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Carbon sequestration potential increased by incomplete anaerobic decomposition of kelp detritus

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ABSTRACT: Kelps are highly productive macroalgae that form habitats along one-quarter of the worlds' coastlines. Emerging evidence suggests that kelps have the potential to sequester carbon through the export of detritus to deep marine sinks, yet how much of this detrital carbon is remineralized through grazing and microbial decomposition before it reaches these sinks remains a critical knowledge gap. We measured decay of *Laminaria hyperborea* detritus in shallow kelp forests (10 m) and adjacent deep fjords (300 m), and experimentally tested the effect of temperature and oxygen conditions similar to those at these habitats in *ex situ* experiments. Initial decay rate (k) was high (–0.107 to –0.183 d^{-1}) with 40–60% of the original carbon biomass being lost within few weeks, after which decay rates slowed down (k = –0.009 to –0.038 d^{-1}). Temperature had little effect on the rate and extent of decomposition within the temperature range tested (4–10°C). Blade detritus decomposed almost completely in 300 d under aerobic conditions. Anaerobic decay of both blade and stipe detritus ceased, in contrast, after 150–200 d, leaving 20–30% of the initial biomass to decompose extremely slowly or not at all. Decomposition was followed by changes in chemical composition; C:N ratios increased substantially, while mannitol and phenolics disappeared almost completely from the detritus matrix. Slow and incomplete anaerobic decomposition suggest that the potential for long-term burial and sequestration of kelp carbon will be enhanced if detritus is exported to nearby deep areas with permanent or periodic hypoxia near the bottom.

KEY WORDS: *Laminaria hyperborea* · Blue carbon · Carbon sink · Burial · Refractory compounds · Macroalgae

1. INTRODUCTION

Blue carbon is defined as carbon (C) captured by marine living organisms (Nellemann et al. 2009), and sequestration of blue C through long-term burial is considered one of several criteria for identifying marine habitats as being blue C ecosystems (Lovelock & Duarte 2019). The importance of blue C has received increased attention (e.g. Mcleod et al. 2011, Duarte 2017, Filbee-Dexter & Wernberg 2020), and coastal wetland habitats, such as seagrass meadows, marshlands and mangrove forests are already recognized as effective long-term C sinks (Chmura et al. 2003, Donato et al. 2011, Fourqurean et al. 2012). The role of macroalgal C in the global C budget is, in contrast, a subject of current debate, and it remains unclear

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whether or not macroalgal C (especially kelp) contributes substantially to C sequestration (e.g. Howard et al. 2017, Krause-Jensen et al. 2018, Smale et al. 2018). Any type of vegetation (terrestrial or aquatic) must meet some basic criteria to contribute meaningfully to C sequestration: (1) it must cover a substantial proportion of the Earth's surface area, (2) it must have a high net production per unit area and time, (3) the consumption of live and dead biomass must be small enough to minimize mineralization of C through respiration at higher trophic levels, and finally (4) part of the detritus must be in a form (or under environmental conditions) such that it decomposes slowly and/or incompletely, because that will increase the probability of permanent burial in soils or sediments.

Large, slow-growing perennial brown algae (kelps and fucoids) constitute the major foundation species along one-quarter of the coastlines globally (Wernberg et al. 2019, Jayathilake & Costello 2020). Kelp systems are among the most productive habitats on Earth, with primary production averaging 500–600 g C m^{-2} yr^{-1} (Krumhansl & Scheibling 2012) and high rates exceeding 2000 g C m^{-2} yr^{-1} (e.g. Mann 1973, Abdullah & Fredriksen 2004). Grazing on live kelp is typically low (0–20% of the production; Burkepile & Hay 2006), although it can be exceptionally high in disturbed systems with outbreaks of herbivores (e.g. sea urchins: Filbee-Dexter & Scheibling 2014, or range-extending fish: Bennett et al. 2015). Most kelp production is thus channeled to the detrital pool within or outside the kelp forest (Krumhansl & Scheibling 2012), and these systems are therefore considered potentially important C donors to blue carbon sediments in adjacent ecosystems (Hill et al. 2015, Krause-Jensen & Duarte 2016, Filbee-Dexter & Wernberg 2020).

The amount of C fixed by, and stored in, live kelp forests can be substantial (e.g. Pedersen et al. 2012, 2020, Smale et al. 2016, Filbee-Dexter & Wernberg 2020), but such storage is transient, because C-fixation is balanced by equivalent losses of C through grazing and formation of detritus, unless the range distribution and/or total kelp biomass is increasing. The same applies to detrital kelp C; inputs to the detrital pool will be balanced by decomposition, unless some of the detritus becomes permanently buried under conditions that disfavor mineralization through microbial respiration.

Detritus is made up by several fractions (i.e. groups of chemical compounds) that decompose at different rates and to a different extent. Low molecular weight compounds, such as amino acids and simple sugars, are typically broken down quickly, whereas structural (e.g. cell wall) compounds decompose more slowly or not at all over measurable time scales (Adair et al. 2008). Aging detritus, therefore, contains often increasing concentrations of relatively inert compounds (Arndt et al. 2013). Decomposition rate and the extent to which detritus decomposes are affected both by intrinsic and extrinsic (environmental) factors. Decomposition rate is positively correlated with the content of nitrogen (N) and phosphorus (P) in the detritus, when compared across plant types ranging from microalgae to trees (Enríquez et al. 1993), but negatively correlated with the amount of structural cell wall compounds, such as lignin, cellulose, hemicellulose and phenolic compounds (e.g. Aber et al. 1990). Kelps and other macroalgae do not contain lignin, and contain less cellulose and hemicellulose than vascular plants, but their cell walls contain other structural compounds (e.g. alginates, xylans, carrageans, agars and phenolics) which may decompose slower and/or less completely than low molecular compounds (Trevathan-Tackett et al. 2015). Decomposition is also affected by environmental conditions, and decay rate usually increases with increasing temperature (Arnosti et al. 1998, Pomeroy & Wiebe 2001, Price & Sowers 2004), although the relationship between decomposition rate and temperature is not straightforward and may depend on microbial physiology, reaction pathway(s), involved time-scales and the magnitude of temperature changes (Arndt et al. 2013). Decomposition also depends on the availability of electron acceptors (Kristensen et al. 1995, Hulthe et al. 1998). Oxygen (O_2) is a powerful electron acceptor, and decomposition is fast under aerobic conditions but slows down when O_2 is depleted and replaced by alternative electron acceptors (e.g. nitrate, sulfate, iron). Environmental conditions that disfavor decomposition (i.e. low temperature and/or anoxia) may thus delay or prevent decomposition and increase the probability of C burial.

Laminaria hyperborea is the dominant kelp species in the NE Atlantic, where it is common from northern Portugal in the south to the Russian Murmansk region in the north (Lüning 1990). Recent studies from the UK and Norway show that *L. hyperborea* produces between 280 and 500 g detrital C m^{-2} yr^{-1} and that the majority of that detritus is delivered as coarse particulate matter such as whole stipes, blades or visible blade fragments (Pessarrodona et al. 2018, Pedersen et al. 2020). Some of that detritus gets trapped within the kelp forest, where it may be consumed and/or shredded by detritivores (Filbee-Dexter et al. 2020) or decompose at relatively high temperature and under aerobic conditions, while the

remaining fractions may be exported and end up as beach cast or, more commonly, enter adjacent, deeper areas (Filbee-Dexter et al. 2018, 2020), where decomposition may proceed at lower temperature and under hypoxic conditions (Gage 2003).

The aim of this study was to investigate decomposition of kelp *L. hyperborea* detritus within high latitude kelp forests and their adjacent deep fjords, known to receive inputs of kelp detritus. We measured decomposition in the laboratory under different temperature and O_2 levels that mimicked environmental conditions encountered within kelp forests and adjacent deep fjords, as well as in the field at shallow (10 m) and deep (300 m) sites. We expected decomposition to be relatively fast and complete in high temperature and aerobic conditions like in the kelp forest, and slower and less complete at lower temperature and low O_2 concentrations as in deeper areas adjacent to kelp forests.

2. MATERIALS AND METHODS

2.1. Collection of material for laboratory experiments

Live kelp material was collected at the mouth of Malangen Fjord, northern Norway (69.6° N, 18.0° E) in October 2016. The material was wrapped in wet paper, packed in sealed plastic bags, and immediately transported by air (<10 h) to Roskilde University, Denmark, where it was kept in the dark in 200 l tanks with seawater (10°C and salinity 34 PSU) for 24 h before being used in the experiment.

2.2. Experimental setup

The setup consisted of 32 tanks (= experimental units), each with a volume of 24 l (dimensions: 30 × 40 × 20 cm). Sixteen tanks were placed in each of 2 identical, thermo-regulated, walk-in culture rooms, where the target temperatures were set to 4 and 10°C, respectively. Temperature in the 2 climate rooms was monitored hourly using HOBO temperature loggers (mean ±1 SD in climate room #1: 3.8 ± 0.7°C, n = 7680; climate room #2: 9.2 ± 0.3°C, n = 7680). All tanks were filled with 8 l of freshly collected and sieved (mesh size = 1 mm) sediment, collected at 1–2 m depth in Roskilde Fjord (Denmark) and with 15 l of natural seawater (salinity 34 PSU). Half the tanks (8) in each culture room were kept aerobic (8.9–10.1 mg O_2 l^{-1}; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m660p053_supp.pdf) by bubbling the water in each of these tanks with atmospheric air, while hypoxic conditions (0.6–0.7 mg O_2 l^{-1}; Table S1) were obtained in the remaining tanks by bubbling their water with N_2.

Blade and stipe materials were cut into smaller pieces using the mid 25–30 cm of the blades and the top 25 cm of the stipes. A subsample of the fragments (n = 8 of each) was frozen and freeze-dried for analysis of initial chemical composition. The remaining fragments were weighed (initial fresh weight; initial FW), and placed in litterbags with a mesh size of 1 mm. Ten litterbags with either blade or stipe fragments were placed in each of the tanks (16 tanks with blade fragments and 16 with stipe fragments). Bags were placed on the sediment surface and covered by a thin layer of sediment (ca. 1 mm) to keep them in close contact with the sediment. The design thus consisted of 8 treatment combinations (i.e. blade or stipe, low or high temperature, low or high O_2 availability), each with 4 replicates. The experiment was conducted in complete darkness to avoid photosynthetic activity in the kelp fragments. The O_2 concentration in the water of each tank was measured bi-weekly using a 'Handy Polaris 2' O_2 probe (OxyGuard), which had been calibrated in seawater (34 PSU and at the same temperatures as in the experiment) containing 0 and 100 % O_2, respectively. Seawater was added to all tanks weekly to compensate for evaporation, and the salinity was adjusted to ca. 34 PSU using tap water when necessary. Water circulation in the tanks was provided by continuously bubbling the water with atmospheric air or N_2 (depending on O_2 treatment).

One randomly chosen litterbag with blade detritus was collected from each tank on Days 7, 21, 49, 77, 105, 126, 149, 193, 229 and 280, while bags with stipe detritus were collected on Days 7, 21, 49, 77, 105, 140, 193, 229, 280 and 308. The contents of each bag were collected, rinsed for debris and sediment, weighed (FW at any sampling time above) and stored at −80°C before being freeze-dried, weighed (dry weight [DW] at any time above), ground to fine powder and stored at −26°C until further analysis.

2.3. Chemical composition

Tissue concentrations of C and N were determined using an EA 1110 CHNS elemental analyzer (CE Instruments). Mannitol content was measured according to Vaskovsky & Isay (1969) on 3–5 mg freeze-dried ground samples that were extracted for 15 min in iso-

propanol (50%) and centrifuged for 5 min at 9000 × *g*. Rhamnose solution, containing periodic acid, was added to the supernatant to react for 5 min, after which the reaction was stopped by adding Nash reagent. The reaction between mannitol and periodic acid was measured at 412 nm on a spectrophotometer (Shimadzu UV-1601). The content of polyphenolics was measured using a modified version of the Folin-Ciocalteu procedure (Ainsworth & Gillespie 2007). Aliquots (ca. 10 mg DW) were mixed with 2.0 ml 95% methanol, and incubated in the dark at room temperature for 24 h, after which they were centrifuged at 2500 × *g* for 5 min. Duplicate samples of the supernatant (each 250 µl) were transferred to 15 ml tubes, mixed with 500 µl F-C reagent, and left to oxidize for 5 min before the oxidation process was stopped by adding of 2.0 ml of 700 mM Na_2CO_3. Samples were left in the dark for 2 h at room temperature, and the absorbance was finally measured at 765 nm using known concentrations of Gallic acid as standards.

2.4. Thermogravimetric analyses

Thermogravimetric analysis (TGA) was used to assess temporal changes in overall chemical composition of the detritus. Thermal degradation of detritus samples obtained at time points 0, 41 and 280 d (308 d for stipe detritus) was measured using a Netzsch TG 209 F3 Tarsus thermogravimetric analyzer (NETZSCH-Gerätebau). An aliquot of ground sample (10–15 mg DW) was placed in an Al_2O_3 crucible and heated under N_2 flow (30 ml min^{-1}). Samples were heated from 35–800°C at a rate of 20°C min^{-1}, including an isothermal ramp at 105°C for 5 min followed by another isothermal step at 800°C for 10 min, while changes in mass were recorded continuously. Weight losses were estimated for each for 4 temperature intervals: 180–300, 300–400, 400–600 and 600–800°C.

2.5. Field experiment

We measured *in situ* kelp decomposition in shallow subtidal (10 m depth) and deep (300 m depth) habitats in Malangen Fjord. Live kelp blades were collected around the study sites between 27 March and 13 May 2018. The material was cut into pieces, patted dry, weighed to the nearest 0.1 g FW and placed into mesh litterbags (1 × 1 cm mesh size) that were enclosed in larger mesh cages (20 × 20 × 40 cm) to exclude sea urchins. Litterbags were deployed in the field within 24 h of collection by attaching them to an anchor and lowering them to the seafloor with a surface float. Divers visually inspected the litterbags at the shallow sites to ensure that they were positioned on sediment. Litterbags (n = 4) were collected from each shallow site on Days 52 and 121 after deployment, while samples at the 2 deep sites (n = 6 $site^{-1}$) were collected after 37 d due to heavy ship traffic in the area. Upon collection, the contents of each bag were rinsed for debris and sediment and weighed (FW) before being oven-dried, ground to fine powder and analyzed for tissue concentrations of C and N.

2.6. Statistical analysis

The factor temperature was, technically speaking, not properly replicated, because tanks exposed to each of the 2 temperatures were placed in 2 separate climate rooms (Hurlbert 1984). The conditions in the 2 climate rooms were, however, completely identical, except for the applied temperature, and therefore we assume that any significant difference in response between groups from different climate rooms was due to differences in temperature.

Decomposition rates were estimated by fitting a decay model with a plateau to the data (i.e. remaining C biomass vs. time):

$$B_t = B_0 \times e^{-k \times t} + R_G \quad (1)$$

where B_0 is the initial detrital mass, B_t is the mass remaining at time t, k is the exponential decay rate and R_G is the refractory fraction, which does not decompose over measurable time scales. Blade detritus lost a significant portion of its biomass during the first week of the experiment, and these data did not fit the model (1). Initial decay rates ($k_{initial}$) obtained over the first week were therefore estimated from data points obtained at Days 0 and 7 assuming exponential decay. Parameter estimates of k and R_G were compared between detritus types (i.e. blade vs. stipe) and between treatments (i.e. aerobic vs. anerobic and 4 vs. 10°C) using Student's t-test for paired observation.

Tissue C:N ratios from the laboratory experiment were compared across time and treatments using 2 factorial repeated measures ANOVA (factors: time, temperature and O_2 level; all considered fixed). Data for mannitol and phenolics did not conform to parametric analysis (i.e. normality of residuals as evaluated by Kolmogorov-Smirnoff's test and/or variance homogeneity as evaluated by Levene's test), so these data were compared across time, O_2 treatment and temperature treatment separately using non-para-

metric 1-factor ANOVA (Kruskal-Wallis [KW] test). Blade and stipe data were analyzed separately because these were sampled at different time points. Overall differences in C:N ratio, mannitol content and phenolics between blade and stipe detritus were compared using Mann-Whitney (MW) *U*-test. Total mass losses during pyrolysis and mass losses obtained in each of the 4 temperature intervals applied were compared over time and across O_2 treatment using 2-factor ANOVA (factors: time and O_2-condition; both considered fixed).

Tissue C:N ratios from deep and shallow field experiments were compared across time and sites using 2-factor ANOVA (factors: time and site; both considered fixed). The proportion of detritus lost after 37 d was compared across deep sites using Student's *t*-test and across shallow sites using a 2-factor ANOVA (factors: time and site). All statistical analyses were performed using SYSTAT v.13.2.

3. RESULTS

3.1. Decomposition in the laboratory experiment

Blade detritus lost 40–60% of its initial C biomass during the first week of the laboratory experiment (Fig. 1A,B), corresponding to decay rates ranging from –0.107 to –0.183 d^{-1} depending on treatment (Table 1). Neither temperature nor O_2 treatment had any significant effect on $k_{initial}$ (paired *t*-test: $t_{Temp} = -1.18$, p = 0.447 and $t_{O2} = -1.58$, p = 0.359). The initial phase of rapid decomposition was followed by a phase with slower decay (k = –0.009 to –0.038 d^{-1}) and, under anaerobic conditions, a third stage with extremely slow or no decomposition at all. Practically all blade detritus had disappeared within 280 d under aerobic conditions, whereas the decay of blade detritus ceased after ca. 4 mo under anaerobic conditions, leaving ca. 20% of the original C biomass at the end of the experiment. Stipe detritus decomposed slower (k = –0.013 to –0.037 d^{-1}) and less completely (R_G = 13.8–29.2% biomass remaining after 308 d) than blade detritus (Fig. 1C,D, Table 1). Decay rates and the amount of refractory detritus in blade and stipe detritus were not affected by temperature (paired *t*-test: $t_k = -1.50$, p = 0.230 and $t_{RG} = 3.16$, p = 0.119), but both were affected by O_2 conditions: decay was faster (paired *t*-test: $t_k = 5.95$, p = 0.027) and the amount of refractory detritus highest (paired *t*-test: $t_{RG} = 6.48$, p = 0.009) under anaerobic conditions.

3.2. Chemical changes in detritus in the laboratory experiment

The C content in blade detritus (Fig. S1, Table S2) decreased from 35.9 ± 0.4 to 29.5 ± 1.8% of DW (mean ± 95% CL) over the first 7 wk ($F_{Time} = 17.2$, p <

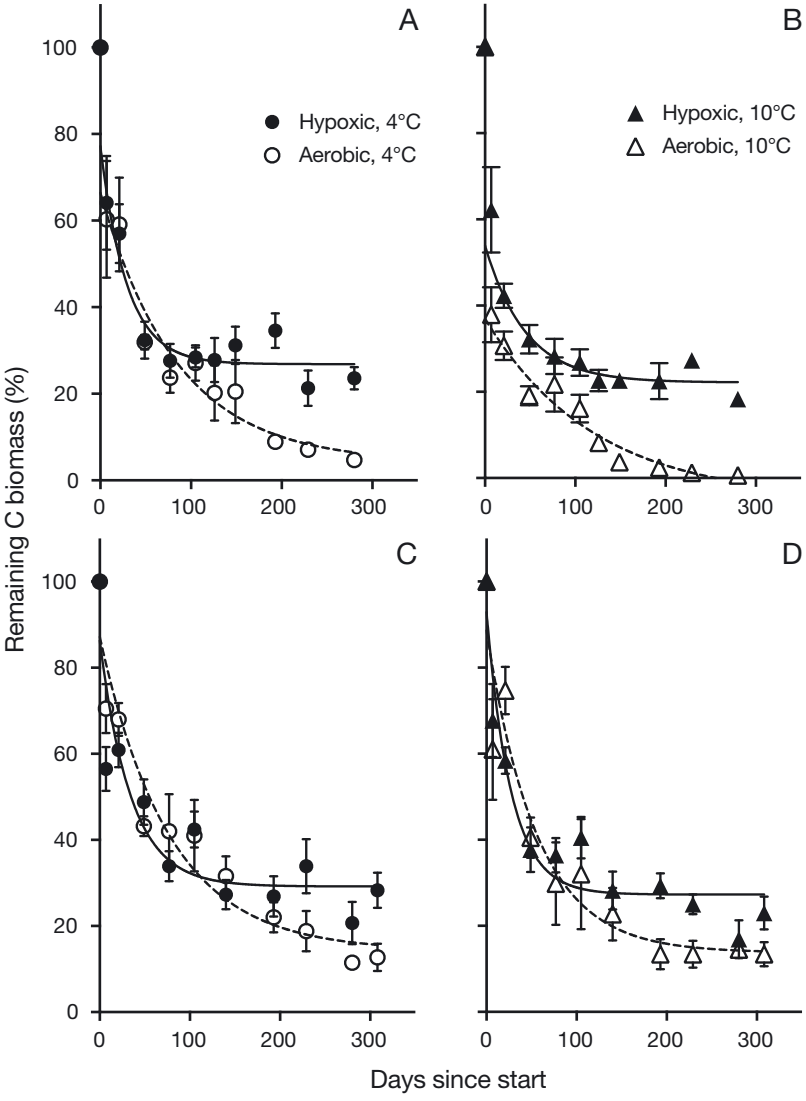

Fig. 1. Changes in detrital carbon (C) biomass over time under hypoxic and aerobic conditions: (A) blade detritus at 4°C, (B) blade detritus at 10°C, (C) stipe detritus at 4°C and (D) stipe detritus at 10°C. Means ±1 SD (n = 4)

Table 1. Mean (±1 SE) parameter estimates of *Laminaria hyperborea* decomposition rate (k) and the refractory pool (R_G) based on changes in carbon biomass over time. The initial decay rate ($k_{initial}$) for blade detritus was estimated from the rapid loss of biomass during the first 7 d of the experiment assuming exponential decay

Treatment	$-k_{initial}$ (d^{-1})	$-k$ (d^{-1})	R_G (% of initial biomass)	R^2 (corrected)
Blade detritus				
Hypoxic 4°C	0.107 ± 0.047	0.034 ± 0.024	26.9 ± 4.8	0.903
Aerobic 4°C	0.123 ± 0.071	0.012 ± 0.008	4.1 ± 13.4	0.945
Hypoxic 10°C	0.112 ± 0.051	0.038 ± 0.022	23.4 ± 3.5	0.695
Aerobic 10°C	0.183 ± 0.050	0.009 ± 0.005	−3.7 ± 9.6	0.785
Stipe detritus				
Hypoxic 4°C		0.029 ± 0.029	29.2 ± 10.4	0.803
Aerobic 4°C		0.013 ± 0.008	14.3 ± 13.4	0.919
Hypoxic 10°C		0.037 ± 0.025	27.3 ± 7.3	0.904
Aerobic 10°C		0.018 ± 0.012	13.8 ± 11.6	0.901

0.001) after which it remained constant during the rest of the experiment. The C content was higher in algae exposed to anaerobic conditions, but only at 10°C ($F_{Temp×O2}$ = 11.3, p = 0.006). The C content in stipe detritus (Fig. S1, Table S2) remained constant over the first 4–5 mo (27.9 ± 1.1% of DW), but then decreased to 25.3 ± 1.2% of DW over the remaining course of the experiment (F_{Time} = 6.8, p < 0.001). The C content was higher in algae exposed to aerobic conditions, but only at 10°C ($F_{Temp×O2}$ = 11.0, p = 0.006).

The N content in blade detritus (Fig. S2, Table S3) increased from 1.19 ± 0.06 to 2.82 ± 0.21% of DW over the course of the experiment (F_{Time} = 38.2, p < 0.001). The N content was higher in algae exposed to 10°C (2.11 ± 0.19 vs. 1.88 ± 0.16% of DW at 4°C; F_{Temp} = 9.7, p = 0.009). The N content in stipe detritus (Fig. S2, Table S3) increased from 1.29 ± 0.06 to 2.89 ± 0.42% of DW over the course of the experiment, but more so under aerobic conditions ($F_{Time×O2}$ = 4.2, p < 0.001). The N content was higher in algae exposed to 10°C (2.24 ± 0.24 vs. 2.01 ± 0.21% of DW at 4°C; F_{Temp} = 11.6, p = 0.005).

The C:N ratio in blade detritus was slightly higher than that in stipe detritus (19.5 ± 1.3 vs. 16.5 ± 0.9, mean ± 95% CL; Fig. 2; MW *U*-test: p = 0.002). The C:N ratio in blade detritus decreased 3- to 4-fold over the course of the experiment (F_{Time} = 58.1, p < 0.001; Table S4). The C:N ratio was slightly lower under aerobic than under anaerobic conditions (18.1 ± 1.8 vs. 20.9 ± 1.9; F_{O2} = 12.7, p = 0.004) and higher at 4°C than at 10°C (20.6 ± 1.8 vs. 18.4 ± 1.9; F_{Temp} = 8.5, p = 0.013). The C:N ratio in stipe detritus decreased 2- to 3-fold over time (F_{Time} = 90.8, p < 0.001). The C:N ratio was slightly lower in stipe detritus exposed to aerobic conditions (15.4 ± 1.3 vs. 17.7 ± 1.2 under anoxic conditions; F_{O2} = 37.7, p < 0.001) and to high temperature (16.1 ± 1.4 at 10°C vs. 17.0 ± 1.2 at 4°C; F_{O2} = 7.0, p = 0.022).

The overall mean content of mannitol in stipe detritus was slightly higher than that in blade detritus (9.73 ± 2.61 vs. 4.16 ± 1.31 mg g^{-1} DW; Fig. 3), albeit not significantly so (*U*-test: p = 0.507). The mannitol content in both blade and stipe detritus decreased substantially within the first week of the experiment (KW_{Blade_Time}: p < 0.001; KW_{Stipe_Time}: p < 0.001) and remained low in both types of detritus during the rest of the experiment. The mannitol content was not affected by O_2 condition (KW_{Blade_O2}: p = 0.683; KW_{Stipe_O2}: p = 0.473), or by temperature (KW_{Blade_Temp}: p = 0.182; KW_{Stipe_Temp}: p = 0.294).

The initial content of polyphenolics in stipe detritus exceeded that in blade detritus (16.2 ± 6.3 vs. 12.5 ± 2.9 mg g^{-1} DW; Fig. 4; *U*-test: p = 0.009). The phenolic content in blade detritus decreased from 12.5 to <3.3 mg g^{-1} DW during the first week of the experiment, after which it remained consistently low (KW_{Time}: p < 0.001). Temperature did not affect the phenolic content in blade detritus (KW_{Temp}: p = 0.835), but the concentration was almost 3-fold higher in detritus kept under anaerobic conditions than under aerobic conditions (KW_{O2}: p < 0.001). Most polyphenolics in the stipe were found in the outer peripheral tissue (32.4 ± 2.0 mg g^{-1} DW vs. 2.2 ± 0.9 in the medulla and cortex). The content of phenolics in stipe detritus decreased gradually from 16.2 to <5.0 mg g^{-1} DW over the first 10–11 wk (KW_{Time}: p < 0.001), after which it remained constantly low. Temperature had no effect on phenolics (KW_{Temp}: p = 0.254), but detritus kept under anaerobic conditions had almost 5 times more polyphenols than that kept under aerobic conditions (KW_{O2}: p = 0.001).

3.3. TGA

There were significant differences in the total loss of organic matter under pyrolysis when detritus from blade or stipe, detritus of different ages and detritus kept under aerobic or anaerobic conditions were compared (Fig. 5, Tables 2, S5 & S6). Fresh blade detritus lost ca. 65% of its DW during pyrolysis while

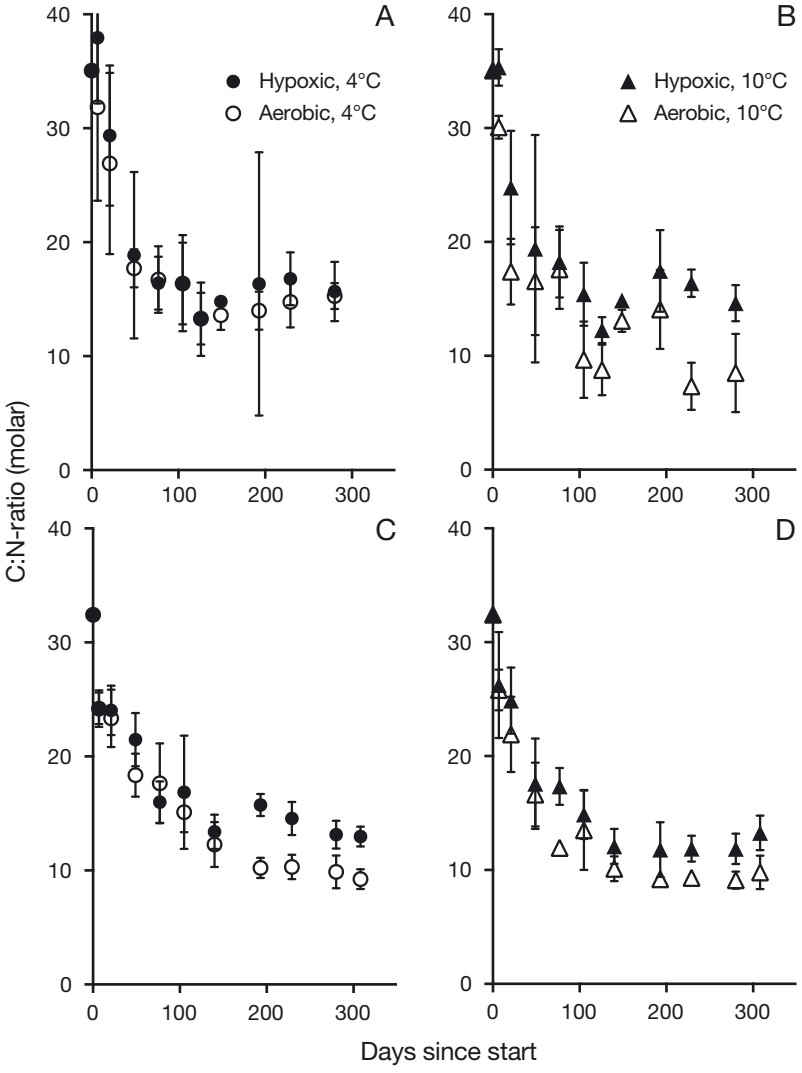

Fig. 2. Changes in tissue C:N ratio in detritus exposed to hypoxic and aerobic conditions: (A) blade detritus at 4°C, (B) blade detritus at 10°C, (C) stipe detritus at 4°C and (D) stipe detritus at 10°C. Means ±1 SD (n = 4)

fresh stipe detritus lost ca. 50%. Total mass loss for both detritus types decreased significantly with increasing age, but the decrease was less pronounced in detritus kept under anaerobic conditions.

Fresh blade detritus lost most mass in the temperature intervals $TI_{180–300°C}$ (23.3%) and $TI_{300–400°C}$ (27.7%) with the highest rate of change at about 312°C while the losses were small in $TI_{400–600°C}$ and $TI_{600–800°C}$ (8.2 and 4.5%, respectively). The thermogravimetric profiles changed with age, and mass losses in $TI_{180–300°C}$ and $TI_{300–400°C}$ were much smaller after 6 wk than in fresh blade detritus, showing that the concentration of easily decomposable compounds had decreased substantially during early decomposition, whereas the concentration of compounds pyrolized between 400 and 800°C remained almost constant. This pattern became even more evident in the oldest detritus (ca. 280 d), where mass losses in $TI_{180–300°C}$ and $TI_{300–400°C}$ were 7.6–12.8 and 10.5–14.2% in detritus kept under aerobic and anaerobic conditions, respectively, thus indicating a lower level of decay in detritus kept under anaerobic conditions. Mass losses within $TI_{180–300°C}$ and $TI_{300–400°C}$ were always larger in detritus kept under hypoxic conditions, thus indicating lower levels of decomposition.

Fresh stipe detritus lost the most mass (24.2%) in $TI_{180–300}$ with the highest rate of change at ca. 253°C, while losses were smaller in $TI_{300–400°C}$ (12.5%), $TI_{400–600°C}$ (8.5%) and $TI_{600–800}$ (4.6%). Changes in mass loss with increasing detritus age occurred mainly in $TI_{180–300}$, where it averaged 14.6% after 6 wk and 9.4% after 300 d. The concentration of compounds being pyrolized above 300°C remained, in contrast, largely constant over the course of the experiment, meaning that they made up an increasing proportion of the remaining material. Experimental treatment (i.e. aerobic vs. anaerobic conditions) had little effect on the relative proportion of lost mass within the different temperature intervals.

3.4. Field experiment

Blade detritus deployed at 10 m remained visually intact after 52 d but showed some signs of tissue damage after 121 d. This blade detritus increased in C biomass to 126.4 ± 13.8% of the initial biomass during the 121 d of deployment (Fig. 6A). Detritus deployed at 300 m depth showed little evidence of tissue degradation after 37 d of deployment, but the C biomass decreased to 84.6 ± 5.2% of its initial mass, corresponding to an average decay rate of $k = -0.005 \pm 0.002\ d^{-1}$ when averaged across sites. The initial C:N ratio in blade detritus used in the field experiment averaged 21.4 ± 2.9 (Fig. 6B). At 10 m depth, the C:N ratio had decreased to 16.1 ± 0.4 at Day 52 and to 16.6 ± 1.4 at Day 121, showing early change in tissue composition followed by little change over the last 90 d, while the C:N ratio in detritus deployed at 300 m decreased to 18.3 ± 1.7 in 37 d. Changes in the C:N

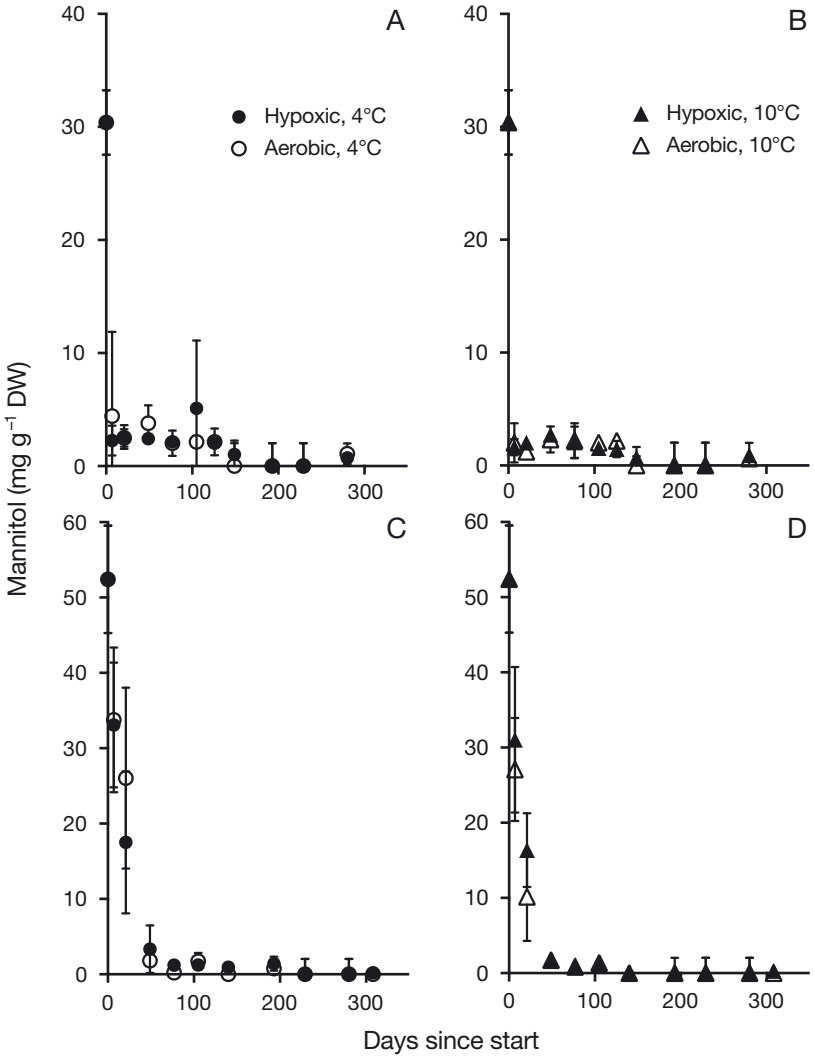

Fig. 3. Changes in mannitol content in kelp detritus kept under hypoxic and aerobic conditions: (A) blade detritus at 4°C, (B) blade detritus at 10°C, (C) stipe detritus at 4°C and (D) stipe detritus at 10°C. Means ±1 SD (n = 4)

ratio were mainly due to an increase in N content (data not shown).

4. DISCUSSION

Decay rates of blade detritus in the laboratory experiment were faster than those observed *in situ*. The field measurements were limited in duration, and the blade material used for these measurements was collected in spring and was therefore 5–6 mo younger than that used in the laboratory experiment, which was collected in October. These differences impeded a direct comparison between the 2 data sets. The decay rates obtained *in situ* show, however, that the onset of decomposition can be substantially lagged, especially at shallow sites with good light conditions. High light availability during the Arctic summer may have enabled the kelp fragments deployed at 10 m to remain viable and increase their C biomass over time, while lack of light at 300 m depth could explain the faster loss of biomass at the 2 deep sites. The slow decay at 300 m in the field compared to laboratory experiments with similar environmental conditions (i.e. darkness, anerobic conditions and 4°C) may be explained by the fact that the material used *in situ* was younger and more viable than that used in the laboratory experiments (de Bettignies et al. 2020).

The decay rates obtained in the laboratory experiments matched those obtained from *in situ* studies on decomposition of old blade detritus from *Laminaria hyperborea* in northern France (k = –0.037 d^{-1}; de Bettignies et al. 2020) but were lower than for marine phytoplankton (k = –0.053 d^{-1}; Cebrian 1999) and faster than for marine, vascular plants (seagrasses: k = –0.012 d^{-1}, marsh plants: k = –0.005 d^{-1}, mangroves: k = –0.006 d^{-1}; Cebrian 1999). Compared to other temperate macroalgae, decay rates of *L. hyperborea* appears to be lower than faster growing genera investigated under almost similar experimental conditions (i.e. 10–15°C and hypoxic O_2 levels); e.g. *Ulva*, *Ceramium*, *Polysiphonia* and *Gracillaria* (range: –0.032 to –0.256 d^{-1}; Buchsbaum et al. 1991, Banta et al. 2004, Pedersen & Johnsen 2017), but comparable to those of other slow-growing brown algae such as *Ascophyllum nodosum*, *Fucus vesiculosus*, *Saccharina latissima, Sargassum muticum* and *Halidrys siliquosa* (range: –0.007 to –0.083 d^{-1}; Josselyn & Mathieson 1980, Buchsbaum et al. 1991, Banta et al. 2004, Pedersen et al. 2005, K. Filbee-Dexter et al. unpubl. data). Furthermore, detritus from *L. hyperborea* contained a significant refractory component (R_G = 14–28 % of the initial biomass), especially when decomposition took place under anaerobic conditions, which is more than for the aforementioned fast-growing algae (range: 0–10 % of the initial biomass), but comparable to that of slow-growing brown algae (range: 0–68.0 %). The slow and incomplete decay of large, slow-growing

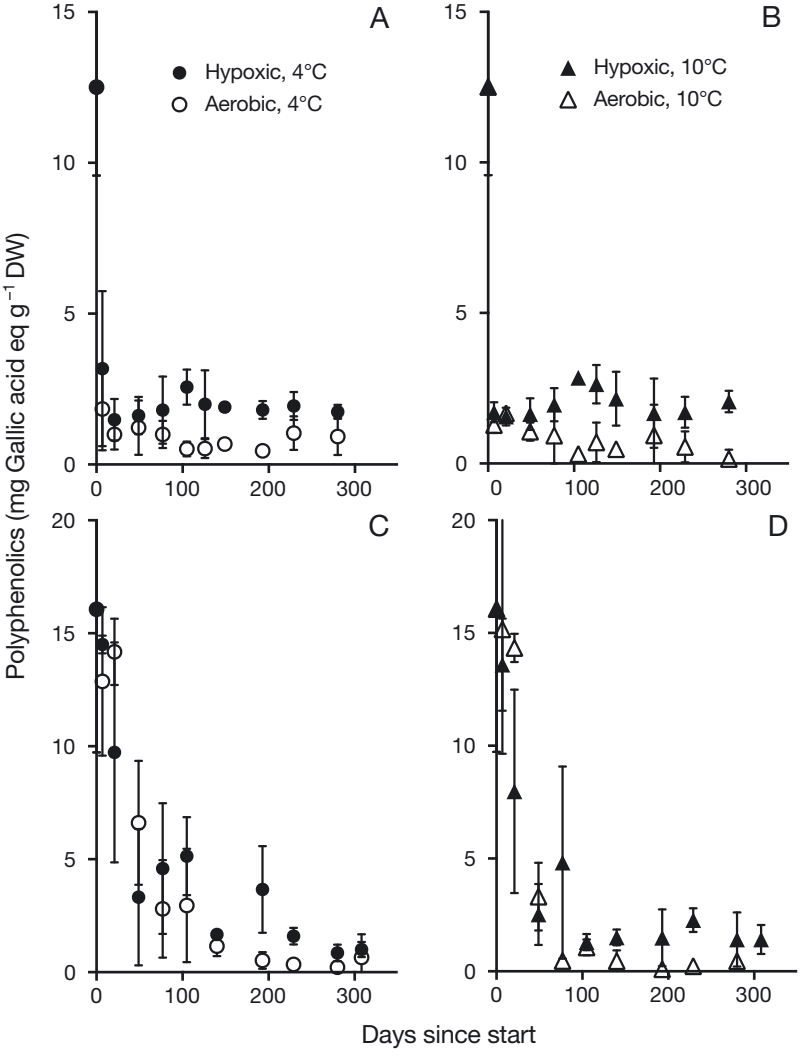

Fig. 4. Changes in content of polyphenolic compounds in kelp detritus kept under hypoxic and aerobic conditions: (A) blade detritus at 4°C, (B) blade detritus at 10°C, (C) stipe detritus at 4°C and (D) stipe detritus at 10°C. Means ±1 SD (n = 4)

brown algae may be explained by a higher proportion of structural versus photosynthetic tissues and a higher content of complex cell wall compounds and polyphenolics than in more fast-growing macroalgal species (e.g. Littler & Littler 1984, Dethier et al. 2014, Trevathan-Tackett et al. 2015).

The decay of kelp detritus was followed by substantial changes in chemical composition that may not only affect the subsequent decay rate and extent, but also affect its quality as food and, thus, the rate by which it may be mineralized through consumption by detritivores. The initial rapid loss of blade biomass during the first week of the laboratory experiment was likely due to leaching of dissolved organic carbon (DOC) during cell lysis, combined with fast breakdown of low molecular compounds, while the subsequent slow decay likely represents breakdown of large storage molecules and cell wall compounds that are more resistant to decomposition.

TGA on fresh kelp detritus revealed that a large proportion of the organic biomass was made up of compounds that were pyrolyzed at temperatures below 400°C. These compounds are considered relatively labile and include amino acids, proteins, hemicellulose and soluble carbohydrates, such as alginic acid and fucoidan, in $TI_{180–300°C}$ and cellulose, lipids and insoluble polysaccharides, such as mannitol and laminarian, in $TI_{300–400°C}$. The compounds pyrolyzed at higher temperatures are considered more resistant to decay, and include lignin (in vascular plants) and insoluble polysaccharide residues in $TI_{400–600°C}$ and organic residues and inorganic salts in $TI_{600–800°C}$ (Anastasakis et al. 2011).

Blade detritus decomposed faster and more completely than stipe detritus, which can be explained by differences in chemical composition. Total mass losses in blade detritus during pyrolysis decreased by 21–32% over the first 49 d of the experiment and by 33–49% over 280 d. This decrease was covered by the disappearance of compounds that were pyrolyzed within the 2 lowest temperature intervals. The fast decay of blade biomass during the first week coincided with a drop in total C content (from 36–33% of DW; Fig. S1), which could largely be explained by the initial loss of mannitol (corresponding to 71% of the initial C loss) and polyphenolics (37% of the initial C loss). The rapid loss of polyphenolics from decaying blade tissue surprised us because these compounds are considered inert (e.g. Buchsbaum et al. 1991). Polyphenolics are, however, present in both soluble and insoluble forms, and the former can dominate in brown algae (e.g. >90% of total in *Fucus vesiculosus*; Koivikko et al. 2005). Soluble polyphenolics can form complexes with alginic acid and become an insoluble, integrated part of the cell wall. DOC released from kelp (*Ecklonia cava*; Wada et al. 2007, 2008) contains large amounts of humic substances, and the fast loss of ca. 90% of the polyphenolics from blade detritus suggests

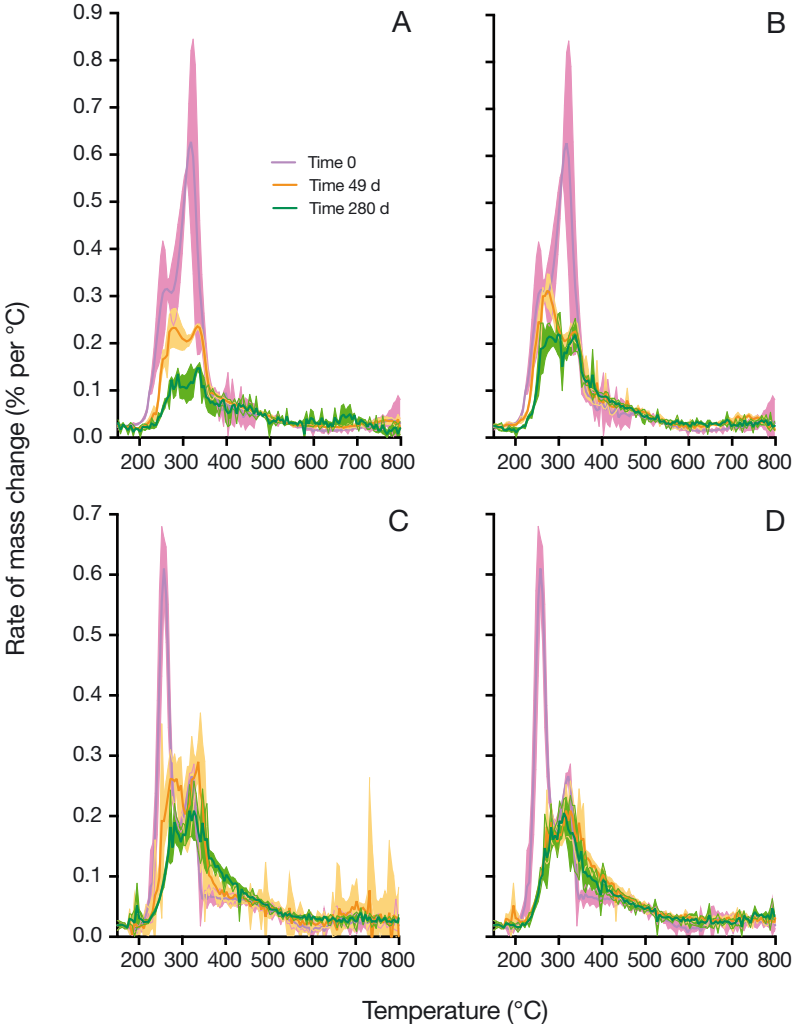

Fig. 5. Rate of mass change during pyrolysis of (A,B) blade and (C,D) stipe detritus representing different stages of decomposition under (A,C) aerobic and (B,D) anaerobic conditions. Thick solid lines: means; error bars: ±1 SD (n = 3)

that most polyphenolics were soluble and could be leached during cell lysis in *L. hyperborea*.

Stipe biomass contained a higher proportion of ash, and total mass loss during pyrolysis decreased less over time than in blade detritus (by 15–27 % over 308 d). Changes in total mass losses during pyrolysis in aging stipe detritus were almost entirely accounted for by the loss of compounds pyrolyzed within $TI_{180–300°C}$ (i.e. proteins, hemicellulose and soluble carbohydrates), while the relative concentration of compounds pyrolyzed above 300°C constituted an increasing fraction of the remaining biomass as the detritus became older. The total concentration of C in the stipe detritus remained almost constant over the course of the experiment, and polyphenolics were lost more slowly than from blade detritus (100–200 d to reach minimum levels). This suggests that a higher proportion of the polyphenolics was related to cell wall structures than in the blades. Decomposition of stipe involved an almost complete disappearance of the central core (i.e. the medulla and cortex) during the first 100–200 d of the experiment, leaving only the peripheral tissue after 308 d. This tissue initially contained more polyphenolics than the medulla and cortex (32.4 vs. 2.2 mg g^{-1} DW). Poly-

Table 2. Thermogravimetric intervals (TI) for blade and stipe detritus measured at the onset of the *Laminaria hyperborea* decomposition experiment (Day 0), after 49 d and after 280 d (for blade detritus) or after 308 d (for stipe detritus). All values are means ±1 SD (n = 3)

Time (Day)	Treatment	Total mass loss (%)	Mass loss within temperature intervals (%)			
			$TI_{180–300}$	$TI_{300–400}$	$TI_{400–600}$	$TI_{600–800}$
Blade						
0	Initial	65.06 ± 1.89	23.38 ± 1.09	27.68 ± 2.26	8.18 ± 0.50	4.45 ± 0.50
49	Aerobic	44.10 ± 3.47	13.73 ± 2.09	14.97 ± 0.62	8.74 ± 0.76	5.56 ± 0.43
280	Aerobic	32.86 ± 1.41	7.55 ± 0.08	10.50 ± 1.07	8.66 ± 0.50	5.36 ± 0.30
49	Hypoxic	51.57 ± 1.77	18.36 ± 1.53	16.23 ± 0.79	10.25 ± 0.37	6.39 ± 0.30
280	Hypoxic	43.74 ± 2.13	12.82 ± 1.07	14.23 ± 1.42	9.74 ± 0.54	5.89 ± 0.39
Stipe						
0	Initial	50.07 ± 0.55	24.18 ± 0.78	12.54 ± 0.41	8.50 ± 0.55	4.60 ± 0.36
49	Aerobic	46.58 ± 1.64	14.01 ± 0.39	15.92 ± 0.75	9.25 ± 0.37	6.27 ± 0.30
308	Aerobic	36.54 ± 1.56	9.10 ± 0.65	12.55 ± 0.86	9.09 ± 0.82	5.35 ± 0.35
49	Hypoxic	48.09 ± 1.14	15.09 ± 1.41	17.54 ± 0.98	9.35 ± 0.20	5.81 ± 0.11
308	Hypoxic	42.71 ± 2.21	9.57 ± 1.20	14.92 ± 0.75	10.92 ± 0.75	6.01 ± 0.13

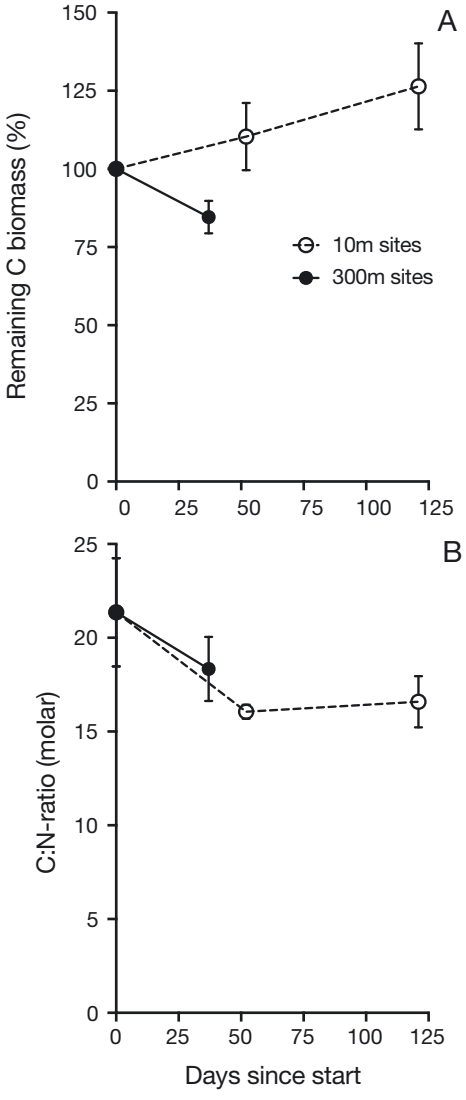

Fig. 6. Average (across replicate sites) change in blade detritus biomass and C:N ratios over time at 10 m depth and 300 m depth: (A) changes in C biomass of blade detritus, (B) changes in C:N ratio of the blade detritus. Means ±1 SD (n = 3 sites at 10 m depth and n = 2 sites at 300 m depth)

phenolics have anti-bacterial effects (Nagayama et al. 2002), and high concentrations may slow down both aerobic and anaerobic decay of major cell wall constituents (e.g. alginate; Moen et al. 1997a,b). High concentrations of phenolics in the peripheral tissue may thus explain the relatively high proportion of refractory matter in stipe detritus.

Decomposition of blade and stipe tissues was followed by a substantial increase in N concentration, leading to a substantial decrease in the C:N ratio. Increases in N concentrations during decay of N-poor detritus is often explained by colonizing microflora that is able to acquire inorganic N from the environment, thereby enriching the detritus matrix (Staaf & Berg 1982). The combined loss of energy-rich, labile compounds during early diagenesis should leave the detritus more inert and less susceptible for decomposers. The substantial loss of polyphenolics and concurrent N enrichment should, on the other hand, have the opposite effect, and increase the food 'quality' of the detritus matrix, thus making it more attractive to larger detritivores (Ayres et al. 1997, Norderhaug et al. 2006), which could potentially stimulate continued decay of the detritus under aerobic conditions.

Decomposition rate and the degree to which organic compounds are decomposed depend partly on temperature and O_2 availability. Increasing temperature is generally expected to stimulate decomposition of organic matter (Arnosti et al. 1998, Pomeroy & Wiebe 2001, Price & Sowers 2004). However, temperature had little effect on the decomposition rate and extent of *L. hyperborea* within the temperature range tested in our experiment (4–10°C). The narrow temperature range was chosen to mimic seasonal temperature variations in the study area, but was obviously too small to yield measurable and significant differences in decomposition rate and extent.

Low availability of O_2 had a clear effect on the decay of *L. hyperborea*. Exposure to anaerobic conditions resulted in slightly higher decay rates and a more incomplete decay of biomass than under aerobic conditions. Several studies have documented the importance of aerobic conditions during decomposition (e.g. Hartnett et al. 1998, Kristensen et al. 1995), but the effect on decay rate is not straightforward and may depend on the chemical composition of the detritus (Arndt et al. 2013). The availability of O_2 has little effect on the decay of low molecular compounds, because the energy yield obtained through aerobic or anaerobic decay of such compounds is similar, whereas the gain of energy from anaerobic decay of more complex compounds is much less than that from aerobic decay (Hulthe et al. 1998). Aerobic decay is therefore expected to be faster than anaerobic decay, but we found the opposite. One possible reason could be that the algal fragments we used were not pre-killed by freezing or heating before the experiment. Most of the tissues would therefore have been alive and physiologically active at the start of the experiment, which could potentially delay cell lysis and initial biomass losses even though the fragments were kept in complete darkness. Exposure to anaerobic conditions may thus have prompted cell death and sped up the decay.

Most macroalgae contain complex chemical compounds and thus should decompose more incom-

pletely under anoxic conditions, as shown by Sassi et al. (1988). The amount of compounds lost during pyrolysis decreased less over time in detritus exposed to anaerobic conditions, showing that decomposition was more incomplete in the absence of O_2. The effect of anoxia was also seen in the content of polyphenolics, which decreased substantially over time in all treatments, but were 3–5 times higher in detritus kept under anaerobic conditions than in that exposed to aerobic conditions after having reached minimum levels. The most obvious effect of anoxia was, however, seen in the amount of remaining biomass (i.e. refractory detritus), which was substantially higher in detritus exposed to anaerobic conditions. This was especially evident in blade detritus, where this component increased from 0–24% of the initial biomass when O_2 was absent. Anoxic conditions thus constitute a critical criterion for long-term preservation of kelp detritus.

Sequestration of kelp C requires that consumption of live and dead kelp is marginal to avoid rapid mineralization of C, that decomposition is slow and incomplete and that the export of detritus from kelp forests to potential blue C sinks is high (Hill et al. 2015). The annual production of kelp detritus in the mouth of Malangen averages 478 g C m^{-2} kelp forest, corresponding to a production of 10517 t detrital C from the 22 km^2 kelp forests in the study area (Pedersen et al. 2020). This detritus is as eroded blade material (23%) and whole stipe (12%) or blades (65%), of which more than 50% is released as a pulse of coarse material during the spring cast of old blades in April and May (Pedersen et al. 2020). *L. hyperborea* is negatively buoyant (Wernberg & Filbee-Dexter 2018), so much of that detritus accumulates within or close to the kelp forests at first. Consumption of detached kelp fragments by sea urchins within the kelp forest can be substantial (60–65% of the standing stock per day; Filbee-Dexter et al. 2020). Slow and incomplete decay of kelp detritus requires further anaerobic conditions, which is rare within kelp forests where the substrate is rocky and water movement substantial. Export of kelp detritus from the kelp sites and into deeper waters with permanent or periodic anoxia therefore needs to be fast to avoid intensive C mineralization through grazing and decomposition.

Kelp detritus often accumulates in deep basins adjacent to kelp forests (Harrold et al. 1998, Dierssen et al. 2009, Filbee-Dexter & Scheibling 2012). The dispersal range of kelp particles depends on the hydrodynamic environment, particle size and sinking speed. About 50% of the whole blades lost through dislodgement and during the spring cast are deposited within 8.5 km of the source populations, whereas the median dispersal range for small kelp particles is 26 km (Filbee-Dexter et al. 2020). The dispersal of visible kelp fragments in the study area was confirmed through video surveys of the seafloor beneath the kelp forests, which revealed substantial depositions of kelp detritus at depths ranging from 30–450 m shortly after it had been released during the spring cast (Filbee-Dexter et al. 2018).

The spatial and temporal variation in O_2 availability in the bottom waters of the study area is unknown, but the water masses in deep basins inside Malangen Fjord and in nearby Harstad and Kilbotn bays are stratified from March–May to October–December. The depth of these basins range from 50–150 m and the O_2 concentration in the bottom water decreases gradually over summer with minimum values ranging from 70–182 µM (i.e. 22–55% saturation; Holte et al. 2005). In contrast, the O_2 concentration in the bottom waters of the coastal shelf just outside Malangen (depth = 329 m) remains aerobic during summer (289 µM O_2 ~96% air saturation; Jørgensen et al. 2005) due to strong tidal currents and the north-bound Norwegian current. The spatial and temporal extent of anoxic conditions near the sediment surface in the study area is thus highly variable and could range from complete aerobic conditions to temporary anoxia in the deeper portions. This variation makes it difficult to evaluate the exact role of aerobic vs. anaerobic decomposition and, thus, the potential for permanent burial of kelp detritus. The annual input of blade detritus to the recipient amounts ca. 7404 t C, assuming that ca. 50% of the produced detritus is consumed by sea urchins before leaving the kelp forest areas and that ca. 60% of the consumed material escapes assimilation and is released as small particulate matter (Mamelona & Pelletier 2005). This material would decompose completely under aerobic conditions while 1777 t C would be recalcitrant under anaerobic conditions. The annual production of stipe material is less (ca. 1262 t C), and aerobic decomposition would leave ca. 141 t as refractory C, while anaerobic conditions would result in ca. 282 t refractory C (using the same assumptions as for the blade material). The potential for burial of kelp C in the area should thus range from 141 t C yr^{-1} (= 1.3% of the detritus production) under completely aerobic conditions to 2059 t C yr^{-1} (= 19.6% of the production) under completely anaerobic conditions. Actual, long-term burial rates may therefore be especially dependent upon the amount of detritus deposited within the 2 deepest basins (>400 m), which cover ca. 10% of the entire study

area. Vilas et al. (2020) estimated that the annual input of kelp detritus to these deep areas is ca. 400 t C, which is <5% of the kelp detritus produced in the area.

Kelp forests are highly productive and should have the potential to serve as important Blue C donors, provided that mineralization of C through grazing and microbial decay is limited. Our results showed that blade material decomposes completely within ca. 10 mo under aerobic conditions, but also that the decay of kelp detritus is relatively slow and incomplete under anaerobic conditions. We conclude that rapid export of kelp detritus from source populations to deep adjacent areas with permanent or periodic anoxia needs to be substantial for sequestration of kelp C to be significant.

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LITERATURE CITED

Abdullah MI, Fredriksen S (2004) Production, respiration and exudation of dissolved organic matter by the kelp *Laminaria hyperborea* along the west coast of Norway. J Mar Biol Assoc UK 84:887–894

Aber JD, Melillo JM, McClaugherty CA (1990) Predicting long-term patterns of mass loss, nitrogen dynamics and soil organic matter formation from initial litter chemistry in forest ecosystems. Can J Bot 68:2201–2208

Adair EC, Parton WJ, Del Grosso SJ, Silver WL, Harmon ME (2008) A simple three-pool model accurately describes patterns of long-term, global litter decomposition in the Long-term Intersite Decomposition Experiment Team (LIDET) data set. Glob Change Biol 14:2636–2660

Ainsworth EA, Gillespie KM (2007) Estimation of total phenolic content and other oxidation substrates in plant tissues using Folin-Ciocalteu reagent. Nat Protoc 2: 875–877

Anastasakis K, Ross AB, Jones JM (2011) Pyrolysis behavior of the main carbohydrates of brown macroalgae. Fuel 90: 598–607

Arndt S, Jørgensen BB, LaRowe DE, Middelburg JJ, Pancost RD, Regnier P (2013) Quantifying the degradation of organic matter in marine sediments: a review and synthesis. Earth Sci Rev 123:53–86

Arnosti C, Jørgensen BB, Sagemann J, Thamdrup B (1998) Temperature dependence of microbial degradation of organic matter in marine sediments: polysaccharide hydrolysis, oxygen consumption and sulfate reduction. Mar Ecol Prog Ser 165:59–70

Ayres MP, Clausen P, MacLean SF Jr, Redman AM, Reichardt PB (1997) Diversity of structure and antiherbivore activity in condensed tannins. Ecology 78: 1696–1712

Banta GT, Pedersen MF, Nielsen SL (2004) Decomposition of marine primary producers: consequences for nutrient recycling and retention in coastal ecosystems. In: Banta GT, Pedersen MF, Nielsen SL (eds) Estuarine nutrient cycling: the influence of primary producers: the fate of nutrients and biomass. Kluwer Academic, Dordrecht, p 187–216

Bennett S, Wernberg T, Harvey ES, Santana-Garcon J, Saunders BJ (2015) Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. Ecol Lett 18:714–723

Buchsbaum R, Valiela I, Swain T, Dzierzeski M, Allen S (1991) Available and refractory nitrogen in detritus of coastal vascular plants and macroalgae. Mar Ecol Prog Ser 72:131–143

Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128–3139

Cebrian J (1999) Patterns in the fate of production in plant communities. Am Nat 154:449–468

Chmura GL, Anisfeld SC, Cahoon DR, Lynch JC (2003) Global carbon sequestration in tidal, saline wetland soils. Global Biogeochem Cycles 17:1111

de Bettignies F, Dauby P, Thomas F, Gobet A and others (2020) Degradation dynamics and processes associated with the accumulation of *Laminaria hyperborea* (Phaeophyceae) kelp fragments: an *in situ* experimental approach. J Phycol 56:1481–1492

Dethier MN, Brown AS, Burgess S, Eisenlord MS and others (2014) Degrading detritus: Changes in food quality of aging kelp tissue varies with species. J Exp Mar Biol Ecol 460:72–79

Dierssen HM, Zimmerman RC, Drake LA, Burdige DJ (2009) Potential export of unattached benthic macroalgae to the deep sea through wind-driven Langmuir circulation. Geophys Res Lett 36:L04602

Donato DC, Kaufmann JB, Murdiyarso D, Kurnianto S, Stidham M, Kanninen M (2011) Mangroves among the most carbon-rich forests in the tropics. Nat Geosci 4: 293–297

Duarte CM (2017) Reviews and syntheses: hidden forests, the role of vegetated coastal habitats in the ocean carbon budget. Biogeosciences 14:301–310

Enríquez S, Duarte C, Sand-Jensen K (1993) Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. Oecologia 94: 457–471

Filbee-Dexter K, Scheibling RE (2012) Hurricane-mediated defoliation of kelp beds and pulsed delivery of kelp detritus to offshore sedimentary habitats. Mar Ecol Prog Ser 455:51–64

Filbee-Dexter K, Scheibling RE (2014) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Mar Ecol Prog Ser 495:1–25

Filbee-Dexter K, Wernberg T (2020) Substantial blue carbon in overlooked Australian kelp forests. Sci Rep 10: 12341

Filbee-Dexter K, Wernberg T, Norderhaug KM, Ramirez-Llodra E, Pedersen MF (2018) Movement of pulsed resource subsidies from kelp forests to deep fjords. Oecologia 187:291–304

Filbee-Dexter K, Pedersen MF, Fredriksen S, Norderhaug KM and others (2020) Carbon export is facilitated by

marine shredders transforming kelp detritus. Oecologia 192:13–25
Fourqurean JW, Duarte CM, Kennedy H, Marbà N and others (2012) Seagrass ecosystems as a globally significant carbon stock. Nat Geosci 5:505–509
Gage JD (2003) Food inputs, utilization, carbon flow and energetics. In: Tyler PA (ed) Ecosystems of the deep oceans. Elsevier, Oxford, p 313–380
Harrold C, Light K, Lisin S (1998) Organic enrichment of submarine-canyon and continental-shelf benthic communities by macroalgal drift imported from nearshore kelp forest. Limnol Oceanogr 43:669–678
Hartnett HE, Keil RG, Hedges JI, Devol AH (1998) Influence of oxygen exposure time on organic carbon preservation in continental margin sediments. Nature 391:572–574
Hill R, Bellgrove A, Macreadie PI, Petrou K, Beardall J, Steven A, Ralph PJ (2015) Can macroalgae contribute to blue carbon? An Australian perspective. Limnol Oceanogr 60:1689–1706
Holte B, Oug E, Dahle S (2005) Soft-bottom fauna and oxygen minima in subarctic north Norwegian marine sill basins. Mar Biol Res 1:85–96
Howard J, Sutton-Grier A, Herr D, Kleypas J and others (2017) Clarifying the role of coastal and marine systems in climate mitigation. Front Ecol Environ 15:42–50
Hulthe G, Hulth S, Hall POJ (1998) Effect of oxygen on degradation rate of refractory and labile organic matter in continental margin sediments. Geochim Cosmochim Acta 62:1319–1328
Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. Ecol Monogr 54:187–211
Jayathilake DRM, Costello MJ (2020) A modelled global distribution of the kelp biome. Biol Conserv 252:108815
Jørgensen BB, Glud RN, Holby O (2005) Oxygen distribution and bioirrigation in Arctic fjord sediments (Svalbard, Barents Sea). Mar Ecol Prog Ser 292:85–95
Josselyn MN, Mathieson AC (1980) Seasonal influx and decomposition of autochthonous macrophyte littler in a North temperate estuary. Hydrobiologia 71:197–208
Koivikko R, Loponen J, Honkanen T, Jormalainen V (2005) Content of soluble, cell-wall-bound and exuded phlorotannins in the brown alga *Fucus vesiculosus*, with implications on their ecological functions. J Chem Ecol 31:195–212
Krause-Jensen D, Duarte CM (2016) Substantial role of macroalgae in marine carbon sequestration. Nat Geosci 9:737–742
Krause-Jensen D, Lavery P, Serrano O, Marbà N, Maque P, Duarte CM (2018) Sequestration of macroalgal carbon: the elephant in the blue carbon room. Biol Lett 14:20180236
Kristensen E, Ahmed SI, Devol AH (1995) Aerobic and anaerobic decomposition of organic matter in marine sediment: Which is fastest? Limnol Oceanogr 40:1430–1437
Krumhansl KA, Scheibling RE (2012) Production and fate of kelp detritus. Mar Ecol Prog Ser 467:281–302
Littler MM, Littler DS (1984) Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. J Exp Mar Biol Ecol 74:13–34
Lovelock CE, Duarte CM (2019) Dimensions of blue carbon and emerging perspectives. Biol Lett 15:20180781
Lüning K (1990) Seaweeds: their environment, biogeography, and ecophysiology. Wiley, New York, NY
Mamelona J, Pelletier É (2005) Green urchin as a significant source of fecal particulate organic matter within nearshore benthic ecosystems. J Exp Mar Biol Ecol 314:163–174
Mann KH (1973) Seaweeds: their productivity and strategy for growth. Science 182:975–981
Mcleod E, Chmura GL, Bouillon S, Salm R and others (2011) Blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering of CO_2. Front Ecol Environ 9:552–560
Moen E, Horn S, Østgaard K (1997a) Alginate degradation during anaerobic digestion of *Laminaria hyperborea* stipes. J Appl Phycol 9:157–166
Moen E, Larsen B, Østgaard K (1997b) Aerobic microbial degradation of alginate in *Laminaria hyperborea* stipes containing different levels of polyphenols. J Appl Phycol 9:45–54
Nagayama K, Iwamura Y, Shibata T, Hirayama I, Nakamura T (2002) Bactericidal activity of phlorotannins from the brown alga *Ecklonia kurome.* J Antimicrob Chemother 50:889–893
Nellemann C, Corcoran E, Duarte CM, Valdés L, DeYoung C, Fonseca L, Grimsditch G (eds) (2009) Blue carbon: the role of healthy oceans in binding carbon. UN Environment, GRID-Arendal, Arendal. www.grida.no
Norderhaug KM, Nygaard K, Fredriksen S (2006) Importance of phlorotannin content and C:N ratio of *Laminaria hyperborea* in determining its palatability as food for consumers. Mar Biol Res 2:367–371
Pedersen MF, Johnsen KL (2017) Nutrient (N and P) dynamics of the invasive macroalga *Gracilaria vermiculophylla*: nutrient uptake kinetics and nutrient release through decomposition. Mar Biol 164:172
Pedersen MF, Staehr PA, Wernberg T, Thomsen MS (2005) Biomass dynamics of exotic *Sargassum muticum* and native *Halidrys siliquosa* in Limfjorden, Denmark — implications of species replacements on turnover rates. Aquat Bot 83:31–47
Pedersen MF, Nejrup LB, Fredriksen S, Christie H, Norderhaug KM (2012) Effects of wave exposure on population structure, demography, biomass and productivity of the kelp *Laminaria hyperborea.* Mar Ecol Prog Ser 451: 45–60
Pedersen MF, Filbee-Dexter K, Norderhaug KM, Fredriksen S, Frisk NL, Fagerli CW, Wernberg T (2020) Detrital carbon production and export in high latitude kelp forests. Oecologia 192:227–239
Pessarrodona A, Moore PJ, Sayer MDJ, Smale DA (2018) Carbon assimilation and transfer through kelp forests in the NE Atlantic is diminished under a warmer ocean climate. Glob Change Biol 24:4386–4398
Pomeroy LR, Wiebe WJ (2001) Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. Aquat Microb Ecol 23:187–204
Price PB, Sowers T (2004) Temperature dependence of metabolic rates for microbial growth, maintenance, and survival. Proc Natl Acad Sci USA 101:4631–4636
Sassi R, Kutner MBB, Moural GF (1988) Studies on the decomposition of drift seaweed from the northeast Brazilian coastal reefs. Hydrobiologia 157:187–192
Smale DA, Burrows MT, Evans AJ, King N, Sayer MDJ, Yunnie ALE, Moore PJ (2016) Linking environmental variables with regional-scale variability in ecological structure and standing stock of carbon within UK kelp forests. Mar Ecol Prog Ser 542:79–95
Smale DA, Moore PJ, Queirós AM, Higgs ND, Burrows MT (2018) Appreciating interconnectivity between habitats is key to blue carbon management. Front Ecol Environ 16:71–73

Staaf H, Berg B (1982) Accumulation and release of plant nutrients in decomposing Scots pine needle litter: long-term decomposition in a Scots pine forest: II. Can J Bot 60:1561–1568

Trevathan-Tackett SM, Kelleway J, Macreadie PI, Beardall J, Ralph P, Bellgrove A (2015) Comparison of marine macrophytes for their distribution to blue carbon sequestration. Ecology 96:3043–3057

Vaskovsky VE, Isay SV (1969) Quantitative determination of formaldehyde liberated with periodate oxidation. Anal Biochem 30:25–31

Vilas D, Coll M, Pedersen T, Corrales X and others (2020) Kelp-carbon uptake by Arctic deep-sea food webs plays a noticeable role in maintaining ecosystem structural and functional traits. J Mar Syst 203: 103268

Wada S, Aoki MN, Tsuchiya Y, Sato T, Shinagawa H, Hama T (2007) Quantitative and qualitative analyses of dissolved organic matter released from *Ecklonia cava* Kjellman, in Oura Bay, Shimoda, Izu Peninsula, Japan. J Exp Mar Biol Ecol 349:344–358

Wada S, Aoki MN, Mikami A, Komatsu T and others (2008) Bioavailability of macroalgal dissolved organic matter in seawater. Mar Ecol Prog Ser 370:33–44

Wernberg T, Filbee-Dexter K (2018) Grazers extend blue carbon transfer by slowing sinking speeds of kelp detritus. Sci Rep 8:17180

Wernberg T, Krumhansl K, Filbee-Dexter K, Pedersen MF (2019) Status and trends for the world's kelp forests. In: Sheppard C (ed) World seas: an environmental evaluation, Vol 3. Ecological issues and environmental impacts. Elsevier, Amsterdam, p 57–78

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