



HAL
open science

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 Davault

► To cite this version:

Nadia Frontier, Florian de Bettignies, Andy Foggo, Dominique Davault. Sustained productivity and respiration of degrading kelp detritus in the shallow benthos: Detached or broken, but not dead. *Marine Environmental Research*, 2021, 166, pp.105277. 10.1016/j.marenvres.2021.105277 . hal-03184625

HAL Id: hal-03184625

<https://hal.science/hal-03184625>

Submitted on 29 Mar 2021

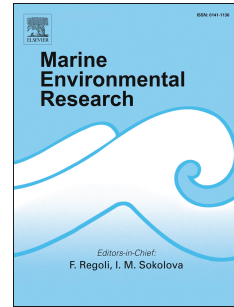
HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Journal Pre-proof

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



PII: S0141-1136(21)00026-X

DOI: <https://doi.org/10.1016/j.marenvres.2021.105277>

Reference: MERE 105277

To appear in: *Marine Environmental Research*

Received Date: 18 October 2020

Revised Date: 28 January 2021

Accepted Date: 4 February 2021

Please cite this article as: Frontier, N., de Bettignies, F., Foggo, A., Davoult, D., Sustained productivity and respiration of degrading kelp detritus in the shallow benthos: detached or broken, but not dead., *Marine Environmental Research*, <https://doi.org/10.1016/j.marenvres.2021.105277>.

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2021 Published by Elsevier Ltd.

CRedit AUTHOR STATEMENT

Nadia Frontier: Conceptualisation, Methodology, Data curation, Formal analysis, Writing – Original Draft. **Florian de Bettignies:** Conceptualisation, Methodology, Writing- Review and Editing. **Andrew Foggo:** Data curation, Formal analysis, Writing- Review and Editing. **Dominique Davault:** Funding acquisition, Resources, Writing- Review and Editing.

Journal Pre-proof

1 **Research paper**

2
3 **Sustained productivity and respiration of degrading kelp detritus in the**
4 **shallow benthos: detached or broken, but not dead.**

5
6
7 Nadia Frontier^{a, b†*}, Florian de Bettignies^{a†}, Andy Foggo^b, Dominique Davoult^a

8 ^a Sorbonne Université, CNRS, UMR 7144 AD2M, Station Biologique de Roscoff, Place
9 Georges Teissier, F-29680 Roscoff, France

10 ^b Marine Biology and Ecology Research Centre, School of Biological and Marine Sciences,
11 University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK

12
13 Running title: Kelp detritus can sustain primary producer functions

14 *Corresponding author: frontier.nadia@gmail.com

15 Postal address: 29A Eythrope Road, Stone, Aylesbury, Buckinghamshire, HP17 8PH

16 † The authors contributed equally to this work

17
18 Running header: Kelp detritus fulfilling primary producer functions

19 All revisions have been highlighted in yellow

20

21

22

23 **ABSTRACT**

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

46 dependent upon the range of habitats to which it is exported. In the context of climate
47 change, shifts in species composition of kelp forests and their detritus are likely to
48 have wide-reaching effects upon the cycling of organic matter in benthic ecosystems.

49

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

52

53 1. INTRODUCTION

54 Within the temperate to sub-polar regions of the globe, kelps are of paramount importance to
55 marine ecosystem functioning. They contribute to the functional integrity of coastal
56 ecosystems as habitat forming species (HFS) via their biogenic structure, through wave
57 energy dissipation and via cycling of carbon (Christie *et al.* 2003; Laffoley & Grimsditch,
58 2009; Teagle *et al.* 2017). As highly productive primary producers, kelps fix carbon dioxide
59 to produce organic matter via photosynthesis (Bartsch *et al.* 2008). The accumulated biomass
60 is eventually released or eroded and exported as detritus in a variety of forms into recipient
61 benthic ecosystems (Duggins *et al.* 1989; Krumhansl and Scheibling 2012; Pessarrodona *et*
62 *al.* 2018a) . This transfer of carbon helps to sustain adjacent food webs. The breakdown of
63 detrital material by erosion and grazing activity provides a source of particulate organic
64 matter (POM) available to filter-feeding invertebrates (Renaud *et al.* 2015; de Bettignies *et*
65 *al.* 2020a; Vilas *et al.* 2020) which in turn can play a major role in mediating carbon fluxes
66 along the sediment-water interface (Queirós *et al.* 2019; Pedersen *et al.* 2020).

67

68 A significant proportion of primary production from marine primary autotrophs is exported as
69 detritus rather than entering the consumer food web (Moore *et al.* 2004). In a global context,

70 as much as 82% of annual kelp biomass may be transferred as detrital subsidies (Krumhansl
71 and Scheibling 2012; de Bettignies *et al.* 2013). Knowing the fate of such detritus is
72 fundamental in understanding the dynamics, connectivity and functioning of coastal
73 ecosystems (Polis *et al.* 1997). Indeed, detritus enhances both primary and secondary
74 production (Polis *et al.* 1997; Marczak *et al.* 2007) whilst contributing to the structure and
75 stability of food webs in recipient ecosystems (Huxel *et al.* 2002). Furthermore, accumulation
76 of detritus can physically modify the habitat structure (Arroyo and Bonsdorff 2016).
77 However, the influences upon recipient ecosystems are dependent upon the timing, frequency
78 and residence time of the detrital deposition (Yang *et al.* 2008).
79
80 Macroalgae represent an as yet under-estimated contributor to the oceanic carbon cycle and
81 in particular to carbon sequestration and long-term storage. Their contribution to global
82 carbon assimilation and sequestration is currently not considered by the IPCC (Ciais *et al.*
83 2013) , and whilst the Global Carbon Project (GCP) identifies coastal habitats as carbon
84 stocks (Friedlingstein *et al.* 2019), their full contribution to the global marine carbon sink
85 remains neglected. Unlike seagrasses or phytoplankton, macroalgae are not routinely
86 considered as contributors to the 'Blue Carbon' budget (McLeod *et al.* 2011; Howard *et al.*
87 2017). Marine macrophytes collectively fix around 1.8 Gt C yr⁻¹ (of which macroalgae
88 contribute ~1.5 Gt C yr⁻¹) (Duarte *et al.* 2013; Duarte and Krause-Jensen 2017; Krause-
89 Jensen and Duarte 2016) in contrast to the ~58 Gt C yr⁻¹ of phytoplankton production
90 (Buitenhuis *et al.* 2013; Middelburg 2019). However, the lability of phytoplankton carbon
91 and the high rate of remineralisation through consumption and degradation mean that only in
92 the region of 0.23 Gt C yr⁻¹ (0.4%) of phytoplankton production becomes sequestered into
93 carbon stores or sinks, whilst the lower rate of consumption and refractory chemical nature of
94 macroalgal detritus mean that ~0.17 Gt C yr⁻¹ (11.4%) is sequestered. Thus, including

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

97

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

116

117 The conspicuous thermally tolerant congeneric kelp (Franco *et al.* 2017; Hargrave *et al.*
118 2017) of Lusitanian origin, *L. ochroleuca* (Bachelot de la Pylaie), has expanded its range
119 northwards from Morocco and across the English Channel in response to the changing

120 climate over the last century. Today, *L. ochroleuca* is expanding its leading edge eastwards
121 and northwards at around 5.4 and 2.5 km per year, respectively (Straub *et al.* 2016). Its range
122 now overlaps substantially with the native assemblage's dominant kelp species, *L.*
123 *hyperborea* (Smale *et al.* 2015; Hargrave *et al.* 2017) which has undergone a ~250 km range
124 contraction at its warm leading-edge since 1970 (Assis *et al.* 2016). In comparison to the
125 pulsed detrital production from *L. hyperborea*, detrital production by *L. ochroleuca* is greater
126 in volume, more frequent and degrades faster between May and October (Pessarrodona *et al.*
127 2018b). The expanding thermal envelope and subsequent spread of *L. ochroleuca* is
128 modifying both the taxonomic and functional composition of HFS, with resulting effects on
129 detrital composition. The re-arrangement of HFS has been shown to have marked ecological
130 implications; extending to adjacent communities which rely on these subsidies of
131 allochthonous material (Bishop *et al.* 2010; Straub *et al.* 2016).

132
133 The ecological function of detritus varies between species. Recent studies (Pessarrodona *et al.*
134 *et al.* 2018b) comparing *L. ochroleuca* and *L. hyperborea* have demonstrated interspecific
135 differences in seasonal detrital decomposition rates, with *L. ochroleuca* exhibiting
136 significantly faster rates (6.5 x) compared to *L. hyperborea* (Pessarrodona *et al.* 2018b) in
137 spring. In addition, the species exhibit differences in timing of detrital production: the May
138 cast from *L. hyperborea* accounting for ~40-60% of annual lamina erosion (Pessarrodona *et al.*
139 *et al.* 2018a) compared with the continual release of detritus from the fronds of *L. ochroleuca*
140 (Pessarrodona *et al.* 2018b). Such alterations to the supply and cycling of organic matter will
141 likely be amplified as sea surface temperatures increase. In the North East Atlantic, a rise of >
142 2°C is forecast in the next 100 years (Philippart *et al.* 2011; Masson-Delmotte *et al.* 2018),
143 which will likely result in the gradual replacement of the native cool-water *L. hyperborea* by
144 the warm-water tolerant *L. ochroleuca*.

145

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

156

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

169

170 **2. MATERIAL AND METHODS**

171 The study was conducted in the Roscoff Biological Station close to the Bay of Morlaix
172 (France). In May 2018, *L. hyperborea* was harvested at La Veille (48°42'36.22"N,
173 3°54'04.81"W) and *L. ochroleuca* at An Nehou (48°41'34.27"N, 3°56'25.52"W) from ~ 8-10
174 m below chart datum. Five typical mature canopy-forming individuals of each kelp species
175 were harvested by severing the stipe just above the holdfast. The mean total length of *L.*
176 *hyperborea* individuals was 348 cm compared to *L. ochroleuca* individuals with a mean
177 length of 169 cm. Within two hours of collection, the sporophytes were submerged in the
178 dark in a 500 L flow-through tank of aerated ambient sea water pumped directly from the Bay
179 and left to acclimate for 48 hours.

180

181 *2.1 Experimental design*

182

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

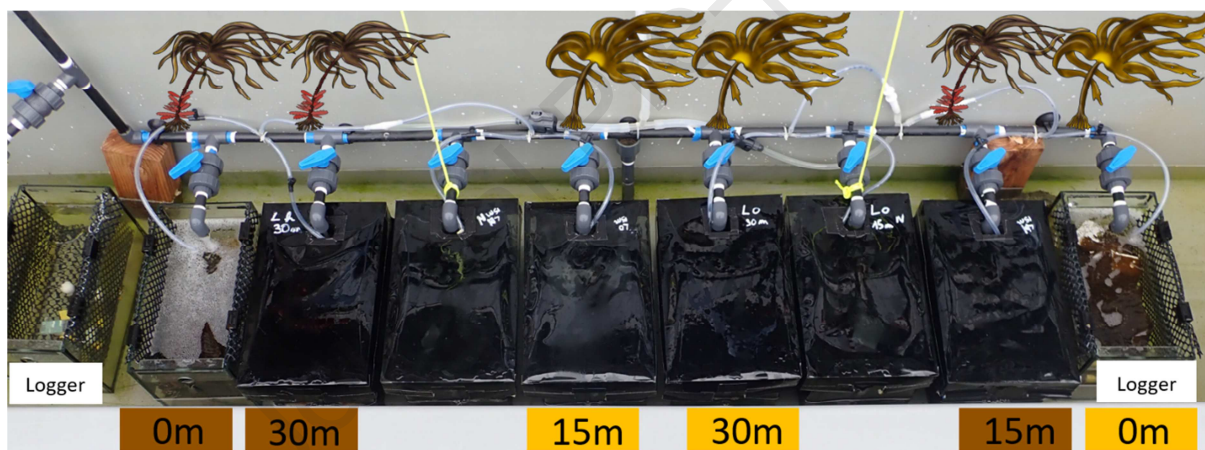
188

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

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

$$195 \quad I(t) = I(z_0)\exp(-kz) \quad \text{equation 1.}$$

196 The irradiance at depth (t) $I(t)$ depends on the light at the surface $I(z_0)$, the depth (z) and the
 197 extinction coefficient of the water in the column (k). The 0 m treatment, representing
 198 strandline and floating detritus, were submerged in 8 cm of water hence $z_0 = 0.08$ m. The
 199 percentage of light available at 0, 15 and 30 m was 98.9%, 12.3% and 1.5% respectively;
 200 these values were utilised when assembling the relevant filters. We did not, however, account
 201 for the change in spectral character as a function of depth (Saulquin *et al.* 2013).
 202



203
 204 **Fig. 1.** Experimental set-up composed of filters for 15 and 30 m aquaria, constant air
 205 bubbling and HOBO loggers. Two unlabelled aquaria were used for experiments that are
 206 outside the scope of this paper. Each aquarium contained five replicate fragments. The
 207 brown squares represent aquaria with *L. hyperborea* fragments and yellow squares contain *L.*
 208 *ochroleuca* fragments.

209

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

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

226 *2.2 Reproductive tissues and biomass change*

227
228 Photographs of each fragment were taken at each time point to monitor visual changes in
229 tissue surface (Figure S1), for example, the presence of sorus (reproductive) tissue (Figure
230 S2). Repeated measures of wet biomass were taken on the same fragment at each time point.
231 Biomass changes were calculated as a percentage of the starting mass remaining at each time
232 point. Completely degraded fragments were removed and their biomass from the preceding
233 time was recorded as mass lost. This aspect of the trial was extended to 108 days and final
234 biomass measurements were recorded after all the fragments from the 30 m treatment had
235 degraded.

236

237 *2.3 Production and respiration measurements*

238 Production and respiration rates were measured using a closed bottle respirometry technique
239 (Migné *et al.* 2002; Biscéré *et al.* 2019). Twenty incubation chambers, each comprising of a
240 1.2 L transparent glass jar closed by a watertight seal, were distributed across four 50 L
241 experimental units. The experimental units were each fitted with optical filters replicating
242 light conditions in the corresponding aquaria and were replenished with the same ambient
243 unfiltered seawater after each set of production and respiration incubations. Fragments were
244 transferred in the dark from their aquaria into the corresponding depth treatment of the
245 experimental unit with each jar containing an individual fragment. Two different incubations
246 were conducted consecutively, measuring both oxygen production and consumption
247 (respiration) respectively. Production was measured during a 60-minute incubation (long
248 enough to allow detection of a change in oxygen concentration whilst avoiding oxygen
249 saturation) under the experimental aquarium conditions. The jars were then opened to allow
250 water exchange for 30 minutes and the containers were covered by dark tarpaulin to halt
251 photosynthetic activity. The jars were subsequently re-sealed and the respiration incubations
252 were conducted on the same fragments for 60 minutes in complete darkness. Dissolved
253 oxygen concentrations were measured before and after both incubations (production and
254 respiration) using a portable multi-meter (HQ40d, Hach®, Loveland, USA) coupled with a
255 luminescent/optical dissolved oxygen probe (Intellical™ LDO101, Hach®, accuracy ± 0.2
256 mg L^{-1}). At the end of the incubations, fragments were retrieved from the jars, gently blotted
257 dry and weighed (WW in g). Production and respiration rates were estimated by calculating
258 the difference between initial and final oxygen O_2 concentrations after being corrected for
259 temperature change (Aminot and K  rouel, 2004). The rates were expressed in $\text{mgO}_2 \text{ kg WW}^{-1}$
260 hr^{-1} . The production rate is a measure of Net Primary Production (NPP), which represents
261 the sum of photosynthesis and respiration in tandem. Meanwhile, Gross Primary Production

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

266

267 *2.4 Photosynthetic efficiency measurement*

268

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

278

279 *2.5 Statistical analyses*

280

281 *2.5.1 Biomass change*

282

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

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

290

291 2.5.2 Production, respiration and photosynthetic parameters

292

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

307

308 2.5.3 Omnibus PERMANCOVA

309

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

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

317

318 3. RESULTS

319 3.1 Degradation dynamics

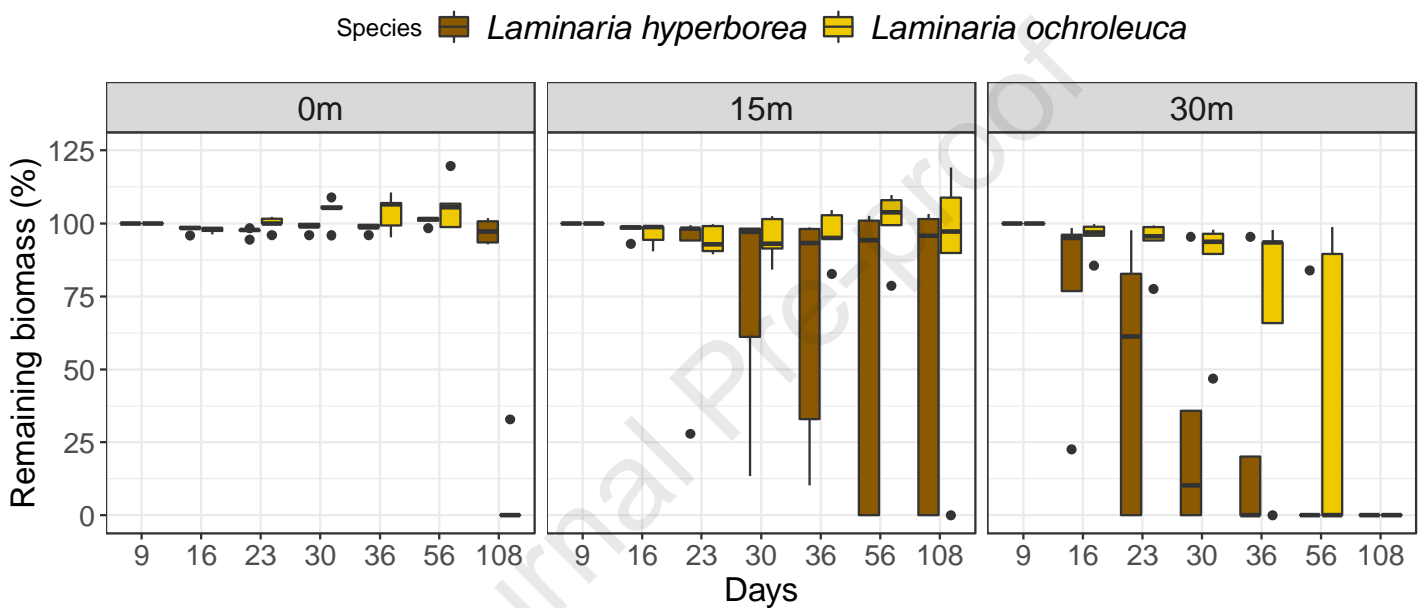
320 The analysis of biomass change with depth indicated strong heterogeneity of response to the
321 environmental factor over time in the different species (3-way interaction pseudo- $F_{2,144} =$
322 12.857, $p < 0.001$; Fig. 2); no evidence of confounding heterogeneity of dispersion was
323 apparent in the MDS plots. The interspecific differences were most apparent in the 15 and 30
324 m treatments, in both cases some of the *L. hyperborea* fragments degraded more quickly than
325 *L. ochroleuca*. Under surface conditions neither species degraded markedly until after 56
326 days. No intact fragments of *L. ochroleuca* remained at the end of the 108 days, while *L.*
327 *hyperborea* fragments were generally still intact at this point. With light attenuated to levels
328 at 15 m, *L. hyperborea* began to degrade after 23 days, whilst *L. ochroleuca* persisted until
329 the end of the study in the majority of cases. At 30 m most *L. hyperborea* fragments had
330 completely broken down after 36 d, in contrast to *L. ochroleuca* where degradation was
331 significantly slower (Fig. 2, Table 1).

332

333 3.2 Reproductive tissues and biomass change

334

335 Clear evidence of sorus material was first detected whilst conducting the final physiological
 336 measurements, 56 days into the experimental period on two *L. ochroleuca* fragments, one in
 337 the 0 m treatment and one in the 15 m treatment. When the study was concluded 108 days
 338 later, two different *L. ochroleuca* fragments had evidence of sorus material on the blade
 339 surface (Figure S2).
 340



341
 342 **Fig. 2.** Remaining biomass at three different simulated depths over time in *Laminaria*
 343 *hyperborea* and *Laminaria ochroleuca* (N = 144). Boxes indicate the interquartile range,
 344 horizontal line inside the bars indicates the median.

345
 346 **Table 1:** Results of permanova analysis (type III SS) of % biomass remaining in the different
 347 species and depths (fixed factors) over 108 days (continuous covariate). Significant terms
 348 (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

349

350 *3.3 Production and respiration measurements*

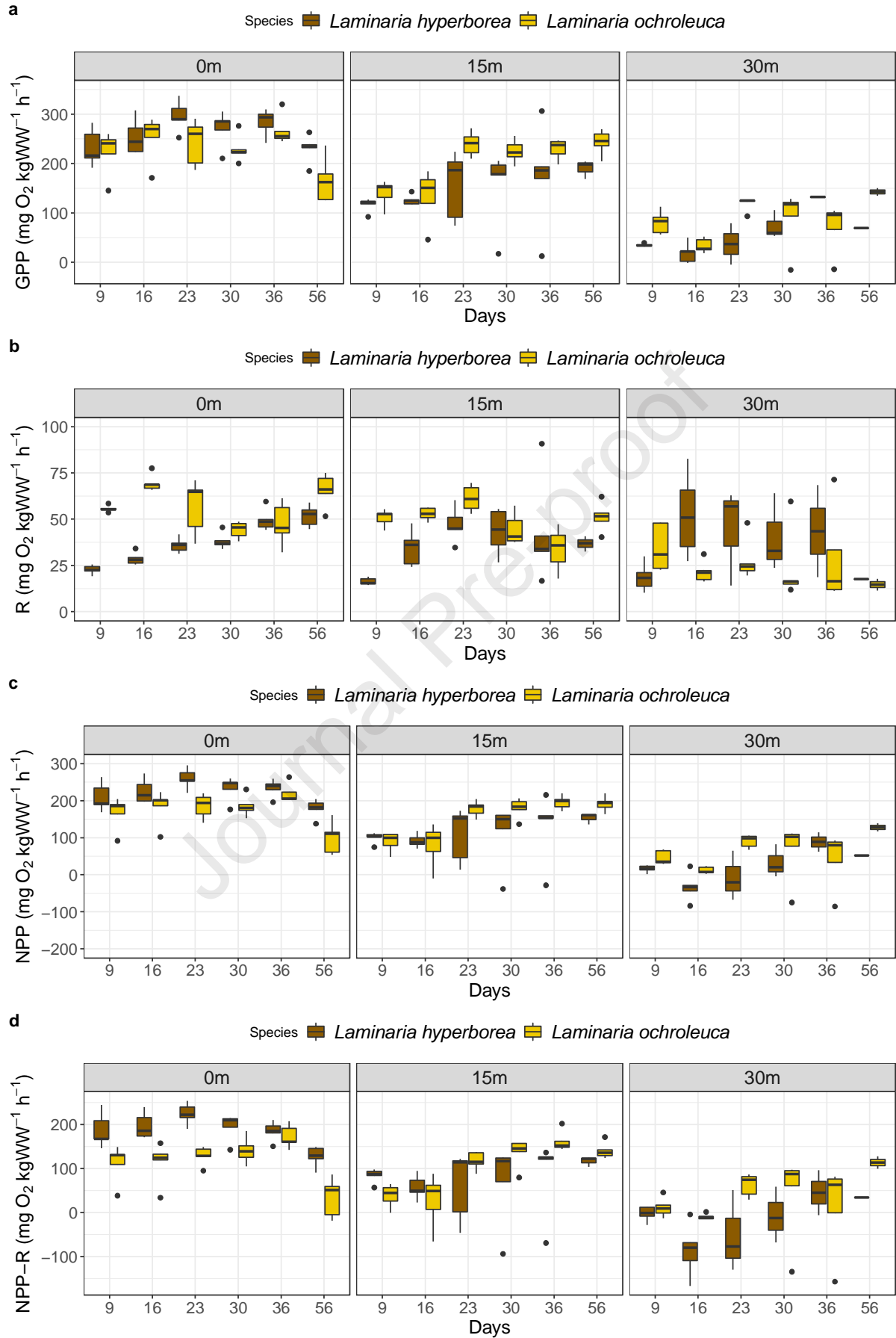
351 As expected, the availability of light was the dominant factor affecting GPP; both in terms of
 352 PAR at the surface ($\chi^2_{1,161} = 15.735$, $p < 0.001$) and as a main effect of photo-attenuation
 353 related to depth ($\chi^2_{2,161} = 92.036$, $p < 0.001$). Contrary to expectation, however,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

358 Respiration (R) was independent of temperature, but differed strongly between species ($\chi^2_{1,$
 359 $161} = 22.555$, $p < 0.001$), and as a function of time ($\chi^2_{1,161} = 8.462$, $p = 0.004$) and depth (χ
 360 $^2_{2,161} = 10.276$, $p = 0.006$), modifying the species effect. Notwithstanding the declining
 361 number of fragments persisting to the end of the trial (Fig. 3), it was clear that R did not
 362 display a simple response over time; only the data for *L. hyperborea* under surface light
 363 levels are suggestive of a simple linear increase over time (Fig. 3b, Table 2).

364 Most importantly, Net Primary Production (NPP) during lit periods remained at, or recovered
 365 to, positive net production levels in the majority of fragments until the end of the 56 day trial
 366 (Fig. 3c, Table 2). As with GPP and R, NPP differed strongly at different depths ($\chi^2_{1,161} =$
 367 88.31 , $p < 0.001$). NPP did not differ statistically between the two species, but the nature of
 368 this experiment restricts these conclusions to brightly lit daylight hours. Assuming

369 equinoctial fully light and dark conditions, with NPP and an additional 12 h of R representing
370 a full day's oxygen flux, suggests a significant effect of species with an additional modifying
371 effect of depth upon this ($\chi^2_{2,161} = 6.244$, $p = 0.044$). Under this '24 h' model, a more realistic
372 interpretation of differential GPP responses between the species can be detected (Fig. 3d,
373 Table 2).
374

Journal Pre-proof



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

381

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

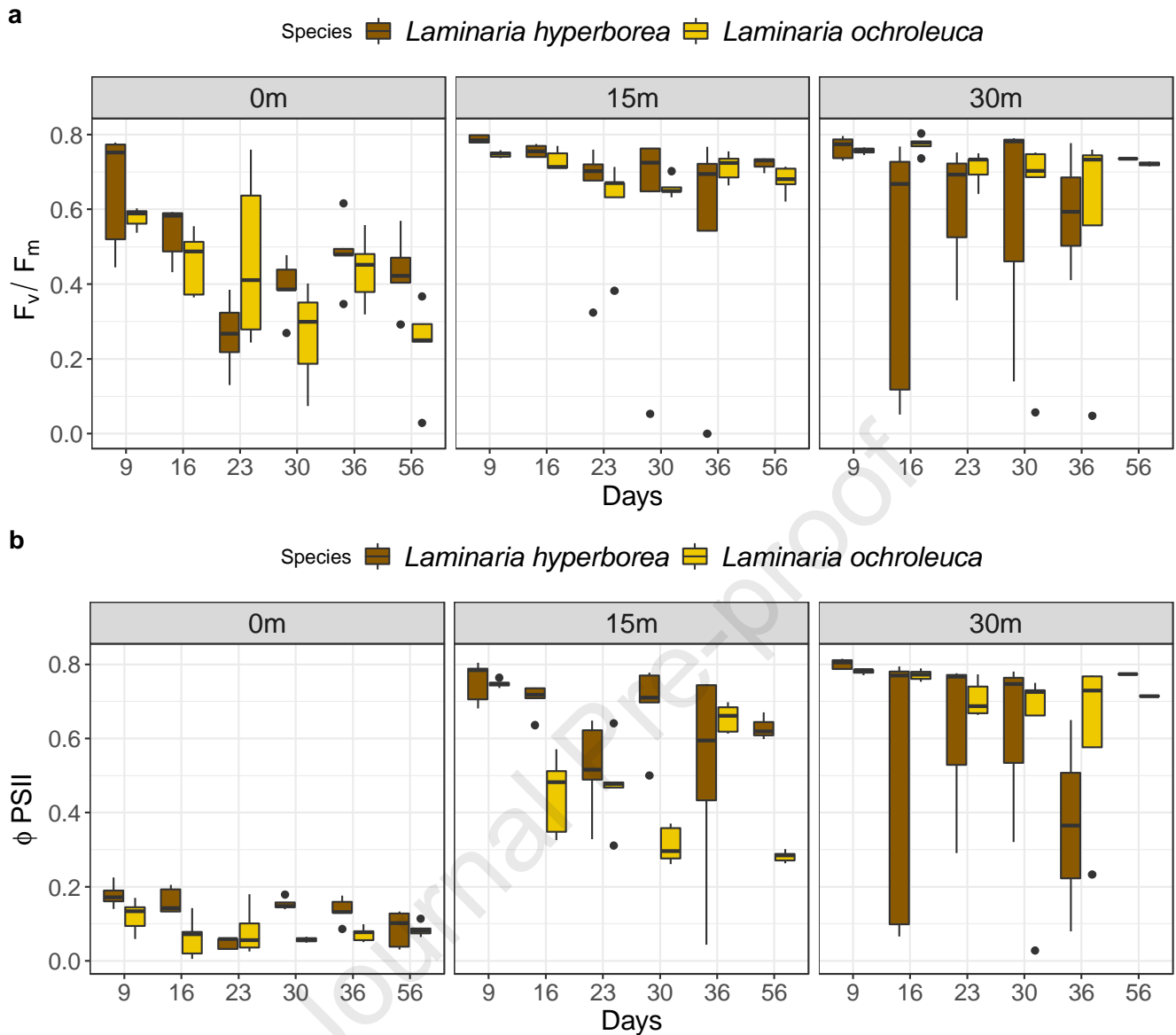
Source	<i>df</i>	Chisq	<i>P</i>
(a) GPP			
PAR	1	15.735	< 0.001
Time (days)	1	0.566	0.452
Species	1	0.000	0.996
Depth	2	92.036	< 0.001
Time: Species	1	5.122	0.024
Species: Depth	2	1.157	0.561
Time: Depth	2	6.316	0.043
Time:Species:Depth	2	4.058	0.131
Fragment ID	1	9.664	0.002
(b) R			
Temp	1	0.098	0.754
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

387

388 *3.4 Photosynthetic response*

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



397

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

401 **Table 3:** Results of likelihood ratio testing based upon generalized least squares fitting to
 402 examine responses of (a) Φ PSII (b) F_v/F_m across time (56 days), between kelp species and
 403 depths (fixed factors) with PAR as a covariate. Significant terms ($P < 0.05$) are indicated in
 404 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

405

406 *3.5 Omnibus permanova*

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

411

412 **Table 4:** Results of omnibus PERMANOVA analysis of standardized data describing GPP,413 R, Φ PSII and F_v/F_m across time (56 days), between kelp species and depth (fixed factors)414 with PAR as a covariate. Significant terms ($P < 0.05$) are indicated in bold.

415

Source	<i>df</i>	Pesudo-F	<i>P</i>
--------	-----------	----------	----------

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

416

417 **4. DISCUSSION**418 *4.1. Production and respiration measurements*

419

420 For the first time, the primary producer functions of algal detritus have been quantified across
421 a simulated depth spectrum. Detritus continued to sustain net production of oxygen across a
422 56-day period, underscoring its capacity to maintain key functions such as carbon fixation.
423 Detrital tissues slightly increased in biomass during the early stages of degradation,
424 demonstrating that measured oxygen production is reflective of fresh material being
425 generated. Over time, the respiration of detrital fragments, as a proxy for stress or associated
426 bacterial activity, increased in some contexts (Sosik and Simenstad, 2013). Evidence of some
427 degradation was further reinforced by a measured decline in photosynthetic performance
428 (Φ PSII and F_v/F_m), in accordance with the initial hypothesis. At the end of the first time
429 period, values between 0.6-0.8 at 15 m and 30 m reflected an optimum performance at depths
430 at which the kelps inhabit (Gorman *et al.*, 2013). Low photosynthetic parameters at 0 m
431 follow reported trends in the literature of decreases in both measurements with increasing
432 irradiances (for *Laminaria digitata*, Delebecq *et al.* 2011).

433

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

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

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

462

463 4.2. Contextualizing the findings

464

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

475

476 Extending the investigation to consider the degradation process across environmental
477 contexts revealed that other measured physiological processes of kelp detritus (NPP, GPP and
478 Φ_{PSII} and F_v/F_m) are not only species specific but also highly dependent on light availability.
479 Depth significantly affected 24-hour oxygen flux and the Species response to the effect of
480 Depth was significantly heterogeneous in the case of both respiration and the 24-hour model
481 of oxygen flux (Fig. 3b and d). Therefore, considering the dynamic nature of detrital
482 transport, the depth to which detritus is exported significantly determines the carbon fixation,
483 respiration and photosynthetic performance of kelp material (Filbee-Dexter and Scheibling,
484 2016). Furthermore, detritus was clearly less productive as a function of decreasing irradiance

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

495

496 4.3. Re-defining kelp detritus

497

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

510 reproduce, then kelp populations structure is likely to be far more fluid than would be indicated by
511 typical spore or gamete dispersal, which is low for individual sporophytes within a kelp forest (~ 5-
512 200 m, Fredriksen *et al.* 1995). This phenomenon compliments the functional role of herbivores in
513 increasing fertilisation success and dispersing kelp spores which germinate post-digestion (Ruz *et al.*
514 2018).

515

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

532

533 *4.4 The role of kelp detritus in benthic ecosystems*

534

535 The vast majority of kelp production enters the detrital pathway (about 82% according to Krumhansl
536 and Scheibling 2012), therefore fundamental variability in the respiration and photosynthetic
537 performance of kelp material across time and under different environmental conditions are important
538 for understanding the persistence and productivity of detrital resources. The composition of kelp
539 forests and thus their detritus, will likely be modified as climate warming persists (Smale et al.
540 2015), with the gradual increase of HFS with high thermal affinities and gradual local extinctions of
541 native HFS with cooler thermal affinities (Wiens 2016). These replacements will likely impact many
542 aspects of the cycling of organic material, from the spatial subsidies exported kelp matter provides,
543 to the fitness of grazers and detritivores feeding upon it, and the rate of carbon sequestration into
544 longer residence forms in the benthos. Pessarrodona *et al.* (2018b) speculated about an alteration in
545 the functional importance of this detrital material due to a variation in the rate of supply from
546 different kelp species. Here we have shown that the continued biological activity of fragmented kelp
547 tissues also differs between species, across time and environments, further altering the contribution
548 of kelp mass to spatial subsidies (Leclerc *et al.* 2013a).

549
550 This study provides a snapshot of the degradation dynamics of two kelps under controlled
551 conditions. There are numerous potential sources for error; for example a change in detrital
552 respiration could be attributed an upregulation of metabolic processes in *L. hyperborea* or to an
553 increase in oxygen consuming saprophytic bacteria and fungi (Fenchel and Jørgensen, 1977;
554 Williams *et al.* 2004). Furthermore, variation in species physiology cannot be generalized across the
555 entirety of benthic ecosystems in the North East Atlantic because despite advances in areas of low-
556 moderate wave exposure (Smale *et al.* 2015), *L. ochroleuca* may not be able to fully replace *L.*
557 *hyperborea* in sites exposed to high wave exposure (Pessarrodona *et al.* 2018b) and therefore the
558 composition of detritus from such assemblages may remain relatively unchanged. Also, the role of
559 macrofaunal colonization and consumption (de Bettignies *et al.* 2020; Ramirez-Llodra *et al.* 2016) of

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

581

582 **5. CONCLUSION**

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

597

598 **DATA AVAILABILITY**

599 Data will be archived in GitHub repository: [https://github.com/nadiafrontier/The-](https://github.com/nadiafrontier/The-degradation-of-kelp-detritus.git)
600 [degradation-of-kelp-detritus.git](https://github.com/nadiafrontier/The-degradation-of-kelp-detritus.git)

601 **FUNDING**

602 This work was supported by the Brittany Regional Council and the French Government
603 through the National Research Agency with regards to the investment expenditure program
604 IDEALG [grant number ANR-10-BTBR-04].

605 **SUPPLEMENTARY INFORMATION**

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

609 **ACKNOWLEDGEMENTS**

610 We thank the marine operation staff at Roscoff Biological Station (*Service Mer &*
611 *Observation SBR*) L. Levêque, Y. Fontana, W. Thomas, M. Camusat, N. Guidal and F. Le
612 Ven for their help with scuba diving kelp collection and T. de Bettignies from the Natural
613 History Museum of Paris. We also thank Marine Roscoff Aquarium Services (*FR2424*),
614 especially R. Garnier and G. Schires for their help with the experimental design and set-up.
615 E. Bocher and M. Kervellec for their assistance in the experimental work. NF, FdB and DD
616 conceived the ideas and designed the study. FdB and NF built the experimental system. NF
617 and FdB conducted the experimental manipulation. AF and NF analysed the data. NF and
618 FdB wrote the first draft and AF extensively contributed to subsequent drafts. All authors
619 gave final approval for publication.

620

621 **REFERENCES**

- 622 **Abdullah MI, Fredriksen S, Christie H. 2017.** The impact of the kelp (*Laminaria*
623 *hyperborea*) forest on the organic matter content in sediment of the west coast of Norway.
624 *Marine Biology Research* **13**: 151–160. doi: 10.1080/17451000.2016.1240369
- 625 **Aminot A, Kerouel R. 2005.** *Hydrologie des écosystèmes marins: paramètres et analyses.*
626 *Méthodes d'analyse en milieu marin.* Ifremer, France.
- 627 **Arroyo N, Bonsdorff E. 2016.** The Role of Drifting Algae for Marine Biodiversity. In:
628 Olafsson E. *Marine Macrophytes as Foundation Species.* 1st edn. CRC Press: Taylor &

- 629 Francis group, 100-123. doi: 10.4324/9781315370781-6
- 630 **Assis J, Lucas AV, Bárbara I, Serrão EÁ. 2016.** Future climate change is predicted to shift
631 long-term persistence zones in the cold-temperate kelp *Laminaria hyperborea*. *Marine*
632 *Environmental Research* **113**: 174–182. doi: 10.1016/j.marenvres.2015.11.005
- 633 **Baedke J, Fábregas-Tejeda A, Nieves Delgado A. 2020.** The holobiont concept before
634 Margulis. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*,
635 **334**: 149–155. doi: 10.1002/jez.b.22931
- 636 **Bajjouk T, Rochette S, Laurans M, Ehrhold A, Hamdi A, Le Niliot P. 2015.** Multi-
637 approach mapping to help spatial planning and management of the kelp species *L. digitata*
638 and *L. hyperborea*: Case study of the Molène Archipelago, Brittany. *Journal of Sea Research*
639 **100**: 2–21. doi: 10.1016/j.seares.2015.04.004
- 640 **Bartsch I, Wiencke C, Bischof K, et al. 2008.** The genus *Laminaria* sensu lato: Recent
641 insights and developments. *European Journal of Phycology* **43**: 1–86. doi:
642 10.1080/09670260701711376
- 643 **Bates D, Maechler, M, Bolker B, Walker, S. 2015.** Fitting Linear Mixed-Effects Models
644 Using lme4. *Journal of Statistical Software* **67**: 1-48. doi:10.18637/jss.v067.i01.
- 645 **Biscéré T, Zampighi M, Lorrain A, et al. 2019.** High pCO₂ promotes coral primary
646 production. *Biology Letters* **15**. doi: 10.1098/rsbl.2018.0777
- 647 **Bischof K, Hanelt D, Wiencke C. 1999.** Acclimation of maximal quantum yield of
648 photosynthesis in the brown alga *Alaria esculenta* under high light and UV radiation. *Plant*
649 *Biology* **1**: 435–444. doi: 10.1111/j.1438-8677.1999.tb00726.x
- 650 **Bishop MJ, Coleman MA, Kelaher BP. 2010.** Cross-habitat impacts of species decline:
651 Response of estuarine sediment communities to changing detrital resources. *Oecologia* **163**:
652 517–525. doi: 10.1007/s00442-009-1555-y
- 653 **Boutler J, Carbioch L, Grall R. 1974.** Quelques observations sur la pénétration de la

- 654 lumière dans les eaux marines au voisinage de Roscoff et ses conséquences écologiques.
655 *Laboratoire d'Océanographie Physique*. Paris, 129–140.
- 656 **Braeckman U, Pasotti F, Vázquez S, et al.** 2019. Degradation of macroalgal detritus in
657 shallow coastal Antarctic sediments. *Limnology and Oceanography*, **64**: 1423–1441. doi:
658 10.1002/lno.11125
- 659 **Buitenhuis ET, Hashioka T, Quéré C Le.** 2013. Combined constraints on global ocean
660 primary production using observations and models. *Global Biogeochemical Cycles* **27**: 847–
661 858. doi: 10.1002/gbc.20074
- 662 **Christie H, Jørgensen NM, Norderhaug KM, Waage-Nielsen E.** 2003. Species
663 distribution and habitat exploitation of fauna associated with kelp (*Laminaria hyperborea*)
664 along the Norwegian coast. *Journal of the Marine Biological Association of the United*
665 *Kingdom* **83**: 687–699. doi: 10.1017/S0025315403007653h
- 666 **Ciais P, Sabine C, Bala G, et al.** 2013. Carbon and other Biogeochemical Cycles. In:
667 *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the*
668 *Fifth Assessment Report of the Intergovernmental Panel on Climate Change*: 465–570.
- 669 **de Bettignies T, Wernberg T, Lavery PS, Vanderklift MA, Mohring MB.** 2013.
670 Contrasting mechanisms of dislodgement and erosion contribute to production of kelp
671 detritus. *Limnology and Oceanography* **58**: 1680–1688. doi: 10.4319/lo.2013.58.5.1680
- 672 **de Bettignies F, Dauby P, Lepoint G. et al.** 2020a. Temporal succession of a macrofaunal
673 community associated with kelp fragment accumulations in an in situ experiment. *Marine*
674 *Ecology Progress Series*. in press. doi: 10.3354/meps13391
- 675 **de Bettignies F, Dauby P, Thomas F, et al.** 2020b. Degradation dynamics and processes
676 associated with the accumulation of *Laminaria hyperborea* (Phaeophyceae) kelp fragments:
677 an in situ experimental approach. *Journal of Phycology*. in press. doi: 10.1111/jpy.13041
- 678 **Delebecq G, Davoult D, Menu D, et al.** 2011. In situ photosynthetic performance of

- 679 *Laminaria digitata* (phaeophyceae) during spring tides in northern Brittany. *Cahiers de*
680 *Biologie Marine* **52**: 405–414. doi: 10.1080/09670262.2015.1104556
- 681 **Duarte CM, Krause-Jensen D. 2017.** Export from seagrass meadows contributes to marine
682 carbon sequestration. *Frontiers in Marine Science* **4**: 1–7. doi: 10.3389/fmars.2017.00013
- 683 **Duarte CM, Losada IJ, Hendriks IE, Mazarrasa I, Marbà N. 2013.** The role of coastal
684 plant communities for climate change mitigation and adaptation. *Nature Climate Change* **3**:
685 961–968. doi: 10.1038/nclimate1970
- 686 **Duggins DO, Simenstad CA, Estes JA. 1989.** Magnification of secondary production by
687 kelp detritus in coastal marine ecosystems. *Science* **245**: 170–173. doi:
688 10.1126/science.245.4914.170
- 689 **Fenchel TM, Jørgensen BB. 1977.** Detritus Food Chains of Aquatic Ecosystems: The Role
690 of Bacteria. : 1–58. doi: 10.1007/978-1-4615-8219-9_1
- 691 **Filbee-Dexter K, Scheibling RE. 2016.** Spatial Patterns and Predictors of Drift Algal
692 Subsidy in Deep Subtidal Environments. *Estuaries and Coasts* **39**: 1724–1734. doi:
693 10.1007/s12237-016-0101-5
- 694 **Filbee-Dexter K, Wernberg T, Norderhaug KM, Ramirez-Llodra E, Pedersen MF.**
695 **2018.** Movement of pulsed resource subsidies from kelp forests to deep fjords. *Oecologia*
696 **187**: 291–304. doi: 10.1007/s00442-018-4121-7
- 697 **Franco JN, Tuya F, Bertocci I, Rodríguez L, Sousa-pinto BMI, Arenas F. 2017.** The
698 ‘golden kelp’ *Laminaria ochroleuca* under global change : Integrating multiple eco-
699 physiological responses with species distribution models. *Journal of Ecology* **106**: 47-58. doi:
700 10.1111/1365-2745.12810
- 701 **Fredriksen S, Sjøtun K, Lein TE, Rueness J, 1995.** Spore dispersal in *Laminaria*
702 *hyperborea* (laminariales, phaeophyceae). *Sarsia*, **80**, pp.47-53. doi:
703 10.1080/00364827.1995.10413579

- 704 **Friedlingstein P, Jones MW, O’Sullivan M, et al. 2019.** Global carbon budget 2019. *Earth*
705 *System Science Data* **11**: 1783–1838. doi: 10.5194/essd-11-1783-201
- 706 **Gevaert F, Creach A, Davoult D, Holl AC, Seuront L, Lemoine Y. 2002.** Photo-inhibition
707 and seasonal photosynthetic performance of the seaweed *Laminaria saccharina* during a
708 simulated tidal cycle: Chlorophyll fluorescence measurements and pigment analysis. *Plant,*
709 *Cell and Environment* **25**: 859–872. doi: 10.1046/j.1365-3040.2002.00869.x
- 710 **Gorman D, Bajjouk T, Populus J, Vasquez M, Ehrhold A. 2013.** Modeling kelp forest
711 distribution and biomass along temperate rocky coastlines. *Marine Biology* **160**: 309–325.
712 doi: 10.1007/s00227-012-2089-0
- 713 **Hader DP, Kumar HD, Smith RC and Worrest RC, 1998.** Effects on aquatic ecosystems.
714 *Journal of photochemistry and photobiology B: Biology.* **46**: 53-68. doi 10.1016/S1011-
715 **1344(98)00185-7**
- 716 **Hagen EM, McCluney KE, Wyant KA, et al. 2012.** A meta-analysis of the effects of
717 detritus on primary producers and consumers in marine, freshwater, and terrestrial
718 ecosystems. *Oikos* **121**: 1507–1515. doi: 10.1111/j.1600-0706.2011.19666.x
- 719 **Hanelt D. 2018.** Photosynthesis assessed by chlorophyll fluorescence. In: Häder D, Erzinger
720 G, *Bioassays: Advanced Methods and Applications*. Amsterdam: Elsevier Inc, 169-196
- 721 **Hargrave MS, Foggo A, Pessarrodona A, Smale DA. 2017.** The effects of warming on the
722 ecophysiology of two co-existing kelp species with contrasting distributions. *Oecologia* **183**:
723 531–543. doi: 10.1007/s00442-016-3776-1
- 724 **Howard J, Sutton-Grier A, Heer D, et al. 2017.** Clarifying the role of coastal and marine
725 systems in climate mitigation. *Frontiers in Ecology and the Environment* **15**: 42–50. doi:
726 10.1038/news050808-1
- 727 **Huxel GR, McCann K, Polis GA. 2002.** Effects of partitioning allochthonous and
728 autochthonous resources on food web stability. *Ecological Research* **17**: 419–432. doi:

- 729 10.1046/j.1440-1703.2002.00501.x
- 730 **Kirk JT, 1994.** *Light and photosynthesis in aquatic ecosystems*, 2nd edn. Cambridge:
731 Cambridge university press. doi: 10.1017/CBO9780511623370
- 732 **Krause-Jensen D, Duarte CM. 2016.** Substantial role of macroalgae in marine carbon
733 sequestration. *Nature Geoscience* **9**: 737–742. doi: 10.1038/ngeo2790
- 734 **Krumhansl KA, Scheibling RE. 2012a.** Production and fate of kelp detritus. *Marine*
735 *Ecology Progress Series* **467**: 281–302. doi: 10.3354/meps09940
- 736 **Krumhansl KA, Scheibling RE. 2012b.** Detrital subsidy from subtidal kelp beds is altered
737 by the invasive green alga *Codium fragile* ssp. *fragile*. *Marine Ecology Progress Series* **456**:
738 73–85. doi: 10.3354/meps09671
- 739 **Laffoley D, Grimsditch G. 2009.** *The management of natural coastal carbon sinks*. Gland:
740 Switzerland: IUCN. doi: 10.1007/s00114-001-0283-x
- 741 **Leclerc J-C, Riera P, Leroux C, Lévêque L, Davoult D. 2013a.** Temporal variation in
742 organic matter supply in kelp forests: Linking structure to trophic functioning. *Marine*
743 *Ecology Progress Series* **494**: 87–105. doi: 10.3354/meps10564
- 744 **Leclerc JC, Riera P, Leroux C, et al. 2013b.** Trophic significance of kelps in kelp
745 communities in Brittany (France) inferred from isotopic comparisons. *Marine Biology* **160**:
746 3249–3258. doi: 10.1007/s00227-013-2306-5
- 747 **Marczak LB, Thompson RM, Richardson JS. 2007.** Meta-analysis: Trophic level, habitat,
748 and productivity shape the food web effects of resource subsidies. *Ecology* **88**: 140–148. doi:
749 10.1890/0012-9658(2007)88[140:MTLHAP]2.0.CO;2
- 750 **Masson-Delmotte V, Zhai P, Pörtner HO, 2018.** IPCC Summary for Policymakers. Global
751 Warming of 1.5°C. IPCC Special Report on the impacts of global warming of 1.5°C above
752 pre-industrial levels and related global greenhouse gas emission pathways, in the context of
753 strengthening the global response to the threat of climate change, sustainable development,

- 754 and efforts to eradicate poverty.
- 755 **McLeod E, Chmura GL, Bouillon S, et al. 2011.** A blueprint for blue carbon: Toward an
756 improved understanding of the role of vegetated coastal habitats in sequestering CO₂.
757 *Frontiers in Ecology and the Environment* **9**: 552–560. doi: 10.1890/110004
- 758 **Middelburg JJ, 2019.** Marine carbon biogeochemistry: a primer for earth system scientists.
759 Springer Briefs in Earth System Sciences. doi: 10.1007/978-3-030-10822-9
- 760 **Migné A, Davoult D, Spilmont N, et al. 2002.** A closed-chamber CO₂-flux method for
761 estimating intertidal primary production and respiration under emerged conditions. *Marine*
762 *Biology* **140**: 865–869. doi: 10.1007/s00227-001-0741-1
- 763 **Moore JC, Berlow EL, Coleman DC, et al. 2004.** Detritus, trophic dynamics and
764 biodiversity. *Ecology Letters* **7**: 584–600. doi: 10.1111/j.1461-0248.2004.00606.x
- 765 **Nielsen SL, Banta GT, Pedersen M, 2004.** Decomposition Of Marine Primary Producers:
766 Consequences For Nutrient Recycling And Retention In Coastal Ecosystems. In: Nielsen
767 S.L., Banta G.T., Pedersen M.F. (eds) *Estuarine Nutrient Cycling: The Influence of Primary*
768 *Producers*. Aquatic Ecology Book Series, **vol 2**. Springer, Dordrecht.
769 https://doi.org/10.1007/978-1-4020-3021-5_7
- 770 **Noisette F, Hurd C. 2018.** Abiotic and biotic interactions in the diffusive boundary layer of
771 kelp blades create a potential refuge from ocean acidification. *Functional Ecology* **32**: 1329–
772 1342. doi: 10.1111/1365-2435.13067
- 773 **Norderhaug KM, Fredriksen S, Nygaard K. 2003.** Trophic importance of *Laminaria*
774 *hyperborea* to kelp forest consumers and the importance of bacterial degradation to food
775 quality. *Marine Ecology Progress Series* **255**: 135–144. doi: 10.3354/meps255135
- 776 **Pedersen MF, Filbee-Dexter K, Norderhaug KM, et al. 2020.** Detrital carbon production
777 and export in high latitude kelp forests. *Oecologia* **192**: 227–239.
- 778 **Pedersen MF, Stæhr PA, Wernberg T, Thomsen MS. 2005.** Biomass dynamics of exotic

- 779 *Sargassum muticum* and native *Halidrys siliquosa* in Limfjorden, Denmark - Implications of
780 species replacements on turnover rates. *Aquatic Botany* **83**: 31–47. doi: 10.1007/s00442-019-
781 04573-z
- 782 **Pereira TR, Azevedo IC, Oliveira P, Silva DM, Sousa-Pinto I. 2019.** Life history traits of
783 *Laminaria ochroleuca* in Portugal: The range-center of its geographical distribution. *Aquatic*
784 *Botany* **152**: 1–9. doi: 10.1016/j.aquabot.2018.09.002
- 785 **Pessarrodona A, Moore PJ, Sayer MDJ, Smale DA. 2018a.** Carbon assimilation and
786 transfer through kelp forests in the NE Atlantic is diminished under a warmer ocean climate.
787 *Global Change Biology* **24**: 4386–4398. doi: 10.1111/gcb.14303 doi: 10.1111/1365-
788 2745.13053
- 789 **Pessarrodona A, Foggo A, Smale DA. 2018b.** Can ecosystem functioning be maintained
790 despite climate-driven shifts in species composition? Insights from novel marine forests.
791 *Journal of Ecology* **107**: 91–104.
- 792 **Philippart CJM, Anadón R, Danovaro R, et al. 2011.** Impacts of climate change on
793 European marine ecosystems: Observations, expectations and indicators. *Journal of*
794 *Experimental Marine Biology and Ecology* **400**: 52–69. doi: 10.1016/j.jembe.2011.02.023
- 795 **Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2019.** Package 'nlme': Linear and
796 Nonlinear Mixed Effects Models_. R package version 3.1-140, URL: [https://CRAN.R-](https://CRAN.R-project.org/package=nlme)
797 [project.org/package=nlme](https://CRAN.R-project.org/package=nlme).
- 798 **Polis GA, Anderson WB, Holt RD. 1997.** Toward an integration of landscape and food
799 webs ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology*
800 *and Systematics* **28**: 289–316. doi: 10.1146/annurev.ecolsys.28.1.289
- 801 **Queirós AM, Stephens N, Widdicombe S, et al. 2019.** Connected macroalgal-sediment
802 systems: blue carbon and food webs in the deep coastal ocean. *Ecological Monographs*. doi:
803 10.1002/ecm.1366

- 804 **Ramirez-Llodra E, Rinde E, Gundersen H, et al. 2016.** A snap shot of the short-term
805 response of crustaceans to macrophyte detritus in the deep Oslofjord. *Scientific Reports* **6**: 1–
806 5. doi: 10.1038/srep23800
- 807 **Renaud PE, Løkken TS, Jørgensen LL, Berge J, Johnson BJ. 2015.** Macroalgal detritus
808 and food-web subsidies along an Arctic fjord depth-gradient. *Frontiers in Marine Science* **2**:
809 1–15. doi: 10.3389/fmars.2015.00031
- 810 **Ruz CS, Muth AF, Tala F, Pérez-Matus A. 2018.** The herbivorous fish, *Aplodactylus*
811 *punctatus*, as a potential facilitator of dispersal of kelp, *Lessonia trabeculata*, in Chile.
812 *Journal of Experimental Marine Biology and Ecology* **500**: 112–119. doi:
813 10.1016/j.jembe.2017.12.007
- 814 **Saulquin B, Hamdi A, Gohin F, Populus J, Mangin A. 2013.** Archimer Estimation of the
815 diffuse attenuation coefficient K dPAR using MERIS and application to seabed habitat
816 mapping. *Remote Sensing of Environment* **128**: 224–233. doi: 10.1016/j.rse.2012.10.002
- 817 **Smale DA, Moore P. 2017.** Variability in kelp forest structure along a latitudinal gradient in
818 ocean temperature. *Journal of Experimental Marine Biology and Ecology* **486**: 255–264. doi:
819 10.1016/j.jembe.2016.10.023
- 820 **Smale DA, Wernberg T, Yunnice A, Vance T. 2015.** The rise of *Laminaria ochroleuca* in
821 the Western English Channel (UK) and comparisons with its competitor and assemblage
822 dominant *Laminaria hyperborea*. *Marine Ecology* **36**: 1033–1044. doi: 10.1111/maec.12199
- 823 **Sorte CJB, Williams SL, Carlton JT. 2010.** Marine range shifts and species introductions:
824 Comparative spread rates and community impacts. *Global Ecology and Biogeography* **19**:
825 303–316. doi: 10.1111/j.1466-8238.2009.00519.x
- 826 **Sosik EA, Simenstad CA. 2013.** Isotopic evidence and consequences of the role of microbes
827 in macroalgae detritus-based food webs. *Marine Ecology Progress Series* **494**: 107–119. doi:
828 10.3354/meps10544

- 829 **Steneck R, Graham B J Bourque D Corbett J M Erlandson MH, Graham MH, et al.**
830 **2002.** Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental*
831 *Conservation* **29**: 436–459. doi: 10.1017/S0376892902000322
- 832 **Straub S, Thomsen MS, Wernberg T. 2016.** The dynamic biogeography of the
833 Anthropocene: The speed of recent range shifts in seaweeds. In: Fraser C, Hu Z. *Seaweed*
834 *Phylogeography: Adaptation and Evolution of Seaweeds under Environmental Change.*
835 Dordrecht:Springer, 63-69. doi: 10.1007/978-94-017-7534-2
- 836 **Swanson AK, Fox, CH. 2007.** Altered kelp (Laminariales) phlorotannins and growth under
837 elevated carbon dioxide and ultraviolet-B treatments can influence associated intertidal food
838 webs. *Global Change Biology*, **13**: 1696–1709. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2486.2007.01384.x)
839 [2486.2007.01384.x](https://doi.org/10.1111/j.1365-2486.2007.01384.x)
- 840 **Teagle H, Hawkins SJ, Moore PJ, Smale DA. 2017.** The role of kelp species as biogenic
841 habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and*
842 *Ecology* **492**: 81–98. doi: 10.1016/j.jembe.2017.01.017
- 843 **Teagle H, Smale DA. 2018.** Climate-driven substitution of habitat-forming species leads to
844 reduced biodiversity within a temperate marine community. *Diversity and Distributions* **24**:
845 1367–1380. doi: 10.1111/ddi.12775
- 846 **Vilas D, Coll M, Pedersen T, et al. 2020.** Kelp-carbon uptake by Arctic deep-sea food webs
847 plays a noticeable role in maintaining ecosystem structural and functional traits. *Journal of*
848 *Marine Systems* **203**: 103268. doi: 10.1016/j.jmarsys.2019.103268
- 849 **Wiens JJ. 2016.** Climate-related local extinctions are already widespread among plant and
850 animal species. *PLoS Biology* **14**: 1–18. doi: 10.1371/journal.pbio.2001104
- 851 **Williams PJB, Giorgio PA, King GM, et al. 2004.** *Respiration in aquatic ecosystems.*
852 Oxford University Press, USA.
- 853 **Yang LH, Bastow JL, Spence KO, Wright AN. 2008.** What can we learn from resource

854 pulses? *Ecology* **89**: 621–634. doi: 10.1890/07-0175.1

855

Journal Pre-proof

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

Nadia Frontier^{a, b†*}, Florian de Bettignies^{a†}, Andy Foggo^b, Dominique Davoult^a

^a Sorbonne Université, CNRS, UMR 7144 AD2M, Station Biologique de Roscoff, Place

Georges Teissier, F-29680 Roscoff, France

Marine Environmental Research Highlights-

- The term ‘detritus’ should be revised when referring to kelp material
- Detached kelp material continues to photosynthesise and fix carbon for months
- Light availability strongly influences productivity and photosynthetic performance
- Material from warm-water and cold-water kelp species degrade at different rates
- The cycling of organic material will likely be modified in a changing climate

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. **(TICK)**

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Journal Pre-proof