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Sustained productivity and respiration of degrading kelp detritus in the shallow benthos: Detached or broken, but not dead

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1 **Research paper**

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3 **Sustained productivity and respiration of degrading kelp detritus in the**
4 **shallow benthos: detached or broken, but not dead.**
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13 Running title: Kelp detritus can sustain primary producer functions

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18 Running header: Kelp detritus fulfilling primary producer functions
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ABSTRACT

Temperate kelp forests contribute significantly to marine primary productivity and fuel many benthic and pelagic food chains. A large proportion of biomass is exported from kelp forests as detritus into recipient marine ecosystems, potentially contributing to Blue Carbon sequestration. The degradation of this organic material is slow and recent research has revealed the preservation of photosynthetic functions over time. However, the physiological correlates of detrital breakdown in *Laminaria* spp. have not yet been studied. The warming climate threatens to reshuffle the species composition of kelp forests and perturb the dynamics of these highly productive ecosystems. The present study compares the physiological response of degrading detritus from two competing North East Atlantic species; the native Boreal *Laminaria hyperborea* and the thermally tolerant Boreal-Lusitanian *L. ochroleuca*. Detrital fragment degradation was measured by a mesocosm experiment across a gradient of spectral attenuation (a proxy for depth) to investigate the changes in physiological performance under different environmental conditions. Degradation of fragments was quantified over 108 days by measuring the biomass, production and respiration (by respirometry) and efficiency of Photosystem II (by PAM fluorometry). Data indicated that whilst degrading, the photosynthetic performance of the species responded differently to simulated depths, but fragments of both species continued to produce oxygen for up to 56 days and sustained positive net primary production. This study reveals the potential for ostensibly detrital kelp to contribute to Blue Carbon fixation through sustained primary production which should be factored into Blue Carbon management. Furthermore, the physiological response of kelp detritus is likely dependent upon the range of habitats to which it is exported. In the context of climate

change, shifts in species composition of kelp forests and their detritus are likely to have wide-reaching effects upon the cycling of organic matter in benthic ecosystems.

Keywords: Climate change; Detritus; North East Atlantic; Oxygen production; PAM fluorescence; Respiration; Trophic transfer

1. INTRODUCTION

Within the temperate to sub-polar regions of the globe, kelps are of paramount importance to marine ecosystem functioning. They contribute to the functional integrity of coastal ecosystems as habitat forming species (HFS) via their biogenic structure, through wave energy dissipation and via cycling of carbon (Christie *et al.* 2003; Laffoley & Grimsditch, 2009; Teagle *et al.* 2017). As highly productive primary producers, kelps fix carbon dioxide to produce organic matter via photosynthesis (Bartsch *et al.* 2008). The accumulated biomass is eventually released or eroded and exported as detritus in a variety of forms into recipient benthic ecosystems (Duggins *et al.* 1989; Krumhansl and Scheibling 2012; Pessarrodona *et al.* 2018a). This transfer of carbon helps to sustain adjacent food webs. The breakdown of detrital material by erosion and grazing activity provides a source of particulate organic matter (POM) available to filter-feeding invertebrates (Renaud *et al.* 2015; de Bettignies *et al.* 2020a; Vilas *et al.* 2020) which in turn can play a major role in mediating carbon fluxes along the sediment-water interface (Queirós *et al.* 2019; Pedersen *et al.* 2020).

A significant proportion of primary production from marine primary autotrophs is exported as detritus rather than entering the consumer food web (Moore *et al.* 2004). In a global context, as much as 82% of annual kelp biomass may be transferred as detrital subsidies (Krumhansl

and Scheibling 2012; de Bettignies *et al.* 2013). Knowing the fate of such detritus is fundamental in understanding the dynamics, connectivity and functioning of coastal ecosystems (Polis *et al.* 1997). Indeed, detritus enhances both primary and secondary production (Polis *et al.* 1997; Marczak *et al.* 2007) whilst contributing to the structure and stability of food webs in recipient ecosystems (Huxel *et al.* 2002). Furthermore, accumulation of detritus can physically modify the habitat structure (Arroyo and Bonsdorff 2016). However, the influences upon recipient ecosystems are dependent upon the timing, frequency and residence time of the detrital deposition (Yang *et al.* 2008).

Macroalgae represent an as yet under-estimated contributor to the oceanic carbon cycle and in particular to carbon sequestration and long-term storage. Their contribution to global carbon assimilation and sequestration is currently not considered by the IPCC (Ciais *et al.* 2013), and whilst the Global Carbon Project (GCP) identifies coastal habitats as carbon stocks (Friedlingstein *et al.* 2019), their full contribution to the global marine carbon sink remains neglected. Unlike seagrasses or phytoplankton, macroalgae are not routinely considered as contributors to the 'Blue Carbon' budget (McLeod *et al.* 2011; Howard *et al.* 2017). Marine macrophytes collectively fix around 1.8 Gt C yr⁻¹ (of which macroalgae contribute ~1.5 Gt C yr⁻¹) (Duarte *et al.* 2013; Duarte and Krause-Jensen 2017; Krause-Jensen and Duarte 2016) in contrast to the ~58 Gt C yr⁻¹ of phytoplankton production (Buitenhuis *et al.* 2013; Middelburg 2019). However, the lability of phytoplankton carbon and the high rate of remineralisation through consumption and degradation mean that only in the region of 0.23 Gt C yr⁻¹ (0.4%) of phytoplankton production becomes sequestered into carbon stores or sinks, whilst the lower rate of consumption and refractory chemical nature of macroalgal detritus mean that ~0.17 Gt C yr⁻¹ (11.4%) is sequestered. Thus, including

seagrasses, marine macrophytes potentially contribute a comparable mass to direct global carbon sequestration to that of phytoplankton.

Species of the order Laminariales are particularly important contributors to coastal primary production (Kirk 1994) and form key constituents of shallow subtidal kelp forests across four continents (Steneck *et al.* 2002; Teagle *et al.* 2017). Along North East Atlantic coastlines, the stipitate canopy-forming *Laminaria hyperborea* dominates shallow subtidal rocky ecosystems (Smale and Moore 2017). Detrital production by *L. hyperborea* is unique because the majority of the previous-season's post-meristematic growth (the 'growth collar') is shed, often intact, between March and May (Bartsch *et al.* 2008); the release of this pulse of biomass contributes significantly to the total detritus production (Pessarrodona *et al.* 2018a). *L. hyperborea*'s detritus is a trophic resource connecting habitats which becomes increasingly accessible to consumers as it degrades (Norderhaug *et al.* 2003) and is an especially important dietary subsidy during periods of low plankton productivity (Leclerc *et al.* 2013a). As well as accumulating in coastal embayments and on beaches, a significant fraction of the carbon fixed by *L. hyperborea* flows into seafloor depressions, low-energy habitats and deep subtidal regions (Filbee-Dexter and Scheibling 2016; Filbee-Dexter *et al.* 2018). Research on *L. hyperborea* has already revealed that its degradation is slow relative to other species and accumulations in shallow subtidal ecosystems are able to maintain photosynthetic activity across several months (de Bettignies *et al.* 2020b), acting as net producers for a sustained period of time dependent upon the illumination regime.

The conspicuous thermally tolerant congeneric kelp (Franco *et al.* 2017; Hargrave *et al.* 2017) of Lusitanian origin, *L. ochroleuca* (Bachelot de la Pylaie), has expanded its range northwards from Morocco and across the English Channel in response to the changing

climate over the last century. Today, *L. ochroleuca* is expanding its leading edge eastwards and northwards at around 5.4 and 2.5 km per year, respectively (Straub *et al.* 2016). Its range now overlaps substantially with the native assemblage's dominant kelp species, *L. hyperborea* (Smale *et al.* 2015; Hargrave *et al.* 2017) which has undergone a ~250 km range contraction at its warm leading-edge since 1970 (Assis *et al.* 2016). In comparison to the pulsed detrital production from *L. hyperborea*, detrital production by *L. ochroleuca* is greater in volume, more frequent and degrades faster between May and October (Pessarrodona *et al.* 2018b). The expanding thermal envelope and subsequent spread of *L. ochroleuca* is modifying both the taxonomic and functional composition of HFS, with resulting effects on detrital composition. The re-arrangement of HFS has been shown to have marked ecological implications; extending to adjacent communities which rely on these subsidies of allochthonous material (Bishop *et al.* 2010; Straub *et al.* 2016).

The ecological function of detritus varies between species. Recent studies (Pessarrodona *et al.* 2018b) comparing *L. ochroleuca* and *L. hyperborea* have demonstrated interspecific differences in seasonal detrital decomposition rates, with *L. ochroleuca* exhibiting significantly faster rates (6.5 x) compared to *L. hyperborea* (Pessarrodona *et al.* 2018b) in spring. In addition, the species exhibit differences in timing of detrital production: the May cast from *L. hyperborea* accounting for ~40-60% of annual lamina erosion (Pessarrodona *et al.* 2018a) compared with the continual release of detritus from the fronds of *L. ochroleuca* (Pessarrodona *et al.* 2018b). Such alterations to the supply and cycling of organic matter will likely be amplified as sea surface temperatures increase. In the North East Atlantic, a rise of > 2°C is forecast in the next 100 years (Philippart *et al.* 2011; Masson-Delmotte *et al.* 2018), which will likely result in the gradual replacement of the native cool-water *L. hyperborea* by the warm-water tolerant *L. ochroleuca*.

144

145 Degradation is dynamic and testing the response of detritus across different environmental
146 conditions is important to contextualise this process. The depth distribution of photosynthetic
147 kelp-forest communities is strongly influenced by light availability (Kirk 1994; Gorman *et al.*
148 2013; Bajjouk *et al.* 2015) and the photosynthetic mechanisms of some kelp species have
149 been demonstrated to respond to changes in underwater light (e.g. in *Saccharina latissima*;
150 and *L. digitata*) (Gevaert *et al.* 2002; Delebecq *et al.* 2011). *L. hyperborea* and *L. ochroleuca*
151 forests have similar natural depth range but little is known about the photosynthetic
152 efficiency of these two species within their depth thresholds. Investigating the degradation of
153 kelp detritus across a gradient of depth will further elucidate its role in the marine
154 environment.

155

156 The aim of this study therefore was to monitor the break-down dynamics and physiological
157 performance of material from *L. hyperborea* and *L. ochroleuca* across a gradient of light
158 attenuation to investigate the influence of depth across time. We examined biomass
159 dynamics, oxygen production, respiration and photosynthetic performance and efficiency of
160 photosystem II of detritus from the two species. We hypothesized that *Laminaria* species
161 have the capacity to resist degradation, maintaining primary production function depending
162 upon the illumination regime. Following the findings of Pessarrodona *et al.* (2018a) we
163 hypothesised that the two species should exhibit differential responses with respect to
164 degradation, with a quicker decomposition and breakdown of physiological capacity for *L.*
165 *ochroleuca* compared to *L. hyperborea*. We also speculated that there would be an effect of
166 the amount of light, and for the first time, empirically tested the influence of depth-related
167 light attenuation as a potential driver of variability in the degradation of kelp material.

2. MATERIAL AND METHODS

The study was conducted in the Roscoff Biological Station close to the Bay of Morlaix (France). In May 2018, *L. hyperborea* was harvested at La Veille (48°42'36.22"N, 3°54'04.81"W) and *L. ochroleuca* at An Nehou (48°41'34.27"N, 3°56'25.52"W) from ~ 8-10 m below chart datum. Five typical mature canopy-forming individuals of each kelp species were harvested by severing the stipe just above the holdfast. The mean total length of *L. hyperborea* individuals was 348 cm compared to *L. ochroleuca* individuals with a mean length of 169 cm. Within two hours of collection, the sporophytes were submerged in the dark in a 500 L flow-through tank of aerated ambient sea water pumped directly from the Bay and left to acclimate for 48 hours.

2.1 Experimental design

For each adult individual, three blade fragments of equal length (20 cm) were cut at a standardised distance (20 cm) above the meristem, away from the distal section of the kelp blade which is subject to greater epiphytic colonisation. Fragments were tagged with a unique ID number, their mass recorded and were randomly allocated to a depth (0, 15 and 30 m) treatment. Thus there were five replicates per species within each depth treatment.

To simulate different light intensities across a depth gradient, light attenuation optical filters (LEE Filters, Andover, UK) were constructed to completely cover the aquaria (Fig. 1). A photon flux simulating light availability at 15 and 30 m was recreated using an average light extinction coefficient (k) of 0.14 (from Boutler *et al.* 1974; spring and summer surveys

around Roscoff) incorporated into equation 1, where light availability at a specified depth equates to:

$$I(t) = I(z_0) \exp(-kz) \quad \text{equation 1.}$$

The irradiance at depth (t) $I(t)$ depends on the light at the surface $I(z_0)$, the depth (z) and the extinction coefficient of the water in the column (k). The 0 m treatment, representing strandline and floating detritus, were submerged in 8 cm of water hence $z_0 = 0.08$ m. The percentage of light available at 0, 15 and 30 m was 98.9%, 12.3% and 1.5% respectively; these values were utilised when assembling the relevant filters. We did not, however, account for the change in spectral character as a function of depth (Saulquin *et al.* 2013).

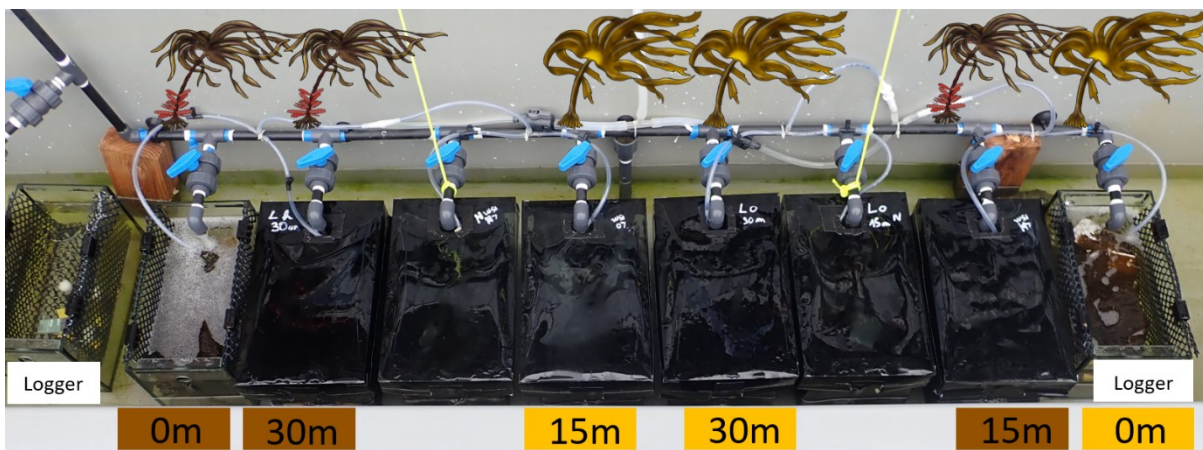


Fig. 1. Experimental set-up composed of filters for 15 and 30 m aquaria, constant air bubbling and HOBO loggers. Two unlabelled aquaria were used for experiments that are outside the scope of this paper. Each aquarium contained five replicate fragments. The brown squares represent aquaria with *L. hyperborea* fragments and yellow squares contain *L. ochroleuca* fragments.

The fragments acclimated for a further 48 hours before being transferred to 8 L aquaria corresponding to their respective species by depth treatment where they remained for the

duration of the experiment. Each aquaria was installed with a wide mesh basket which held the fragments in 8 cm of water and raised them 5 cm from the bottom. The baskets facilitated water circulation whilst constant aeration promoted diffusion across the boundary layer (Noisette and Hurd 2018). The six aquaria were held in a circulating water bath system supplied with a continual flow of unfiltered seawater (renewal rate of 10 times the aquarium volume per hour) located outside (Fig. 1). The fragments were therefore exposed to ambient temperature and irradiance in order to re-create their natural environment. Two aquaria were fitted with temperature/light loggers (HOBO Pendant Temperature/Light Weatherproof Pendant Data Logger 16K) recording at 10-minute intervals. Data was regularly downloaded to ensure conditions did not deviate significantly from outside conditions. Physiological measurements (see below) began 9 days after the fragments were transferred into the experimental system and observations were repeated at 7-day intervals thereafter across five-time periods, (T1-T5) with a 19 day gap between T5 and T6, for a total duration of 56 days.

2.2 Reproductive tissues and biomass change

Photographs of each fragment were taken at each time point to monitor visual changes in tissue surface (Figure S1), for example, the presence of sorus (reproductive) tissue (Figure S2). Repeated measures of wet biomass were taken on the same fragment at each time point. Biomass changes were calculated as a percentage of the starting mass remaining at each time point. Completely degraded fragments were removed and their biomass from the preceding time was recorded as mass lost. This aspect of the trial was extended to 108 days and final biomass measurements were recorded after all the fragments from the 30 m treatment had degraded.

2.3 Production and respiration measurements

Production and respiration rates were measured using a closed bottle respirometry technique (Migné *et al.* 2002; Biscéré *et al.* 2019). Twenty incubation chambers, each comprising of a 1.2 L transparent glass jar closed by a watertight seal, were distributed across four 50 L experimental units. The experimental units were each fitted with optical filters replicating light conditions in the corresponding aquaria and were replenished with the same ambient unfiltered seawater after each set of production and respiration incubations. Fragments were transferred in the dark from their aquaria into the corresponding depth treatment of the experimental unit with each jar containing an individual fragment. Two different incubations were conducted consecutively, measuring both oxygen production and consumption (respiration) respectively. Production was measured during a 60-minute incubation (long enough to allow detection of a change in oxygen concentration whilst avoiding oxygen saturation) under the experimental aquarium conditions. The jars were then opened to allow water exchange for 30 minutes and the containers were covered by dark tarpaulin to halt photosynthetic activity. The jars were subsequently re-sealed and the respiration incubations were conducted on the same fragments for 60 minutes in complete darkness. Dissolved oxygen concentrations were measured before and after both incubations (production and respiration) using a portable multi-meter (HQ40d, Hach®, Loveland, USA) coupled with a luminescent/optical dissolved oxygen probe (Intellical™ LDO101, Hach®, accuracy ± 0.2 mg L⁻¹). At the end of the incubations, fragments were retrieved from the jars, gently blotted dry and weighed (WW in g). Production and respiration rates were estimated by calculating the difference between initial and final oxygen O₂ concentrations after being corrected for temperature change (Aminot and K  rouel, 2004). The rates were expressed in mgO₂ kg WW⁻¹ hr⁻¹. The production rate is a measure of Net Primary Production (NPP), which represents the sum of photosynthesis and respiration in tandem. Meanwhile, Gross Primary Production

(GPP) was calculated by adding the dark respiration rate (R) to the NPP to derive the total oxygen produced via photosynthesis. The seawater temperature and incident photosynthetically active radiation (PAR, 400-700 nm, $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, Li-Cor QuantumSA-190, LI-COR®, Lincoln, USA), were recorded every minute during the trials.

2.4 Photosynthetic efficiency measurement

To reveal to the extent to which fragments' photosynthetic apparatuses were active, the operating efficiency of photosystem II (ΦPSII) and the maximal quantum yield of PSII photochemistry (F_v/F_m) were measured using a portable pulse-amplitude-modulated fluorometer (PAM, Heinz Walz, Effeltrich, Germany). *In vivo* ΦPSII was measured in ambient light whereas F_v/F_m measurements were obtained from fragments that had been dark adapted for 15 minutes (following Hargrave *et al.* 2017), before being flashed with a 0.8 s saturating white light pulse ($2500 \mu\text{mol photons.m}^{-2} \text{ s}^{-1}$). F_v/F_m values normally range between 0.7-0.8 for Phaeophyceae and values below are indicative of a stress response (Bischof *et al.* 1999; Hanelt, 2018)

2.5 Statistical analyses

2.5.1 Biomass change

As a consequence of bimodality in the bounded biomass data, a Euclidean distance-based permutational ancova (PERMANCOVA) was used in PRIMER ver 6.1 (Primer-E, Plymouth) to test effects of species and depth (fixed factors) over time (continuous covariate), with fragment identity (the plant from which the fragment was cut) as a random factor. P values

were obtained from type III sums of squares. MDS plots were inspected as a way of identifying potential issues relating to heterogeneities of dispersion, though no formal tests were performed due to the complexity of the model.

2.5.2 Production, respiration and photosynthetic parameters

The effects of species and depths across time on net and gross oxygen production (NPP and GPP), dark respiration (R) and combining NPP with 12 h of R to represent a full day's rate of oxygen flux (NPP-R), were tested with linear mixed effect models using Maximum Likelihood (package *lme4* in R 3.6.1) (Bates *et al.* 2015; R Core Team 2019). To account for variation in abiotic conditions across the experiment, mean PAR was used as a continuous covariate for oxygen production and mean temperature for dark respiration (PAR and temperature were strongly correlated). Fragment identity was included as a random factor and p values were obtained from type III Wald χ^2 tests. Plots of residuals versus fits were used to check assumptions of analyses. Data describing the photosynthetic parameters Fv/Fm and Φ PSII were analysed by similar model structure using generalised least squares (glS) fitting (package *nlme*, Pinheiro *et al.* 2019) due to heterogeneities of variance; PAR was again used as a continuous covariate; no random factor could be included in the glS model, between-plant variability being accounted for in the overall model fit. P values were derived as described above.

2.5.3 Omnibus PERMANCOVA

To examine the *in toto* physiological response of the two species, a multivariate approach was employed. A z-transformation was used to normalise the physiological variables (GPP,

R, Fv/Fm and Φ PSII), and a Euclidean distance – based multivariate similarity matrix was produced in PRIMER ver 6.1. This was then used as the basis for a mixed model PERMANCOVA with 999 permutations of a reduced model employing the same structure as the linear models described above; p values were obtained from type III sums of squares using a pseudo-F statistic.

3. RESULTS

3.1 Degradation dynamics

The analysis of biomass change with depth indicated strong heterogeneity of response to the environmental factor over time in the different species (3-way interaction pseudo- $F_{2,144} = 12.857$, $p < 0.001$; Fig. 2); no evidence of confounding heterogeneity of dispersion was apparent in the MDS plots. The interspecific differences were most apparent in the 15 and 30 m treatments, in both cases some of the *L. hyperborea* fragments degraded more quickly than *L. ochroleuca*. Under surface conditions neither species degraded markedly until after 56 days. No intact fragments of *L. ochroleuca* remained at the end of the 108 days, while *L. hyperborea* fragments were generally still intact at this point. With light attenuated to levels at 15 m, *L. hyperborea* began to degrade after 23 days, whilst *L. ochroleuca* persisted until the end of the study in the majority of cases. At 30 m most *L. hyperborea* fragments had completely broken down after 36 d, in contrast to *L. ochroleuca* where degradation was significantly slower (Fig. 2, Table 1).

3.2 Reproductive tissues and biomass change

Clear evidence of sorus material was first detected whilst conducting the final physiological measurements, 56 days into the experimental period on two *L. ochroleuca* fragments, one in the 0 m treatment and one in the 15 m treatment. When the study was concluded 108 days later, two different *L. ochroleuca* fragments had evidence of sorus material on the blade surface (Figure S2).

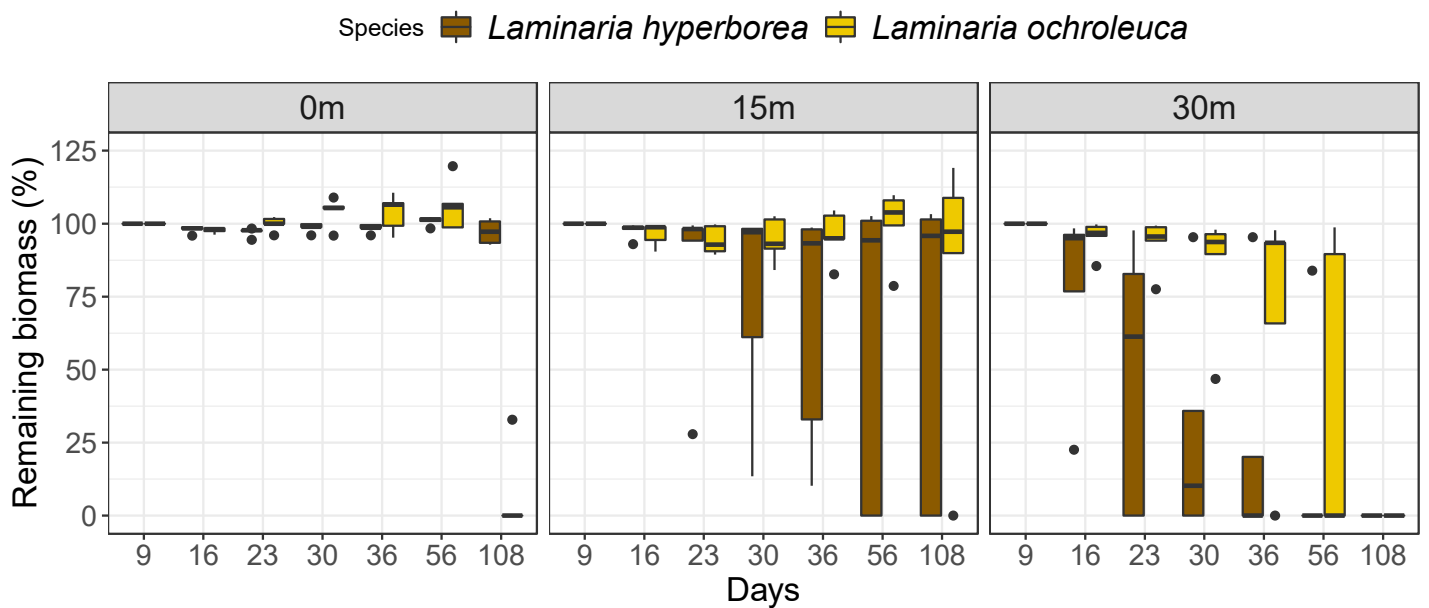


Fig. 2. Remaining biomass at three different simulated depths over time in *Laminaria hyperborea* and *Laminaria ochroleuca* (N = 144). Boxes indicate the interquartile range, horizontal line inside the bars indicates the median.

Table 1: Results of permanova analysis (type III SS) of % biomass remaining in the different species and depths (fixed factors) over 108 days (continuous covariate). Significant terms (P<0.05) are indicated in bold.

Source	Df	Pesudo-F	P
Time	1	119.37	0.001

Species	1	2.977	0.104
Depth	2	12.686	0.002
Time:Species	1	18.33	0.001
Species:Depth	2	2.893	0.066
Time: Depth	2	14.448	0.001
Time:Species:Depth	2	12.857	0.001
Fragment ID	24	6.331	0.001

348

349 3.3 Production and respiration measurements

350 As expected, the availability of light was the dominant factor affecting GPP; both in terms of
351 PAR at the surface ($\chi^2_{1,161} = 15.735$, $p < 0.001$) and as a main effect of photo-attenuation
352 related to depth ($\chi^2_{2,161} = 92.036$, $p < 0.001$). Contrary to expectation, however, across the
353 degradation period GPP did not decline as expected, and whilst the two species responded
354 differently to the passage of time ($\chi^2_{1,161} = 5.122$, $p = 0.024$), it was apparent that overall
355 oxygen evolution was indicative of the metabolic integrity of surviving tissues remaining
356 remarkably intact often beyond 36 days post-detachment (Fig. 3a, Table 2).

357 Respiration (R) was independent of temperature, but differed strongly between species ($\chi^2_{1,161} = 22.555$, $p < 0.001$), and as a function of time ($\chi^2_{1,161} = 8.462$, $p = 0.004$) and depth ($\chi^2_{2,161} = 10.276$, $p = 0.006$), modifying the species effect. Notwithstanding the declining
360 number of fragments persisting to the end of the trial (Fig. 3), it was clear that R did not
361 display a simple response over time; only the data for *L. hyperborea* under surface light
362 levels are suggestive of a simple linear increase over time (Fig. 3b, Table 2).

363 Most importantly, Net Primary Production (NPP) during lit periods remained at, or recovered
364 to, positive net production levels in the majority of fragments until the end of the 56 day trial
365 (Fig. 3c, Table 2). As with GPP and R, NPP differed strongly at different depths ($\chi^2_{1,161} = 88.31$, $p < 0.001$). NPP did not differ statistically between the two species, but the nature of
366 this experiment restricts these conclusions to brightly lit daylight hours. Assuming

368 equinoctial fully light and dark conditions, with NPP and an additional 12 h of R representing
369 a full day's oxygen flux, suggests a significant effect of species with an additional modifying
370 effect of depth upon this ($\chi^2_{2,161} = 6.244$, $p = 0.044$). Under this '24 h' model, a more realistic
371 interpretation of differential GPP responses between the species can be detected (Fig. 3d,
372 Table 2).
373

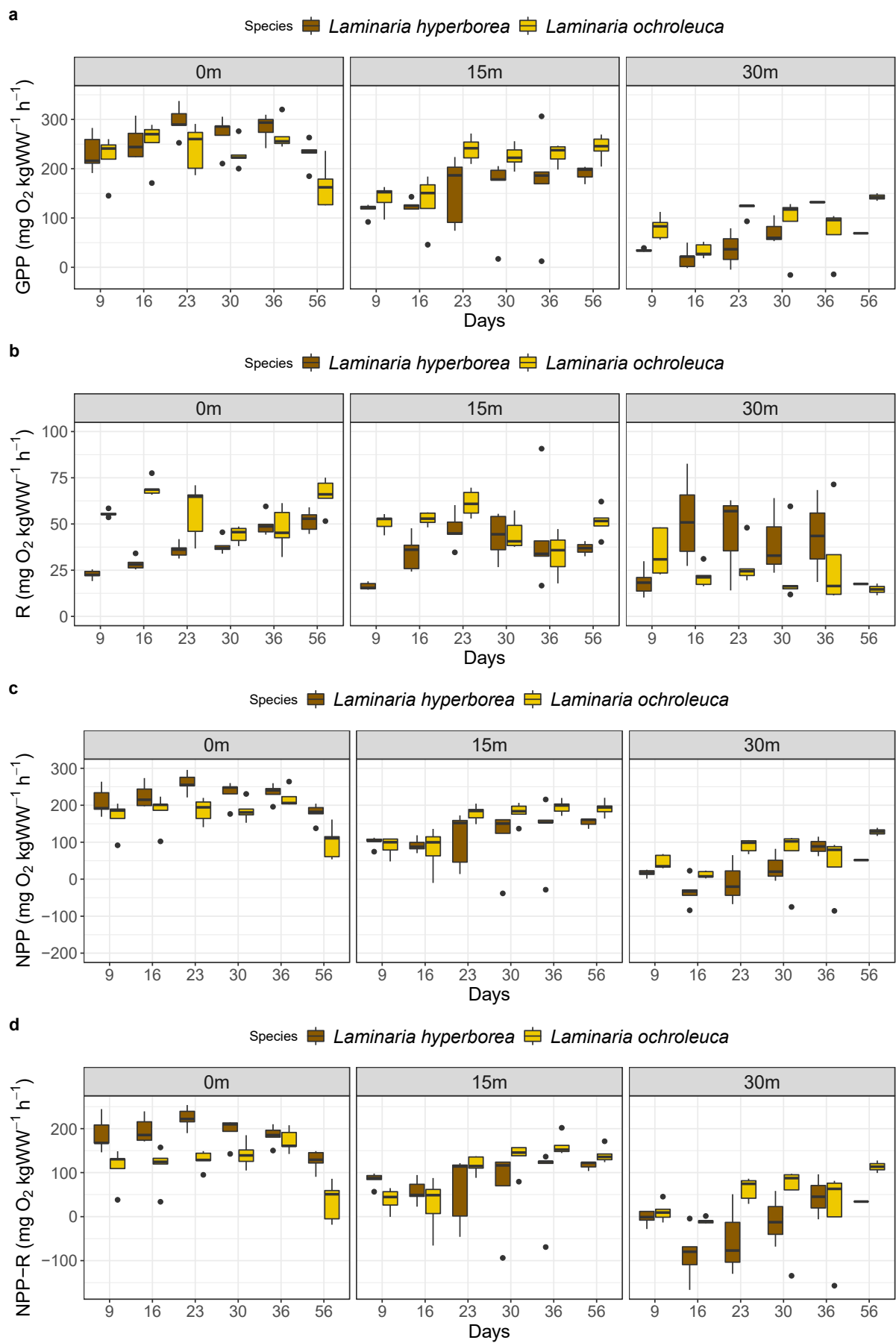


Fig. 3. (a) Gross Primary Production (GPP), (b) Respiration (R), and (c) Net Primary Production (NPP) and (d) ‘24 hour’ model of oxygen flux (NPP-R) rates, expressed as oxygen consumption or production, at three different simulated depths over time for *Laminaria hyperborea* and *Laminaria ochroleuca* (N = 161). Boxes indicate the interquartile range, horizontal line inside the bars indicates the median.

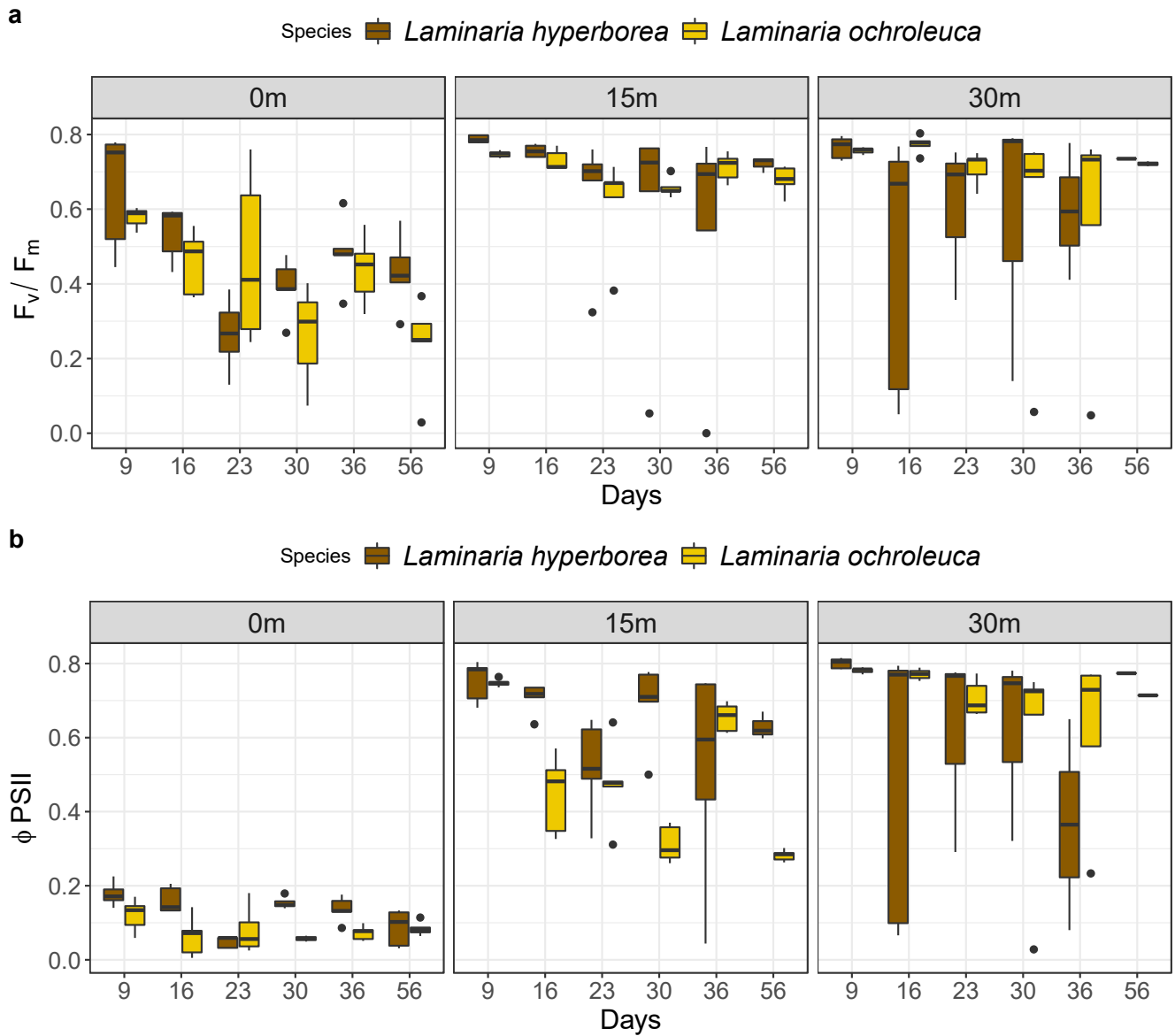
Table 2: Results of likelihood ratio tests based upon linear mixed effect models examining responses of (a) Gross Primary Production (GPP), (b) Respiration, (c) Net Primary Production (NPP) and (d) ‘24 hour’ model of oxygen flux (NPP-R) rates across time (56 days), between kelp species and depth (fixed factors) with PAR or Temperature as a covariate. Significant terms ($P < 0.05$) are indicated in bold.

Source	df	Chisq	P
(a) GPP			
PAR	1	15.735	< 0.001
Time (days)	1	0.566	0.452
Species	1	0.000	0.996
Depth	2	92.036	< 0.001
Time: Species	1	5.122	0.024
Species: Depth	2	1.157	0.561
Time: Depth	2	6.316	0.043
Time:Species:Depth	2	4.058	0.131
Fragment ID	1	9.664	0.002
(b) R			
Temp	1	0.098	0.754
Time (days)	1	6.110	0.013
Species	1	22.555	< 0.001
Depth	2	2.234	0.327
Time:Species	1	8.462	0.004
Species: Depth	2	10.276	0.006
Time: Depth	2	1.369	0.504
Time: Species: Depth	2	0.047	0.977
Fragment ID	1	3.727	0.054
(c) NPP			
PAR	1	9.160	0.002

Time (days)	1	3.833	0.050
Species	1	2.032	0.154
Depth	2	88.311	< 0.001
Time:Species	1	1.246	0.262
Time: Depth	2	7.147	0.028
Species: Depth	2	3.589	0.166
Time: Species: Depth	2	3.704	0.157
Fragment ID	1	11.22	0.001
(d) NPP- R			
PAR	1	4.050	0.044
Time (days)	1	7.924	0.005
Species	1	6.215	0.013
Depth	2	74.259	< 0.001
Time:Species	1	0.007	0.933
Time: Depth	2	6.861	0.032
Species: Depth	2	6.244	0.044
Time: Species: Depth	2	2.893	0.235
Fragment ID	1	11.226	< 0.001

3.4 Photosynthetic response

PAR was a significant covariate for the Φ PSII response ($\chi^2_1 = 7.901$, $p < 0.01$). Despite time exerting a non-statistically significant effect on Φ PSII (as it did upon NPP and GPP), the response of detrital fragments clearly declined over the degradation period (Fig. 4a) but became highly variable at increasing depth, swamping any trend. Fig. 4b shows that F_v/F_m displayed a similarly noisy decline over time. There was no significant difference in the photosynthetic response between the species. Both parameters were significantly affected by depth. No interactions were significant and therefore the photosynthetic behaviour of detrital resources from different species was not affected by time or by depth (Figs 4 a-b, Table 3).



396

397 **Fig. 4.** (a) Φ PSII and (b) F_v/F_m measurements at three different simulated depths over time
 398 for *Laminaria hyperborea* and *Laminaria ochroleuca* (N = 161). Boxes indicate the
 399 interquartile range, horizontal line inside the bars indicates the median.

400 **Table 3:** Results of likelihood ratio testing based upon generalized least squares fitting to
 401 examine responses of (a) Φ PSII (b) F_v/F_m across time (56 days), between kelp species and
 402 depths (fixed factors) with PAR as a covariate. Significant terms ($P < 0.05$) are indicated in
 403 bold.

Source	<i>df</i>	Chisq	<i>P</i>
(a) Φ PSII			
PAR	1	7.901	0.005
Time	1	0.221	0.638
Species	1	0.935	0.334
Depth	2	51.403	<0.001
Time:Species	1	0.694	0.405
Species: Depth	2	2.700	0.260
Time:Species:Depth	2	1.331	0.514
(b) F_v/F_m			
PAR	1	13.418	0.001
Time	1	1.620	0.203
Species	1	0.230	0.632
Depth	2	5.981	0.050
Time:Species	1	0.428	0.513
Species: Depth	2	2.654	0.265
Time:Species:Depth	2	1.641	0.440

404

405 3.5 Omnibus permanova

406 The combined response of GPP, R, Φ PSII and F_v/F_m variables was strongly affected by the
407 light availability in terms of PAR ($\chi^2_1 = 11.176$, $p < 0.001$) and Depth ($\chi^2_1 = 21.585$, $p <$
408 0.001). A realistic picture of detrital degradation revealed species responded differently to the
409 passage of time ($\chi^2_1 = 9.327$, $p < 0.001$) but not depth (Table 4).

410

411 **Table 4:** Results of omnibus PERMANOVA analysis of standardized data describing GPP,
412 R, Φ PSII and F_v/F_m across time (56 days), between kelp species and depth (fixed factors)
413 with PAR as a covariate. Significant terms ($P < 0.05$) are indicated in bold.

414

Source	<i>df</i>	Pesudo-F	<i>P</i>
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GPP, R, ΦPSII, F_v/F_m			
PAR	1	11.176	0.001
Time	1	4.837	0.012
Species	1	8.729	0.001
Depth	2	21.585	0.001
Time:Species	1	9.327	0.001
Species: Depth	2	2.269	0.081
Time:Species:Depth	2	0.848	0.519

4. DISCUSSION

4.1. Production and respiration measurements

For the first time, the primary producer functions of algal detritus have been quantified across a simulated depth spectrum. Detritus continued to sustain net production of oxygen across a 56-day period, underscoring its capacity to maintain key functions such as carbon fixation. Detrital tissues slightly increased in biomass during the early stages of degradation, demonstrating that measured oxygen production is reflective of fresh material being generated. Over time, the respiration of detrital fragments, as a proxy for stress or associated bacterial activity, increased in some contexts (Sosik and Simenstad, 2013). Evidence of some degradation was further reinforced by a measured decline in photosynthetic performance (Φ PSII and F_v/F_m), in accordance with the initial hypothesis. At the end of the first time period, values between 0.6-0.8 at 15 m and 30 m reflected an optimum performance at depths at which the kelps inhabit (Gorman *et al.*, 2013). Low photosynthetic parameters at 0 m follow reported trends in the literature of decreases in both measurements with increasing irradiances (for *Laminaria digitata*, Delebecq *et al.* 2011).

Respiration is a central process in kelp decomposition (de Bettignies *et al.* 2020b) and measured increases in the rate of oxygen consumption were mirrored by a decline in the

435 detrital biomass. However, it is important to note that the measurements reflect the holobiont
436 respiration of *Laminaria* tissue together with its ensemble of microorganisms (Baedke *et al.*
437 2020). The results of this study reveal that the respiration response differed between the two
438 species across time. Detritus from *L. hyperborea* exhibited higher rates of respiration
439 compared to *L. ochroleuca* over time in the 30 m treatment and only under surface conditions
440 was a linear increase in respiration detected for *L. hyperborea*. This differential response
441 between the species may be indicative of stress or higher biofilm activity associated with *L.*
442 *hyperborea* fragments. *L. hyperborea* degraded faster than *L. ochroleuca* at 15 m and 30 m,
443 suggesting that low light conditions may impede the regeneration of damaged tissue for *L.*
444 *hyperborea* which points to the role of light in determining the detrital fate of some species
445 (Hader *et al.* 1998; Swanson and Fox 2007). Furthermore, in some instances, during the
446 initial stages of degradation at 0 and 15 m, *L. ochroleuca* positively increased in biomass
447 compared to *L. hyperborea* (Fig. 2). However, this trend was reversed after 56 days in the 0
448 m treatment when all *L. ochroleuca* fragments were completely degraded in sharp contrast to
449 the relatively intact fragments of *L. hyperborea*. 4.2 Considering the first 40 days of this trial,
450 this result is comparable, yet contrary to the findings of Pessarrodona *et al.*'s (2018b) *in situ*
451 study comparing the biomass loss from the same study species. Pessarrodona *et al.* (2018b)
452 report that *L. ochroleuca* lost biomass at a faster rate than *L. hyperborea* in spring, prior to
453 the latter shedding of old fronds. The present study separated the change in mass across
454 regular time intervals and elongated the temporal scale of degradation to 108 days, as well as
455 eliminating physical erosion as a mechanism of degradation, casting light on the purely
456 organic dimension of how kelp matter breaks down. Our results suggest that *L. hyperborea*
457 has the potential to be a more persistent spatial subsidy and thus may reside in the ecosystem
458 for longer under attenuated illumination. However, hydrodynamics and physical processes

such as abrasion and grazing may further confound elucidation of the decomposition process.
(Nielsen *et al.* 2004; Braeckman *et al.* 2019).

4.2. Contextualizing the findings

These differences in persistence will become increasingly important as *L. ochroleuca* gradually replaces *L. hyperborea*, in habitats where the two species coexist, (Teagle and Smale 2018) and will be further exacerbated by the seasonal modification of detrital production between the species; ultimately affecting the quality and supply of organic kelp derived material entering the detrital pathway (Bishop *et al.* 2010). The extent to which benthic ecosystems in the North East Atlantic are dependent on detritus derived from *L. hyperborea* remains unquantified. However, modifications in the turnover of organic material, transport (Pedersen *et al.* 2005), trophic connectivity (Leclerc *et al.* 2013b), organic matter content (Abdullah *et al.* 2017) and a homogenization of the nutrient supply from kelp detritus derived from different species will likely have ramifying effects across food webs.

Extending the investigation to consider the degradation process across environmental contexts revealed that other measured physiological processes of kelp detritus (NPP, GPP and Φ_{PSII} and F_v/F_m) are not only species specific but also highly dependent on light availability. Depth significantly affected 24-hour oxygen flux and the Species response to the effect of Depth was significantly heterogeneous in the case of both respiration and the 24-hour model of oxygen flux (Fig. 3b and d). Therefore, considering the dynamic nature of detrital transport, the depth to which detritus is exported significantly determines the carbon fixation, respiration and photosynthetic performance of kelp material (Filbee-Dexter and Scheibling, 2016). Furthermore, detritus was clearly less productive as a function of decreasing irradiance

from 0 m > 15 m > 30 m (Fig. 4a). Photosynthetic capacity was critically impaired at 0 m, probably as a result of photoinhibition (Delebecq *et al.* 2011), but remained mostly invariant between 15 and 30 m. Although the activity of the photosynthetic apparatus was maintained in low light conditions, the decline in oxygen production is indicative that detritus is a less effective primary producer at 30 m. The differing responses of respiration in the two species over time and at different depths highlight that the process of degradation needs to be considered across different environmental conditions with a temporal dimension. Species' respiration fluctuated across time and their response was dependent on light attenuation, which indicates that one species may have the physiological capacity to persist for longer than its congener at a specific depth.

4.3. Re-defining kelp detritus

An unexpected result was that *L. ochroleuca* fragments developed visible sorus tissue at the tissue surface indicating that such fragments remain capable of maintaining reproductive functions (Fig S1). Moreover, this was detected first for two fragments during the final time period (T6) in July. Visible sorus remained at the blade surface two independent *L. ochroleuca* fragments when the experiment ended 108 days post fragment preparation in September. This time window is in accordance with the reproductive period for *L. ochroleuca* (Pereira *et al.* 2019), further revealing the metabolic competency of the kelps post-detachment. Further research would be necessary to determine spore viability from such tissues. de Bettignies *et al.* (2020b) reported a similar phenomenon for *L. hyperborea* in October after subjecting detrital fragments to 5 months of degradation *in situ*. In terms of reproductive capacity, some of the energy generated by detrital photosynthesis is invested into the generation of reproductive tissue which potentially has considerable implications for the dispersal of these species. If current-borne kelp detritus can still

reproduce, then kelp populations structure is likely to be far more fluid than would be indicated by typical spore or gamete dispersal, which is low for individual sporophytes within a kelp forest (~ 5-200 m, Fredriksen *et al.* 1995). This phenomenon compliments the functional role of herbivores in increasing fertilisation success and dispersing kelp spores which germinate post-digestion (Ruz *et al.* 2018).

Another important outcome of the present study and other recent work on physiological viability of macroalgal ‘detritus’ (de Bettignies *et al.* 2020b) is a questioning of the rationale behind defining this material as ‘detritus’. Currently, cast or detached macroalgal fragments are considered as ‘non-living’ organic matter generated by the growth and production of living organisms (Hagen *et al.* 2012): a viewpoint that is based upon terrestrial botanical science. Although such tissues may be no longer attached, and as our data suggests, may be in the process of slowly entering the detrital food web, they remain ‘alive’ and physiologically competent for much longer than would be typical for tissues of land plants. This ‘productive necromass’ – physiologically persistent and viable, unattached or fragmented algal biomass – continues to photosynthesize and, in the right conditions, can continue to fix carbon for months after it would otherwise be inaccurately defined as detrital. Our study has demonstrated that kelp detritus can sustain productivity for long periods of time and therefore detrital contribution to Blue Carbon is likely to be much greater than has been previously accounted for. Accordingly, incorporating productivity from macroalgal detritus could account for important increases to the contribution of macroalgae in the Blue Carbon economy.

4.4 The role of kelp detritus in benthic ecosystems

The vast majority of kelp production enters the detrital pathway (about 82% according to Krumhansl and Scheibling 2012), therefore fundamental variability in the respiration and photosynthetic performance of kelp material across time and under different environmental conditions are important for understanding the persistence and productivity of detrital resources. The composition of kelp forests and thus their detritus, will likely be modified as climate warming persists (Smale et al. 2015), with the gradual increase of HFS with high thermal affinities and gradual local extinctions of native HFS with cooler thermal affinities (Wiens 2016). These replacements will likely impact many aspects of the cycling of organic material, from the spatial subsidies exported kelp matter provides, to the fitness of grazers and detritivores feeding upon it, and the rate of carbon sequestration into longer residence forms in the benthos. Pessarrodona *et al.* (2018b) speculated about an alteration in the functional importance of this detrital material due to a variation in the rate of supply from different kelp species. Here we have shown that the continued biological activity of fragmented kelp tissues also differs between species, across time and environments, further altering the contribution of kelp mass to spatial subsidies (Leclerc *et al.* 2013a).

This study provides a snapshot of the degradation dynamics of two kelps under controlled conditions. There are numerous potential sources for error; for example a change in detrital respiration could be attributed an upregulation of metabolic processes in *L. hyperborea* or to an increase in oxygen consuming saprophytic bacteria and fungi (Fenchel and Jørgensen, 1977; Williams *et al.* 2004). Furthermore, variation in species physiology cannot be generalized across the entirety of benthic ecosystems in the North East Atlantic because despite advances in areas of low-moderate wave exposure (Smale *et al.* 2015), *L. ochroleuca* may not be able to fully replace *L. hyperborea* in sites exposed to high wave exposure (Pessarrodona *et al.* 2018b) and therefore the composition of detritus from such assemblages may remain relatively unchanged. Also, the role of macrofaunal colonization and consumption (de Bettignies *et al.* 2020; Ramirez-Llodra *et al.* 2016) of

the kelps in question could change the degradation dynamics completely. Hargrave *et al.* (2016) reported lower concentrations of grazer-deterrent polyphenolics and flavonoids in *L. ochroleuca* than in another common NE Atlantic congener: *L. digitata*, with higher grazing rate by herbivorous gastropods in the former. Meanwhile, Pessarrodona *et al.* (2018b) found a similar herbivore preference for *L. ochroleuca* over *L. hyperborea*, recording a faster degradation of the former. If detritivore preference for the more palatable *L. ochroleuca* mirrors that of grazers, then the reconciliation of the slower degradation of *L. ochroleuca* in the earlier stages of the present study with the faster *in situ* degradation of *L. ochroleuca* observed by Pessarrodona *et al.* (2018b) could be attributed to mechanical effects, especially of saprovores aiding conversion of frond tissue into coarse particulate organic matter and facilitating ingress by saprophytic micro-organisms. Future study should therefore aim to evaluate the importance of the ecological consequences of environmentally realistic deposits of macroalgal detritus with their attendant bacterial and detritivorous assemblages and also continue to compare the detrital compositions from species at risk of local extinction from a variety of range-expanding or invasive algae (Sorte *et al.* 2010), taking into account different environmental contexts in which kelp degradation may occur, testing the degradation response *in situ* across a gradient of turbulence, and explicitly focusing on detritivores as a driver of tissue fragmentation and a facilitator of micro-organismal colonization. These questions have indeed been addressed in other contexts spanning from shallow shorelines to the deep sea whilst the shallow subtidal has often been considered as a mere transitional deposition area. However, we argue that detrital accumulations can exert measurable impacts on ecosystem functioning and deserve enhanced attention.

5. CONCLUSION

Kelp fragments remained physiologically competent for 56 days and possibly reproductively active for up to 108 days after they were cut from the thallus. The fragments' photosynthetic apparatus continued to function adequately to allow short-term (~ 56 days in *L. ochroleuca*) net gains in biomass which was sustained under ambient light levels. Light availability was the greatest determinant of photosynthetic performance, and net and gross primary production, whilst light and interspecific differences dominated the response of respiration. The range-expanding *L. ochroleuca* broke down more slowly under attenuated illumination, challenging previous findings. We believe that a re-evaluation of recently formed macroalgal detritus as 'living material' is due and should certainly be considered when evaluating the functional integrity and spatial subsidies afforded by kelp forests. The predicted expansion of the thermally tolerant species, *L. ochroleuca*, and replacement of the less tolerant *L. hyperborea* across extensive areas is likely to alter the cycling of organic matter. Overall, these findings demonstrate the indispensable need to consider detritus as an important autotrophic resource, even after exportation, depending on the environmental conditions.

DATA AVAILABILITY

Data will be archived in GitHub repository: <https://github.com/nadiafrontier/The-degradation-of-kelp-detritus.git>

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SUPPLEMENTARY INFORMATION

Supplementary tables 1-4 contain abridged statistical tables following permanova, linear mixed effect models and generalised least squares analysis to support the summary statistics quoted in the manuscript.

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SUPPLEMENTARY MATERIAL

Sustained productivity and respiration of degrading kelp detritus in the shallow benthos: detached or broken, but not dead.

Nadia Frontier, Florian de Bettignies, Andy Foggo, Dominique Davoult

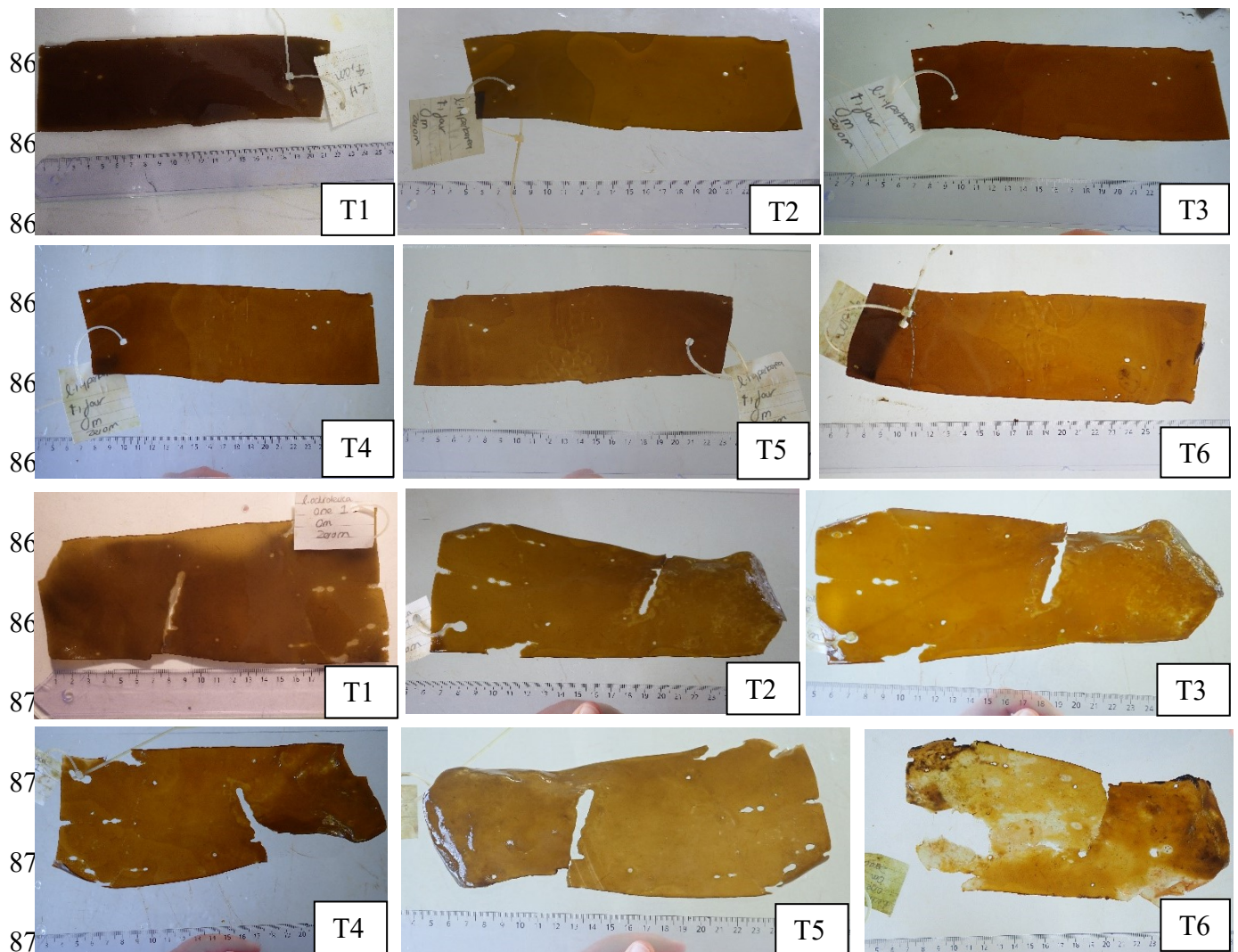
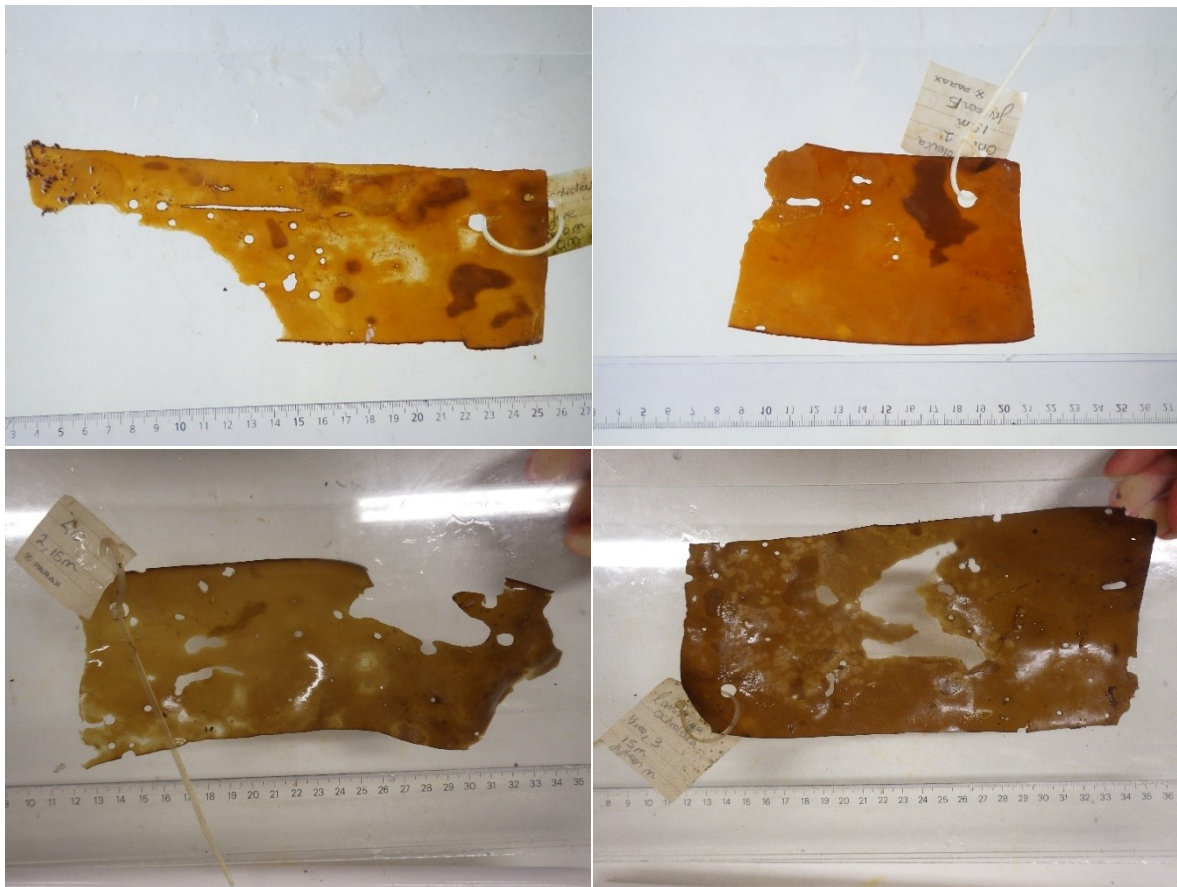


Figure S1: The transition of fragments through time (56 days) for *Laminaria hyperboeaa*, (lines 1 and 2) and *Laminaria ochroleuca* (lines 3 and 4) both in the 0 m depth treatment.

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880 **Figure S2:** Moving clockwise from top left: Sorus material (dark patches) from *Laminaria*
881 *ochroleuca* fragments at 0 m and 15 m at Time 6, 56 days into the degradation period. Sorus
882 material from two different *Laminaria ochroleuca* fragments at 15 m, 108 days post fragment
883 detachment when the experiment terminated.

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