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Nutritional quality of giant kelp declines due to warming ocean temperatures

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Giant kelp *Macrocystis pyrifera* forms extensive forests on temperate reefs, providing habitat and food for a diversity of marine life. Kelp biomass varies in response to changing ocean temperatures, but physiological responses as reflected in the nutritional quality of kelp tissue are poorly understood. Over a 19-year period in southern California, we found that nutritional quality of giant kelp tissue declined; nitrogen content of giant kelp tissue declined by 18%, while carbon content proportionally increased. This decline in nutritional quality was associated with increasing seawater temperatures and with regional and local scale processes including upwelling as indicated by the biologically effective upwelling transport index, the El Niño-Southern oscillation and the North Pacific Gyre oscillation. Changes in kelp stoichiometry with seawater temperature have important implications for nutrition and behavior of key consumers, such as sea urchins. Our results suggest that the consequences of projected declines in kelp abundance due to climate change may be compounded by reductions in its nutritional quality.

Keywords: C:N, giant kelp, herbivores, nitrogen, nutritional quality, warming

Introduction

Global temperatures have risen considerably in recent decades, and while greater warming has occurred over land, nearly all sea surface temperatures are warmer today compared to a century ago (Hansen et al. 2006). Upper ocean waters (0–700 m) have warmed significantly since 1970, especially in the Pacific Ocean, based on ocean heat content observations (Abraham et al. 2013). With continued ocean warming, projections indicate declines in marine biomass at all trophic levels and reduced primary production (Lotze et al. 2019). Temperate coastal ecosystems and their associated flora and fauna are highly sensitive to episodic warming events and ocean climate cycles (Cavanaugh et al. 2011, 2019). These regional and ocean basin scale processes have produced dramatic change in regions such as Tasmania, New Zealand, Europe and northern California with declines in abundance and biomass of various kelp species, including *Macrocystis pyrifera*, *Nereocystis luetkeana*, *Durvillaea* spp. and *Laminaria digitata* (Johnson et al. 2011, Raybaud et al. 2013, Rogers-Bennett and Catton 2019, Thomsen et al. 2019). Such episodic warming events may be harbingers of the



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projected effects of long-term climate change on kelps over more readily observed timescales (Di Lorenzo and Mantua 2016, Smale et al. 2019).

Kelp forests are highly productive ecosystems in temperate coastal seas (Steneck et al. 2002) where kelps are considered a foundation species that structure the surrounding community (Falkenberg et al. 2012, Miller et al. 2018), providing numerous ecosystem functions including habitat structure, food resources, nutrient cycling and subsidies to other habitats, and support high biodiversity (Dayton 1985, Steneck et al. 2002). Grazers, such as sea urchins, abalone, crustaceans and gastropods, feed directly on kelp while other organisms rely on kelp-derived carbon via indirect pathways (Koenigs et al. 2015, Yorke et al. 2019). More than 80% of kelp forest net primary production is exported as detritus to adjacent marine ecosystems (Cebrian 1999, Krumhansl and Scheibling 2012) where it becomes a valuable habitat and food resource (Vetter and Dayton 1999, Dugan et al. 2003). The availability of kelp as a resource, both within the kelp forest and as a subsidy to adjacent ecosystems, may be threatened as the growing effects of global climate change on primary productivity and ocean circulation are realized (Harley et al. 2006).

Marine macroalgae form the base of many aquatic food webs; thus the effects of climate change on the abundance and nutritional quality of macroalgae are likely to have multi-trophic implications (Harley et al. 2012). Existing evaluations of changes in macroalgal nutritional quality in the context of abiotic factors, like temperature, are poorly constrained and often derived from controlled experiments rather than in situ field conditions. Findings from studies of macroalgae grown in warmer seawater have ranged widely, from no effect (Simonson et al. 2015) to mixed effects (Phelps et al. 2017), including increased nitrogen content (Wilson et al. 2015). The nutritional content of macroalgae affects feeding preferences (Van Alstyne et al. 2009), consumption rates (Boyer et al. 2004) and the physiological performance of algal consumers (Hemmi and Jormalainen 2002).

Long-term ecological data series provide a means of exploring questions regarding the in situ effects of prolonged and episodic ecosystem change (Hughes et al. 2017, Kominoski et al. 2018, Gaiser et al. 2020), particularly warming events in marine ecosystems (Frölicher et al. 2018). These concerns are of particular interest for kelp forests dominated by large canopy-forming kelps, such as giant kelp *Macrocystis pyrifera*, found along the majority of the west coast of North America. Using data collected as part of the Santa Barbara Coastal Long Term Ecological Research program, we evaluated the nutritional quality (C:N) of giant kelp on nearshore rocky reefs in the Santa Barbara Channel over a 19-year period (Reed and Miller 2021), and its relationship with local sea surface temperature and Pacific basin-scale ocean climate cycles. Prior analyses showed gradually declining kelp biomass on local reefs over this time period, in addition to pronounced effects on some components of kelp forest communities due to an anomalous Pacific warming event, also known as 'the Blob' (Reed et al. 2016). Kelp canopy cover in the region is temporally and spatially variable, and

responses of kelp to environmental conditions or perturbations may vary significantly on local scales compared with regional scales (Bell et al. 2015). We hypothesized that the nutritional quality of giant kelp tissue declined over the same period that local kelp biomass declined, a change that may have compounding effects on kelp forest ecosystems and consumers as well as the ecosystems subsidized by exported kelp production.

Methods

Sample collection and processing

The Santa Barbara Coastal Long-Term Ecological Research (SBC LTER) program is located in the Santa Barbara Channel, California, USA (34°24'30.0"N, 119°50'65.0"W). The SBC LTER maintains long-term datasets on giant kelp *Macrocystis pyrifera* production along with associated macroalgal and faunal communities. Carbon (C) and nitrogen (N) content of giant kelp blades were measured monthly at each of three long-term kelp forest monitoring sites (Arroyo Burro, Mohawk and Arroyo Quemado) (Supporting information). In this study we used % C, % N and C:N values for giant kelp measured monthly from May 2002 through January 2021 (Reed and Miller 2021). From February 2011 to May 2012, the Arroyo Quemado site did not have a surface canopy of giant kelp, so there is no data available from this site during that time period. Sampling also did not take place at any sites during April, May and June 2020 due to COVID-19. At each site, a surface kelp blade was collected one to two meters back from the growing tip of 15 different individual plants. The blades were scraped to remove any epiphytes and a core (2.9 cm diameter) was taken from each blade near the pneumatocyst. The cores were dipped in 10% HCl and rinsed with DI water to remove any residual calcium carbonate (Hepburn et al. 2007). The 15 cores were combined to create a composite sample, dried at 60°C for a minimum of 48 h, and then ground into a homogenous sample. The homogenized samples from each site were analyzed in duplicate for C and N content using an elemental analyzer (precision \pm 0.3%).

Data analyses

We examined the monthly trends in kelp nutritional content (% C, % N and C:N), the relationship between C:N values and seawater temperature, which is greatly influenced by oceanographic season, and the relationship of C:N values with oceanographic indices describing decadal-scale climate cycles that can modulate seasonal conditions and ocean climate. Local ocean temperature was used in analyses as prior research has shown it is strongly correlated to local nutrient availability (Brzezinski et al. 2013) and kelp growth (Cavanaugh et al. 2011, 2019). Local (daily, 1 km gridded) satellite-derived sea surface temperatures (SST) were averaged by month and compared to C:N values with no temporal lag

(National Climatic Data Center 2007, JPL MUR MEaSUREs Project 2015). Several oceanographic indices were also considered as potential drivers of kelp C:N ratios, including the Pacific Decadal oscillation (PDO), the Madden Julian oscillation (MJO), the El Niño-Southern oscillation (ENSO), the coastal upwelling transport index (CUTI), the Bakun upwelling index, the North Pacific Gyre oscillation (NPGO) (Di Lorenzo et al. 2008) and the biologically effective upwelling transport index (BEUTI) (Jacox et al. 2018). Data formatting, visualization and analyses were performed using the tidyverse, EnvStats, nlme and MuMIn packages in RStudio (ver. 1.4.1106) (Millard 2013, Wickham et al. 2019, Bartoń 2020, Pinheiro et al. 2021, <www.r-project.org>).

Prior to conducting any analyses, replicate samples, from the original composite sample, were averaged for C:N, % C and % N values. Furthermore, C:N values were log-transformed prior to constructing any of the models below, as is recommended for ecological stoichiometric ratios (Isles et al. 2020).

To identify temporal trends, we performed a series of Kendall tests. Mann–Kendall tests may be used to determine if the dependent values (e.g. C:N) are broadly increasing or decreasing as the dataset progresses in time; in other words, this non-parametric test identifies the presence of monotonic trends. Seasonal Kendall tests may also be used to identify monotonic increasing or decreasing trends, but data are grouped according to defined intervals to account for seasonality, and comparisons are not made across the boundaries of these intervals (Helsel 2020). First, Seasonal Kendall tests were performed for C:N, % C and % N values to identify a monotonic trend while accounting for the known seasonal (i.e. monthly) variability in giant kelp nutritional content; the results of these tests are presented in Table 1. Then, the dataset was grouped by month (across all years), and Mann–Kendall tests were performed for each month, effectively removing the seasonal patterns and instead examining only data from a certain month for a monotonic trend through time; the results of these tests are presented in Table 2. These analyses used the *kendallSeasonalTrendTest* and *kendallTrendTest* functions, respectively, from the EnvStats package in R (Millard 2013). Each Seasonal Kendall test also included a test for heterogeneity (χ^2) which, when found to be significant ($p < 0.05$), indicates there is a significant seasonal (i.e. monthly) trend in an opposing direction from the overall trend. Furthermore, to calculate overall trends in nutritional content, we calculated the mean values for the first year of data collection, used the slopes of the Seasonal Kendall test for each parameter to estimate change over 19 years, and calculated the percent difference for the resulting values.

To identify relationships between nutritional content and various physical parameters (e.g. temperature), we constructed a series of linear mixed effects models. This approach allowed us to address the lack of independence between samples due to the repeated sampling design (Zuur et al. 2009). At time of analysis, NPGO values were only available through July 2020, so six months less of the kelp nutrition dataset were used for that index's model. Model creation began with fixed effects and random effects using a random intercept structure. Model selection followed the protocol outlined by Zuur et al. (2009, Chapter 5), beginning with a linear model, accounting for variance structure, optimizing the fixed structure and validating the best model fit using distribution of residuals and Akaike information criterion values. The *lme* function within the nlme package was used to create and validate each model (Pinheiro et al. 2021), and the *r.squaredGLMM* function within the MuMIn package was used to calculate conditional R^2 values for each model (Bartoń 2020). The final linear mixed effects model structure for each of the indices included the appropriate index and sampling date (month and year of kelp C:N sample and corresponding index value) as interacting fixed effects and sampling site as a random effect to account for the three sites sampled each month.

Global kelp C:N review

In addition to our examination of nutritional content of Santa Barbara Channel giant kelp, global literature on kelp nutritional content (C:N) from in situ as well as laboratory studies was reviewed. We included nine widely distributed genera of kelps, covering all major ocean basins. Only C:N values measured from in situ samples or un-manipulated (i.e. control) experimental treatments were included. We present the range of mean C:N values reported for each kelp species and indicate any studies that provided time series data for a period greater than one year, although not necessarily on a monthly basis.

Results

Mean values of carbon to nitrogen (C:N) ratios of giant kelp blades varied from 6.70 to 47.84 in samples collected from 2002 through 2021 (Fig. 1A). C:N values displayed an annual pattern, with greater values during the warmer stratified season, from approximately August through November, and smaller values during the cooler upwelling season, from March through June (Fig. 2). The results of the Seasonal Kendall test indicated a significant, positive monotonic trend

Table 1. Results of Seasonal Kendall tests performed for log(C:N), % C and % N values across the entire dataset (2002–2021) and at all three locations sampled (15 blades per month). Significant trends ($p < 0.05$) are denoted in bold.

Parameter	Tau	Slope	Intercept	df	χ^2	$p(\chi^2)$	z	$p(z)$
log(C:N)	0.26	0.0097	−17.47	11	9.72	0.56	9.47	< 0.0001
% C	0.25	0.27	−574.10	11	10.21	0.51	9.02	< 0.0001
% N	−0.14	−0.024	44.14	11	20.65	0.037	−5.24	< 0.0001

Table 2. Results of Mann–Kendall tests performed for each season (i.e. month) for log(C:N), % C and % N values. Significant effects ($p < 0.05$) are denoted in bold.

	log(C:N)						% C						% N														
	Slope		z		p		Tau		Slope		Int.		z		p		Tau		Slope		Int.		z		p		
	Tau	Slope	Int.	z	p	Tau	Slope	Int.	z	p	Tau	Slope	Int.	z	p	Tau	Slope	Int.	z	p	Tau	Slope	Int.	z	p		
January	0.32	0.011	-21.69	3.36	0.0008	0.23	0.26	-495.26	2.41	0.016	-0.21	-0.034	70.71	-2.15	0.032												
February	0.26	0.010	-19.44	2.77	0.0055	0.38	0.45	-879.54	4.01	0.0001	-0.076	-0.017	35.53	-0.80	0.42												
March	0.23	0.0080	-14.92	2.41	0.016	0.29	0.34	-651.17	3.02	0.0025	-0.052	-0.011	24.71	-0.55	0.59												
April	0.18	0.0044	7.85	1.76	0.078	0.28	0.48	-932.92	2.78	0.0055	0.044	0.012	-21.58	0.44	0.66												
May	0.23	0.0069	-12.77	2.43	0.015	0.32	0.42	-818.99	3.30	0.0010	-0.022	-0.0032	9.43	-0.22	0.83												
June	0.25	0.010	-19.35	2.62	0.0088	0.29	0.39	-754.56	3.05	0.0023	-0.12	-0.025	52.76	-1.20	0.23												
July	0.31	0.014	-27.18	3.37	0.0008	0.21	0.20	-360.94	2.32	0.021	-0.30	-0.047	95.63	-3.31	0.0009												
August	0.43	0.018	-35.75	4.72	< 0.0001	0.23	0.26	-497.04	2.53	0.011	-0.37	-0.054	109.67	-3.98	0.0001												
September	0.21	0.0084	-15.60	2.32	0.02	0.14	0.10	11.83	0.14	0.89	-0.18	-0.026	54.35	-1.98	0.048												
October	0.091	0.0038	-6.26	0.96	0.34	0.19	0.24	-444.52	2.01	0.044	-0.025	-0.0034	8.34	-0.25	0.80												
November	0.31	0.014	-26.44	3.35	0.0008	0.22	0.20	-380.06	2.44	0.015	-0.25	-0.039	79.93	-2.70	0.0070												
December	0.22	0.0079	-14.64	2.37	0.018	0.32	0.38	-741.09	3.48	0.0005	-0.061	-0.0082	18.43	-0.66	0.51												

in log(C:N) values through time ($p < 0.0001$), and there were no significant opposing seasonal trends, as indicated by the test for heterogeneity ($p=0.56$) (Table 1). Our results suggest the overall mean annual C:N values of giant kelp increased by approximately 44% (12.71 to 18.28, Fig. 1A) over the past 19 years which translates to an increase of 0.29 units per year in C:N content of kelp blade tissue. Kendall tests were performed for each month, and all months displayed a significant positive trend, except April ($p=0.08$) and October ($p=0.34$) (Table 2). C:N values frequently exceeded 20, especially during the ‘Blob’ warming event (2013–2015) (Di Lorenzo and Mantua 2016) and again between August 2017 and November 2020.

Mean values of carbon and nitrogen content of giant kelp blades ranged from 21.03% to 44.52% and 0.57% to 4.34%, respectively, in samples collected from 2002 through 2021 (Fig. 1C–D). The results of the Seasonal Kendall test performed for carbon content indicated a significant positive monotonic trend in % C through time ($p < 0.0001$), and the test for heterogeneity indicated that there were no significant opposing seasonal trends ($p=0.51$) (Table 1). The results of the monthly Mann–Kendall tests indicate all months displayed a significant, positive trend, except September ($p=0.89$) (Table 2). The Seasonal Kendall test performed for nitrogen content indicated a significant negative monotonic trend in %N through time ($p < 0.0001$), and the test for heterogeneity indicated that there was a significant opposing seasonal trend ($p=0.04$) (Table 1). The results of monthly Mann–Kendall tests indicate that there was instead a positive, monotonic trend in nitrogen content during the month of April, although this trend was not found to be significant ($p=0.66$) (Table 2). The remaining Mann–Kendall tests performed by season (i.e. month) found a significant, negative trend in January ($p=0.03$), July ($p=0.001$), August ($p < 0.0001$), September ($p=0.048$) and November ($p=0.007$). Since the opposing seasonal trend in April was not deemed significant, we felt confident in assigning a negative value to the overall trend for nitrogen content through time, as indicated by the overall Seasonal Kendall test.

Monthly values of the carbon content of kelp blades routinely exceeded 35%, particularly since 2010 (Fig. 1C). Monthly values of kelp tissue nitrogen content have regularly fallen below 1.5% since the onset of the ‘Blob’ warming event in 2013 (Fig. 1D). From September 2013 to August 2015 and again from August 2019 to March 2020, the nitrogen content of multiple kelp samples fell below 1.1%, which is considered the threshold at which kelp has exhausted its internal nitrogen reserves (Gerard 1982). Our results suggest the overall carbon content of giant kelp increased by approximately 18% (28.39 to 33.52%) over the past 19 years while overall nitrogen content also decreased by approximately 18% (2.48 to 2.02%).

Based on the strong temporal trends in C and N content for local populations of giant kelp, we investigated relationships between C:N ratios and abiotic environmental factors using a series of linear mixed effects models. As noted above, all models were created using log-transformed C:N values

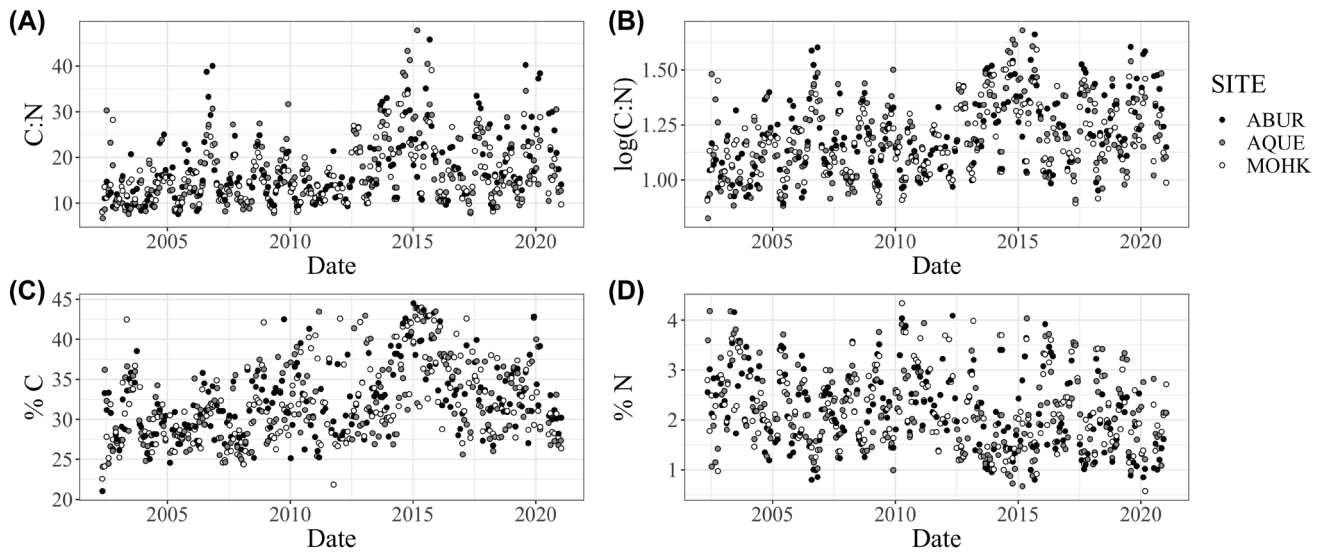


Figure 1. Monthly values of (A) C:N, (B) log(C:N), (C) % carbon and (D) % nitrogen content of giant kelp *Macrocystis pyrifera* blades collected from three sites (Arroyo Burro, Arroyo Quemado, Mohawk) from May 2002 to January 2021. Each point represents the mean of replicates collected at a single site.

(Fig. 1B). The first abiotic predictor investigated was satellite-derived sea surface temperature, and the final model structure included temperature and sampling date as interacting fixed effects and sampling site as a random effect. The model results revealed a significant positive correlation between temperature and log(C:N) values (linear mixed effects model (LMEM), $p < 0.0001$) (Table 3, Fig. 3A).

In addition to local seawater temperature, we investigated seven oceanographic indices as predictors of log(C:N) values of giant kelp. Log(C:N) values were significantly negatively

correlated with four regional ocean climate indicators – the Bakun index, BEUTI, CUTI and the NPGO index (LMEM, $p < 0.0001$ for all) (Table 3, Fig. 3B–D, G). In addition, log(C:N) values were significantly positively correlated with ENSO (LMEM, $p < 0.0001$) (Table 3, Fig. 3E). The MJO and PDO indices were not significant predictors of log(C:N) values (LMEM, $p > 0.05$ for both) (Table 3, Fig. 3F, H). For the remainder of the manuscript, we chose to focus on the BEUTI, ENSO index and NPGO index as predictors of kelp nutritional content since these indices were the strongest

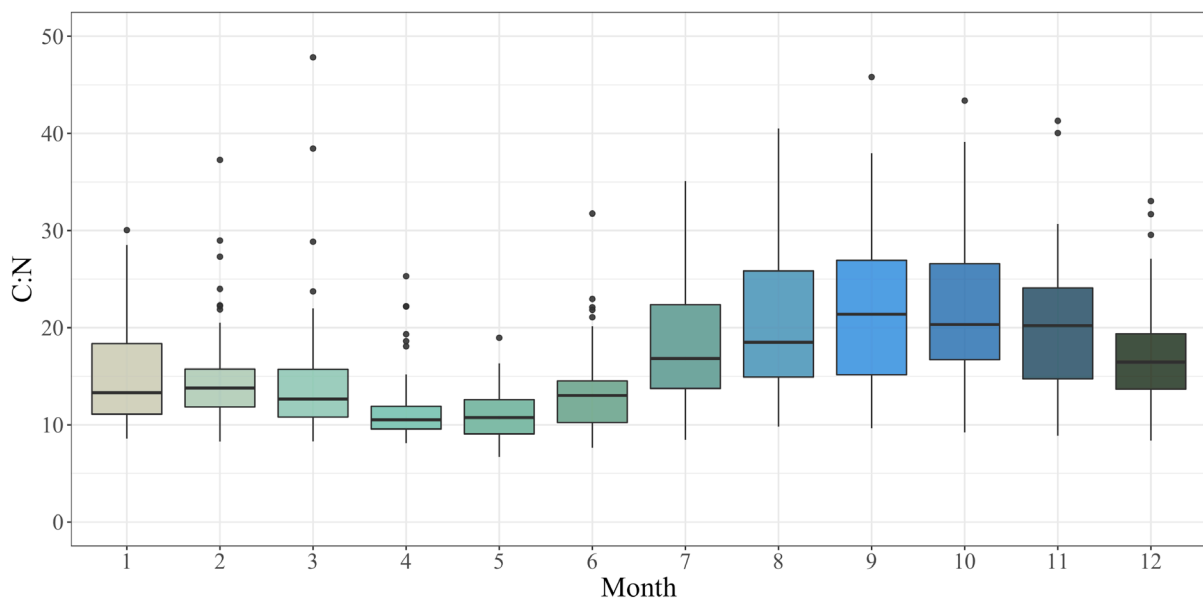


Figure 2. Boxplots of giant kelp *Macrocystis pyrifera* tissue C:N values measured from May 2002 through January 2021 and aggregated (and colored) by month of the year. Thick black lines denote the 50th percentile values, and box boundaries denote the 25th to 75th percentile ranges. Upper whiskers extend no further than 1.5 times the interquartile range (IQR), and lower whiskers extend to the smallest value, no further than 1.5 times the IQR. Remaining outliers are plotted individually.

Table 3. Results of linear mixed effects models constructed using temperature and various oceanographic indices as predictors of log(C:N) values. Each of the below models reports the results for a physical parameter, sampling date (i.e. month sampled) and their interaction effect. Each model also incorporates sampling site as a random effect. Significant fixed effects ($p < 0.05$) are denoted in bold.

Dependent variable	Fixed effect	Value	SE	df	F	p	Entire model R ²
log(C:N)	Temperature	0.048	0.005	1,635	432.96	< 0.0001	0.4378
	Sampling date	0.001	0.0006	1,635	52.39	< 0.0001	
	Temperature × Sampling date	-3.0e-5	3.8e-5	1,635	0.73	0.3938	
log(C:N)	Bakun	-0.0003	1.2e-4	1,635	28.44	< 0.0001	0.1610
	Sampling date	0.0009	1.5e-4	1,635	93.61	< 0.0001	
	Bakun × Sampling date	4.0e-7	8.8e-7	1,635	0.19	0.6596	
log(C:N)	BEUTI	-0.019	0.004	1,635	218.84	< 0.0001	0.3367
	Sampling date	0.0010	0.0001	1,635	102.44	< 0.0001	
	BEUTI × Sampling date	-5.1e-5	3.0e-5	1,635	2.87	0.0908	
log(C:N)	CUTI	-0.13	0.040	1,635	44.84	< 0.0001	0.1798
	Sampling date	8.6e-4	0.0002	1,635	94.61	< 0.0001	
	CUTI × Sampling date	8.6e-5	0.0003	1,635	0.07	0.7882	
log(C:N)	ENSO	0.054	0.018	1,635	25.04	< 0.0001	0.1643
	Sampling date	9.3e-4	9.4e-5	1,635	98.67	< 0.0001	
	ENSO × Sampling date	-1.5e-4	1.3e-4	1,635	1.32	0.2511	
log(C:N)	MJO	0.031	0.023	1,635	1.55	0.2132	0.1354
	Sampling date	9.4e-4	9.6e-5	1,635	94.14	< 0.0001	
	MJO × Sampling date	-3.2e-4	1.6e-4	1,635	3.81	0.0515	
log(C:N)	NPGO	-0.036	0.014	1,617	52.24	< 0.0001	0.1445
	Sampling date	8.9e-4	1.2e-4	1,617	47.98	< 0.0001	
	NPGO × Sampling date	1.8e-4	8.3e-5	1,617	4.87	0.0276	
log(C:N)	PDO	-0.024	0.014	1,635	0.54	0.4634	0.1350
	Sampling date	9.8e-4	9.9e-5	1,635	94.58	< 0.0001	
	PDO × Sampling date	2.3e-4	1.2e-4	1,635	4.02	0.0455	

predictors of log(C:N) content after sea surface temperature (Table 3). Our findings suggest that local seawater temperature, as well as regional ocean climate, are significant predictors of C:N content in giant kelp tissue.

Discussion

Our results show that values of C:N in giant kelp blade tissue were significantly positively correlated with seawater temperature. This finding, combined with the predicted increase in the frequency of ocean warming events (Hoegh-Guldberg et al. 2018), suggest a future where key marine primary producers, such as kelp, may not only be lower in abundance but also have significantly reduced nutritional value. Warming periods can cause large declines in kelp forest size, at least in some regions (Johnson et al. 2011, Raybaud et al. 2013), as well as reduce the resilience of kelp to disturbance events, such as wave action or grazing by consumers (Wernberg et al. 2010). Our results suggest that the nutritional content of giant kelp may also decline significantly with warming, which is perhaps in part due to giant kelp's inability to store nitrogen reserves for longer than approximately three weeks (Gerard 1982).

In addition to short-term warming events, our findings suggest that decadal trends in large scale ocean climate indices (NPGO, ENSO, BEUTI) may drive variability in the nutritional quality of kelp tissue. The NPGO index values can be used to explain variations in salinity, nutrients and chlorophyll-a in the California Current, with larger,

more positive values associated with greater circulation and upwelling (Di Lorenzo et al. 2008). Previous analyses found that NPGO values, as well as temperature (and nutrient content by proxy), to be significant predictors of giant kelp canopy biomass in North America (Bell et al. 2015). Since 1950, the variance of the NPGO index has increased from ± 2 to ± 3 standard units (Di Lorenzo et al. 2008). If the variance of the NPGO index continues to amplify, our results suggest that the C:N values of giant kelp tissue will oscillate in response, magnifying the effect of more frequent warming events on both kelp abundance and nutritional quality. Furthermore, since a regime shift that took place in 1977, southern California kelp forests have been subject to a climate of decreased nutrients, which has amplified nutrient stress on kelp growth following El Niño-Southern oscillation events (Parnell et al. 2010). The multivariate ENSO index indicates the strength of ENSO conditions in the tropical Pacific Ocean as the first principal component of sea level pressure, sea surface temperature, zonal and meridional surface wind components, near-surface air temperature and total cloudiness (Wolter and Timlin 2011). Our model results demonstrate a significant positive correlation between the ENSO index and kelp nutritional content, which suggests giant kelp respond to variations in nutrient availability as influenced by factors associated with ENSO dynamics in the tropical Pacific Ocean (Wolter and Timlin 2011). Our results also show a significant relationship between nutritional quality and BEUTI, an oceanographic index that predicts nitrate flux due to upwelling in the surface mixed

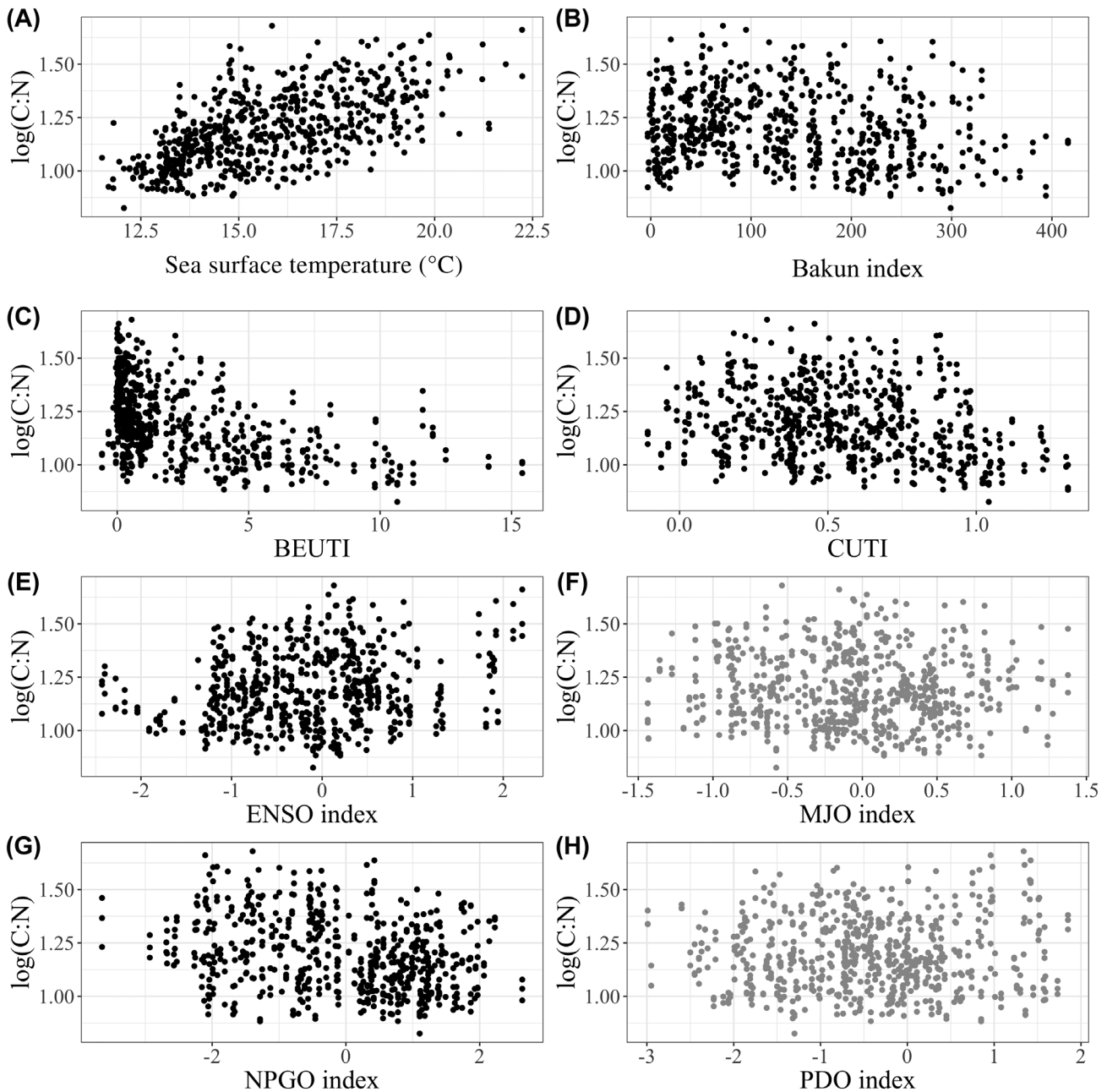


Figure 3. Monthly $\log(\text{C:N})$ values for giant kelp *Macrocystis pyrifera* blades plotted against (A) sea surface temperature from satellite-derived data, (B) Bakun index values, (C) biologically effective upwelling transport index (BEUTI) values, (D) coastal upwelling transport index (CUTI) values, (E) El Niño seasonal oscillation (ENSO) index values, (F) Madden Julian oscillation (MJO) index values, (G) North Pacific Gyre oscillation (NPGO) index values and (H) Pacific decadal oscillation (PDO) index values. Oceanographic indices that were found to be a significant predictor of $\log(\text{C:N})$ values (i.e. a significant fixed effect) are denoted in black. Each point represents the mean of replicates collected at a single site (Arroyo Burro, Arroyo Quemado, Mohawk) monthly from May 2002 to January 2021. Note, NPGO index data was only available through July 2020.

layer along the US west coast, with larger values associated with greater upwelling and higher nitrate concentrations (Jacox et al. 2018). Climate change may amplify the frequency and intensity of warming events on both shorter-term and decadal scales (Frölicher and Laufkötter 2018). Conversely, long-term warming may increase upwelling intensity in the California Current region due to stronger

alongshore winds and enhanced upper-ocean stratification (Xiu et al. 2018). The response of primary consumers and higher trophic levels to variation in C:N values of kelp will likely vary depending on the combined effect of these multiple processes, the timescales at which kelp nutritional quality changes and the life history and demography of different consumer species.

Time-series data collected from kelp forests around the world suggest ocean climate is correlated with significant fluctuations in kelp biomass (Bell et al. 2015, Wernberg et al. 2016, Pfister et al. 2018, Smale 2020). However, our understanding of the effects of ocean climate on kelp nutritional content has been limited by the fact that few studies include more than a single year of data, and published C:N values vary widely (6–60) among kelp species and studies (Table 4). Our time series data on giant kelp tissue, spanning nearly two decades, indicate that C:N values increased when kelp was exposed to warmer seawater temperatures and these values generally increased over our nearly two decade study period. In coastal waters off southern California, temperature and nitrogen availability are tightly coupled (Parnell et al. 2010) and driven largely by three dominant oceanographic seasons: December through March, when winter storms cause strong wave action and significant runoff from land to sea; March through May, when wind-driven coastal upwelling delivers cold, nutrient-rich deep waters to the photic zone; and June through November, when warm, strongly stratified conditions can lead to relatively low nutrient concentrations (McPhee-Shaw et al. 2007). As a result of this marked seasonality,

nitrogen content in kelp tissue displays a strong annual cycle, whereas carbon content does not (Brzezinski et al. 2013).

Through all oceanographic seasons, dissolved nutrient concentrations, specifically nitrate, are negatively correlated with seawater temperature in the northeastern Pacific, off the coast of southern California (Zimmerman and Kremer 1984). Despite the knowledge of the close relationship between temperature and nutrient availability in certain regions of the ocean, few studies have demonstrated a significant correlation between increasing seawater temperatures and decreasing nutritional content of kelp tissue. Experimental studies raising juvenile sporophytes of *Macrocystis pyrifera* from eastern Tasmania (Mabin et al. 2019) and southern California (Brown et al. 2014) as well as thalli of *Saccharina latissima* collected in the Arctic (Olischläger et al. 2014) at varied temperatures have found that kelp tissues cultivated at higher temperatures had lower nutritional content when seawater nutrients were held constant. A longitudinal study conducted in southwest Australia demonstrated that the nutritional content of the kelp *Ecklonia radiata* also declined with increasing water temperature (Staehr and Wernberg 2009). To our knowledge, our study is the first to demonstrate this

Table 4. Published values of tissue C:N for globally-distributed kelp species. Values represent means across varying numbers of replicate samples. See the Supporting information for full reference list. Studies where C:N was measured over a period greater than 1 year (12 months) are indicated with an asterisk (*).

Genus	Species	C:N	Sources
<i>Alaria</i>	<i>crassifolia</i>	8.9	Johnston 1971
A.	<i>esculenta</i>	23–30	Gordillo et al. 2006, 2015
A.	<i>marginata</i>	12.5–14.5	Pelletreau and Muller-Parker 2002, McDonald and Bingham 2010
<i>Durvillaea</i>	<i>antarctica</i>	30	Suárez-Jiménez et al. 2017
<i>Ecklonia</i>	<i>radiata</i>	17–52	Atkinson and Smith 1983, Miller 2004, Staehr and Wernberg 2009, Falkenberg et al. 2013, Britton et al. 2016, Gladstone-Gallagher et al. 2016, Wernberg et al. 2019
<i>E.</i>	<i>maxima</i>	15–17.8	Probyn and McQuaid 1985
<i>Laminaria</i>	<i>angustata</i>	23.3	Johnston 1971
L.	<i>dentiger</i>	21.7	Atkinson and Smith 1983
L.	<i>digitata</i>	19.4–28.6	Mann 1972, Schaal et al. 2010, Xia et al. 2016
L.	<i>groenlandica</i>	12.4–17	Harrison et al. 1986
L.	<i>hyperborea</i>	6–60	Sjøtun et al. 1996, Norderhaug et al. 2003, Leclerc et al. 2013
L.	<i>japonica</i>	10–50	Johnston 1971, Mizuta et al. 1997
L.	<i>longicuris</i>	13.8–16.7	Mann 1972
L.	<i>religiosa</i>	15.4	Johnston 1971
L.	<i>saccharina</i>	7.1–30	Subandar et al. 1993, Henley and Dunton 1995, Ahn et al. 1998, Gevaert et al. 2001*, Pelletreau and Muller-Parker 2002, Gordillo et al. 2006
L.	<i>solidungula</i>	10–26	Dunton and Schell 1986, Henley and Dunton 1995, Gordillo et al. 2006
<i>Lessonia</i>	<i>nigrescens</i>	16.6	Reddin et al. 2015
<i>Macrocystis</i>	<i>pyrifera</i>	7.5–47.2	(This paper), Jackson 1977, Wheeler and North 1981*, Atkinson and Smith 1983, Rosell and Srivastava 1985*, van Tussenbroek 1989, Hurd et al. 1994, 1996, 2000, Brown et al. 1997, 2014, Pennings et al. 2000, Hepburn et al. 2006, 2007, Davenport and Anderson 2007, Stephens and Hepburn 2014, 2016, Fernández et al. 2015, Hamersley et al. 2015, Dobkowski et al. 2017, Suárez-Jiménez et al. 2017
<i>Nereocystis</i>	<i>luetkeana</i>	9.8–24	Atkinson and Smith 1983, Rosell and Srivastava 1985*, Ahn et al. 1998, Pennings et al. 2000, Pelletreau and Muller-Parker 2002, Dethier et al. 2014, Dobkowski et al. 2017
<i>Saccharina</i>	<i>japonica</i>	7.1	Wang et al. 2013
S.	<i>latissima</i>	7–45	McDonald and Bingham 2010, Handå et al. 2013, Olischläger et al. 2014, Gordillo et al. 2015
<i>Undaria</i>	<i>pinnatifida</i>	8.4–23.6	Johnston 1971, Yoshikawa et al. 2001, Dean and Hurd 2007, Sfriso and Facca 2013, Suárez-Jiménez et al. 2017

relationship based on data from repeated sampling of natural populations at a decadal scale.

The variation of giant kelp C:N values observed in our nearly two decade (19-year) dataset encompasses almost the entire range of C:N values measured for kelp species (Table 4). The potential for such change within a species highlights the need to track and evaluate the nutritional quality of kelps, a key basal resource for many marine ecosystems and species. The apparently declining nutritional quality of kelp available to consumers in the Santa Barbara Channel has widespread implications for kelp forest food webs and for the food webs of recipient ecosystems that rely on exported kelp (Fig. 4). Kelp is not only a basal resource within the kelp forest but also on sandy beaches (Dugan et al. 2003, Bishop et al. 2010, Dufour et al. 2012) and deep-water benthos (Vetter and Dayton 1999, Filbee-Dexter and Scheibling 2014) as most annual kelp production becomes detritus (Krumhansl and Scheibling 2012). On sandy beaches, kelp wrack inputs influence the abundance and biomass of macroinvertebrate

kelp consumers, which support higher trophic levels, such as shorebirds (Dugan et al. 2003, Lastra et al. 2008, Schlacher et al. 2017). Exported kelp is similarly important to deep water benthic consumers, including urchins and other invertebrates (Britton-Simmons et al. 2009, Filbee-Dexter and Scheibling 2014) as well as deep-sea canyon communities (Vetter and Dayton 1999, Filbee-Dexter et al. 2018). In these ecosystems, kelp subsidies are the dominant resource for primary consumer species, highlighting the importance of kelp nutritional quality.

In ecosystems where primary producers have high nutritional quality, trophic transfers are more efficient and consumers more productive; therefore, nutritional quality can shape the extent of top-down control by consumers and other processes such as nutrient recycling and carbon accumulation (Cebrian 1999, Cebrian et al. 2009). Research in terrestrial ecosystems has attributed insect population declines to both warming and nutrient dilution of their food resources (Welti et al. 2020). Decreased nutritional quality may result

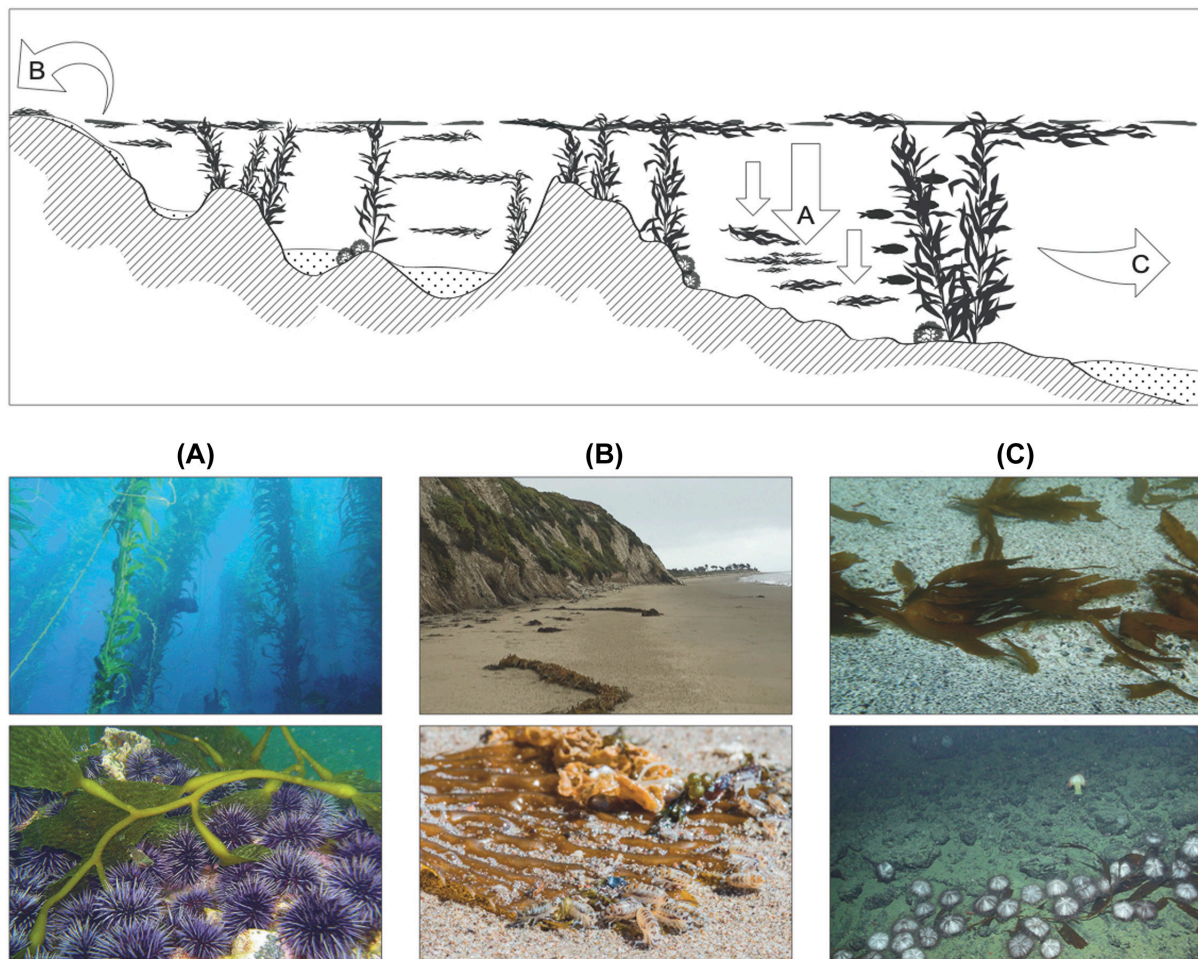


Figure 4. Conceptual diagram (top) of the trophic fate of giant kelp detritus in (A) kelp forest, (B) beach and (C) offshore canyon ecosystems (adapted from Ebeling et al. 1980). Images of the ecosystems and associated consumers are below. (A) Purple sea urchins, *Strongylocentrotus purpuratus*, consume a kelp frond on the seafloor in a kelp forest. (B) Talitrid amphipods, or beach hoppers, consume kelp wrack cast up on a sandy beach (photo, Nicholas Schooler). (C) Fragile pink sea urchins, *Strongylocentrotus fragilis*, consume kelp on the seafloor in Monterey Canyon (kelp and urchin photos, courtesy of Monterey Bay Aquarium Research Institute).

in compensatory feeding by consumers (Cruz-Rivera and Hay 2000) such that they eat a greater quantity of the same food to compensate for the reduction in nutritional quality. This behavior can affect the probability of an ecosystem state change, such as shifts from kelp forest to urchin barren, which have been observed following reductions in ecosystem nutrient status elsewhere (Boada et al. 2017). Fluctuations, and more specifically declines, in the nutritional quality of kelp will have cascading effects on the food webs of ecosystems that depend on kelp subsidies and may lead consumers to seek out additional food resources.

In addition to the changing nutritional quality of primary producers, the nutritional demands of consumers may shift with increasing temperatures (Cross et al. 2015, Rosenblatt and Schmitz 2016, Anderson et al. 2017, Carr et al. 2018). For example, phosphorus demand in relation to carbon can increase as temperatures rise (Ruiz et al. 2020); if a similar trend applies for nitrogen, this would compound the nutritional stress on kelp consumers. However, consumer carbon demand can also increase above the temperature at which the threshold elemental ratio is minimized, resulting in a U-shaped response in consumer nutritional demands (Ruiz et al. 2020). Increased carbon demand may be met by excess carbon in the diet, and if metabolism and consumption increases scale equally with rising temperatures, consumer C:N nutritional demands may not change (Anderson et al. 2017). Furthermore, organisms at different ends of their range distribution may have opposing responses to increasing temperatures (Ruiz et al. 2020), an organism's threshold elemental ratio is related to feeding strategy (detritivore, herbivore, predator) (Frost et al. 2006), and, ultimately, there may be a disconnect in the timing between changes in producers and responses in consumers which could affect their mutual success (Mertens et al. 2015). There is also a strong inverse effect of increased temperature on body size of consumers which could further alter nutritional needs (Jaramillo et al. 2017). In sum, the relationships between autotroph nutrient quality and heterotroph nutrient demands and their interactions with increasing temperatures is complex and will have significant consequences for the future structure of food webs in a changing climate.

As a foundation species, giant kelp provides physical structure and habitat to a diverse assemblage of reef-associated species (Steneck et al. 2002, Miller et al. 2018) and food resources to many herbivores and detritivores (Yorke et al. 2019). Sea urchins and abalone, for example, depend on kelp as their main food source, and both are important components of the kelp forest food web (Dayton 1985). In addition, both taxa are targeted by commercial and recreational fisheries. In California, red urchins *Strongylocentrotus franciscanus* are harvested for their roe in one of the state's most valuable fisheries (California Department of Fish and Wildlife 2013). Urchin growth and gonad quality are dependent on food quality (McBride et al. 2004) and sea water temperature (Azad et al. 2011), which we found were negatively correlated in the Santa Barbara Channel (Table 3). Similarly, growth rates of abalone are highly

sensitive to water temperature and food quantity and quality (Vilchis et al. 2005). Overfishing, combined with a disease associated with ocean warming, has contributed to large-scale declines in wild abalone (Neuman et al. 2010) and recent closures of recreational and commercial fisheries in California. Greater dietary protein content is directly linked to greater wet weight, gonad size and test sizes of sea urchins (Hammer et al. 2012) as well as greater body weight and shell size of abalone (Naidoo et al. 2006). Our data show that giant kelp nitrogen content ranged from 0.57% to 4.34%, which translates to a range in protein content of 2.85% to 21.7%, using the seaweed-specific conversion factor of 5 (Angell et al. 2016). Mean annual nitrogen content of giant kelp declined from 2.47% to 2.02% over the course of this study, corresponding to a 18% decline in protein content from 12.38% to 10.10%. This implies that sea urchins, abalone and other consumers would need to ingest 18% more kelp to receive the same nutritional benefit. In addition to these direct effects on consumers, changes in kelp nutritional quality could have indirect effects on the state of entire reef ecosystems. For example, when abundant, sea urchins can overgraze kelp forests, creating persistent urchin barrens. Decreased kelp nutritional content could increase the likelihood of such ecosystem state change by increasing the amount of kelp needed by urchins, thus reducing ecosystem resilience (Boada et al. 2017).

Conclusion

Our results suggest that giant kelp, the foundation species of highly productive kelp forests that support biodiverse coastal ecosystems, has experienced a nearly 45% decline in the nutritional quality of blade tissue over the course of 19 years. Reductions in kelp nutritional quality, in addition to declines in kelp biomass, in response to increased sea surface temperatures have important implications for kelp forest food webs and kelp-subsidized ecosystems. Overall, these climate driven changes to a key foundation species may lead to a reduced role for kelp in temperate marine food webs under future conditions. Long-term studies of marine ecosystems that consider food quality in addition to primary production will provide greater insights and more accurate projections of the responses of ecosystem structure and function to changing ocean climate.

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Data availability statement

Data are available from the Environmental Data Initiative: <<https://doi.org/10.6073/pasta/7b5ec12ad274b4943464fae35cc39452>> (Santa Barbara Coastal LTER et al. 2021).

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