 2.68) whereas the GAM fit for temperature using the same CalCOFI data was $\sim 95\%$ (GCV = 5.86) with equivalent degrees of freedom for both fits ($\sim 8-9$). The greater variation of nitrate as a function of temperature is evident in Fig. 13, especially at nitrate concentrations most frequently observed on the inner shelf ($< 2 \mu\text{mol L}^{-1}$); (2) North et al. (1993) analyzed kelp data lumped across the regime shift; (3) North, by necessity, used canopy data, which can be biased by the episodic submergence of canopy by currents and the seasonality of canopy disappearance without associated kelp mortality. The combination of these factors has deemphasized the importance of nutrient control of *M. pyrifera* after the regime shift. The greater amount of variance captured by the model utilizing lagged σ_t also emphasizes the importance of nutrient lag effects at the scale of 1 yr. The relationship between kelp PC1 and sea level at SIO Pier is consistent with Tegner et al. (1996), in which sea level was significantly but weakly correlated with kelp harvest. Sea level and the depth of the 25.1 σ_t isopycnal, while correlated, appear to be somewhat uncoupled.

The σ_t threshold was based on its strong correlation with giant kelp density. Computationally, it represents the fraction of each year that σ_t is ≥ 25.1 . Functionally, the $\sigma_t = 25.1$ isocline likely indicates the shallowest waters whose nitrate concentration is near the lower limit of kelp growth as indicated in Fig. 1 and, therefore, the σ_t threshold represents a lower bound of nitrate for kelp growth. However, neither the nitrate- σ_t relationship, nor the σ_t threshold developed in this study, is likely useful to estimate *M. pyrifera* growth, because neither nitrate uptake as a function of nitrate concentration (Gerard 1982) nor the dependence of kelp growth on nitrate (Zimmerman and Kremer 1984) are linear.

Response of Macrocyctis pyrifera—The response of *M. pyrifera* to the nutrient climate shift in 1977 represents a different type of biological response to a climatic regime shift than has been previously described. Frequency distributions of giant kelp canopy were not bi- or multimodal as described for biological regime shifts in other systems. The response of giant kelp across the regime shift was not one in which its mean condition was displaced. Rather, it was how *M. pyrifera* responded to years in which the nutrient climate was conducive for kelp growth against a background of low-frequency autocorrelated physical conditions (Rudnick and Davis 2003) that define the 1976–1977 regime shift. The frequency of ENSO events did not change across this regime shift; rather, their effects on the nutrient climate on the inner shelf differed across the regime shift due to the deepening of the 25.1 σ_t isopycnal. This deepening appears to have increased the amplitude of nutrient stress associated with the El Niños after the regime shift. Plankton dynamics in the southern California Bight might also be similarly affected by such synergistic forcing (Miller et al. 2004), in which the biological response to ENSO events depends at least partly on the phase of background lower frequency climate forcing. In this sense, the change in giant kelp response to good nutrient years

across the regime shift represents a type of discontinuous regime shift, similar to that described in Collie et al. (2004) and Scheffer et al. (2001), in which the biological response to climate forcing depends on the lower frequency physical condition (i.e., red-shifted hysteresis) of the system.

Although it is clear that giant kelp responded differently to interannual nutrient forcing across the regime shift, the mechanisms are not clear. The kelp forests of southern California prior to the 1976–1977 regime shift were different than today. Comparisons of historical sea urchin abundances off Pt. Loma and La Jolla, the largest forests in California indicate that prior to the regime shift, red (*Strongylocentrotus franciscanus*), purple (*S. purpuratus*), and white (*Lytechinus anamesus*) sea urchins were more abundant (Parnell et al. 2006) and the effects of sea urchin grazing on kelp recovery were greater (Tegner and Dayton 1991). Further, the size or stipe numbers of giant kelp after the regime shift appears truncated. Median plant sizes (stipe number) after the regime shift were less than half that prior to the regime shift (Tegner et al. 1996), a pattern that persists at present. Abundance, species richness, and recruitment of some fishes decreased across the 1976–1977 regime shift and their species composition has shifted toward more southern species (Holbrook et al. 1997).

Many factors, both natural and anthropogenic, have been invoked to explain periods of historically high or low giant kelp abundance, though not in the context of climate at temporal scales longer than ENSO. Many studies have at least partly attributed localized kelp-forest disturbances to human disturbances such as pollution and sedimentation (North et al. 1993; Foster and Schiel 2010) and resource utilization (Tegner and Dayton 2000). However, pollution and sedimentation are not likely a major cause of the kelp response we describe here because their effects on kelps are localized in time and space (Dayton et al. 1992) and cannot have affected kelp forests over the length scale of our study region. Resource utilization such as recreational and commercial fishing are also not likely primary factors because the timing of the regime shift does not coincide with abrupt changes in these activities (Dayton et al. 1998). Foster and Schiel (2010) concluded that anthropogenic disturbances were likely important for localized kelp-forest declines dating back to the 1950s but were not likely important at regional scales.

Storm waves, often associated with El Niños, can fundamentally affect kelp-forest community structure (Dayton et al. 1992) and have been associated with transitions from barrens to kelp forests (Harris et al. 1984; Ebeling et al. 1985). The timing of storm waves relative to ENSO-period nutrient forcing is important for the trajectory of kelp-forest recovery (Tegner et al. 1997). Mechanical disturbance due to large wave events can rip out kelp forests and decimate sea urchins (Harris et al. 1984; Dayton et al. 1989; Seymour et al. 1989). The effects of storm waves on kelp abundance are complex. Storm-wave effects depend on the hysteresis of the interaction between individual kelp plants, the grazer community, and the underlying nutrient climate (Tegner and Dayton 1991). Because of this, direct relationships between storm waves and kelp abundances are not clear (Tegner et al. 1996). However, wave data, which date only to 1974 in our study

region, indicate a trebling of major wave events since the late 1970s (Seymour 1996) and meteorological reconstructions of storm tracks indicate a step increase in storm intensity in 1973 (Chang and Fu 2002) when storm intensities in the North Pacific increased $\sim 30\%$. Therefore, kelp forests in southern California have been subjected to more intense storms in addition to a decreased nutrient climate since the regime shift.

The cross-regime age structure of giant kelp in Pt. Loma is consistent with both a reduced nutrient climate and increased storm frequency. Within this context, the increased response of kelps to nutrients since the regime shift represents regionally synchronous boom and bust cycles in which mortality appears greater and more homogenous across entire kelp forests and appears less modulated by consumers. The match–mismatch hypothesis (Stenseth et al. 2002), which relates the synchrony of secondary production (reproduction and growth) with food supply, might be applied as a framework to investigate such a response. The degree of asynchrony between kelp production and sea urchin grazing demand (Tegner and Dayton 1991) and population-regulating processes such as recruitment may have changed fundamentally across the regime shift. More broadly, the response of giant kelp to the regime shift appears to conform to the classic model of community regulation of Menge and Sutherland (1987), in which environmental stress and recruitment regulate the intensity of herbivory, predation, and competition. Within this model, the time scales of nutrient and wave climates as environmental stressors are related to large-scale, low-frequency North Pacific climate processes. The larger amplitude response of giant kelp to nutrient-replete conditions after the regime shift may, therefore, be the result of low-frequency hysteresis in which the intensity of consumer and competitive processes are reduced.

We also suggest that what appears to be increased control of the kelp forests by climate after the regime shift may actually be due to a modulation of the kelp response to interannual variability by decadal or lower frequency climate processes acting on all (or several) levels of the kelp-forest community. Implicit in this hypothesis is the possibility that at least some of what is perceived as uncoupling between simple proxies of kelp and climate, and which might be invoked as evidence of top-down (consumer) control, is really due to climate control. In such cases, correlation analyses may be misinforming. Therefore, the true dependencies of biological processes on climate are best unmasked mechanistically.

Finally, we also suggest that the profound and sudden response of kelp forests in our region to the 1976–1977 regime shift and the sensitivity of the forests to a slight deepening of the $25.1 \sigma_t$ isopycnal indicates that future climate shifts involving further deepening could lead to rapid changes in *M. pyrifera* populations. This has strong bio-geographical implications regarding the southern distribution of giant kelp. *Macrocystis pyrifera* extends south along the Pacific coast of Baja California to San Ignacio Lagoon (located > 850 km south of our study region) but only in areas of strong upwelling. These southern kelp forests are heavily affected by ENSO events (Ladah et al.

1999). Future decadal scale deepening of the thermocline could suddenly reduce the latitudinal distribution of giant kelp and functionally eliminate this key species from much of Baja California.

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