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

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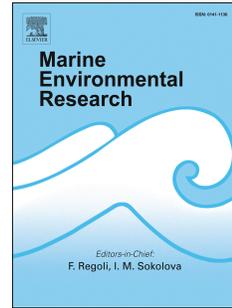
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**CRediT AUTHOUR STATEMENT**

**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 Davoult:**  Funding acquisition, Resources, Writing- Review and Editing.

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

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12

13     Running title: Kelp detritus can sustain primary producer functions

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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

4

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*

134 *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*

139 *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 $2^{o}$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:

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

196    The irradiance at depth (t) $I_{(t)}$ depends on the light at the surface $I_{(Z0)}$, 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).

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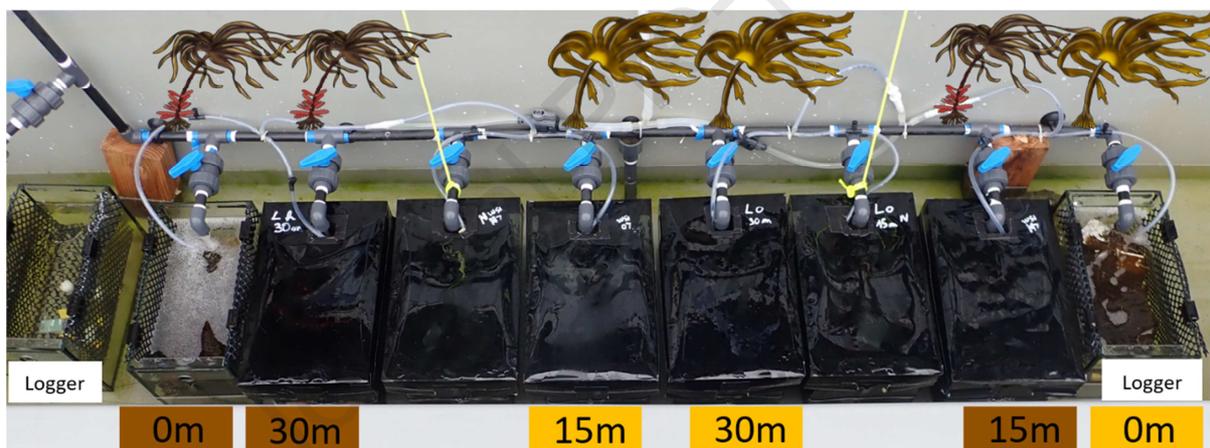


203

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.

225

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 $\pm$ 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 Kérouel, 2004). The rates were expressed in $mgO_2$ kg WW $^{-}$

260   $^1$ 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, µmol photons m $^{-2}$ 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 µmol photons.m $^{-2}$ 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 $\chi^2$ tests. Plots of residuals versus fits were used to

301     check assumptions of analyses. Data describing the photosynthetic parameters Fv/Fm and

302     ΦPSII 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 ΦPSII), 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).

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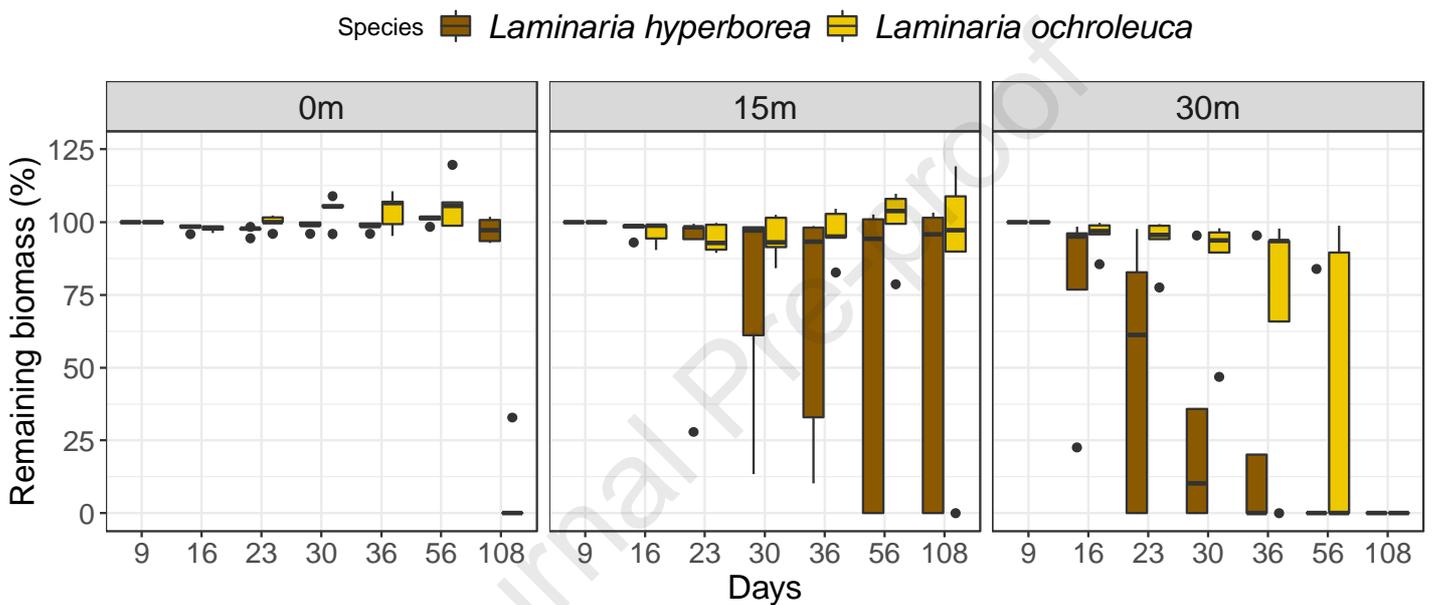


341

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

*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 ($\chi^2_{1,161}$

359  = 22.555, p < 0.001), and as a function of time ($\chi^2_{1,161}$ = 8.462, p = 0.004) and depth ($\chi^2_{2,161}$

360  = 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

15

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

**a**



**b**



**c**



375

**d**
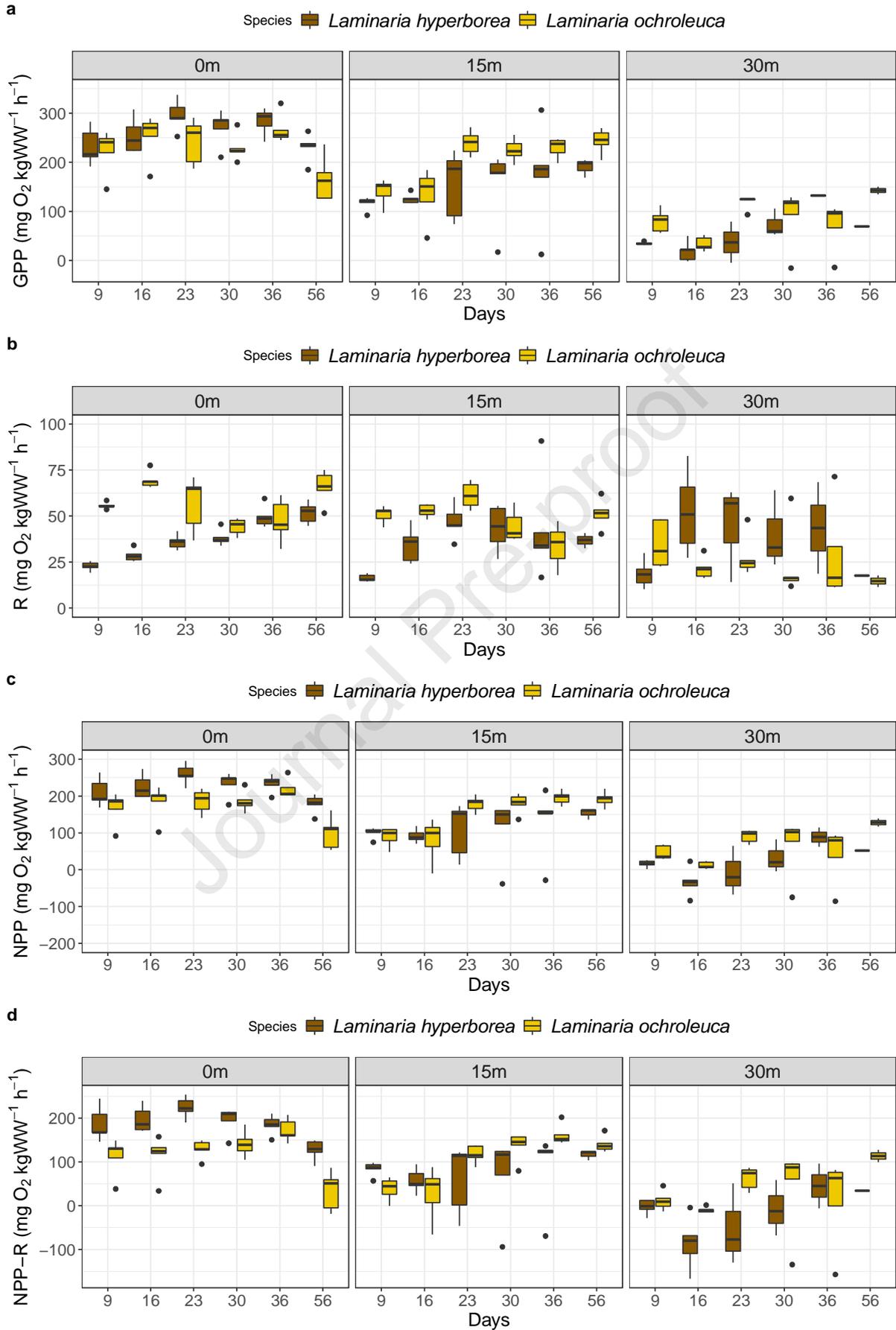
376  **Fig. 3.** (a) Gross Primary Production (GPP), (b) Respiration (R), and (c) Net Primary

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 | *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** |

18

| | | | |
|---|---|---|---|
| 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

*3.4 Photosynthetic response*

388

389 PAR was a significant covariate for the $\Phi$PSII response ($\chi^2_1 = 7.901$, p < 0.01). Despite time

390 exerting a non-statistically significant effect on $\Phi$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).

19

**a**



**b**



397
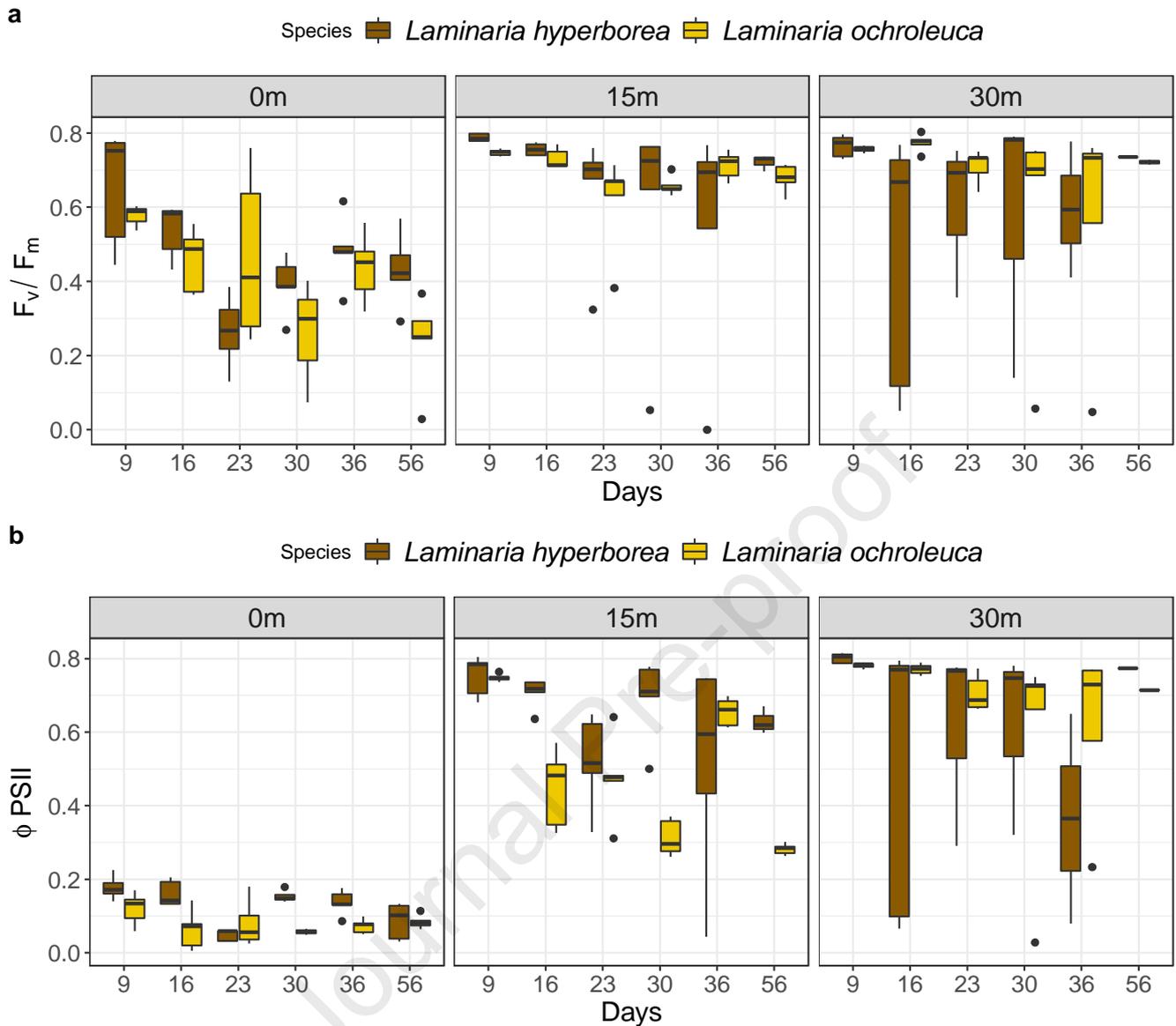
**Fig. 4.** (a) ΦPSII and (b) $F_v/F_m$ measurements at three different simulated depths over time

for *Laminaria hyperborea* and *Laminaria ochroleuca* (N = 161). Boxes indicate the

interquartile range, horizontal line inside the bars indicates the median.

**Table 3**: Results of likelihood ratio testing based upon generalized least squares fitting to

examine responses of (a) ΦPSII (b) $F_v/F_m$ across time (56 days), between kelp species and

depths (fixed factors) with PAR as a covariate. Significant terms (P < 0.05) are indicated in

bold.

| Source | df | Chisq | P |
|---|---|---|---|
| (a) $\Phi$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

*3.5 Omnibus permanova*

The combined response of GPP, R, $\Phi$PSII and $F_v/F_m$ variables was strongly affected by the

light availability in terms of PAR ($\chi^2_1 = 11.176$, p < 0.001) and Depth ($\chi^2_1 = 21.585$, p <

0.001). A realistic picture of detrital degradation revealed species responded differently to the

passage of time ($\chi^2_1 = 9.327$, p < 0.001) but not depth (Table 4).

**Table 4**: Results of omnibus PERMANOVA analysis of standardized data describing GPP,

R, $\Phi$PSII and $F_v/F_m$ across time (56 days), between kelp species and depth (fixed factors)

with PAR as a covariate. Significant terms (P < 0.05) are indicated in bold.

415

| Source | df | Pesudo-F | P |
|---|---|---|---|

| 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 (ΦPSII 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

22

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     $\Phi$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-deterring 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-

600 degradation-of-kelp-detritus.git

601 **FUNDING**

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.

620

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855

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

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**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: