# Research

# Nutritional quality of giant kelp declines due to warming ocean temperatures

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Subject Editor: Alexandre Bec Editor-in-Chief: Dries Bonte Accepted 21 September 2021 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 multitrophic 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 kendall-TrendTest functions, respectively, from the EnvStats package in R (Millard 2013). Each Seasonal Kendall test also included a test for heterogeneity  $(\chi^2)$  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<sup>2</sup> 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 | $\chi^2$ | p (χ <sup>2</sup> ) | 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 |

| $ \begin{array}{{ c c c c c c c c c c c c c c c c c c $   | . Kesults ( |       |        |          |      |          |       |       |         |      |        |        |         |        |       |        |
|---|-------------|-------|--------|----------|------|----------|-------|-------|---------|------|--------|--------|---------|--------|-------|--------|
| TauSlopeInt.zpTauSlopeInt.z0.320.011 $-21.69$ 3.360.00080.230.26 $-495.26$ 2.410.016 $-0.21$ $-0.034$ 70.71 $-2.15$ 00.260.010 $-19.44$ 2.770.00550.380.45 $-879.54$ 4.010.0017 $-0.076$ $-0.017$ 35.53 $-0.80$ 00.230.0080 $-14.92$ 2.410.0160.290.34 $-651.17$ 3.02 $0.0075$ $-0.017$ 35.53 $-0.80$ 00.180.00447.85 $1.76$ 0.0780.280.48 $-932.92$ $2.78$ $0.0075$ $-0.011$ $24.71$ $-0.55$ 00.230.0069 $-12.77$ $2.43$ 0.0150.32 $0.422$ $-818.99$ $3.30$ $0.0010$ $-0.022$ $-0.011$ $24.71$ $-0.55$ 00.250.010 $-19.35$ $2.62$ 0.0080.29 $0.34$ $-551.17$ $3.02$ $0.011$ $24.71$ $-0.55$ 00.250.010 $-19.35$ $2.62$ 0.008 $0.29$ $0.32$ $0.742$ $-818.99$ $3.30$ $0.0012$ $-0.022$ $-1.20$ 00.210.014 $-27.18$ $3.37$ 0.008 $0.22$ $0.025$ $0.026$ $-3.943$ $-0.22$ 00.210.018 $-35.75$ $4.72$ $<0.008$ $0.21$ $0.021$ $-0.31$ $-0.32$ $-0.022$ $-1.20$ 00.21 <t< th=""><th></th><th></th><th></th><th>log(C:N)</th><th></th><th></th><th></th><th></th><th>% C</th><th></th><th></th><th></th><th></th><th>% N</th><th></th><th></th></t<> |             |       |        | log(C:N) |      |          |       |       | % C     |      |        |        |         | % N    |       |        |
| $ \begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$   |             | Tau   | Slope  | Int.     | Z    | d        | Tau   | Slope | Int.    | Z    | d      | Tau    | Slope   | Int.   | Z     | d      |
| $ \begin{array}{cccccccccccccccccccccccccccccccccccc$   |             | 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  |
| $ \begin{array}{cccccccccccccccccccccccccccccccccccc$   |             | 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   |
| 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           0.23         0.0069 $-12.77$ 2.43 <b>0.015</b> 0.32         0.42 $-818.99$ 3.30 <b>0.0010</b> $-0.022$ $-0.032$ $9.43$ $-0.22$ 0           0.25         0.010 $-19.35$ 2.62 <b>0.0088</b> 0.29         0.39 $-754.56$ 3.05 <b>0.0010</b> $-0.025$ $52.76$ $-1.20$ 0           0.31         0.014 $-27.18$ $3.37$ <b>0.0088</b> 0.21 $0.20$ $-360.94$ $2.32$ <b>0.047</b> $95.63$ $-3.31$ <b>0</b> 0.13         0.018 $-35.75$ $4.72$ <b>&lt;0.0011</b> $0.23$ $0.24$ $2.53$ <b>0.011</b> $-0.37$ $-0.025$ $53.76$ $-1.20$ $0$ 0.14 $0.014$ $-15.60$ $0.23$ $0.214$ $0.24$ $2.32$ $0.021$ $-0.027$ $-0.025$  |             | 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   |
| $ \begin{array}{c ccccccccccccccccccccccccccccccccccc$  |             | 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   |
| $\begin{array}{cccccccccccccccccccccccccccccccccccc$  |             | 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   |
| $ \begin{array}{c ccccccccccccccccccccccccccccccccccc$  |             | 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   |
| 0.43       0.018       -35.75       4.72       < 0.001  |             | 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 |
| 0.21       0.0084       -15.60       2.32 <b>0.02</b> 0.014       0.010       11.83       0.14       0.89       -0.18       -0.026       54.35       -1.98 <b>0</b> 0.091       0.0038       -6.26       0.96       0.34       0.19       0.24       -444.52       2.01 <b>0.044</b> -0.025       -0.0034       8.34       -0.25       0         0.31       0.014       -26.44       3.35 <b>0.0008</b> 0.22       0.20       -380.06       2.44 <b>0.015</b> -0.039       79.93       -2.70 <b>0</b> 0.22       0.079       -14.64       2.37 <b>0.018</b> 0.32       0.38       -741.09       3.48 <b>0.005</b> -0.061       -0.0682       18.43       -0.66       0  |             | 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 |
| 0.091         0.0038         -6.26         0.34         0.19         0.24         -444.52         2.01 <b>0.044</b> -0.025         -0.034         8.34         -0.25         0           0.31         0.014         -26.44         3.35 <b>0.0008</b> 0.22         0.20         -380.06         2.44 <b>0.015</b> -0.039         79.93         -2.70 <b>0</b> 0.22         0.079         -14.64         2.37 <b>0.018</b> 0.38         -741.09         3.48 <b>0.005</b> -0.061         -0.062         18.43         -0.66         0  |             | 0.21  | 0.0084 | -15.60   | 2.32 | 0.02     | 0.014 | 0.010 | 11.83   | 0.14 | 0.89   | -0.18  | -0.026  | 54.35  | -1.98 | 0.048  |
| 0.31 0.014 -26.44 3.35 <b>0.0008</b> 0.22 0.20 -380.06 2.44 <b>0.015</b> -0.25 -0.039 79.93 -2.70 <b>0</b> .<br>0.22 0.0079 -14.64 2.37 <b>0.018</b> 0.32 0.38 -741.09 3.48 <b>0.0005</b> -0.061 -0.0082 18.43 -0.66 0  |             | 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   |
| 0.22 0.0079 -14.64 2.37 <b>0.018</b> 0.32 0.38 -741.09 3.48 <b>0.0005</b> -0.061 -0.0082 18.43 -0.66 0  |             | 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 |
|   |             | 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 satellitederived 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      | р        | Entire model R <sup>2</sup> |
|--------------------|------------------------------------|---------|--------|-------|--------|----------|-----------------------------|
| log(C:N)           | Temperature                        | 0.048   | 0.005  | 1,635 | 432.96 | < 0.0001 | 0.4378                      |
| 0                  | Sampling date                      | 0.001   | 0.0006 | 1,635 | 52.39  | < 0.0001 |                             |
|                    | Temperature $\times$ 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                      |
| C                  | 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                      |
| C                  | 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  $\pm$ 2 to  $\pm$  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(C:N) values for giant kelp *Macrocystis pyrifera* blades plotted against (A) sea surface temperature from satellitederived 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(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 shorterterm 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  |
|-------------|--------------|-----------|--|
| Alaria      | crassifolia  | 8.9       | Johnston 1971  |
| А.          | esculenta    | 23-30     | Gordillo et al. 2006, 2015   |
| А.          | marginata    | 12.5-14.5 | Pelletreau and Muller-Parker 2002, McDonald and Bingham 2010   |
| Durvillaea  | antarctica   | 30        | Suárez-Jiménez et al. 2017   |
| Ecklonia    | radiata      | 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   |
| Ε.          | maxima       | 15-17.8   | Probyn and McQuaid 1985  |
| Laminaria   | angustata    | 23.3      | Johnston 1971  |
| <i>L</i> .  | dentiger     | 21.7      | Atkinson and Smith 1983  |
| L.          | digitata     | 19.4-28.6 | Mann 1972, Schaal et al. 2010, Xia et al. 2016   |
| L.          | groenlandica | 12.4-17   | Harrison et al. 1986   |
| L.          | hyperborea   | 6-60      | Sjøtun et al. 1996, Norderhaug et al. 2003, Leclerc et al. 2013  |
| L.          | japonica     | 10-50     | Johnston 1971, Mizuta et al. 1997  |
| L.          | longicruris  | 13.8–16.7 | Mann 1972  |
| L.          | religiosa    | 15.4      | Johnston 1971  |
| L.          | saccharina   | 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.          | solidungula  | 10-26     | Dunton and Schell 1986, Henley and Dunton 1995, Gordillo et al. 2006   |
| Lessonia    | nigrescens   | 16.6      | Reddin et al. 2015   |
| Macrocystis | pyrifera     | 7.5–47.2  | (This paper), Jackson 1977, Wheeler and North 1981*, Atkinson and Smith 1983,<br>Rosell and Srivastava 1985*, van Tussenbroek 1989, Hurd et al. 1994, 1996, 2000,<br>Brown et al. 1997, 2014, Pennings et al. 2000, Hepburn et al. 2006, 2007,<br>Davenport and Anderson 2007, Stephens and Hepburn 2014, 2016,<br>Fernández et al. 2015, Hamersley et al. 2015, Dobkowski et al. 2017, Suárez-<br>Jiménez et al. 2017 |
| Nereocystis | luetkeana    | 9.8–24    | Atkinson and Smith 1983, Rosell and Srivastava 1985*, Ahn et al. 1998,<br>Pennings et al. 2000, Pelletreau and Muller-Parker 2002, Dethier et al. 2014,<br>Dobkowski et al. 2017   |
| Saccharina  | japonica     | 7.1       | Wang et al. 2013   |
| <i>S</i> .  | latissima    | 7–45      | McDonald and Bingham 2010, Handå et al. 2013, Olischläger et al. 2014,<br>Gordillo et al. 2015   |
| Undaria     | pinnatifida  | 8.4–23.6  | Johnston 1971, Yoshikawa et al. 2001, Dean and Hurd 2007, Sfriso and Facca 2013,<br>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



(A)





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: <a href="https://doi.org/10.6073/pasta/7b5ec12ad274b4943464fae35cc39452">https://doi.org/10.6073/pasta/7b5ec12ad274b4943464fae35cc39452</a>> (Santa Barbara CoastalLTER et al. 2021).

#### References

- Abraham, J. P. et al. 2013. A review of global ocean temperature observations: implications for ocean heat content estimates and climate change. – Rev. Geophys. 51: 450–483.
- Ahn, O. et al. 1998. Ammonium and nitrate uptake by *Laminaria* saccharina and Nereocystis luetkeana originating from a salmon sea cage farm. – J. Appl. Phycol. 10: 333–340.
- Anderson, T. R. et al. 2017. Will invertebrates require increasingly carbon-rich food in a warming world? – Am. Nat. 190: 725–742.
- Angell, A. R. et al. 2016. The protein content of seaweeds: a universal nitrogen-to-protein conversion factor of five. J. Appl. Phycol. 28: 511–524.
- Atkinson, M. J. and Smith, S. V. 1983. C:N:P ratios of benthic marine plants. – Limnol. Oceanogr. 28: 568–574.
- Azad, A. K. et al. 2011. Effects of diet and temperature on ingestion, absorption, assimilation, gonad yield and gonad quality of the purple sea urchin *Strongylocentrotus purpuratus*. – Aquaculture 317: 187–196.
- Bartoń, K. 2020. MuMIn: multi-model inference. ver. 1.43.17. <a href="https://CRAN.R-project.org/package=MuMIn">https://CRAN.R-project.org/package=MuMIn</a>>.
- Bell, T. W. et al. 2015. Geographical variability in the controls of giant kelp biomass dynamics. J. Biogeogr. 42: 2010–2021.
- Bishop, M. J. et al. 2010. Cross-habitat impacts of species decline: response of estuarine sediment communities to changing detrital resources. – Oecologia 163: 517–525.
- Boada, J. et al. 2017. Immanent conditions determine imminent collapses: nutrient regimes define the resilience of macroalgal communities. – Proc. R. Soc. B 284: 20162814.
- Boyer, K. E. et al. 2004. Elevated nutrient content of tropical macroalgae increases rates of herbivory in coral, seagrass and mangrove habitats. – Coral Reefs 23: 530–538.

- Britton-Simmons, K. H. et al. 2009. Spatial subsidy in the subtidal zone: utilization of drift algae by a deep subtidal sea urchin. – Aquat. Biol. 5: 233–243.
- Britton, D. et al. 2016. Ocean acidification reverses the positive effects of seawater pH fluctuations on growth and photosynthesis of the habitat-forming kelp, *Ecklonia radiata*. – Sci. Rep. 6: 26036.
- Brown, M. B. et al. 2014. Effects of climate change on the physiology of giant kelp, *Macrocystis pyrifera* and grazing by purple urchin, *Strongylocentrotus purpuratus*. – Algae 29: 203–215.
- Brown, M. T. et al. 1997. Seasonal growth of the giant kelp *Macrocystis pyrifera* in New Zealand. Mar. Biol. 129: 417–424.
- Brzezinski, M. et al. 2013. Multiple sources and forms of nitrogen sustain year-round kelp growth on the inner continental shelf of the Santa Barbara Channel. – Oceanography 26: 114–123.
- California Department of Fish and Wildlife (CA DFW) 2013. Status of the fisheries report: an update through 2011 [Marine Region]. – <www.wildlife.ca.gov/marine/status/index.asp>.
- Carr, L. A. et al. 2018. Temperature influences herbivory and algal biomass in the Galápagos Islands. – Front. Mar. Sci. 5: 279.
- Cavanaugh, K. et al. 2011. Environmental controls of giant-kelp biomass in the Santa Barbara Channel, California. – Mar. Ecol. Prog. Ser. 429: 1–17.
- Cavanaugh, K. C. et al. 2019. Spatial variability in the resistance and resilience of giant kelp in Southern and Baja California to a multiyear heatwave. – Front. Mar. Sci. 6: 413.
- Cebrian, J. 1999. Patterns in the fate of production in plant communities. – Am. Nat. 154: 449–468.
- Cebrian, J. et al. 2009. Producer nutritional quality controls ecosystem trophic structure. – PLoS One 4: e4929.
- Cross, W. F. et al. 2015. Interactions between temperature and nutrients across levels of ecological organization. – Global Change Biol. 21: 1025–1040.
- Cruz-Rivera, E. and Hay, M. E. 2000. Can quantity replace quality? Food choice, compensatory feeding and fitness of marine mesograzers. – Ecology 81: 201–219.
- Davenport, A. C. and Anderson, T. W. 2007. Positive indirect effects of reef fishes on kelp performance: the importance of mesograzers. – Ecology 88: 1548–1561.
- Dayton, P. K. 1985. Ecology of kelp communities. Annu. Rev. Ecol. Syst. 16: 215–245.
- Dean, P. R. and Hurd, C. L. 2007. Seasonal growth, erosion rates and nitrogen and photosynthetic ecophysiology of *Undaria pinnatifida* (Heterokontophyta) in southern New Zealand. – J. Phycol. 43: 1138–1148.
- Dethier, M. N. et al. 2014. Degrading detritus: changes in food quality of aging kelp tissue varies with species. J. Exp. Mar. Biol. Ecol. 460: 72–79.
- Di Lorenzo, E. and Mantua, N. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nat. Clim. Change 6: 1042–1047.
- Di Lorenzo, E. et al. 2008. North Pacific Gyre oscillation links ocean climate and ecosystem change. – Geophys. Res. Lett. 35: L08607.
- Dobkowski, K. A. et al. 2017. Picky Pugettia: a tale of two kelps. - Mar. Biol. 164: 210.
- Dufour, C. et al. 2012. Macrofaunal colonisation of stranded Durvillaea antarctica on a southern New Zealand exposed sandy beach. – N. Z. J. Mar. Freshwater Res. 46: 369–383.
- Dugan, J. E. et al. 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. – Estuar. Coastal Shelf Sci. 58: 25–40.

- Dunton, K. and Schell, D. 1986. Seasonal carbon budget and growth of *Laminaria solidungula* in the Alaskan High Arctic. – Mar. Ecol. Prog. Ser. 31: 57–66.
- Ebeling, A. W. et al. 1980. Annual variability of reef-fish assemblages in kelp forests off Santa Barbara, California. Fish. Bull. 78: 361–377.
- Falkenberg, L. J. et al. 2012. Stability of strong species interactions resist the synergistic effects of local and global pollution in kelp forests. PLoS One 7: e33841.
- Falkenberg, L. J. et al. 2013. Contrasting resource limitations of marine primary producers: implications for competitive interactions under enriched CO<sub>2</sub> and nutrient regimes. – Oecologia 172: 575–583.
- Fernández, P. A. et al. 2015. Effects of ocean acidification on the photosynthetic performance, carbonic anhydrase activity and growth of the giant kelp *Macrocystis pyrifera*. – Photosynth. Res. 124: 293–304.
- Filbee-Dexter, K. and Scheibling, R. 2014. Detrital kelp subsidy supports high reproductive condition of deep-living sea urchins in a sedimentary basin. – Aquatic Biol. 23: 71–86.
- Filbee-Dexter, K. et al. 2018. Movement of pulsed resource subsidies from kelp forests to deep fjords. – Oecologia 187: 291–304.
- Frölicher, T. L. and Laufkötter C. 2018. Emerging risks from marine heat waves. Nat. Commun. 9: 650.
- Frölicher, T. L. et al. 2018. Marine heatwaves under global warming. – Nature 560: 360–364.
- Frost, P. C. et al. 2006. Threshold elemental ratios of carbon and phosphorus in aquatic consumers. Ecol. Lett. 9: 774–779.
- Gaiser, E. E. et al. 2020. Long-term ecological research and evolving frameworks of disturbance ecology. – BioScience 70: 141–156.
- Gerard, V. A. 1982. Growth and utilization of internal nitrogen reserves by the giant kelp *Macrocystis pyrifera* in a low-nitrogen environment. – Mar. Biol. 66: 27–35.
- Gevaert, F. et al. 2001. Carbon and nitrogen content of *Laminaria* saccharina in the eastern English Channel: biometrics and seasonal variations. J. Mar. Biol. Assoc. UK 81: 727–734.
- Gladstone-Gallagher, R. V. et al. 2016. Effects of detrital subsidies on soft-sediment ecosystem function are transient and source dependent. – PLoS One 11: e0154790.
- Gordillo, F. J. L. et al. 2006. The response of nutrient assimilation and biochemical composition of Arctic seaweeds to a nutrient input in summer. – J. Exp. Bot. 57: 2661–2671.
- Gordillo, F. J. L. et al. 2015. Ocean acidification modulates the response of two Arctic kelps to ultraviolet radiation. J. Plant Physiol. 173: 41–50.
- Hamersley, M. R. et al. 2015. Nitrogen fixation associated with the decomposition of the giant kelp *Macrocystis pyrifera*. Aquatic Bot. 125: 57–63.
- Hammer, H. S. et al. 2012. Effect of feed protein and carbohydrate levels on feed intake, growth and gonad production of the sea urchin, *Lytechinus variegatus*. – J. World Aquacult. Soc. 43: 145–158.
- Handå, A. et al. 2013. Seasonal- and depth-dependent growth of cultivated kelp *Saccharina latissima* in close proximity to salmon *Salmo salar* aquaculture in Norway. Aquaculture 414–415: 191–201.
- Hansen, J. et al. 2006. Global temperature change. Proc. Natl Acad. Sci. USA 103: 14288–14293.
- Harley, C. D. G. et al. 2006. The impacts of climate change in coastal marine systems: climate change in coastal marine systems. Ecol. Lett. 9: 228–241.

- Harley, C. D. G. et al. 2012. Effects of climate change on global seaweed communities. J. Phycol. 48: 1064–1078.
- Harrison, P. J. et al. 1986. Nitrogen uptake kinetics in three yearclasses of *Laminaria groenlandica* (Laminariales: Phaeophyta).
  Mar. Biol. 93: 29–35.
- Helsel, D. R. et al. 2020. Statistical methods in water resources (Report No. 4-A3), techniques and methods. – US Geological Survey, Reston, VA.
- Hemmi, A. and Jormalainen, V. 2002. Nutrient enrichment increases performance of a marine herbivore via quality of its food alga. – Ecology 83: 1052–1064.
- Henley, W. J. and Dunton, K. H. 1995. A seasonal comparison of carbon, nitrogen and pigment content in *Laminaria solidungula* and *L. saccharina* (Phaeophyta) in the Alaskan Arctic. – J. Phycol. 31: 325–331.
- Hepburn, C. D. et al. 2006. Colony structure and seasonal differences in light and nitrogen modify the impact of sessile epifauna on the giant kelp *Macrocystis pyrifera* (L.) C Agardh. – Hydrobiologia 560: 373–384.
- Hepburn, C. D. et al. 2007. Exposure to waves enhances the growth rate and nitrogen status of the giant kelp *Macrocystis pyrifera*. – Mar. Ecol. Prog. Ser. 339: 99–108.
- Hoegh-Guldberg, O. et al. 2018. Impacts of 1.5°C of global warming on natural and human systems. – In: Global warming of 1.5°C. An IPCC Special Report on the impact of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development and efforts to eradicate poverty. – IPCC, <https:// unfccc.int/topics/science/workstreams/cooperation-with-theipcc/ipcc-special-report-on-global-warming-of-15-degc>.
- Hughes, B. B. et al. 2017. Long-term studies contribute disproportionately to ecology and policy. – BioScience 67: 271–281.
- Hurd, C. L. et al. 1994. Effect of bryozoan colonization on inorganic nitrogen acquisition by the kelps *Agarum fimbriatum* and *Macrocystis integrifolia*. – Mar. Biol. 121: 167–173.
- Hurd, C. L. et al. 1996. Effect of seawater velocity on inorganic nitrogen uptake by morphologically distinct forms of *Macrocystis integrifolia* from wave-sheltered and exposed sites. – Mar. Biol. 126: 205–514.
- Hurd, C. L. et al. 2000. Influence of bryozoan colonization on the physiology of the kelp *Macrocystis integrifolia* (Laminariales, Phaeophyta) from nitrogen-rich and -poor sites in Barkley Sound, British Columbia, Canada. – Phycologia 39: 435–440.
- Isles, P. D. F. 2020. The misuse of ratios in ecological stoichiometry. – Ecology 101: e03153.
- Jackson, G. A. 1977. Nutrients and production of giant kelp, *Macrocystis pyrifera*, off southern California. Limnol. Oceanogr. 22: 979–995.
- Jacox, M. G. et al. 2018. Coastal upwelling revisited: Ekman, Bakun and improved upwelling indices for the U.S. west coast. – J. Geophys. Res. 123: 1–19.
- Jaramillo, E. et al. 2017. Macroscale patterns in body size of intertidal crustaceans provide insights on climate change effects. – PLoS One 12: e0177116.
- Johnson, C. R. et al. 2011. Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. – J. Exp. Mar. Biol. Ecol. 400: 17–32.
- Johnston, H. W. 1971. A detailed chemical analysis of some edible Japanese seaweeds. – In: Proc. 7th Int. Seaweed Symp., pp. 429–435.

- JPL MUR MEaSUREs Project 2015. GHRSST level 4 MUR global foundation sea surface temperature analysis (4.1). doi: 10.5067/GHGMR-4FJ04 <a href="https://podaac-www.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1>">https://podaac-www.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1></a>.
- Kominoski, J. S. et al. 2018. Advancing theories of ecosystem development through long-term ecological research. – BioScience 68: 554–562.
- Koenigs, C. et al. 2015. Top predators rely on carbon derived from giant kelp *Macrocystis pyrifera*. – Mar. Ecol. Progr. Ser. 537: 1–8.
- Krumhansl, K. and Scheibling, R. 2012. Production and fate of kelp detritus. – Mar. Ecol. Prog. Ser. 467: 281–302.
- Lastra, M. et al. 2008. Processing of allochthonous macrophyte subsidies by sandy beach consumers: estimates of feeding rates and impacts on food resources. – Mar. Biol. 154: 163–174.
- Leclerc, J. C. et al. 2013. Temporal variation in organic matter supply in kelp forests: linking structure to trophic functioning. – Mar. Ecol. Prog. Ser. 494: 87–105.
- Lotze, H. K. et al. 2019. Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. – Proc. Natl Acad. Sci. USA 116: 12907–12912.
- Mabin, J. T. et al. 2019. Physiological response to temperature, light and nitrates in the giant kelp *Macrocystis pyrifera* from Tasmania, Australia. – Mar. Ecol. Prog. Ser. 614: 1–19.
- Mann, K. H. 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. I. Zonation and biomass of seaweeds. – Mar. Biol. 12: 1–10.
- McBride, S. C. et al. 2004. Comparison of gonad quality factors: color, hardness and resilience, of *Strongylocentrotus franciscanus* between sea urchins fed prepared feed or algal diets and sea urchins harvested from the northern California fishery. – Aquaculture 233: 405–422.
- McDonald, P. S. and Bingham, B. L. 2010. Comparing macroalgal food and habitat choice in sympatric, tube-building amphipods, *Ampithoe lacertosa* and *Peramphithoe humeralis*. – Mar. Biol. 157: 1513–1524.
- McPhee-Shaw, E. E. et al. 2007. Mechanisms for nutrient delivery to the inner shelf: observations from the Santa Barbara Channel. – Limnol. Oceanogr. 52: 1748–1766.
- Mertens, N. L. et al. 2015. Escaping herbivory: ocean warming as a refuge for primary producers where consumer metabolism and consumption cannot pursue. – Oecologia 179: 1223–1229.
- Millard, S. P. 2013. EnvStats: an R packge for environmental statistics. – Springer, <www.springer.com>.
- Miller, R. J. et al. 2018. Giant kelp, *Macrocystis pyrifera*, increases faunal diversity through physical engineering. Proc. R. Soc. B 285: 20172571.
- Miller, S. M. 2004. Ecophysiology of *Ecklonia radiata* (Alariaceae: Laminariales) in Doubtful Sound, Fiordland. – PhD thesis, Univ. of Otago, New Zealand.
- Mizuta, H. et al. 1997. The relationship between nitrogen and carbon contents in the sporophytes of *Laminaria japonica* (Phaeophyceae). Fish. Sci. 63: 553–556.
- Naidoo, K. et al. 2006. A comparison of various seaweed-based diets and formulated feed on growth rate of abalone in a landbased aquaculture system. – J. Appl. Phycol. 18: 437–443.
- National Climatic Data Center 2007. GHRSST level 4 AVHRR\_ OI global blended sea surface temperature analysis (ver. 1.0). doi: 10.5067/GHAAO-4BC01 <a href="https://podaac.jpl.nasa.gov/dataset/NCDC-L4LRblend-GLOB-AVHRR\_OI">https://podaac.jpl.nasa.gov/ dataset/NCDC-L4LRblend-GLOB-AVHRR\_OI</a>.
- Neuman, M. et al. 2010. Overall status and threats assessment of black abalone (*Haliotis cracherodii* Leach, 1814) populations in California. – J. Shellfish Res. 29: 577–586.

- Norderhaug, K. et al. 2003. Trophic importance of *Laminaria hyperborea* to kelp forest consumers and the importance of bacterial degradation to food quality. Mar. Ecol. Prog. Ser. 255: 135–144.
- Olischläger, M. et al. 2014. Biochemical composition of temperate and Arctic populations of *Saccharina latissima* after exposure to increased pCO<sub>2</sub> and temperature reveals ecotypic variation. – Planta 240: 1213–1224.
- Parnell, P. E. et al. 2010. The response of giant kelp *Macrocystis* pyrifera in southern California to low-frequency climate forcing. – Limnol. Oceanogr. 55: 2686–2702.
- Pelletreau, K. and Muller-Parker, G. 2002. Sulfuric acid in the phaeophyte alga *Desmarestia munda* deters feeding by the sea urchin *Strongylocentrotus droebachiensis.* – Mar. Biol. 141: 1–9.
- Pennings, S. C. et al. 2000. Feeding preferences of supralittoral isopods and amphipods. Can. J. Zool. 78: 1918–1929.
- Pfister, C. A. et al. 2018. The dynamics of kelp forests in the Northeast Pacific Ocean and the relationship with environmental drivers. – J. Ecol. 106: 1520–1533.
- Phelps, C. M. et al. 2017. Future climate change scenarios differentially affect three abundant algal species in southwestern Australia. – Mar. Environ. Res. 126: 69–80.
- Pinheiro, J. et al. 2021. nlme: linear and nonlinear mixed effects models. v 3.1-152. – <a href="https://CRAN.R-project.org/package=nlme">https://CRAN.R-project.org/package=nlme</a>>.
- Probyn, T. A. and McQuaid, C. D. 1985. In-situ measurements of nitrogenous nutrient uptake by kelp *Ecklonia maxima* and phytoplankton in a nitrate-rich upwelling environment. – Mar. Biol. 88: 149–154.
- Raybaud, V. et al. 2013. Decline in kelp in west Europe and climate. – PLoS One 8: e66044.
- Reddin, C. J. et al. 2015. Coastal upwelling drives intertidal assemblage structure and trophic ecology. PLoS One 10: e0130789.
- Reed, D. and Miller, R. 2021. SBC LTER: reef: *Macrocystis pyrifera* CHN content (carbon, hydrogen, nitrogen) ver. 20. – Environ. Data Initiative. doi: 10.6073/pasta/7b5ec12ad274b4943464fa e35cc39452
- Reed, D. et al. 2016. Extreme warming challenges sentinel status of kelp forests as indicators of climate change. – Nat. Commun. 7: 13757.
- Rogers-Bennett, L. and Catton, C. A. 2019. Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. – Sci. Rep. 9: 15050.
- Rosell, K. G. and Srivastava, L. 1985. Seasonal variations in total nitrogen, carbon and amino acids in *Macrocystis integrifolia* and *Nereocystis luetkeana* (Phaeophyta). – J. Phycol. 21: 304–309.
- Rosenblatt, A. E. and Schmitz, O. J. 2016. Climate change, nutrition and bottom–up and top–down food web processes. – Trends Ecol. Evol. 31: 965–975.
- Ruiz, T. et al. 2020. U-shaped response unifies views on temperature dependency of stoichiometric requirements. – Ecol. Lett. 23: 860–869.
- Santa Barbara Coastal LTER et al. 2021. Data from: Nutritional quality of giant kelp declines due to warming ocean temperatures. Environmental Data Initiative: .
- Schaal, G. et al. 2010. Trophic ecology in a Northern Brittany (Batz Island, France) kelp *Laminaria digitata* forest, as investigated through stable isotopes and chemical assays. – J. Sea Res. 63: 24–35.
- Schlacher, T. A. et al. 2017. Algal subsidies enhance invertebrate prey for threatened shorebirds: a novel conservation tool on ocean beaches? Estuar. Coastal Shelf Sci. 191: 28–38.
- Sfriso, A. and Facca, C. 2013. Annual growth and environmental relationships of the invasive species *Sargassum muticum* and

*Undaria pinnatifida* in the lagoon of Venice. – Estuar. Coastal Shelf Sci. 129: 162–172.

- Simonson, E. et al. 2015. Kelp in hot water: II. Effects of warming seawater temperature on kelp quality as a food source and settlement substrate. – Mar. Ecol. Prog. Ser. 537: 105–119.
- Sjøtun, K. et al. 1996. Seasonal growth and carbon and nitrogen content in canopy and first-year plants of *Laminaria hyperborea* (Laminariales, Phaeophyceae). – Phycologia 35: 1–8.
- Smale, D. A. 2020. Impacts of ocean warming on kelp forest ecosystems. – New Phytol. 225: 1447–1454.
- Smale, D. A. et al. 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. – Nat. Clim. Change 9: 306–312.
- Staehr, P. A. and Wernberg, T. 2009. Physiological responses of *Ecklonia radiata* (Laminariales) to a latitudinal gradient in ocean temperature. – J. Phycol. 45: 91–99.
- Steneck, R. S. et al. 2002. Kelp forest ecosystems: Biodiversity, stability, resilience and future. – Environ. Conserv. 29: 436–459.
- Stephens, T. A. and Hepburn, C. D. 2014. Mass-transfer gradients across kelp beds influence *Macrocystis pyrifera* growth over small spatial scales. – Mar. Ecol. Prog. Ser. 515: 97–109.
- Stephens, T. A. and Hepburn, C. D. 2016. A kelp with integrity: *Macrocystis pyrifera* prioritises tissue maintenance in response to nitrogen fertilisation. – Oecologia 182: 71–84.
- Suárez-Jiménez, R. et al. 2017. Importance of the invasive macroalga Undaria pinnatifida as trophic subsidy for a beach consumer. – Mar. Biol. 164: 113.
- Subandar, A. et al. 1993. Laminaria culture for reduction of dissolved inorganic nitrogen in salmon farm effluent. – J. Appl. Phycol. 5: 455–463.
- Thomsen, M. S. et al. 2019. Local extinction of bull kelp *Durvillaea* spp. due to a marine heatwave. Front. Mar. Sci. 6: 84.
- Van Alstyne, K. L. et al. 2009. Nutritional preferences override chemical defenses in determining food choice by a generalist herbivore, *Littorina sitkana.* – J. Exp. Mar. Biol. Ecol. 379: 85–91.
- van Tussenbroek, B. I. 1989. Seasonal growth and composition of fronds of *Macrocystis pyrifera* in the Falkland Islands. – Mar. Biol. 100: 419–430.
- Vetter, E. W. and Dayton, P. K. 1999. Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons. – Mar. Ecol. Prog. Ser. 186: 137–148.
- Vilchis, L. I. et al. 2005. Ocean warming effects on growth, reproduction and survivorship of southern California abalone. – Ecol. Appl. 15: 469–480.

- Wang, Y. et al. 2013. Variation of photosynthetic performance, nutrient uptake and elemental composition of different generations and different thallus parts of *Saccharina japonica*. – J. Appl. Phycol. 25: 631–637.
- Welti, E. A. R. et al. 2020. Nutrient dilution and climate cycles underlie declines in a dominant insect herbivore. – Proc. Natl Acad. Sci. USA 117: 7271–7275.
- Wernberg, T. et al. 2010. Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. – Ecol. Lett. 13: 685–694.
- Wernberg, T. et al. 2016. Climate-driven regime shift of a temperate marine ecosystem. – Science 353: 169–172.
- Wernberg, T. et al. 2019. Biology and ecology of the globally significant kelp *Ecklonia radiata*. – In: Hawkins, S. J. et al. (eds), Oceanography and marine biology: an annual review, pp. 265–324. CRC Press.
- Wheeler, P. A. and North, W. J. 1981. Nitrogen supply, tissue composition and frond growth rates for *Macrocystis pyrifera* off the coast of Southern California. – Mar. Biol. 64: 59–69.
- Wickham, H. et al. 2019. Welcome to the tidyverse. J. Open Source Softw. 4: 1686.
- Wilson, K. L. et al. 2015. Effects of increasing water temperatures on survival and growth of ecologically and economically important seaweeds in Atlantic Canada: implications for climate change. – Mar. Biol. 162: 2431–2444.
- Wolter, K. and Timlin, M. S. 2011. El Niño/Southern Oscillation behaviour since 1871 as diagnosed in an extended multivariate ENSO index. – Int. J. Climatol. 31: 1074–1087.
- Xia, A. et al. 2016. Production of hydrogen, ethanol and volatile fatty acids through co-fermentation of macro- and micro-algae. – Bioresour. Technol. 205: 118–125.
- Xiu, P. et al. 2018. Future changes in coastal upwelling ecosystems with global warming: the case of the California Current System. – Sci. Rep. 8: 2866.
- Yorke, C. E. et al. 2019. Sea urchins mediate the availability of kelp detritus to benthic consumers. – Proc. R. Soc. B 286: 20190846.
- Yoshikawa, T. et al. 2001. Active erosion of Undaria pinnatifida Suringar (Laminariales, Phaeophyceae) mass-cultured in Otsuchi Bay in northeastern Japan. – J. Exp. Mar. Biol. Ecol. 266: 51–65.
- Zimmerman, R. C. and Kremer, J. N. 1984. Episodic nutrient supply to a kelp forest ecosystem in Southern California. – J. Mar. Res. 42: 591–604.
- Zuur, A. F. et al. 2009. Mixed effects models and extensions in ecology with R, Statistics for biology and health. Springer.