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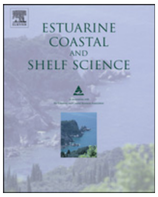

Vertical distribution of *Macrocystis pyrifera* nutrient exposure in southern California

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ABSTRACT

We examined water column temperature time series profiles for several years at two locations in a single kelp (*Macrocystis pyrifera*) forest to characterize the alongshore variability of the nutrient climate that giant kelp is exposed to and compare it to the response of giant kelp. The differences in nutrient climate are due to differential alongshore vertical variations in temperature, a well-established proxy of nitrate, due to the topographically induced internal wave dynamics within the kelp forest. We observed the greatest temperature variability during summer and most of this variability occurred near the surface. The 14.5 °C isotherm, indicating the presence of nitrate, ranged the entire vertical extent of the water column, and was shallowest during the winter and in the southern portion of the kelp forest. Predicted water column integrated nitrate varies from 0 μmol NO_3^-/m^2 to 431 μmol NO_3^-/m^2 yielding a time series daily average of 0.12 gN/m^2day (North La Jolla) and 0.18 gN/m^2day (South La Jolla). Redfield conversion of these values puts the time series daily average for carbon production (upper limit) between 0.8 and 1.2 gC/m^2day for the north and south parts of the bed respectively, and shows considerable variation at several time scales. Giant kelp in the southern portion of the forest exhibited greater stipe densities (a proxy for kelp production) than individuals in the northern portion, corresponding with the alongshore nutrient climate variability. The depth of the nutricline varied by up to 10 m over time scales as short as hours. Variability was greatest at diurnal and semi-diurnal frequencies, with shallower water column depths showing greatest variability. These depth-specific variations in temperature and nutrient exposure may have biologically important consequences for *M. pyrifera* especially during low nutrient seasons.

1. Introduction

Giant kelp, *Macrocystis pyrifera*, is the largest algal species on earth and has a broad geographic range. Individuals span the water column, often bridging gradients in temperature and nutrients needed for growth. A significant input of nutrients is required to support the large and rapid biological production of these forests. *Macrocystis pyrifera* productivity in California ranges from 0.95 to 6.8 gC/m^2day (Towle and Pearse, 1973; Mann, 2000). Using the empirical stoichiometric Redfield ratio 106:16:1 (C:N:P), this leads to estimates that 0.14–1.03 gN/m^2day and 0.01–0.06 gP/m^2day are required to support such growth. Low nutrient conditions limit growth and survivorship as well as negatively affect adult reproductive output and juvenile recruitment (Gerard, 1982b; Steneck et al., 2002). Nutrients are typically stratified in the water column and linked with temperature and density (Kamykowski and Zentara, 1986), with greater nutrient concentrations below the thermocline. Thus, there is variation across the alga in the opportunities for nutrient acquisition. Geographically, the stratification of nutrients increases toward the southern range of *M. pyrifera* (in North America). Temperature and nitrate concentrations can vary on multiple temporal and spatial scales with profound consequences for kelp biology.

Giant kelp production decreases with warming temperatures (Jackson, 1977; North and Zimmerman, 1984). El Niño – Southern Oscillation (ENSO), an inter-annual and Pacific wide climate pattern that involves a warming of the surface waters in the eastern Pacific and extending to higher latitudes in the eastern boundary currents, presents alternating periods of high and low nutrient conditions. In southern California, storm and wave activity increases during El Niño years, which increases the incidence of *Macrocystis pyrifera* being detached from their substrate (Seymour et al., 1989). Loss of canopy can in turn affect the light reaching the bottom and the ability of competitors to monopolize substrate. One of the largest El

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Niño events in recent history (1982–1984) greatly reduced *M. pyrifera* stands with dramatic follow-on effects for understory algal species (Tegner and Dayton, 1991; Tegner et al., 1997; Dayton et al., 1998).

The San Diego region supports two of the largest kelp beds in California, Point Loma and La Jolla, yet unlike nutrient-replete regions to the north, the San Diego area experiences seasons (i.e. summer) when nutrients are limiting (Jackson, 1977). Internal waves are critical in "nutritionally marginal" habitats of southern California, especially during warm water events (Zimmerman and Robertson, 1985). The offshore nitracline in addition to internal waves can affect the availability of nitrate to the inner shelf (Lucas et al., 2011). Sub-mesoscale coastal eddies represent another potential means of nutrient transport to kelp forests (Bassin et al., 2005).

Macrocystis pyrifera is one of the few algae that possess sieve tube elements that allow for internal transport of metabolites such as mannitol and amino acids (Sykes, 1908; Schmitz and Srivastava, 1979; Manley, 1983). One kelp individual could be limited in both light (at depth) and nutrients (at the surface) at the same time, yet still be able to grow. The existence of the sieve tube transport system, which spans the water column, provides a mechanism by which deeper-water nitrate can support growth despite low nitrate levels at the ocean surface. This system may help explain why *M. pyrifera* also can sustain growth in the absence of surface nutrients for limited periods of time. Starting with high internal nitrogen reserves, *M. pyrifera* can sustain relatively rapid growth for at least 2–3 weeks in the absence of a significant external nitrogen supply (Gerard, 1982a) though low overall nutrient availability in southern California limits this ability (Zimmerman and Kremer, 1986). Prior nutrient history can affect that response.

An interesting aspect of the great length of *Macrocystis pyrifera* fronds is that water column spanning individuals may be exposed to very different nutrient concentrations across their vertical extent. To explore water column variability in the nutrient environment at short spatial scales (within a kelp bed; <10 km) along the length of the typical height of *M. pyrifera*, we examine a thermistor string time series of ~4 years. The objectives of this study were to define the nutrient climate and the variable physical environment of *M. pyrifera* within a single kelp forest, examine low frequency (seasonal) to high frequency (hourly) temperature and predicted nitrate events, focusing on depth differences and discuss them in relation to *M. pyrifera* biology and giant kelp performance estimated *in situ* at the same study locations.

2. Methods

2.1. Description of study sites

The La Jolla kelp forest is the second largest kelp forest in California, after Pt. Loma, with approximate dimensions 8 km

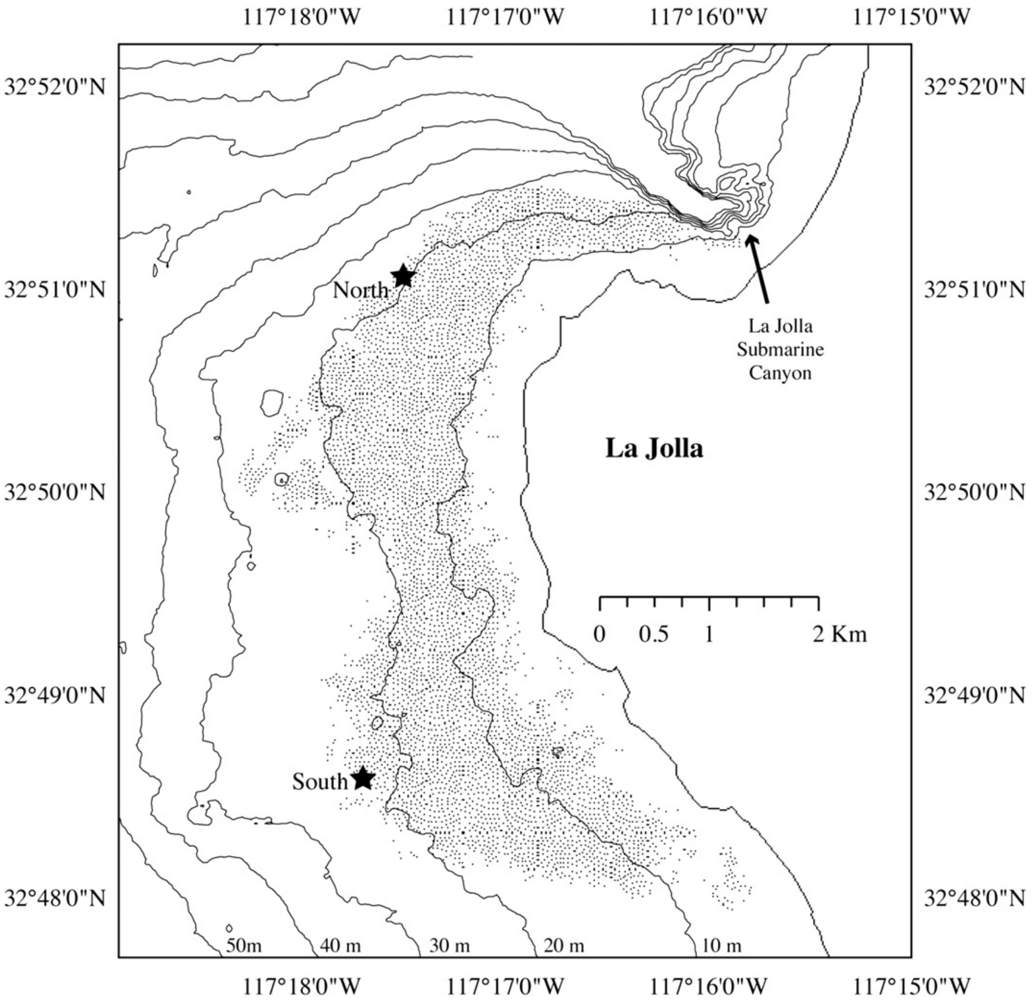

Fig. 1. Map of the La Jolla kelp forest and nearby submarine canyon. The stippled area is where *Macrocystis pyrifera* has been observed at least once in aerial photographs taken 1967–1999). The North La Jolla and South La Jolla thermistor strings were anchored 22 m deep and are indicated by stars. Bathymetric contours are at 10 m increments.

alongshore × 1.5 km cross-shelf (Fig. 1). The bed occupies an area of mainly rocky substrate with cobble and sand patches interspersed. The northern end of the forest is located near a submarine canyon and the San Diego-La Jolla Ecological Reserve and the southern portion of the kelp forest wraps around a headland. We chose to look at the temperature and predicted nutrient climate of two sites in this kelp bed: North La Jolla (N 32° 51.0′; W° 117 17.5′) and South La Jolla (N 32° 48.6′; W 117° 17.7′). The North La Jolla site is close to the submarine canyon and has stronger currents than the South La Jolla site, which is located behind the headland. Documented biological differences include greater kelp persistence in the south as seen from aerial photos, while the north has a more dynamic canopy and more dominant understory (Parnell et al., 2006).

2.2. Temperature data collection

To quantify horizontal and vertical differences in temperature and hence nutrient availability at the two locations, thermistor chain data were collected from July 2007 through March 2011 at 10 min intervals using TidBit temperature data loggers with ∼0.2° resolution, and ∼5 min response time (Onset, Bourne, Massachusetts, USA). TidBits were placed on the bottom and at 2, 6, 10, 14, and 18 m above the bottom at both sites and at the surface (21 and 22 m above bottom) at South La Jolla (Fig. 2).

2.3. Temperature as a proxy for nutrient availability

There is a strong linear relationship between nitrate and temperature in the southern California nearshore at temperatures below 14.5 °C, with colder waters possessing more nitrate (Kamykowski and Zentara, 1986; Zimmerman and Kremer, 1986; Dayton et al., 1999; Lucas et al., 2011). However, anomalous temperature-nitrate events with greater than expected nitrate at warmer temperatures have been documented in the southern part of the range (Ladah, 2003). In this study, we estimate seawater nitrate concentrations from an empirically-derived temperature-nitrate relationship using offshore California Cooperative Oceanic Fisheries Investigations (CalCOFI) temperature and bottle nitrate data from 1959 to 2010 from line 93.3, station 28.0, located offshore of La Jolla (N 32° 54′; W 117° 23′). This data was subset by the range of temperatures seen in our time series: 9.73 °C–24.86 °C ($n = 1904$). A linear fit to temperatures 14.5 °C and below ($n = 1439$) yielded the equation: nitrate (μmol/L) $= -5.8$ temperature (°C) $+81.7$ with $R^2 = 0.90$, which was then used to calculate predicted nitrate values. At temperatures above 14.5 °C, nitrate levels are typically insignificant (i.e. median ≤0.1 μmol/L). We assume that this relationship is maintained inshore despite complex mixing that occurs in the nearshore. Parnell et al. (2010) show that nitrate/temperature and nitrate/density relationships from waters 5 m depth off Scripps Pier were consistent with those measured offshore at nearby CalCOFI stations. Water column integrated nitrate was calculated for a square meter of bottom at each 10 min time step by linearly interpolating the thermistor chain data to get temperature values and calculated nitrate values (using the equation above) throughout the water column, which were then summed in 10 cm bins. Conversions to carbon were calculated using the Redfield ratio (106C:16N). For comparisons between sites we used time periods for which both sites had data.

2.4. Power spectral density

Power spectral density calculations for the temperature time series used the Welch's averaged periodogram method with a section length of 14 days, zero overlap and application of a standard Hamming window. Power spectra were calculated at 0 m above bottom and 18 m above bottom at each of the two study sites and also at 6 m above bottom for South La Jolla.

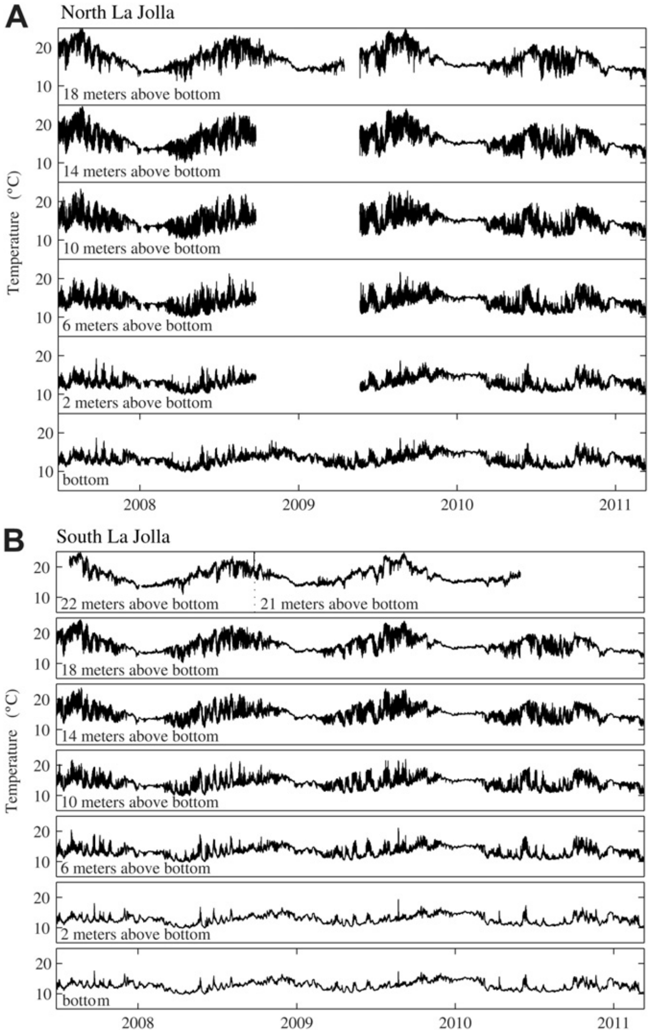

Fig. 2. Temperature time series for North and South La Jolla. From July 2007 through March 2011, temperature was continuously recorded at depths of 0, 2, 6, 10, 14, and 18 m above the bottom at two locations: (A) North La Jolla, and (B) South La Jolla. South La Jolla also had an additional tidbit at 22 m above bottom from July 27th 2007 through September 24th 2008, then at 21 m above bottom through May 30th 2010.

2.5. Kelp stipe and plant data collection

Total number of *Macrocystis pyrifera* stipes and plants within the same cohort were counted quarterly along 25 × 4 m band transects throughout the length of the study at both North and South La Jolla sites (four transects per site). For each quarter, mean (±standard error) numbers of stipes per plant were calculated. Differences among sites in the mean number of stipes per plant were assessed using the Wilcoxon rank sum test.

3. Results

During this ∼4 year time series, we see periods of greater temperature variability during the summer, and lower variability during the winter months (Figs. 2 and 3A & B). This within depth variability is greater at 18 m above bottom compared to bottom depth (Fig. 3A & B, Table 1). In the North La Jolla time series, there is an eight-month gap resulting from the mooring being ripped from

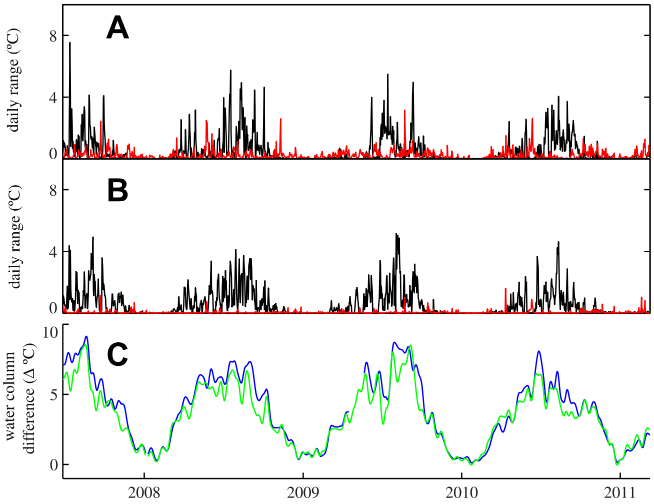

Fig. 3. Daily averaged range in temperature through time for 18 m above bottom (black) and bottom (red) at (A) North La Jolla and (B) South La Jolla. Panel (C) shows water column differences (18 m above bottom temperature minus bottom temperature) through time using one-week running mean filter for North La Jolla (blue) and South La Jolla (green).

the base during a storm; only the top and bottom tidbits were recovered. Because of this gap, we chose to focus on comparisons of the 18 m and bottom time series for some of our analyses (Table 1; Figs. 3 and 4). The mean temperatures were slightly warmer in North La Jolla compared to South La Jolla. Water column differences change predictably throughout the year; we see seasonal patterns of greater stratification in summer months and more homogenous temperatures in the winter (Fig. 3C). In North La Jolla, the dominant frequency signal is the diurnal peak, while at South La Jolla, the semi-diurnal peak is more prominent (Fig. 4). Variance is greater at 18 m above bottom compared to the bottom at both sites, though the difference is stronger at South La Jolla (Table 1). The rate of decay (slope) increases with depth, implying that frequencies higher than semi-diurnal have lower thermal variance at depth compared to the surface. For our study, the Oceanic Niño Index, a measure of the occurrence and strength of El Niño/La Niña events, included the 2009–2010 El Niño event and the 2010–2011 La Niña event (Nam et al., 2011). We did not see a significant peak in the power spectra greater than diurnal. The length of our section window in the power spectra calculations precludes seeing variation longer than 14 days and our sampling interval of 10 min limits analysis to events occurring at 20 min or longer time scales. Additionally, the length of this time series is limited in resolving longer time scale events such as ENSO which is recurrent on ~3–7 year time scales.

Of biological interest for *Macrocystis pyrifera* is the vertical position in the water column of the 14.5 °C isotherm at which nitrate reaches appreciable levels in this region. Depending on the depth of this isotherm, different segments of a *M. pyrifera* individual will have access to nitrate. The depth of this isotherm throughout the time series varies the entire length of the water column at both sites (Fig. 5). There are periods where the waters surrounding an individual are likely to be completely depleted of nitrate and periods when waters containing nitrate bathe the entire individual. For the majority of time, the depth of nitrate coverage lies somewhere along the length of the individual. Trends are similar at both locations, although the 14.5 °C isotherm is generally shallower at South La Jolla (Fig. 5, bottom panel). The proportion of time that the instruments positioned 18 m above bottom recorded temperatures below 14.5 °C was approximately 20% while at the bottom the proportion was ~80% and highly variable throughout the year (Table 1). The proportion of time for exposure to temperatures below 14.5 °C was higher and the corresponding temperatures were lower at South La Jolla than for North La Jolla. This implies that kelps at the south site spend a greater time exposed to nutrients and that the nutrient levels during exposure events are higher than at the north site. Because *M. pyrifera* spans the water column, predicted water column nitrate through time may be a more appropriate measure of kelp exposure to nitrate (Fig. 6). General seasonal patterns are again similar at the two sites, although the south is exposed to higher nitrate (Fig. 6, bottom panel), meaning for a given m^2 of bottom, there are potentially more nutrients available for growth. Biological differences were seen between the two locations in the number of stipes per plant (Fig. 7); the two sites generally track each other (i.e. lower stipes per plant values in 2008 and increasing values in 2010), though South La Jolla (which consistently has more nutrient availability) has higher stipes per plant (Fig. 7). Integrated nitrate values range from 0 µmol NO$_3^-$/m^2 to 431 µmol NO$_3^-$/m^2 with a time series daily

Table 1
Temperature summaries by month at North and South La Jolla for the 18 m above bottom and bottom time series. The following statistics were calculated: mean temperature, range, variance, and the percentage of the time series that the temperature was less than or equal to 14.5 °C and the average of those values.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
North La Jolla 18 m above bottom	Mean temp	14.34	14.47	14.64	15.47	17.69	19.02	19.06	20.14	19.02	18.20	16.85	15.04	16.99
	Range	1.58	2.09	4.00	5.35	7.31	6.16	10.00	8.17	8.84	6.21	3.88	3.04	5.55
	Variance	0.06	0.10	0.40	0.71	0.85	1.30	5.16	3.13	2.42	1.19	0.66	0.55	1.38
	Below 14.5 °C	0.67	0.63	0.28	0.14	0.04	0.01	0.06	0.04	0.03	0.01	0.03	0.23	0.18
North La Jolla bottom	Mean temp	13.68	13.50	12.02	11.68	11.69	12.56	12.54	13.05	13.35	14.25	14.06	14.08	13.04
	Range	2.39	2.79	3.89	4.18	5.15	4.98	4.86	4.56	5.20	5.77	4.43	3.63	4.32
	Variance	0.21	0.33	0.59	0.61	0.90	1.11	0.81	0.57	0.63	0.92	0.73	0.82	0.68
	Below 14.5 °C	0.77	0.75	0.95	0.99	0.98	0.93	0.95	0.89	0.85	0.57	0.60	0.52	0.81
South La Jolla 18 m above bottom	Mean temp	14.18	14.30	14.13	14.80	16.50	17.77	17.77	18.67	17.40	17.67	16.09	14.86	16.18
	Range	1.26	1.42	3.51	5.97	7.01	7.10	9.78	9.05	8.26	5.55	4.70	3.00	5.55
	Variance	0.06	0.07	0.46	1.33	1.72	2.41	5.71	4.01	3.46	1.11	0.77	0.61	1.81
	Below 14.5 °C	0.71	0.70	0.54	0.30	0.10	0.07	0.13	0.09	0.09	0.01	0.10	0.28	0.26
South La Jolla bottom	Mean temp	13.56	13.20	11.37	11.20	11.30	12.20	12.17	12.54	12.96	13.92	13.71	13.98	12.68
	Range	2.08	2.64	2.38	3.19	3.42	4.35	3.03	3.39	3.54	3.49	4.05	3.75	3.28
	Variance	0.26	0.40	0.36	0.36	0.60	0.99	0.45	0.33	0.42	0.54	0.65	1.09	0.54
	Below 14.5 °C	0.76	0.78	0.98	1.00	1.00	0.97	0.99	0.97	0.97	0.69	0.69	0.53	0.86

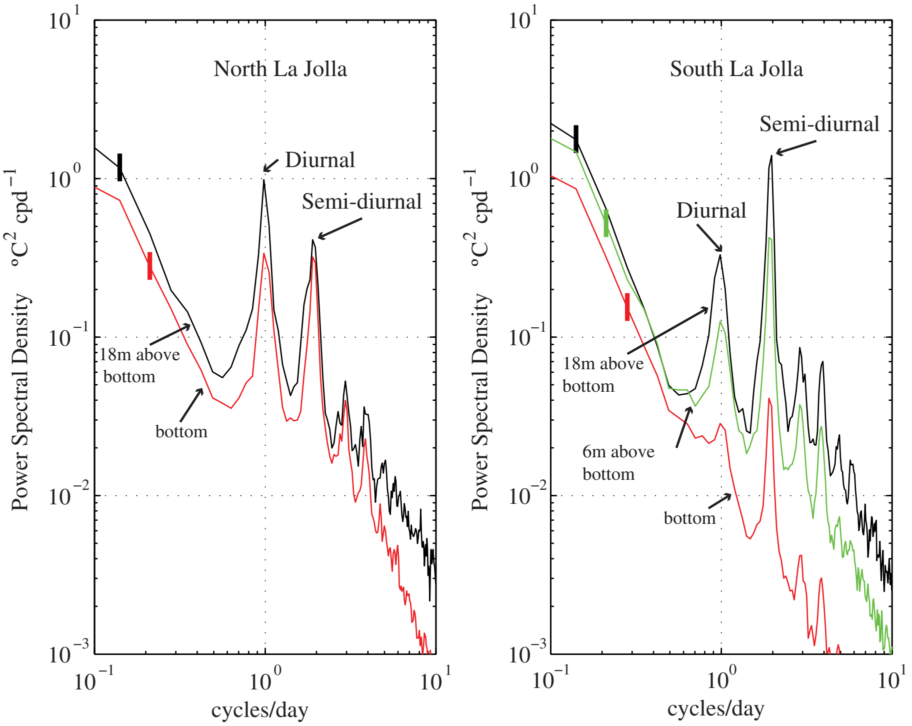

Fig. 4. A periodogram estimating the power spectral density calculated using Welch's averaged periodogram method with a section length of two weeks, zero overlap, and a Hamming window. Vertical bars represent the 95% confidence interval for a given depth.

average of 0.12–0.18 gN/m^{2}day; corresponding to upper daily limit between 0.8 and 1.2 gC/m^{2}day.

On monthly, daily and even over several hours, the depth of the 14.5 °C isotherm (Fig. 8A & B) and thus available predicted nutrients (Fig. 8C & D) can vary by as much as 10 m (Fig. 8).

4. Discussion

Environmental forcing is variable across a variety of temporal and spatial scales; likewise, the response of giant kelp is likely to vary across these scales. Both study sites show similar seasonal patterns in terms of temperature and nutrients (Figs. 2, and 4–6), and in the biological measurements of stipes per plant (Fig. 7). Local scale diversity patterns (i.e. within a kelp bed) can be the result of processes at larger spatiotemporal scales (Witman et al., 2004). Farther north near Pt. Conception, California, diurnal-period internal waves have along-shelf coherence of $>$50 km (Cudaback and McPhee-Shaw, 2009). Presumably, the same larger scale forcing (i.e. greater than the size of this kelp bed) could be acting on the La Jolla kelp bed. Shifts in stratification at the scale of the Southern California Bight are expected with climate change and

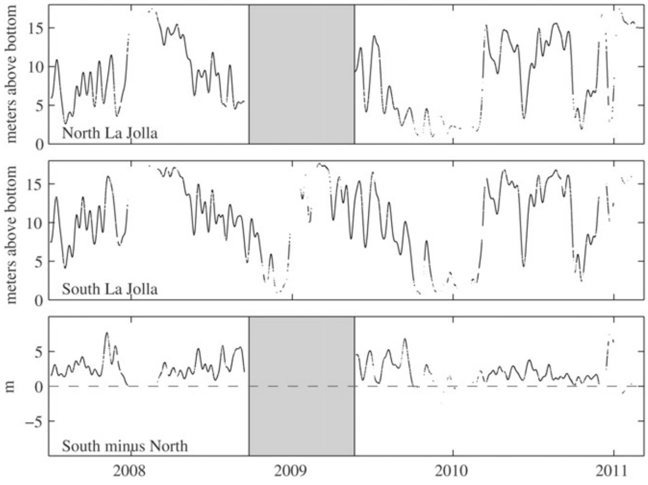

Fig. 5. Depth in meters above bottom of the 14.5 °C isotherm through time shown for North La Jolla in the top panel and South La Jolla in the middle panel (1-week running mean filtered data). At depths below this isotherm predicted levels of nitrate are $>$0 μmol/L. The third panel shows the difference in meters of the depth of the 14.5 °C isotherm between the two sites through time. Positive values indicate a shallower isotherm in the south (more of the water column bathed in nitrate) as compared to North La Jolla. Grey box indicates missing data.

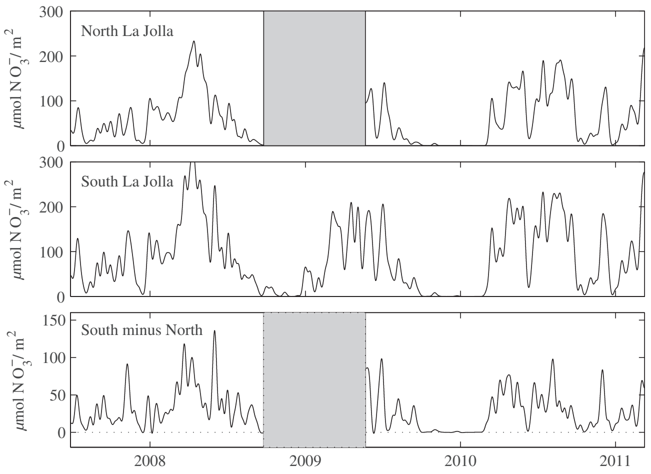

Fig. 6. Predicted water column integrated nitrate through time for a m^2 of substrate (1-week running mean filtered data) calculated using the equation: nitrate (μmol/L) $= -5.8$ temperature (°C)+81.7 (fit $<$ 14.5 °C) which is based on CalCOFI line 93.3, station 28 temperature-nitrate measurements collected from 1959 to 2010. Grey box indicates missing data.

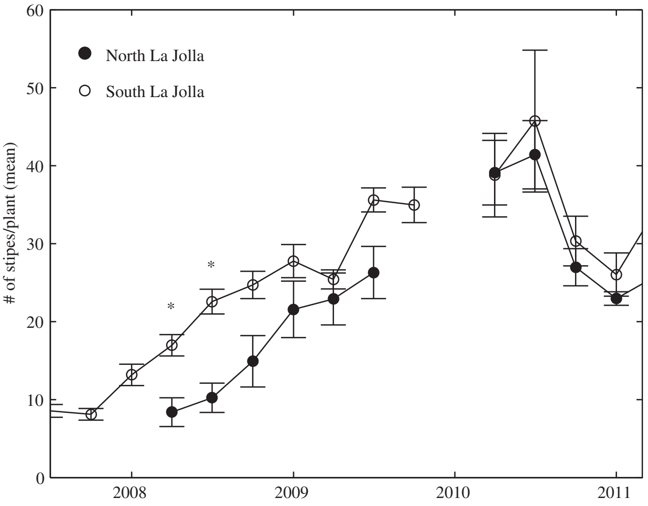

Fig. 7. Quarterly averaged stipes per plant at North La Jolla (solid symbols) and South La Jolla (open symbols) through time. Error bars indicate standard error and asterisks indicate significant differences at $\alpha \leq 0.05$ according to Wilcoxon rank sum test.

would likely affect the physical forcing of giant kelp. Alongshore winds can also affect nearshore cross-shelf circulation at kilometer scale distances (Pringle and Riser, 2003).

Smaller scale differences (i.e. within a kelp bed; Figs. 3C and 4–6) in temperature and nutrient exposure could potentially be explained by the complex undersea topography and nearby headland which may be setting up complex secondary circulation flows in the nearshore (Wolanski and Hamner, 1988). Both physical differences (i.e. shelf nearby canyon topography, currents) and biological structure (i.e. biogenic alteration of flow) may alter the physical environment kelps experience. Nutrient concentrations vary in the alongshore direction (Jackson, 1977). The physical structure of the kelp bed itself attenuates horizontal transport and vertical mixing (Jackson and Winant, 1983; Jackson, 1998; Rosman et al., 2010) which can have effects on nutrient availability. The magnitude of this effect scales to the size of the bed (Gaylord et al., 2007). Even with a similar nitrate climate, growth, morphology and tissue composition of giant kelp can vary within a kelp forest (Stewart et al., 2008). Thus, within-bed nutrient gradients can influence morphology indicating that the nitrate climate can affect change in regulatory mechanisms and metabolism of kelp. Significant differences between sites in stipes per plant were seen in two quarters during 2008 (Fig. 7). These biological differences corresponded to the highest integrated nitrate peaks of the study's time series (Fig. 6).

The nutrient and temperature history can be quite distinct at different depths: the bottom is characterized by cold temperatures with warm water deviations, the mid-water depths (i.e. the thermocline) has variation in both directions; and the surface warm water is punctuated by cold spikes (Fig. 2). This variable temperature and nutrient environment has different biological relevance depending on depth. The majority of photosynthesis occurs in the surface canopy with half of the standing crop lying between the surface and 1.5 m as fronds reach and spread along the surface (McFarland and Prescott, 1959; Towle and Pearse, 1973; Gerard, 1986). Nitrate and colder temperatures are important for recruitment and juvenile *Macrocystis pyrifera* growth, processes that occur near the benthos (Dean and Jacobsen, 1984). Nutrient uptake and photosynthetic capacity of blades will vary depending on ambient conditions at a given depth. For example, nitrate uptake is higher in the dark, a factor correlated with depth in the kelp forest (Wheeler and Srivastava, 1984).

It is also important to consider the total integrated kelp biomass at different depths as this may potentially affect the total amount of available surface for nitrate uptake in a kelp individual. A large fraction of the kelp's surface area floats at or near the surface; up to 60% of the total weight of plant can be found between the surface

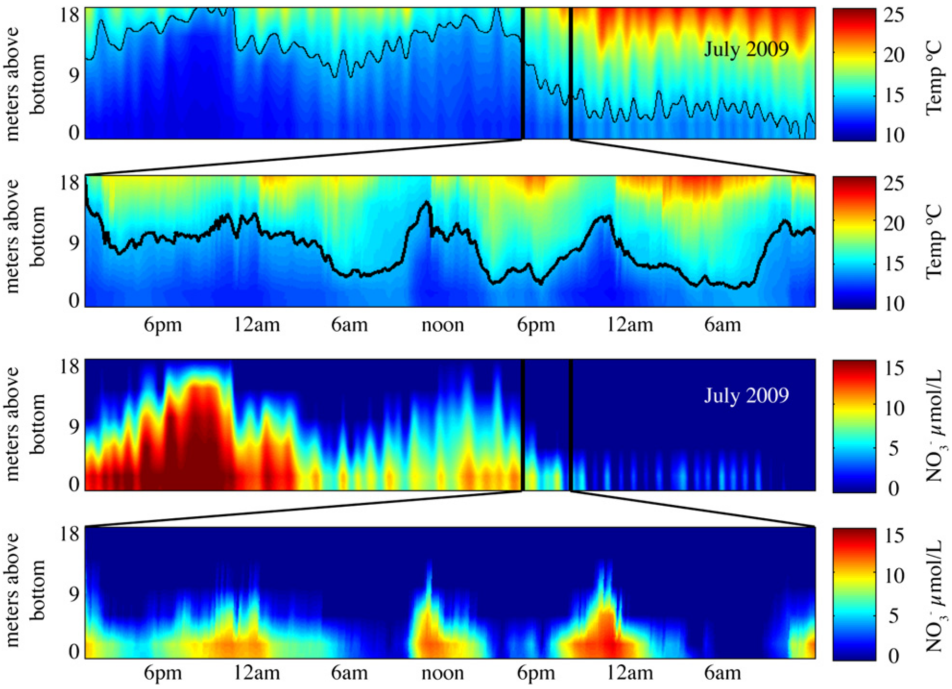

Fig. 8. Linearly interpolated temperature plot using 6 h running mean filtered temperature data for the month of July 2009 (top panel) and an expanded view of July 19–21st (second panel), as an example demonstrating that the depth of the 14.5 °C isotherm can vary by several meters over the span of a few hours. Black lines represent the 14.5 °C isotherm. The bottom two panels are interpolated predicted nitrate (calculated as in Fig. 7) for the same time periods as the top two panels.

and a depth of 4 ft, though the proportion of tissues is highly variable amongst plants (North and Hubbs, 1968). Measurements of ten 60 ft fronds from La Jolla showed weights concentrated near the upper end; 75% of the cumulative weight was in the upper half of fronds (North, 1971). A recent study also showed higher ratios of frond wet mass (kg) to frond length (m) for canopy fronds vs. subsurface fronds (Reed et al., 2009). Differences in nitrate concentrations in the upper portions may have a proportionally larger effect on kelp physiology due to higher biomass and surface area at these shallower depths.

Warm water and accompanying low surface nutrient conditions found during the late summer and more pronounced during El Niño years, may increase with climate change. Hydrographic time series of the upper 500 m of the coast of southern California and daily temperature records at Scripps Institution of Oceanography's pier have documented the rise in sea surface temperature over the last several decades (Roemmich, 1992). Climate and wind patterns are likely to change due to changes in land–sea interactions leading to changes in upwelling (Bakun, 1990; Diffenbaugh et al., 2004; King et al., 2011). As spring (70%) and winter (10%) upwelling provide 80% of total nutrient input in the Southern California Bight (McPhee-Shaw et al., 2007), this could have significant impacts on *Macrocystis* nutrition and health (Doney et al., 2012).

Biological impacts resulting from climate change driven environmental changes, such as altered upwelling strength, will likely vary depending on the geographic location of the kelp bed. Geographically isolated populations have exhibited environmentally consistent physiological specialization to ambient nutrient availability including growth rates, tissue nitrogen content and amino acid concentrations (Espinoza and Chapman, 1983; Kopczak et al., 1991). Kopczak et al. (1991) measured the responses of *Macrocystis* to nitrate availability from populations in Monterey Bay (high nutrients, affected by storms), Santa Barbara (a transition zone), and Santa Catalina (low wave stress, low nutrients). While maximum growth rates were similar among sites, those rates occurred at different nitrate concentrations; maximum rates occurred at lower nitrate concentrations for the algae that were acclimated to more oligotrophic conditions. The sites also differed in the amount of tissue nitrogen content, with more tissue nitrogen in algae from more oligotrophic conditions. Thus, isolated populations have evolved different responses to nitrate availability. This is in concordance with earlier work finding growth on restricted nitrogen supply leads to an increased ability to take up NO_3^- from low concentrations (Haines and Wheeler, 1978). Nutrients may be especially important for recruitment and survival at the equatorward range limits of the species where low nutrient conditions are more prevalent (Hernández-Carmona et al., 2001).

While the physical environment structures kelp communities on a variety of scales, that is not the only factor affecting their persistence. Biological processes including consumption by urchins or competition with other species may also play structuring roles (Dayton et al., 1984, 1999; Dayton, 1985) and these factors may have elements controlled by the physical environment. Stronger currents in the northern part of the La Jolla bed, or internal tidal bores, could bring in an increased flux of urchin larvae (Pineda, 1991, 1999; Parnell et al., 2006). Alternatively, the stronger persistence of the kelp forest in South La Jolla and its potential to decrease water flow (Rosman et al., 2010), could serve to retain kelp spores within that area, acting as a positive feedback. Epibionts may actually serve a beneficial role, providing an alternate nitrogen source via ammonium to kelp (Hepburn and Hurd, 2005). Also, with higher environmental nitrate levels, *Macrocystis pyrifera* canopy cover would be expected to increase, resulting in less light reaching the benthos, making it difficult for other algae to compete.

Daily changes in the thermocline depth are largely a function of tidal and internal wave activity. From power spectra we see the importance of diurnal and semi-diurnal tidal energy altering the depth of the thermocline and nitracline in this time series (Fig. 4). The structure of the kelp bed can change current flow, though the semi-diurnal frequency has the least damping (Jackson and Winant, 1983). The 14.5 °C isotherm can vary by several meters over the span of minutes to hours (Figs. 5 and 8), and *Macrocystis pyrifera* is able to take up nutrients on these time scales (Haines and Wheeler, 1978; Haxen and Lewis, 1981). The arrival of cold-water, high nutrient internal waves, which can change the nutrient levels of the water surrounding kelp on the order of minutes to hours, is an especially important nutrient input mechanism during summer stratified months (McPhee-Shaw et al., 2007). It is largely unknown exactly how kelps are reacting physiologically to these short time scale events and utilizing reserves under limiting conditions. However, a recent study observed increased nitrogen levels in algal tissues in response to a higher ambient internal wave driven nitrate environment in the intertidal green alga *Ulva lactuca* (Pérez-Mayorga et al., 2011). Genomic-enabled approaches are increasingly being applied in marine ecology, especially as a way to assess physiological response to environmental conditions (Dupont et al., 2007; Hofmann and Place, 2007). The water column spanning *M. pyrifera* is a unique system with which to explore physiological response to measured physical environmental gradients using these approaches.

The methods and analysis presented here are a simple, yet illuminating way to monitor nutrient influences in kelp forests. Time series of expanded duration would allow for characterization of longer time scale events such as ENSO. Expanding this approach by coupling telemetered thermistor chain with productivity studies and satellite imagery (e.g., Cavanaugh et al., 2010) in several kelp beds along the coast could potentially provide resource managers with predictive capabilities of changes in productivity or even collapse. Future studies should include flow measurements to resolve flux measurements. The development and integration of tools to study *Macrocystis pyrifera* physiological response on short time scales would also be a valuable addition. It is important to know the time and space scales of hydrographic variation in order to understand, measure and study the time and space scales of kelp biological response (Denny et al., 2004).

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