Ocean temperature controls kelp decomposition and carbon sink potential

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Abstract

Compelling new evidence shows that kelp production contributes an important and underappreciated flux of carbon in the ocean. Major questions remain, however, about the controls on the cycling of this organic carbon in the coastal zone, and their implications for future carbon sequestration. Here we used field experiments distributed across 28° latitude, and the entire range of two dominant kelps in the northern hemisphere, to measure decomposition rates of kelp detritus on the seafloor in relation to environmental factors. Ocean temperature was the strongest control on detritus decomposition in both species, and it was positively related to decomposition. This suggests that decomposition could accelerate with ocean warming under climate change, increasing remineralization and reducing overall kelp carbon sequestration. However, we also demonstrate the potential for high kelp-carbon storage in cooler (northern) regions, which could be targeted by climate mitigation strategies to expand blue carbon sinks.

Introduction

The cycling of organic carbon in the ocean is a critical yet unresolved component of the global carbon cycle [1,2]. Consequently, there has been a strong focus on resolving inorganic carbon (CO_2) uptake and primary productivity on global scales [3]. Yet, decomposition rates of organic carbon at the ecosystem scale, which are known to vary with environmental conditions such as temperature [e.g., 4,5], could be equally important in determining the balance between pools of organic and inorganic carbon [6–8]. At the land-sea interface, carbon cycling by macroalgae and other macrophytes has recently emerged as an important process by which CO_2 is captured, stored, and potentially sequestered in the ocean [9,10]. As such, quantifying rates of decomposition of macroalgal detritus in the marine environment is essential to estimate its potential contribution to blue carbon [11] and its fate in the global carbon cycle more generally.

Decomposition rates of organic carbon vary geographically, and this is a challenge for current climate models, which usually use spatially uniform relationships to represent major processes or pathways [1,12–14]. On land, models that consider spatiotemporal dependencies in temperature, microbial, and mineral surface interactions predict weaker and more variable soil-carbon–climate feedbacks than models using average rates [15]. In the open ocean, the global biological pump has large regional variability, with particulate organic carbon (POC) decomposition rates ranging over two orders of magnitude. As a result of these spatial differences, commonly applied rates of POC decomposition based on measures from a few areas have overestimated the global flux of POC to the seafloor [16]. Similarly, variation in deep sea benthic communities appears to drive strong heterogeneity in carbon turnover rates following deposition [1] and latitudinal differences in microbial activity are expected to drive slower degradation rates of dissolved organic carbon at higher latitudes [4].

The dynamics of temperature-decomposition relationships are also complex [17]. Organic matter tends to be remineralized faster in warmer compared to cooler environments, and the temperature-dependent decomposition of carbon has been highlighted as a key source of uncertainty in future global carbon

models [5,18,19]. Understanding the environmental drivers underlying spatial variation in carbon turnover is critical because it effectively controls how current rates of carbon cycling could be changed with global warming. In particular, it informs whether environmental and biological changes will create positive feedbacks on the entire carbon cycle that lead to further warming, as opposed to negative feedbacks that buffer impacts and buy time to reduce emissions.

Large brown macroalgae at high latitudes form kelp forests, which assimilate substantial quantities of CO_2 by virtue of their exceptional productivity and large spatial extent [20,21]. Many kelp forests are declining globally, particularly in regions with high seawater temperatures and rapid warming [22–25]. In contrast, kelp forests in cooler regions are relatively stable, and in some cases kelp is even increasing in abundance [24,26–29]. Changes in the abundance of kelp, and the environmental conditions they experience, may have consequences for the global carbon cycle. More than 80% of kelp production enters the coastal ecosystem as detritus, where it eventually strands on beaches, sinks to the seafloor, or is decomposed [20,30]. In general, the slower the decomposition of kelp detritus in the ocean, the greater chance it has for sequestration in the deep ocean and the longer it takes to re-enter the atmosphere as CO_2 [16,31]. For example, macroalgal detritus that reaches open ocean depths >1000 m is considered trapped in water masses where the CO_2 is retained for significant time periods (i.e., >1000 years) before returning to the ocean surface and eventually the atmosphere [9,32]. Detritus that is retained in some nearshore areas, such as deep fjords or basins with high rates of sedimentation may also be buried for 100s to 1000s of years, effectively removing it from the short-term carbon cycle [33–36].

Here we conducted a broadly distributed field experiment at 35 sites spanning 12 geographic regions across the northern hemisphere (Fig. 1) to measure decomposition rates of kelp detritus in coastal habitats and to assess the influence of an ocean climate gradient on decomposition. Experiments on two dominant species of kelp (*Laminaria hyperborea* and *Saccharina latissima*) were deployed through a collaborative network of researchers in the northeast Pacific Ocean (n = 1), the subarctic Norwegian Sea (n = 1), the Gulf of Alaska (n = 1), the northeast Atlantic Ocean (n = 4), and the northwest Atlantic Ocean (n = 5). Our study sites spanned 28° in latitude, 169° in longitude, and encompassed the entire distribution of the two kelp species and a gradient in mean sea temperature of ~14°C. We hypothesized that the large spatial range in environmental conditions would drive significant differences in kelp-carbon decomposition rates, and that turnover would be faster in areas with warmer temperature, lower light, and higher water movement.

Results

Our study regions experienced markedly different temperature conditions, with average temperatures ranging from 6 to 21 °C and regional minimum and maximum temperatures spanning from 2 to 24 °C, over the 4 to 18-week study (Fig. 1).

Across all our study regions, kelp biomass decomposed at an average rate of 0.74 ± 0.87 % d^{-1} (± SD) reaching 50 % loss after 67 days, on average. Decomposition rates for both species were inversely related to latitude along the 28° gradient (Fig. 2). The most rapid biomass loss occurred at the southernmost sites in Rhode Island Sound, USA (1.76 ± 0.39 % d^{-1}) and Portugal (2.63 ± 0.66 % d^{-1}). Biomass loss was similar among the Norwegian Sea, the Gulf of Alaska, and other regions in cooler parts of the northeast Atlantic Ocean, with extremely slow decomposition rates (0 – 0.28 % d^{-1}) over the 72 - 121 d duration of the experiment, and evidence that kelp detritus continued to grow after deployment, especially in the Norwegian Sea and Gulf of Alaska (Fig. 2).

We used generalized linear mixed models to describe relationships between decomposition rates and environmental conditions on the seafloor (water temperature [average and range], light, water movement), as well as algal material traits (species, % carbon), while accounting for study region and site (Table 1, Supplementary Table 2). These models showed a significant positive relationship between kelp decomposition rate and average water temperature (Fig. 3a), which explained 72% of the variation of all fixed and random effects, suggesting that the observed patterns were largely driven by sea temperature. There was a negative correlation between average temperature and latitude across our study sites (Pearson's R = -0.59, $p < 0.001$, n = 35), but there was variation around this trend due to the influence of factors independent of latitude on temperature, such as ocean currents (e.g., Gulf Stream and Labrador Currents). We found no evidence that differences in water movement or light intensity influenced kelp decomposition, which we expected would either increase mechanical breakdown or delay tissue death by maintaining low levels of photosynthesis. Average light intensity was highly variable across the study regions (range 10 – 100 Lux), but average water movement was similar (range 0.98 – 1.15 g^3), likely due to consistent wave dampening by the cages which could explain its low importance in the model.

The two kelp species had different decomposition rates, with *S. latissima* losing biomass significantly faster than *L. hyperborea* (Fig. 3b, Table 1). Decomposition rates were more variable among regions than among sites within regions suggesting that heterogeneity in local conditions did not influence the larger spatial patterns in decomposition (Table 1). Initial % carbon content also had a significant effect on the decomposition rates during the experiment, with slower decomposition rates for detritus with higher carbon content (Table 1, Fig. 3c).

Over the experiment, the average nitrogen content increased significantly in both *S. latissima* and *L. hyperborea* detritus in some regions (*S. latissima*: France and Rhode I Sound; *L. hyperborea*: France and Scotland), suggesting that the kelp tissue became nitrogen enriched as it underwent degradation in these regions (Fig. 4), possibly via increased microbial abundance or activity. We did not detect a relationship between changes in kelp tissue composition (C:N or % nitrogen) and temperature, light, or water movement over the course of the experiment (Supplementary Table 3). The nitrogen content in kelp tissue at the onset of the study was highly variable among regions (Fig. 4), which likely reflects different background nutrient levels or initial kelp condition.

Discussion

Our experiments revealed a significant relationship between temperature and kelp detritus decomposition rates across the northern hemisphere, with markedly slower decomposition in cooler northern regions relative to warmer southern regions. Temperature dependence of organic-matter decomposition constitutes an important link between climate change and the global carbon cycle [5], including in the ocean where there are large actively cycling pools of organic matter [38,39]. There is a widely held view that decomposition rates and carbon turnover are faster at lower latitudes, due to increased microbial activity and metabolic rates of detritivores in warmer climates [8,17,40]. However, empirical evidence shows that these patterns do not hold in many systems, and such temperature relationships may not be universal [41–45]. Nevertheless, these relationships have important implications for potential positive feedbacks of climate change, and they underpin predictions of increased permafrost decomposition from microbial activity [7] and faster soil degradation from increased decomposer activity [6,46] with global warming. The present study shows that such a relationship exists for kelp detritus on a large spatial scale. Our study also identifies cool regions as possible hotspots for kelp carbon storage and sequestration by providing evidence that kelp detritus in these regions remains intact for longer, increasing its dispersal potential to carbon sinks [47]. This potentially has important consequences for global patterns of carbon cycling in the coastal zone.

The temperature-dependent rates of kelp decomposition uncovered here suggest that future kelp detritus turnover will become more rapid as coastal zones warm. Faster turnover means that detritus will have shorter residence time and lower potential to be exported and transported to deep marine sediments or water bodies or sequestered by burial in shallow soft sediments [9,47]. This would imply a loss of potential carbon sequestration within the current distribution of kelp forests [e.g., 48] under future warming. This change would also alter the nature of kelp as a resource subsidy, which will have ramifications for detrital food webs within the kelp forests and in adjacent habitats that rely on this source of production [20].

Importantly, although decomposition varied across regions, kelp detritus decomposed slower than many other dominant sources of organic carbon in the ocean (e.g., zooplankton casings, feces and debris, phytodetritus, bacteria), and at rates similar to other forms of benthic vegetation (e.g., seagrass and other seaweeds) (Table 2). This could be related to the physicochemical properties of kelp material, such as the presence of structural compounds and phenols [49]. Also, it could be because the material, even as detritus, can remain viable and photosynthetically active for extended periods in shallow subtidal areas with sufficient light to maintain net photosynthesis [50]. Although critical information about export of this detrital material is still lacking in many regions [11], our findings show that kelp detritus has long residence times in the coastal zone, and therefore high potential to be transported to deeper regions [36,47]. This is consistent with evidence that a substantial amount of kelp reaches deep marine sinks where it can be sequestered in the long-term [11,32,51].

We found a significant negative relationship between initial carbon content in detritus and decomposition rate, which could indicate that more carbon-rich tissue was less palatable to microorganisms or detritivores. This is supported by other studies showing detritus quality is a key predictor of decomposition [52,53]. The nitrogen enrichment of detritus that occurred in some regions may be explained by increased microbial colonization [54,55]. However, we detected no relationship between nitrogen enrichment and temperature over the course of the experiment. This finding differs from those of distributed decomposition experiments in freshwater systems that suggest warmer temperature shifts decomposition from detritivore to microbial pathways[53].

Kelp forests are currently changing in distribution and abundance due to climate change [21,24], with implications for the storage and cycling of kelp carbon. *S. latissima* and *L. hyperborea* are disappearing at their warmer southern range edges [56–58]. Kelp forests in other north Atlantic regions, such as around the British Isles, have undergone structural changes following climate-driven shifts in kelp species distributions [59], also leading to concomitant shifts in rates and timings of carbon fixation and release [60]. Along the west coast of North America, loss of predators and marine heatwaves are driving shifts from kelp forests to sea urchins barrens in some areas [61–63]. Our findings imply an overall reduction in rates of kelp carbon decomposition as oceans warm, which represents faster carbon cycling and lost storage potential. However, the predicted expansion of kelp forests along Arctic coasts due to reduced sea ice[64] could lead to extensive and more productive kelp forests in cooler regions, where decomposition rates are slower and long term carbon sequestration more likely [27,64,but see 65]. The consistent changes in decomposition across latitudes highlights the issues with representing major processes underpinning carbon cycling in the ocean in a uniform manner across space. While these patterns should be better understood, incorporating them into estimates of carbon cycling in a future ocean will improve current predictions and better resolve the climate mitigation potential of kelp forests. Indeed, understanding key processes such as decomposition at the ecosystem level should lead to a fuller understanding of carbon cycling on a global scale.

Methods

Fieldwork and laboratory analyses were conducted by a collaborative network covering the global range of two dominant and broadly distributed kelp species (*S. latissima* and *L. hyperborea*) (Fig. 1). Field decomposition rates of kelp detritus were quantified in concurrent, standardized litterbag experiments deployed in 12 regions throughout the northern hemisphere. Litterbag experiments are widely used to quantify decomposition rates in the field [66] by measuring the mass loss of plant material enclosed in mesh bags that allow water flow and microbial colonization while excluding large grazers and preventing biomass advection. In each region, three sites, approximately 0.5 to 10 km apart, were selected on sand or coarse sediment adjacent to rocky reefs in areas with low to moderate wave and current exposure (Supplementary Table 1). Litterbags were pre-assembled and shipped to all partners, ensuring identical treatments were deployed in all regions. We targeted overall patterns of kelp loss rather than attempting to distinguish between mesograzers (or detritivores) and microbial activity. Consequently, we did not vary

mesh size of the litterbags as this can substantially alter light and water flow, which may affect kelp decomposition.

In each of the 12 regions divers haphazardly collected 24 adult blades with minimal to no epibionts of each targeted species. Six regions collected and deployed two species (*S. latissima* and *L. hyperborea*), and six regions deployed one species (*S. latissima*) (Supplementary Table 1). From each blade a 20-g piece of kelp tissue was sectioned ~15 cm from the base and at least 15 cm from the distal end and weighed to the nearest 0.01 g. This approach was chosen to maximize blade uniformity across regions as older distal tissue would be less uniform depending on age and fouling. Using newly formed basal tissue also minimized phenological or seasonal differences in detrital material from slight variation in timing of the trials across regions, which may influence the decomposition rates. Additional kelp samples (n = 8-10) were collected for each species for baseline C:N analyses.

A single kelp piece was loosely packed into each litterbag (plastic ~1 x 1-cm mesh bags) and placed into cages (four litterbags in each of the two cages for each species at each site), to allow access of smaller mesograzers. Cages were 20 cm by 20 cm by 40 cm and made of plastic 1 x 1 cm mesh ('gutter guard'). Each cage was tethered with cable ties to a weight on the seafloor at ~8-m depth. In order to accurately quantify the impact of ocean climate on decomposition, we selected this cage size to exclude grazing by large herbivores in our experiments, which can drive localized increases in the turnover, size, and availability of kelp detritus in some areas [36] and could overwhelm measures of turnover in areas where they were locally abundant. All kelp pieces were kept damp after collection, stored in a dark cooler and deployed within 24 hours of collection.

Environmental variables known to influence decomposition were measured concurrently throughout the experiment at each site. Hourly light and temperature were measured by an Onset HOBO pendant temperature and light logger fixed to the top of a cage at each site. Only light records for the first two weeks of deployment were used to account for fouling of the sensor, which could shade and confound measurements over time. To estimate wave action, an Onset HOBO G logger was placed inside a mesh bag and added to a cage at each site to log hourly movement of the litterbags. We used the average product of logged acceleration along 3 axes (x, y and z, units of g^3) of the period as a relative measure of movement of the litterbags.

Approximately 4-6 weeks into the experiment half the litterbags were collected (two from each cage). The remaining litterbags were collected after 12-18 weeks. Litterbags were lost at some sites (Supplementary Table 1). Samples were processed within 10 h of collection. All kelp fragments were removed from bags, patted dry, and weighed to the nearest 0.01 g. Weighed samples were rinsed in distilled water, oven dried at 60 °C for 48 h, and then shipped to the University of California (Davis, CA, USA) where they were analyzed for nitrogen and carbon tissue content.

We compared the obtained values of kelp decomposition to that of other marine detritus using data from litterbags or incubations obtained from the literature (Supplementary Table 4). For each type of organic

material (seaweed, seagrass, mangrove, other particulate detritus (e.g., marine snow, zooplankton feces or debris), and dissolved organic material (DOM)) we calculated residence times (days to 50% loss). This metric enabled comparison between materials with different decay functions. We did not include refractory pools of DOM or below-ground decomposition.

Analysis

Rates of kelp loss (average rate of biomass loss for each retrieval time at each site) as a function of environmental conditions and kelp tissue properties were analyzed by generalized linear mixed effects models. Sites were averaged because litterbags in the same cage were not independent replicates. We also calculated k values, using the equation $y = e^{-kt}$, where y is the proportion of biomass remaining at a time point and t is the time elapsed since the beginning of the experiment (days), but linear rates of loss fit our dataset better. The lagged onset of decomposition in some of our study regions may explain why our linear decomposition rates, although similar to other regional decomposition experiments on kelp detritus [50,55], deviated from patterns of exponential decay shown for other types of organic material [67]. Because we were examining kelp decomposition, any negative rates of loss (biomass increase or growth) were assigned a value of 0 in our model, as a growing kelp is undergoing little to no decomposition. This was important for sites in the subarctic, where kelp detritus continued to grow after deployment. Our predictor variables were obtained from logger data and stable isotope measures. The fixed effects were kelp species, average water temperature, range in water temperature, average light conditions, and relative water movement during the experimental period, as well as site nested within region as the random effects. We used two variables to capture temperature conditions, the average temperature over the deployment and the temperature range (the difference between the 10^{th} and 90^{th} percentiles) as temperature ranges varied markedly, from 0.6 to 18.6 °C. Average temperatures and peak temperatures (90^{th} percentile) were highly correlated among sites (Pearson's $R = 0.96$, $p < 0.001$), so peak temperatures were not included in our model. Temperature loggers were lost in the Gulf of Maine region, so temperatures were obtained from the closest meteorological weather buoy (19 km away).

We accounted for differences in starting kelp conditions using initial % carbon content in kelp tissue as fixed effects in the model. This variable was correlated with initial % nitrogen and C:N ratio (Pearson's correlation tests, $R > 0.7$), so only initial % carbon was included in the model. Carbon content was modelled separately using a subset of the data, because these measures were not available for Gulf of Maine, Rhode I Sound, and the Gulf of St Lawrence. The main relationships between the other key variables (light, temperature, species) were similar in both models. To confirm the latitudinal gradient was statistically significant, we ran another model using the continuous variable of 'latitude' as a predictor of biomass loss instead of a categorical variable (region name) (Supplementary Information 1). We did not use 'latitude' in our final model because it was correlated with temperature and the environmental gradients underlying these latitudinal differences provided more interesting and operational information on spatial patterns of carbon turnover.

We tested for significant nitrogen enrichment of *S. latissima* and *L. hyperborea* using a 2-way ANOVA comparing %N at the start and end of the experiment among regions. Post-hoc comparisons were conducted for each region using Tukey's tests.

All analyses were conducted in R (version 3.5.3). We used the glmer function from package *lme4* to fit the generalized linear mixed-effects models. Decomposition models were fit with a gamma distribution and identity link function. We checked model residuals for violation of model assumptions and to investigate the suitability of the chosen distribution (i.e. deviance residuals vs. theoretical quantiles), dispersion and heteroscedasticity, using package *DHARMa* (Supplementary Information 1). To stabilize parameter estimation, we standardized mean light by dividing it by 100, so it matched the scale of the other predictor variables. We used likelihood ratio tests with single-term deletions to assess the importance of each fixed effect predictor in the models. Relationships between the most important predictor variables and decomposition rates were illustrated with package *visreg*, which shows the relationship between a single predictor and the model outcome while holding the other predictors constant [68].

Declarations

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Author contributions: DS, KFD, KK, TW, MFP, KMN, MB, PJM, KH, and KHD conceived the study. KFD, TW, DS, and KK designed the experiment. CF and DY led the stable isotope analyses. KFD collated and analyzed the data, made the figures and led the writing of the manuscript. TW, CJF, DS, JB, KK, MP, and PJM and provided statistical advice on data analysis and helped interpret the results. All authors funded, organized and/or participated in the fieldwork, edited the manuscript and agreed to its publication in its current form.

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Tables

Table 1. Summary of generalized linear mixed-effects models (GLMM) relating the decomposition (% d-1) of kelp detritus to environmental conditions and tissue properties at 12 regions of the northern hemisphere. Temperature (average and range) is temperature at the seafloor over the duration of the experiment. Light is average light (Lux) over the first 2 weeks of the experiment. The % carbon is the initial carbon content in the kelp detritus, and water movement is average g forces within the cages over the experiment. GLMMs are with gamma distribution and identity link function. Model 1 uses the full dataset (n = 12 regions) with predictors temperature (range, average), light and species, and model 2 uses a subset of the data (n = 9 regions) with additional predictors % carbon content and water movement, because these variables were not obtained at all 12 regions. Importance of fixed effects parameters were evaluated using likelihood ratio tests with single-term deletions. Shown for each deletion are percentage of deviance explained (%De) and Chi-squared statistic used to compare model with deletion to full model. Site and region represent random effects.

Model 1 **Fixed effects**	**Log-Likelihood**	**% De**	**Chi^2**	**p**
All parameters	-11,470			
Average temperature	-15,208	32.8	7,47	**0,006**
Temperature range	-11,48	0,31	0,02	0,887
Light	-11,640	1.66	0,33	0,566
Species	-14,966	28.1	6,45	**0,011**
Random effects	**N**	**Variance**	**SD**	
(1 | Site:Region)	34	0.014	0.118	
(1 | Region)	12	0.156	0.395	
Residual		0.032	0.178	

Model 2 **Fixed Effects**	**Log-Likelihood**	**% De**	**Chi^2**	**P**
All parameters	-10.33			
Average temperature	-15.24	47.5	9.82	**0.002**
Temperature range	-10.81	4.6	0.94	0.332
% carbon	-13.53	30.9	6.39	**0.012**
Light	-10.55	2.1	0.43	0.510
Water movement	-10.46	1.2	0.24	0.621
Species	-15.26	47.7	9.85	**0.002**
Random effects	**N**	**Variance**	**SD**	
(1 | Site:Region)	26	0.020	0.143	
(1 | Region)	9	0.090	0.300	
Residual		0.024	0.154	

Figures

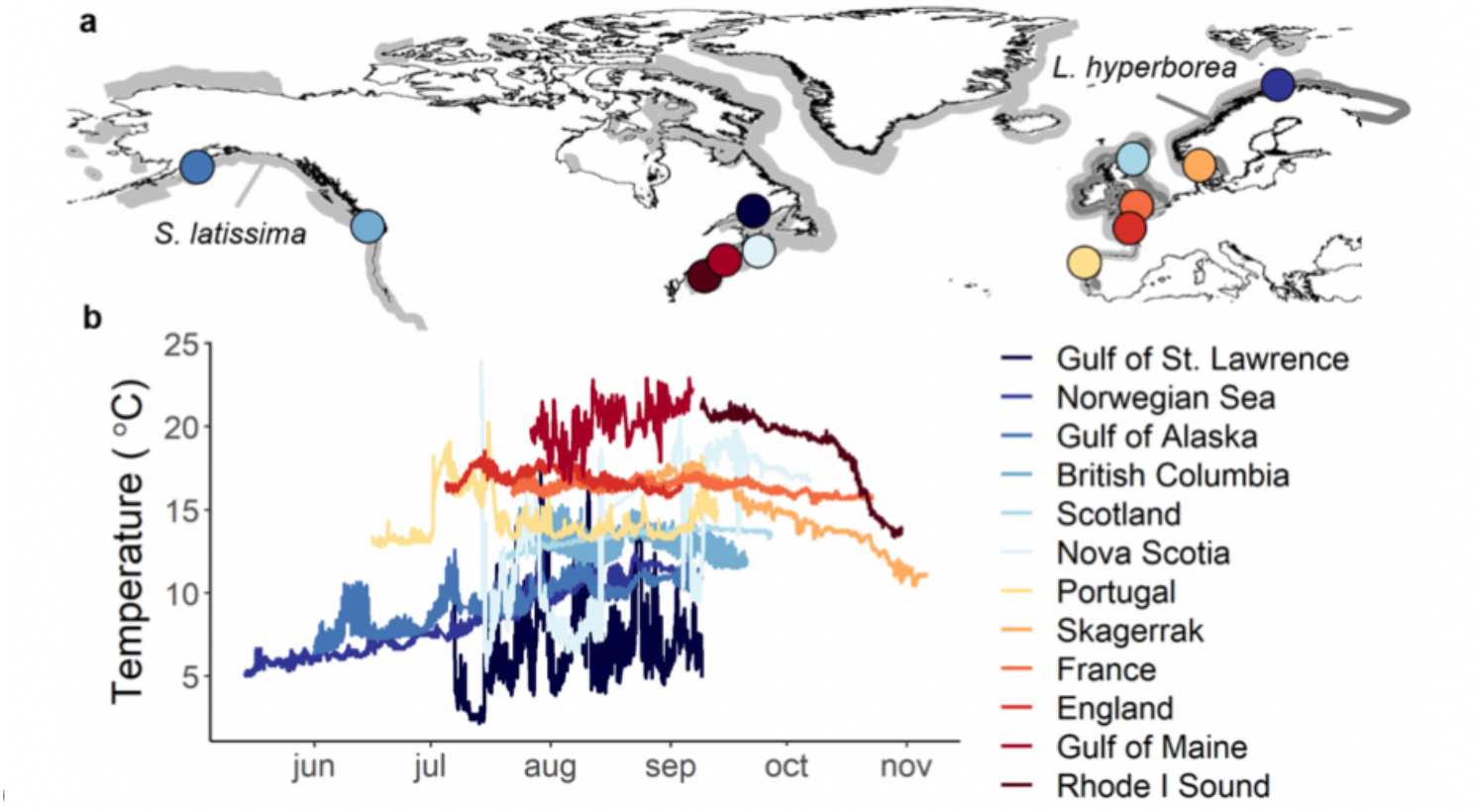

Figure 1

Study regions and temperatures. Map of study regions (a) and temperature records (b) over the duration of the experiment. Distributions of Saccharina latissima and Laminaria hyperborea kelps, modified from 37, are shown in light and dark gray respectively. Additional details in Supplementary Table 1. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

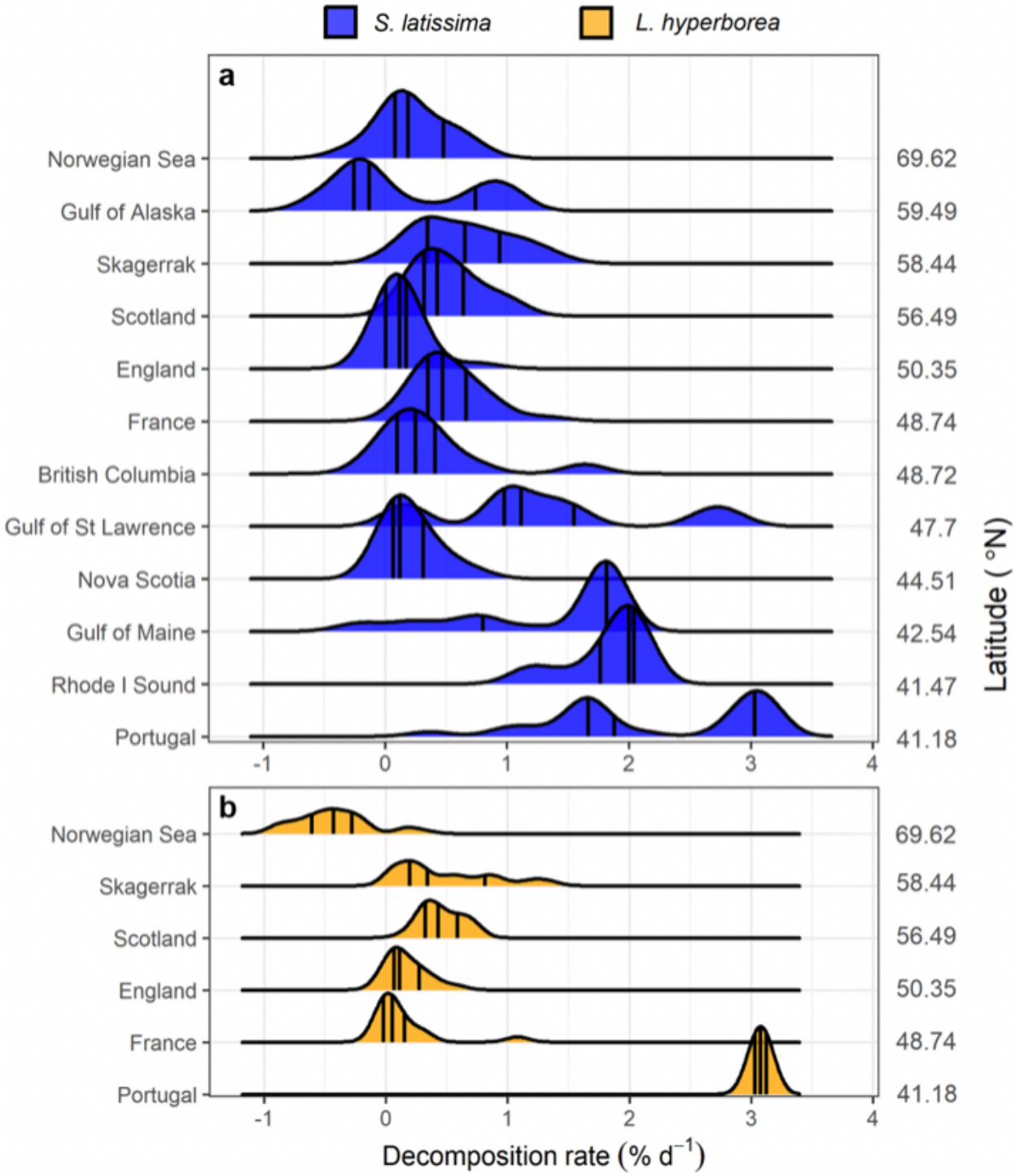

Figure 2

Kelp decomposition rates. Probability density functions of decomposition rates of (a) Saccharina latissima and (b) Laminaria hyperborea throughout the northern hemisphere. Curves show frequency of observations, pooled across sites in each region and ordered by latitude. Black middle lines show medians, and outer lines show the 25th and 75th quantiles. Y axes units are the proportion of observations, ranging from 0 to 0.18 (a) and from 0 to 0.9 (b) for each site.

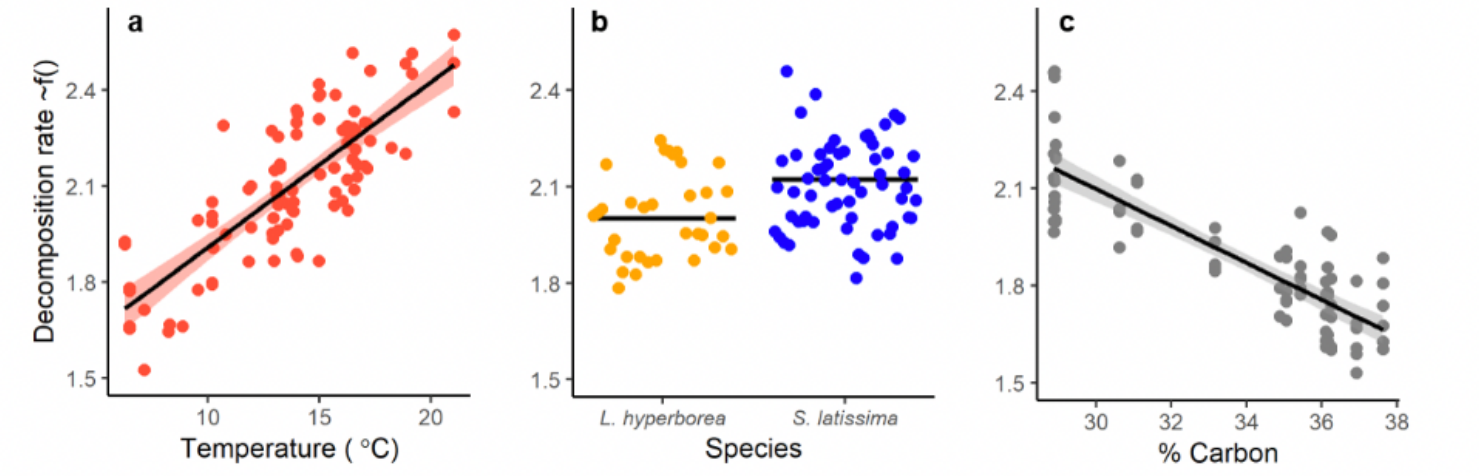

Figure 3

Drivers of decomposition. Relationships between kelp decomposition rate (% d-1) and significant predictor variables in generalized linear models: (a) average water temperature during the experiment, (b) species, and (c) initial % carbon content, from the generalized linear mixed effect models, with all other variables in the model held fixed. Black lines are the expected value from the model, shaded error bar (a & c) is confidence interval, and points are partial residuals for each sampling time at each site. Relationship with % carbon is based on a subset of 9 out of 12 regions for which data existed.

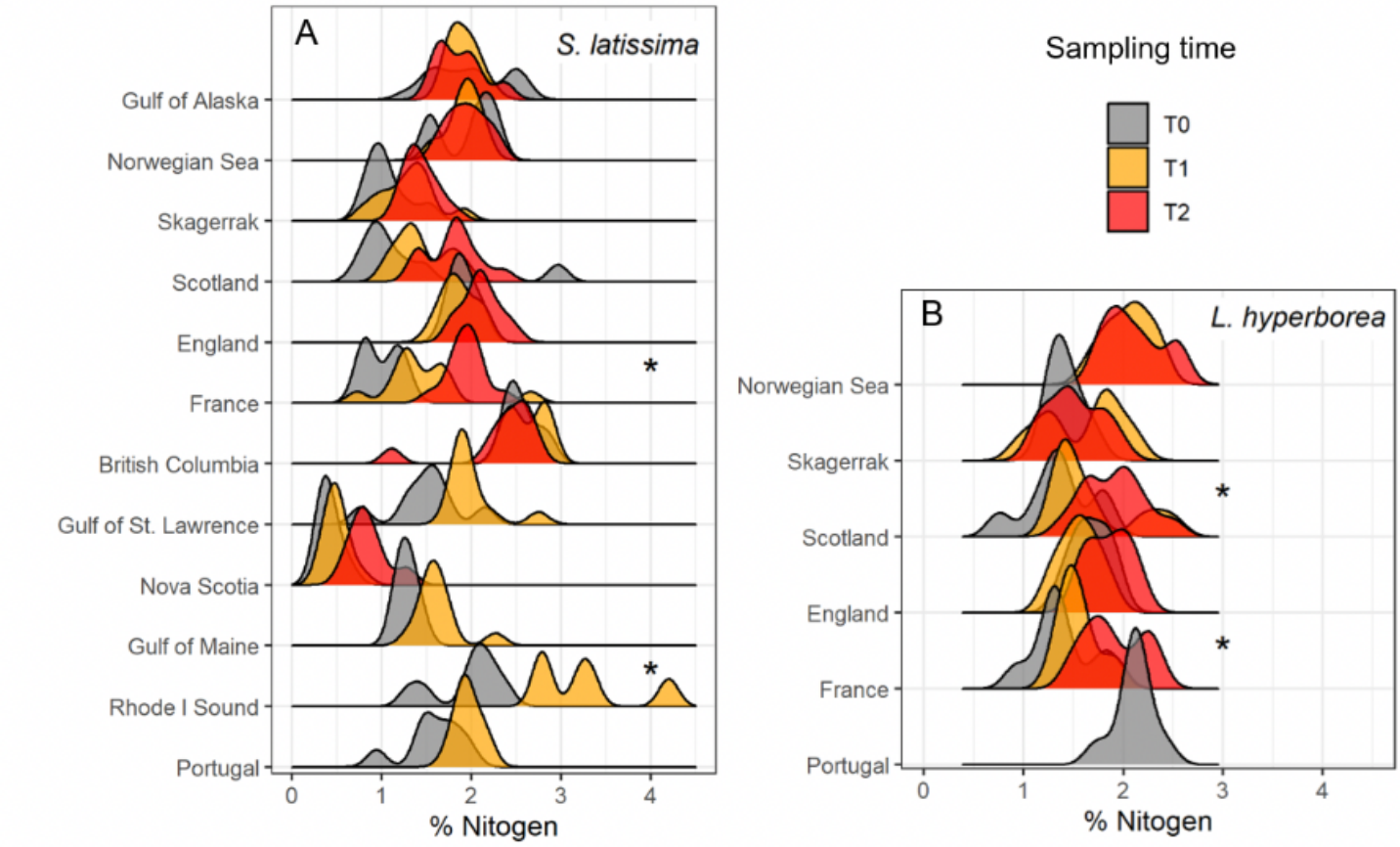

Figure 4

Change in detritus quality. Total nitrogen content in kelp detritus over the experiment for Saccharina latissima and Laminaria hyperborea. Data are frequency measures of % nitrogen from tissue samples taken at the onset of the experiment (T0), the first sampling time (T1) and the final sampling (T2). Y axes units are the proportion of observations. Measures are pooled across sites for each region and ordered by decreasing latitude. Values are missing for later samplings in some regions because insufficient biomass remained for analysis at the time of sampling (* denotes statistical significance, post hoc tests in Supplementary Table 3).

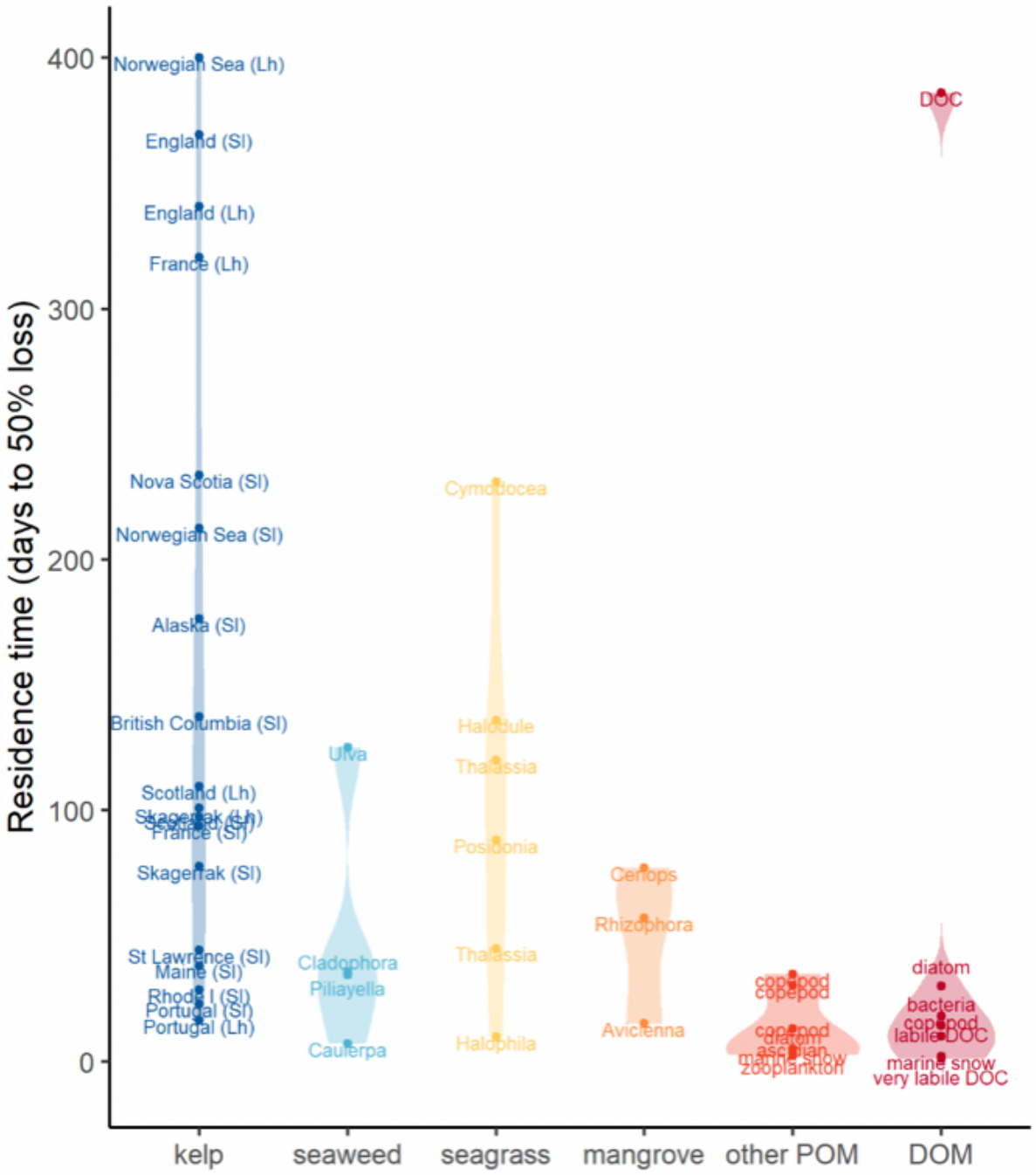

Figure 5

Figure 4. Residence time of marine detritus. Residence times (days to 50% decomposition) reported for different types of marine detritus, including kelps from our study regions (SI = Saccharina latissima; Lh = Laminaria hyperborea) and measures reported in the literature for other seaweeds, seagrass, mangrove detritus (leaf), other particulate organic material (POM) and dissolved organic material (DOM) (Supplementary Table 4). POM consist of zooplankton debris, feces, fauna casings and marine snow.

DOM is labile DOC or DOM released from zooplankton debris or marine snow during incubations. Refractory DOC is not shown and residence times for this organic carbon pool range from years to decades or more.

Supplementary Files

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