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

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1   **Research paper**

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3   **Sustained productivity and respiration of degrading kelp detritus in the**

4   **shallow benthos: detached or broken, but not dead.**

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13   Running title: Kelp detritus can sustain primary producer functions

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18   Running header: Kelp detritus fulfilling primary producer functions

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22 **ABSTRACT**

23   Temperate kelp forests contribute significantly to marine primary productivity and

24   fuel many benthic and pelagic food chains. A large proportion of biomass is exported

25   from kelp forests as detritus into recipient marine ecosystems, potentially contributing

26   to Blue Carbon sequestration. The degradation of this organic material is slow and

27   recent research has revealed the preservation of photosynthetic functions over time.

28   However, the physiological correlates of detrital breakdown in *Laminaria* spp. have

29   not yet been studied. The warming climate threatens to reshuffle the species

30   composition of kelp forests and perturb the dynamics of these highly productive

31   ecosystems. The present study compares the physiological response of degrading

32   detritus from two competing North East Atlantic species; the native Boreal *Laminaria*

33   *hyperborea* and the thermally tolerant Boreal-Lusitanian *L. ochroleuca*. Detrital

34   fragment degradation was measured by a mesocosm experiment across a gradient of

35   spectral attenuation (a proxy for depth) to investigate the changes in physiological

36   performance under different environmental conditions. Degradation of fragments was

37   quantified over 108 days by measuring the biomass, production and respiration (by

38   respirometry) and efficiency of Photosystem II (by PAM fluorometry). Data indicated

39   that whilst degrading, the photosynthetic performance of the species responded

40   differently to simulated depths, but fragments of both species continued to produce

41   oxygen for up to 56 days and sustained positive net primary production. This study

42   reveals the potential for ostensibly detrital kelp to contribute to Blue Carbon fixation

43   through sustained primary production which should be factored into Blue Carbon

44   management. Furthermore, the physiological response of kelp detritus is likely

45   dependent upon the range of habitats to which it is exported. In the context of climate

46   change, shifts in species composition of kelp forests and their detritus are likely to

47   have wide-reaching effects upon the cycling of organic matter in benthic ecosystems.

48

49   **Keywords:** Climate change; Detritus; North East Atlantic; Oxygen production; PAM

50   fluorescence; Respiration; Trophic transfer

51

1. INTRODUCTION

53   Within the temperate to sub-polar regions of the globe, kelps are of paramount importance to

54   marine ecosystem functioning. They contribute to the functional integrity of coastal

55   ecosystems as habitat forming species (HFS) via their biogenic structure, through wave

56   energy dissipation and via cycling of carbon (Christie *et al*. 2003; Laffoley & Grimsditch,

57   2009; Teagle *et al.* 2017). As highly productive primary producers, kelps fix carbon dioxide

58   to produce organic matter via photosynthesis (Bartsch *et al.* 2008). The accumulated biomass

59   is eventually released or eroded and exported as detritus in a variety of forms into recipient

60   benthic ecosystems (Duggins *et al.* 1989; Krumhansl and Scheibling 2012; Pessarrodona *et*

61   *al.* 2018a) . This transfer of carbon helps to sustain adjacent food webs. The breakdown of

62   detrital material by erosion and grazing activity provides a source of particulate organic

63   matter (POM) available to filter-feeding invertebrates (Renaud *et al.* 2015; de Bettignies *et*

64   *al*. 2020a; Vilas *et al.* 2020) which in turn can play a major role in mediating carbon fluxes

65   along the sediment-water interface (Queirós *et al.* 2019; Pedersen *et al.* 2020).

66

67   A significant proportion of primary production from marine primary autotrophs is exported as

68   detritus rather than entering the consumer food web (Moore *et al.* 2004). In a global context,

69   as much as 82% of annual kelp biomass may be transferred as detrital subsidies (Krumhansl

70   and Scheibling 2012; de Bettignies *et al.* 2013). Knowing the fate of such detritus is

71   fundamental in understanding the dynamics, connectivity and functioning of coastal

72   ecosystems (Polis *et al.* 1997). Indeed, detritus enhances both primary and secondary

73   production (Polis *et al.* 1997; Marczak *et al.* 2007) whilst contributing to the structure and

74   stability of food webs in recipient ecosystems (Huxel *et al.* 2002). Furthermore, accumulation

75   of detritus can physically modify the habitat structure (Arroyo and Bonsdorff 2016).

76   However, the influences upon recipient ecosystems are dependent upon the timing, frequency

77   and residence time of the detrital deposition (Yang *et al.* 2008).

78

79   Macroalgae represent an as yet under-estimated contributor to the oceanic carbon cycle and

80   in particular to carbon sequestration and long-term storage. Their contribution to global

81   carbon assimilation and sequestration is currently not considered by the IPCC (Ciais *et al.*

82   2013) , and whilst the Global Carbon Project (GCP) identifies coastal habitats as carbon

83   stocks (Friedlingstein *et al.* 2019), their full contribution to the global marine carbon sink

84   remains neglected. Unlike seagrasses or phytoplankton, macroalgae are not routinely

85   considered as contributors to the 'Blue Carbon' budget (McLeod et al. 2011; Howard *et al.*

86   2017). Marine macrophytes collectively fix around 1.8 Gt C yr $^{-1}$ (of which macroalgae

87   contribute ~1.5 Gt C yr $^{-1}$) (Duarte *et al.* 2013; Duarte and Krause-Jensen 2017; Krause-

88   Jensen and Duarte 2016) in contrast to the ~58 Gt C yr $^{-1}$ of phytoplankton production

89   (Buitenhuis *et al.* 2013; Middelburg 2019). However, the lability of phytoplankton carbon

90   and the high rate of remineralisation through consumption and degradation mean that only in

91   the region of 0.23 Gt C yr $^{-1}$ (0.4%) of phytoplankton production becomes sequestered into

92   carbon stores or sinks, whilst the lower rate of consumption and refractory chemical nature of

93   macroalgal detritus mean that ~0.17 Gt C yr $^{-1}$ (11.4%) is sequestered. Thus, including

94 seagrasses, marine macrophytes potentially contribute a comparable mass to direct global

95 carbon sequestration to that of phytoplankton.

96

97 Species of the order Laminariales are particularly important contributors to coastal primary

98 production (Kirk 1994) and form key constituents of shallow subtidal kelp forests across four

99 continents (Steneck *et al.* 2002; Teagle *et al.* 2017). Along North East Atlantic coastlines, the

100 stipitate canopy-forming *Laminaria hyperborea* dominates shallow subtidal rocky

101 ecosystems (Smale and Moore 2017). Detrital production by *L. hyperborea* is unique because

102 the majority of the previous-season's post-meristematic growth (the 'growth collar') is shed,

103 often intact, between March and May (Bartsch *et al.* 2008); the release of this pulse of

104 biomass contributes significantly to the total detritus production (Pessarrodona *et al.* 2018a).

105 *L. hyperborea'*s detritus is a trophic resource connecting habitats which becomes increasingly

106 accessible to consumers as it degrades (Norderhaug *et al.* 2003) and is an especially

107 important dietary subsidy during periods of low plankton productivity (Leclerc *et al.* 2013a).

108 As well as accumulating in coastal embayments and on beaches, a significant fraction of the

109 carbon fixed by *L. hyperborea* flows into seafloor depressions, low-energy habitats and deep

110 subtidal regions (Filbee-Dexter and Scheibling 2016; Filbee-Dexter *et al.* 2018). Research on

111 *L. hyperborea* has already revealed that its degradation is slow relative to other species and

112 accumulations in shallow subtidal ecosystems are able to maintain photosynthetic activity

113 across several months (de Bettignies *et al.* 2020b), acting as net producers for a sustained

114 period of time dependent upon the illumination regime.

115

116 The conspicuous thermally tolerant congeneric kelp (Franco *et al.* 2017; Hargrave *et al.*

117 2017) of Lusitanian origin, *L. ochroleuca* (Bachelot de la Pylaie)*,* has expanded its range

118 northwards from Morocco and across the English Channel in response to the changing

119   climate over the last century. Today, *L. ochroleuca* is expanding its leading edge eastwards

120   and northwards at around 5.4 and 2.5 km per year, respectively (Straub *et al.* 2016). Its range

121   now overlaps substantially with the native assemblage's dominant kelp species, *L.*

122   *hyperborea* (Smale *et al.* 2015; Hargrave *et al.* 2017) which has undergone a ~250 km range

123   contraction at its warm leading-edge since 1970 (Assis *et al.* 2016). In comparison to the

124   pulsed detrital production from *L. hyperborea*, detrital production by *L. ochroleuca* is greater

125   in volume, more frequent and degrades faster between May and October (Pessarrodona *et al.*

126   2018b). The expanding thermal envelope and subsequent spread of *L. ochroleuca* is

127   modifying both the taxonomic and functional composition of HFS, with resulting effects on

128   detrital composition. The re-arrangement of HFS has been shown to have marked ecological

129   implications; extending to adjacent communities which rely on these subsidies of

130   allochthonous material (Bishop *et al.* 2010; Straub *et al.* 2016).

131

132   The ecological function of detritus varies between species. Recent studies (Pessarrodona *et*

133   *al.* 2018b) comparing *L. ochroleuca* and *L. hyperborea* have demonstrated interspecific

134   differences in seasonal detrital decomposition rates, with *L. ochroleuca* exhibiting

135   significantly faster rates (6.5 x) compared to *L. hyperborea* (Pessarrodona *et al.* 2018b) in

136   spring. In addition, the species exhibit differences in timing of detrital production: the May

137   cast from *L. hyperborea* accounting for ~40-60% of annual lamina erosion (Pessarrodona *et*

138   *al.* 2018a) compared with the continual release of detritus from the fronds of *L. ochroleuca*

139   (Pessarrodona *et al.* 2018b). Such alterations to the supply and cycling of organic matter will

140   likely be amplified as sea surface temperatures increase. In the North East Atlantic, a rise of >

141   2°C is forecast in the next 100 years (Philippart *et al.* 2011; Masson-Delmotte *et al.* 2018),

142   which will likely result in the gradual replacement of the native cool-water *L. hyperborea* by

143   the warm-water tolerant *L. ochroleuca*.

144

145 Degradation is dynamic and testing the response of detritus across different environmental

146 conditions is important to contextualise this process. The depth distribution of photosynthetic

147 kelp-forest communities is strongly influenced by light availability (Kirk 1994; Gorman *et al.*

148 2013; Bajjouk *et al.* 2015) and the photosynthetic mechanisms of some kelp species have

149 been demonstrated to respond to changes in underwater light (e.g. in *Saccharina latissima*;

150 and *L. digitata*) (Gevaert *et al.* 2002; Delebecq *et al.* 2011). *L. hyperborea* and *L. ochroleuca*

151 forests have similar natural depth range but little is known about the photosynthetic

152 efficiency of these two species within their depth thresholds. Investigating the degradation of

153 kelp detritus across a gradient of depth will further elucidate its role in the marine

154 environment.

155

156 The aim of this study therefore was to monitor the break-down dynamics and physiological

157 performance of material from *L. hyperborea* and *L. ochroleuca* across a gradient of light

158 attenuation to investigate the influence of depth across time. We examined biomass

159 dynamics, oxygen production, respiration and photosynthetic performance and efficiency of

160 photosystem II of detritus from the two species. We hypothesized that *Laminaria* species

161 have the capacity to resist degradation, maintaining primary production function depending

162 upon the illumination regime. Following the findings of Pessarrodona *et al.* (2018a) we

163 hypothesised that the two species should exhibit differential responses with respect to

164 degradation, with a quicker decomposition and breakdown of physiological capacity for *L.*

165 *ochroleuca* compared to *L. hyperborea*. We also speculated that there would be an effect of

166 the amount of light, and for the first time, empirically tested the influence of depth-related

167 light attenuation as a potential driver of variability in the degradation of kelp material.

168

2. MATERIAL AND METHODS

The study was conducted in the Roscoff Biological Station close to the Bay of Morlaix

(France). In May 2018, *L. hyperborea* was harvested at La Veille (48°42'36.22"N,

3°54'04.81"W) and *L. ochroleuca* at An Nehou (48°41'34.27"N, 3°56'25.52"W) from ~ 8-10

m below chart datum. Five typical mature canopy-forming individuals of each kelp species

were harvested by severing the stipe just above the holdfast. The mean total length of *L.*

hyperborea individuals was 348 cm compared to *L. ochroleuca* individuals with a mean

length of 169 cm. Within two hours of collection, the sporophytes were submerged in the

dark in a 500 L flow-through tank of aerated ambient sea water pumped directly from the Bay

and left to acclimate for 48 hours.

2.1 Experimental design

For each adult individual, three blade fragments of equal length (20 cm) were cut at a

standardised distance (20 cm) above the meristem, away from the distal section of the kelp

blade which is subject to greater epiphytic colonisation. Fragments were tagged with a unique

ID number, their mass recorded and were randomly allocated to a depth (0, 15 and 30 m)

treatment. Thus there were five replicates per species within each depth treatment.

To simulate different light intensities across a depth gradient, light attenuation optical filters

(LEE Filters, Andover, UK) were constructed to completely cover the aquaria (Fig. 1). A

photon flux simulating light availability at 15 and 30 m was recreated using an average light

extinction coefficient (k) of 0.14 (from Boutler *et al*. 1974; spring and summer surveys

192   around Roscoff) incorporated into equation 1, where light availability at a specified depth

193   equates to:

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

195   The irradiance at depth (t) $I_{(t)}$ depends on the light at the surface $I_{(z0)}$, the depth (z) and the

196   extinction coefficient of the water in the column (k). The 0 m treatment, representing

197   strandline and floating detritus, were submerged in 8 cm of water hence $z_0 = 0.08$ m. The

198   percentage of light available at 0, 15 and 30 m was 98.9%, 12.3% and 1.5% respectively;

199   these values were utilised when assembling the relevant filters. We did not, however, account

200   for the change in spectral character as a function of depth (Saulquin *et al.* 2013).
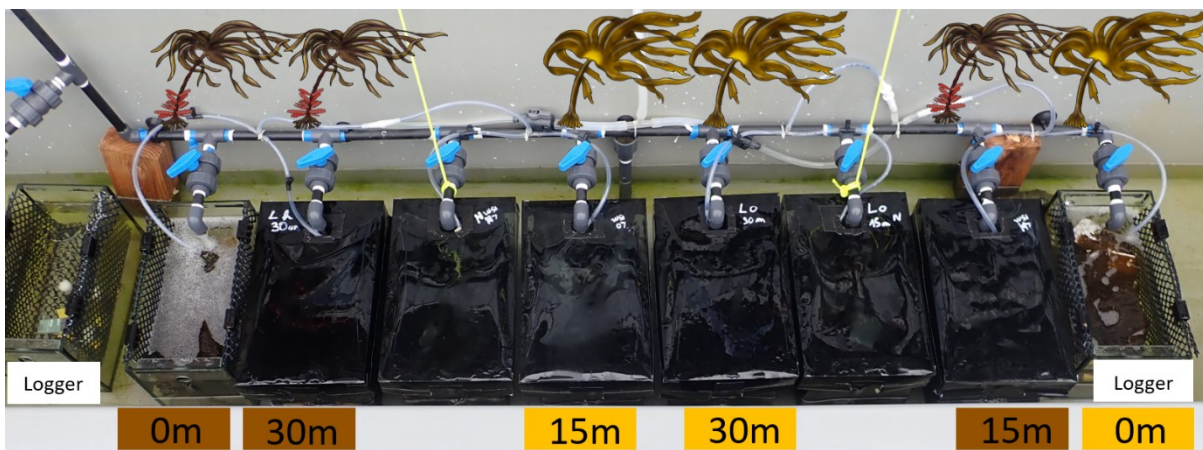
201

202

203   **Fig. 1.** Experimental set-up composed of filters for 15 and 30 m aquaria, constant air

204   bubbling and HOBO loggers. Two unlabelled aquaria were used for experiments that are

205   outside the scope of this paper. Each aquarium contained five replicate fragments. The

206   brown squares represent aquaria with *L. hyperborea* fragments and yellow squares contain *L.*

207   *ochroleuca* fragments.

208

209   The fragments acclimated for a further 48 hours before being transferred to 8 L aquaria

210   corresponding to their respective species by depth treatment where they remained for the

211 duration of the experiment. Each aquaria was installed with a wide mesh basket which held

212 the fragments in 8 cm of water and raised them 5 cm from the bottom. The baskets facilitated

213 water circulation whilst constant aeration promoted diffusion across the boundary layer

214 (Noisette and Hurd 2018). The six aquaria were held in a circulating water bath system

215 supplied with a continual flow of unfiltered seawater (renewal rate of 10 times the aquarium

216 volume per hour) located outside (Fig. 1). The fragments were therefore exposed to ambient

217 temperature and irradiance in order to re-create their natural environment. Two aquaria were

218 fitted with temperature/light loggers (HOBO Pendant Temperature/Light Weatherproof

219 Pendant Data Logger 16K) recording at 10-minute intervals. Data was regularly downloaded

220 to ensure conditions did not deviate significantly from outside conditions. Physiological

221 measurements (see below) began 9 days after the fragments were transferred into the

222 experimental system and observations were repeated at 7-day intervals thereafter across five-

223 time periods, (T1-T5) with a 19 day gap between T5 and T6, for a total duration of 56 days.

224

225 *2.2 Reproductive tissues and biomass change*

226

227 Photographs of each fragment were taken at each time point to monitor visual changes in

228 tissue surface (Figure S1), for example, the presence of sorus (reproductive) tissue (Figure

229 S2). Repeated measures of wet biomass were taken on the same fragment at each time point.

230 Biomass changes were calculated as a percentage of the starting mass remaining at each time

231 point. Completely degraded fragments were removed and their biomass from the preceding

232 time was recorded as mass lost. This aspect of the trial was extended to 108 days and final

233 biomass measurements were recorded after all the fragments from the 30 m treatment had

234 degraded.

235

236   *2.3 Production and respiration measurements*

237   Production and respiration rates were measured using a closed bottle respirometry technique

238   (Migné *et al*. 2002; Biscéré *et al.* 2019). Twenty incubation chambers, each comprising of a

239   1.2 L transparent glass jar closed by a watertight seal, were distributed across four 50 L

240   experimental units. The experimental units were each fitted with optical filters replicating

241   light conditions in the corresponding aquaria and were replenished with the same ambient

242   unfiltered seawater after each set of production and respiration incubations. Fragments were

243   transferred in the dark from their aquaria into the corresponding depth treatment of the

244   experimental unit with each jar containing an individual fragment. Two different incubations

245   were conducted consecutively, measuring both oxygen production and consumption

246   (respiration) respectively. Production was measured during a 60-minute incubation (long

247   enough to allow detection of a change in oxygen concentration whilst avoiding oxygen

248   saturation) under the experimental aquarium conditions. The jars were then opened to allow

249   water exchange for 30 minutes and the containers were covered by dark tarpaulin to halt

250   photosynthetic activity. The jars were subsequently re-sealed and the respiration incubations

251   were conducted on the same fragments for 60 minutes in complete darkness. Dissolved

252   oxygen concentrations were measured before and after both incubations (production and

253   respiration) using a portable multi-meter (HQ40d, Hach®, Loveland, USA) coupled with a

254   luminescent/optical dissolved oxygen probe (Intellical™ LDO101, Hach®, accuracy $\pm$ 0.2

255   mg L $^{-1}$). At the end of the incubations, fragments were retrieved from the jars, gently blotted

256   dry and weighed (WW in g). Production and respiration rates were estimated by calculating

257   the difference between initial and final oxygen O_2 concentrations after being corrected for

258   temperature change (Aminot and Kérouel, 2004). The rates were expressed in mgO_2 kg WW $^{-}$

259   ^{1} hr $^{-1}$. The production rate is a measure of Net Primary Production (NPP), which represents

260   the sum of photosynthesis and respiration in tandem. Meanwhile, Gross Primary Production

261 (GPP) was calculated by adding the dark respiration rate (R) to the NPP to derive the total

262 oxygen produced via photosynthesis. The seawater temperature and incident

263 photosynthetically active radiation (PAR, 400-700 nm, μmol photons m $^{-2}$ s $^{-1}$, Li-Cor

264 QuantumSA-190, LI-COR®, Lincoln, USA), were recorded every minute during the trials.

265

266 *2.4 Photosynthetic efficiency measurement*

267

268 To reveal to the extent to which fragments' photosynthetic apparatuses were active, the

269 operating efficiency of photosystem II (ΦPSII) and the maximal quantum yield of PSII

270 photochemistry (F_v/F_m) were measured using a portable pulse-amplitude-modulated

271 fluorometer (PAM, Heinz Walz, Effeltrich, Germany). *In vivo* ΦPSII was measured in

272 ambient light whereas F_v/F_m measurements were obtained from fragments that had been dark

273 adapted for 15 minutes (following Hargrave *et al.* 2017), before being flashed with a 0.8 s

274 saturating white light pulse (2500 μmol photons.m $^{-2}$ s $^{-1}$). F_v/F_m values normally range

275 between 0.7-0.8 for Phaeophyceae and values below are indicative of a stress response

276 (Bischof *et al.* 1999; Hanelt, 2018)

277

278 *2.5 Statistical analyses*

279

280 *2.5.1 Biomass change*

281

282 As a consequence of bimodality in the bounded biomass data, a Euclidean distance-based

283 permutational ancova (PERMANCOVA) was used in PRIMER ver 6.1 (Primer-E, Plymouth)

284 to test effects of species and depth (fixed factors) over time (continuous covariate), with

285 fragment identity (the plant from which the fragment was cut) as a random factor. P values

286   were obtained from type III sums of squares. MDS plots were inspected as a way of

287   identifying potential issues relating to heterogeneities of dispersion, though no formal tests

288   were performed due to the complexity of the model.

289

290   *2.5.2 Production, respiration and photosynthetic parameters*

291

292   The effects of species and depths across time on net and gross oxygen production (NPP and

293   GPP), dark respiration (R) and combining NPP with 12 h of R to represent a full day's rate of

294   oxygen flux (NPP-R), were tested with linear mixed effect models using Maximum

295   Likelihood (package *lme4* in R 3.6.1) (Bates *et al.* 2015; R Core Team 2019). To account for

296   variation in abiotic conditions across the experiment, mean PAR was used as a continuous

297   covariate for oxygen production and mean temperature for dark respiration (PAR and

298   temperature were strongly correlated). Fragment identity was included as a random factor and

299   p values were obtained from type III Wald χ^2 tests. Plots of residuals versus fits were used to

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

301   ΦPSII were analysed by similar model structure using generalised least squares (gls) fitting

302   (package *nlme,* Pinheiro *et al*. 2019) due to heterogeneities of variance; PAR was again used

303   as a continuous covariate; no random factor could be included in the gls model, between-

304   plant variability being accounted for in the overall model fit. P values were derived as

305   described above.

306

307   *2.5.3 Omnibus PERMANCOVA*

308

309   To examine the *in toto* physiological response of the two species, a multivariate approach

310   was employed. A z-transformation was used to normalise the physiological variables (GPP,

311 R, Fv/Fm and ΦPSII), and a Euclidean distance – based multivariate similarity matrix was

312 produced in PRIMER ver 6.1. This was then used as the basis for a mixed model

313 PERMANCOVA with 999 permutations of a reduced model employing the same structure as

314 the linear models described above; p values were obtained from type III sums of squares

315 using a pseudo-F statistic.

316

317 **3. RESULTS**

318 *3.1 Degradation dynamics*

319 The analysis of biomass change with depth indicated strong heterogeneity of response to the

320 environmental factor over time in the different species (3-way interaction pseudo-$F_{2,144}$ =

321 12.857, p <0.001; Fig. 2); no evidence of confounding heterogeneity of dispersion was

322 apparent in the MDS plots. The interspecific differences were most apparent in the 15 and 30

323 m treatments, in both cases some of the *L. hyperborea* fragments degraded more quickly than

324 *L. ochroleuca*. Under surface conditions neither species degraded markedly until after 56

325 days. No intact fragments of *L. ochroleuca* remained at the end of the 108 days, while *L.*

326 *hyperborea* fragments were generally still intact at this point. With light attenuated to levels

327 at 15 m, *L. hyperborea* began to degrade after 23 days, whilst *L. ochroleuca* persisted until

328 the end of the study in the majority of cases. At 30 m most *L. hyperborea* fragments had

329 completely broken down after 36 d, in contrast to *L. ochroleuca* where degradation was

330 significantly slower (Fig. 2, Table 1).

331

332 *3.2 Reproductive tissues and biomass change*

333

334   Clear evidence of sorus material was first detected whilst conducting the final physiological

335   measurements, 56 days into the experimental period on two *L. ochroleuca* fragments, one in

336   the 0 m treatment and one in the 15 m treatment. When the study was concluded 108 days

337   later, two different *L. ochroleuca* fragments had evidence of sorus material on the blade
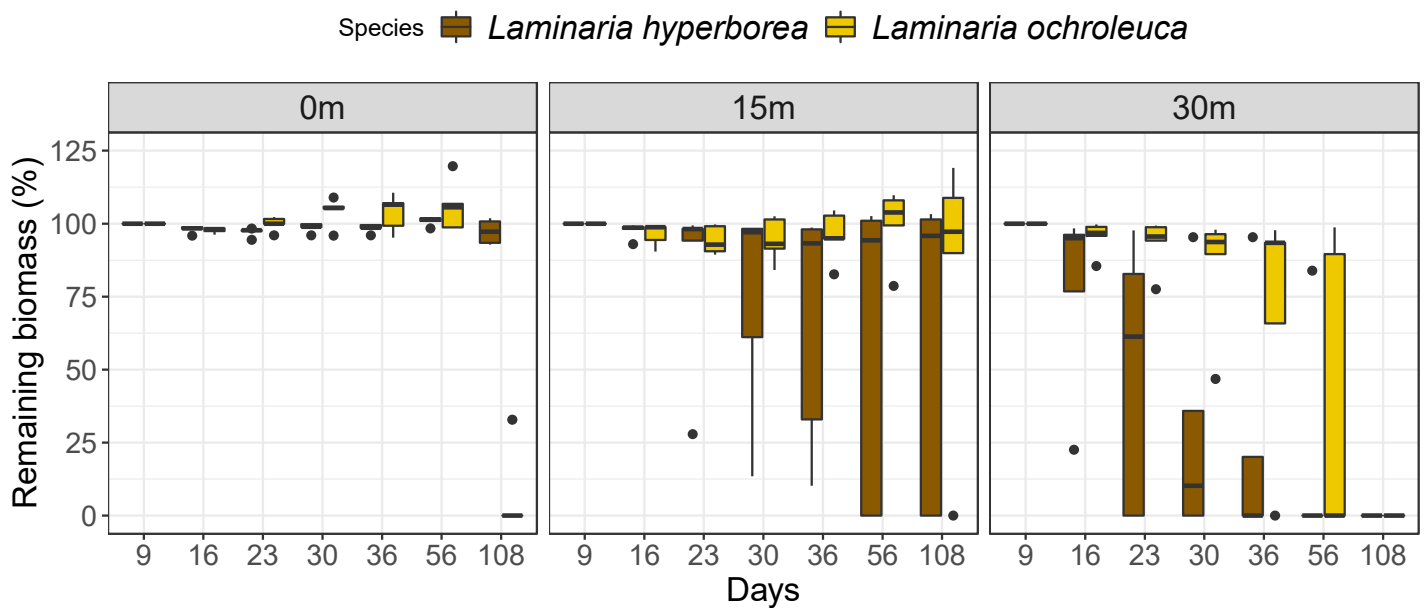
338   surface (Figure S2).

339

340

341   **Fig. 2.** Remaining biomass at three different simulated depths over time in *Laminaria*

342   *hyperborea* and *Laminaria ochroleuca* (N = 144). Boxes indicate the interquartile range,

343   horizontal line inside the bars indicates the median.

344

345   **Table 1:** Results of permanova analysis (type III SS) of % biomass remaining in the different

346   species and depths (fixed factors) over 108 days (continuous covariate). Significant terms

347   (P<0.05) are indicated in bold.

Source	*Df*	Pesudo-F	*P*
Time	1	119.37	**0.001**

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

348

349 *3.3 Production and respiration measurements*

350 As expected, the availability of light was the dominant factor affecting GPP; both in terms of

351 PAR at the surface ($\chi^2_{1,161}$ = 15.735, p < 0.001) and as a main effect of photo-attenuation

352 related to depth ($\chi^2_{2,161}$ = 92.036, p < 0.001). Contrary to expectation, however, across the

353 degradation period GPP did not decline as expected, and whilst the two species responded

354 differently to the passage of time ($\chi^2_{1,161}$ = 5.122, p = 0.024), it was apparent that overall

355 oxygen evolution was indicative of the metabolic integrity of surviving tissues remaining

356 remarkably intact often beyond 36 days post-detachment (Fig. 3a, Table 2).

357 Respiration (R) was independent of temperature, but differed strongly between species ($\chi^2_{1,}$

358 $_{,161}$ = 22.555, p < 0.001), and as a function of time ($\chi^2_{1,161}$ = 8.462, p = 0.004) and depth (χ

359 $^2_{2,161}$ = 10.276, p = 0.006), modifying the species effect. Notwithstanding the declining

360 number of fragments persisting to the end of the trial (Fig. 3), it was clear that R did not

361 display a simple response over time; only the data for *L. hyperborea* under surface light

362 levels are suggestive of a simple linear increase over time (Fig. 3b, Table 2).

363 Most importantly, Net Primary Production (NPP) during lit periods remained at, or recovered

364 to, positive net production levels in the majority of fragments until the end of the 56 day trial

365 (Fig. 3c, Table 2). As with GPP and R, NPP differed strongly at different depths ($\chi^2_{1,161}$ =

366 88.31, p < 0.001). NPP did not differ statistically between the two species, but the nature of

367 this experiment restricts these conclusions to brightly lit daylight hours. Assuming

368   equinoctial fully light and dark conditions, with NPP and an additional 12 h of R representing

369   a full day's oxygen flux, suggests a significant effect of species with an additional modifying

370   effect of depth upon this ($\chi^2_{2,161} = 6.244$, p = 0.044). Under this '24 h' model, a more realistic

371   interpretation of differential GPP responses between the species can be detected (Fig. 3d,
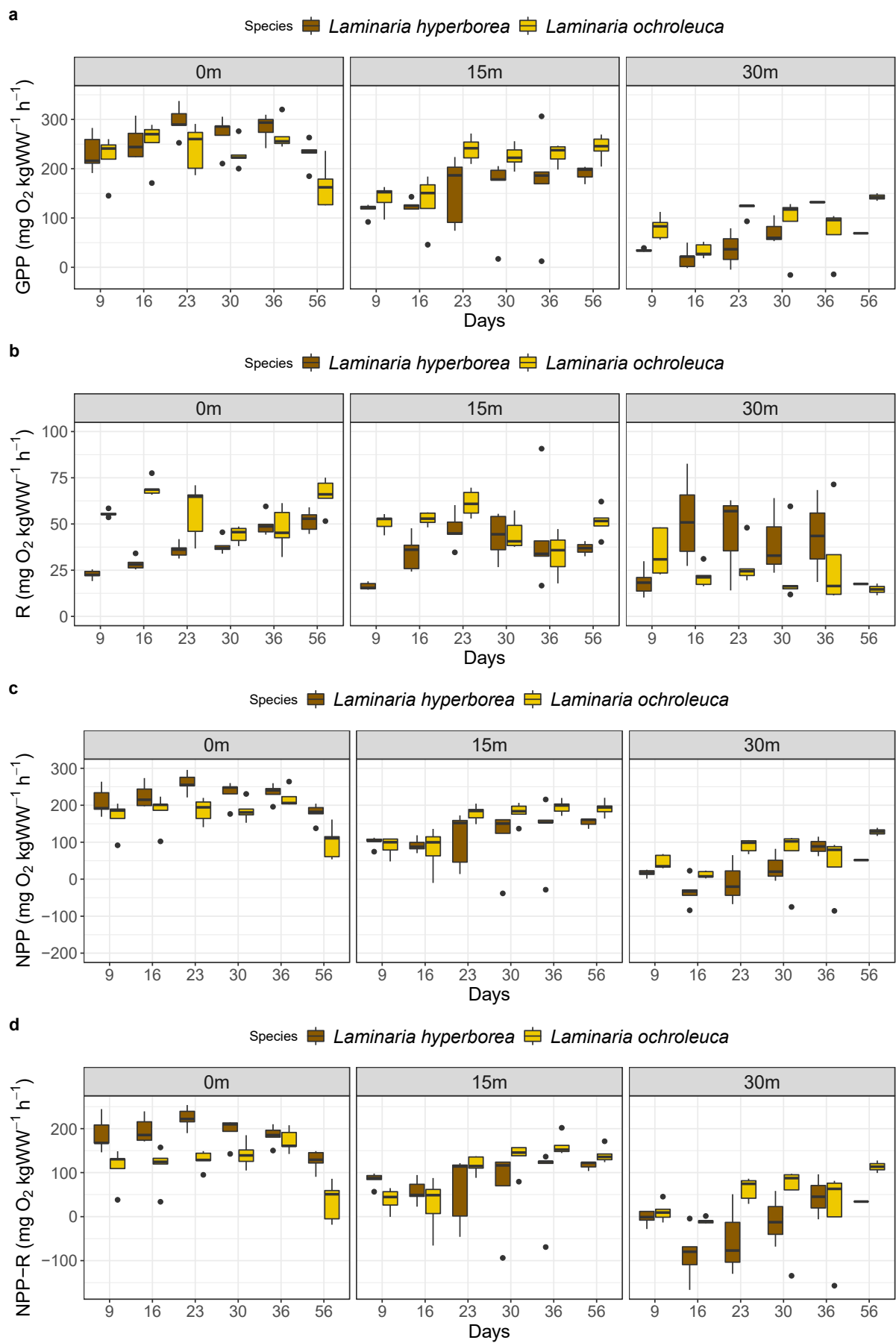
372   Table 2).

373

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

Production (NPP) and (d) '24 hour' model of oxygen flux (NPP-R) rates, expressed as

oxygen consumption or production, at three different simulated depths over time for

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

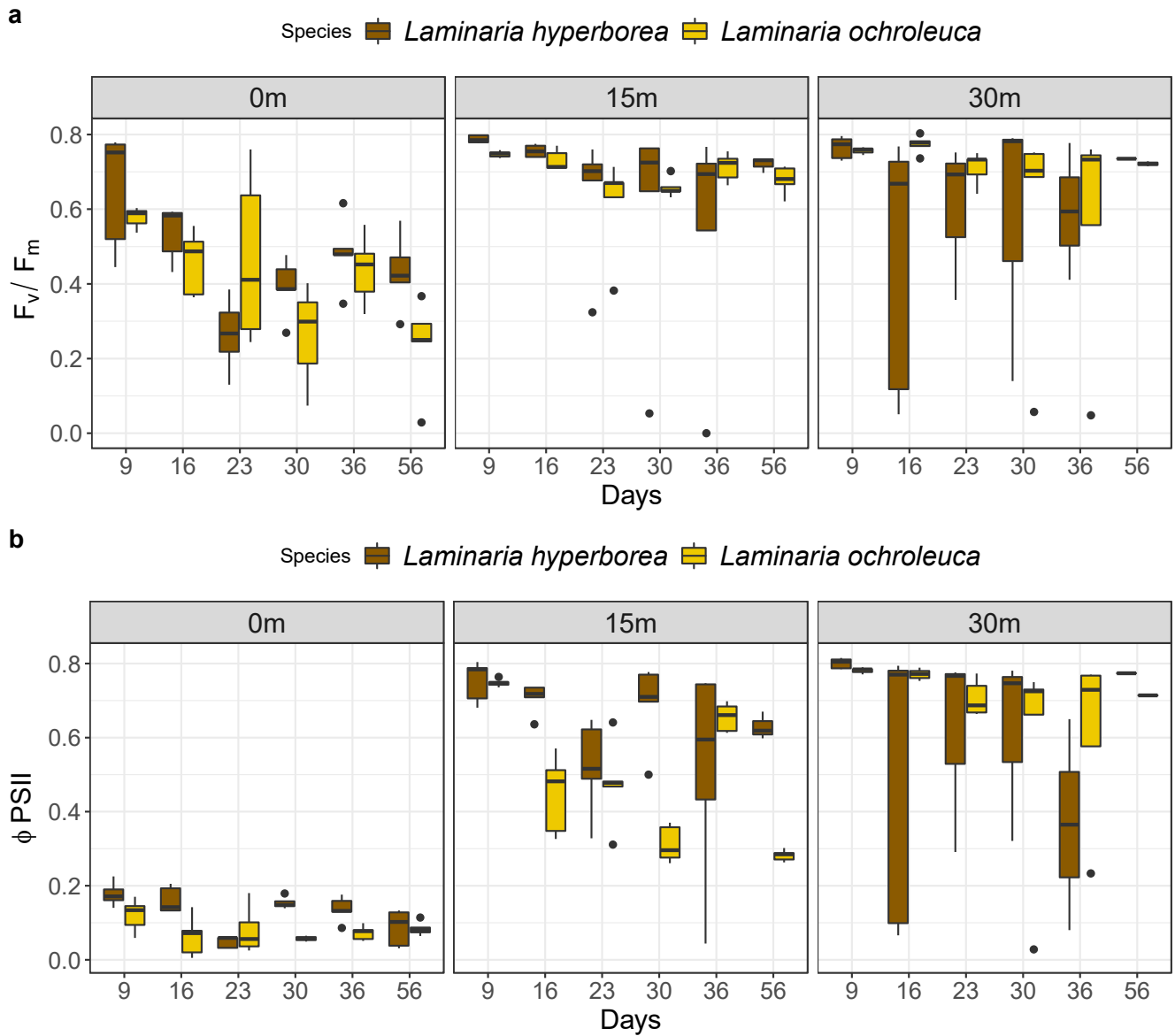range, horizontal line inside the bars indicates the median.

Table 2: Results of likelihood ratio tests based upon linear mixed effect models examining

responses of (a) Gross Primary Production (GPP), (b) Respiration, (c) Net Primary

Production (NPP) and (d) '24 hour' model of oxygen flux (NPP-R) rates across time (56

days), between kelp species and depth (fixed factors) with PAR or Temperature as a

covariate. Significant terms ($P < 0.05$) are indicated in bold.

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

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

386

3.4 Photosynthetic response

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

exerting a non-statistically significant effect on ΦPSII (as it did upon NPP and GPP), the

response of detrital fragments clearly declined over the degradation period (Fig. 4a) but

became highly variable at increasing depth, swamping any trend. Fig. 4b shows that F_v/F_m

displayed a similarly noisy decline over time. There was no significant difference in the

photosynthetic response between the species. Both parameters were significantly affected by

depth. No interactions were significant and therefore the photosynthetic behaviour of detrital

resources from different species was not affected by time or by depth (Figs 4 a-b, Table 3).

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) ΦPSII			
PAR	1	7.901	**0.005**
Time	1	0.221	0.638
Species	1	0.935	0.334
Depth	2	51.403	**<0.001**
Time:Species	1	0.694	0.405
Species: Depth	2	2.700	0.260
Time:Species:Depth	2	1.331	0.514
(b) F_v/F_m			
PAR	1	13.418	**0.001**
Time	1	1.620	0.203
Species	1	0.230	0.632
Depth	2	5.981	**0.050**
Time:Species	1	0.428	0.513
Species: Depth	2	2.654	0.265
Time:Species:Depth	2	1.641	0.440

404

3.5 Omnibus permanova

The combined response of GPP, R, ΦPSII 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, ΦPSII 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.

414

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

415

416   **4. DISCUSSION**

417   *4.1. Production and respiration measurements*

418

419   For the first time, the primary producer functions of algal detritus have been quantified across

420   a simulated depth spectrum. Detritus continued to sustain net production of oxygen across a

421   56-day period, underscoring its capacity to maintain key functions such as carbon fixation.

422   Detrital tissues slightly increased in biomass during the early stages of degradation,

423   demonstrating that measured oxygen production is reflective of fresh material being

424   generated. Over time, the respiration of detrital fragments, as a proxy for stress or associated

425   bacterial activity, increased in some contexts (Sosik and Simenstad, 2013). Evidence of some

426   degradation was further reinforced by a measured decline in photosynthetic performance

427   (ΦPSII and F_v/F_m), in accordance with the initial hypothesis. At the end of the first time

428   period, values between 0.6-0.8 at 15 m and 30 m reflected an optimum performance at depths

429   at which the kelps inhabit (Gorman *et al.,* 2013). Low photosynthetic parameters at 0 m

430   follow reported trends in the literature of decreases in both measurements with increasing

431   irradiances (for *Laminaria digitata*, Delebecq *et al.* 2011).

432

433   Respiration is a central process in kelp decomposition (de Bettignies *et al.* 2020b) and

434   measured increases in the rate of oxygen consumption were mirrored by a decline in the

435   detrital biomass. However, it is important to note that the measurements reflect the holobiont

436   respiration of *Laminaria* tissue together with its ensemble of microorganisms (Baedke *et al.*

437   2020). The results of this study reveal that the respiration response differed between the two

438   species across time. Detritus from *L. hyperborea* exhibited higher rates of respiration

439   compared to *L. ochroleuca* over time in the 30 m treatment and only under surface conditions

440   was a linear increase in respiration detected for *L. hyperborea*. This differential response

441   between the species may be indicative of stress or higher biofilm activity associated with *L.*

442   *hyperborea* fragments. *L. hyperborea* degraded faster than *L. ochroleuca* at 15 m and 30 m,

443   suggesting that low light conditions may impede the regeneration of damaged tissue for *L.*

444   *hyperborea* which points to the role of light in determining the detrital fate of some species

445   (Hader *et al.* 1998; Swanson and Fox 2007). Furthermore, in some instances, during the

446   initial stages of degradation at 0 and 15 m, *L. ochroleuca* positively increased in biomass

447   compared to *L. hyperborea* (Fig. 2). However, this trend was reversed after 56 days in the 0

448   m treatment when all *L. ochroleuca* fragments were completely degraded in sharp contrast to

449   the relatively intact fragments of *L. hyperborea*. 4.2 Considering the first 40 days of this trial,

450   this result is comparable, yet contrary to the findings of Pessarrodona *et al.'s* (2018b) *in situ*

451   study comparing the biomass loss from the same study species. Pessarrodona et al. (2018b)

452   report that *L. ochroleuca* lost biomass at a faster rate than *L. hyperborea* in spring, prior to

453   the latter shedding of old fronds. The present study separated the change in mass across

454   regular time intervals and elongated the temporal scale of degradation to 108 days, as well as

455   eliminating physical erosion as a mechanism of degradation, casting light on the purely

456   organic dimension of how kelp matter breaks down. Our results suggest that *L. hyperborea*

457   has the potential to be a more persistent spatial subsidy and thus may reside in the ecosystem

458   for longer under attenuated illumination. However, hydrodynamics and physical processes

459   such as abrasion and grazing may further confound elucidation of the decomposition process.

460   (Nielsen *et al*. 2004; Braeckman *et al*. 2019).

461

462   *4.2. Contextualizing the findings*

463

464   These differences in persistence will become increasingly important as *L. ochroleuca*

465   gradually replaces *L. hyperborea,* in habitats where the two species coexist, (Teagle and

466   Smale 2018) and will be further exacerbated by the seasonal modification of detrital

467   production between the species; ultimately affecting the quality and supply of organic kelp

468   derived material entering the detrital pathway (Bishop *et al.* 2010). The extent to which

469   benthic ecosystems in the North East Atlantic are dependent on detritus derived from *L.*

470   *hyperborea* remains unquantified. However, modifications in the turnover of organic

471   material, transport (Pedersen *et al.* 2005), trophic connectivity (Leclerc *et al.* 2013b), organic

472   matter content (Abdullah *et al.* 2017) and a homogenization of the nutrient supply from kelp

473   detritus derived from different species will likely have ramifying effects across food webs.

474

475   Extending the investigation to consider the degradation process across environmental

476   contexts revealed that other measured physiological processes of kelp detritus (NPP, GPP and

477   ΦPSII and F_v/F_m) are not only species specific but also highly dependent on light availability.

478   Depth significantly affected 24-hour oxygen flux and the Species response to the effect of

479   Depth was significantly heterogeneous in the case of both respiration and the 24-hour model

480   of oxygen flux (Fig. 3b and d). Therefore, considering the dynamic nature of detrital

481   transport, the depth to which detritus is exported significantly determines the carbon fixation,

482   respiration and photosynthetic performance of kelp material (Filbee-Dexter and Scheibling,

483   2016). Furthermore, detritus was clearly less productive as a function of decreasing irradiance

484 from 0 m > 15 m > 30 m (Fig. 4a). Photosynthetic capacity was critically impaired at 0 m,

485 probably as a result of photoinhibition (Delebecq *et al.* 2011), but remained mostly invariant

486 between 15 and 30 m. Although the activity of the photosynthetic apparatus was maintained

487 in low light conditions, the decline in oxygen production is indicative that detritus is a less

488 effective primary producer at 30 m. The differing responses of respiration in the two species

489 over time and at different depths highlight that the process of degradation needs to be

490 considered across different environmental conditions with a temporal dimension. Species'

491 respiration fluctuated across time and their response was dependent on light attenuation,

492 which indicates that one species may have the physiological capacity to persist for longer

493 than its congener at a specific depth.

494

495 *4.3. Re-defining kelp detritus*

496

497 An unexpected result was that *L. ochroleuca* fragments developed visible sorus tissue at the tissue

498 surface indicating that such fragments remain capable of maintaining reproductive functions (Fig

499 S1). Moreover, this was detected first for two fragments during the final time period (T6) in July.

500 Visible sorus remained at the blade surface two independent *L. ochroleuca* fragments when the

501 experiment ended 108 days post fragment preparation in September. This time window is in

502 accordance with the reproductive period for *L. ochroleuca* (Pereira *et al*. 2019), further revealing the

503 metabolic competency of the kelps post-detachment. Further research would be necessary to

504 determine spore viability from such tissues. de Bettignies *et al.* (2020b) reported a similar

505 phenomenon for *L. hyperborea* in October after subjecting detrital fragments to 5 months of

506 degradation *in situ*. In terms of reproductive capacity, some of the energy generated by detrital

507 photosynthesis is invested into the generation of reproductive tissue which potentially has

508 considerable implications for the dispersal of these species. If current-borne kelp detritus can still

509   reproduce, then kelp populations structure is likely to be far more fluid than would be indicated by

510   typical spore or gamete dispersal, which is low for individual sporophytes within a kelp forest (~ 5-

511   200 m, Fredriksen *et al.*1995). This phenomenon compliments the functional role of herbivores in

512   increasing fertilisation success and dispersing kelp spores which germinate post-digestion (Ruz *et al.*

513   2018).

514

515   Another important outcome of the present study and other recent work on physiological

516   viability of macroalgal 'detritus' (de Bettignies *et al.* 2020b) is a questioning of the rationale

517   behind defining this material as 'detritus'. Currently, cast or detached macroalgal fragments

518   are considered as 'non-living' organic matter generated by the growth and production of

519   living organisms (Hagen *et al.* 2012): a viewpoint that is based upon terrestrial botanical

520   science. Although such tissues may be no longer attached, and as our data suggests, may be

521   in the process of slowly entering the detrital food web, they remain 'alive' and

522   physiologically competent for much longer than would be typical for tissues of land plants.

523   This 'productive necromass' – physiologically persistent and viable, unattached or

524   fragmented algal biomass – continues to photosynthesize and, in the right conditions, can

525   continue to fix carbon for months after it would otherwise be inaccurately defined as detrital.

526   Our study has demonstrated that kelp detritus can sustain productivity for long periods of

527   time and therefore detrital contribution to Blue Carbon is likely to be much greater than has

528   been previously accounted for. Accordingly, incorporating productivity from macroalgal

529   detritus could account for important increases to the contribution of macroalgae in the Blue

530   Carbon economy.

531

532   *4.4 The role of kelp detritus in benthic ecosystems*

533

534 The vast majority of kelp production enters the detrital pathway (about 82% according to Krumhansl

535 and Scheibling 2012), therefore fundamental variability in the respiration and photosynthetic

536 performance of kelp material across time and under different environmental conditions are important

537 for understanding the persistence and productivity of detrital resources. The composition of kelp

538 forests and thus their detritus, will likely be modified as climate warming persists (Smale et al.

539 2015), with the gradual increase of HFS with high thermal affinities and gradual local extinctions of

540 native HFS with cooler thermal affinities (Wiens 2016). These replacements will likely impact many

541 aspects of the cycling of organic material, from the spatial subsidies exported kelp matter provides,

542 to the fitness of grazers and detritivores feeding upon it, and the rate of carbon sequestration into

543 longer residence forms in the benthos. Pessarrodona *et al.* (2018b) speculated about an alteration in

544 the functional importance of this detrital material due to a variation in the rate of supply from

545 different kelp species. Here we have shown that the continued biological activity of fragmented kelp

546 tissues also differs between species, across time and environments, further altering the contribution

547 of kelp mass to spatial subsidies (Leclerc *et al.* 2013a).

548

549 This study provides a snapshot of the degradation dynamics of two kelps under controlled

550 conditions. There are numerous potential sources for error; for example a change in detrital

551 respiration could be attributed an upregulation of metabolic processes in *L. hyperborea* or to an

552 increase in oxygen consuming saprophytic bacteria and fungi (Fenchel and Jørgensen, 1977;

553 Williams *et al.* 2004). Furthermore, variation in species physiology cannot be generalized across the

554 entirety of benthic ecosystems in the North East Atlantic because despite advances in areas of low-

555 moderate wave exposure (Smale *et al.* 2015), *L. ochroleuca* may not be able to fully replace *L.*

556 *hyperborea* in sites exposed to high wave exposure (Pessarrodona *et al.* 2018b) and therefore the

557 composition of detritus from such assemblages may remain relatively unchanged. Also, the role of

558 macrofaunal colonization and consumption (de Bettignies *et al.* 2020; Ramirez-Llodra *et al.* 2016) of

559 the kelps in question could change the degradation dynamics completely. Hargrave *et al.* (2016)

560 reported lower concentrations of grazer-deterring polyphenolics and flavonoids in *L. ochroleuca* than

561 in another common NE Atlantic congener: *L. digitata*, with higher grazing rate by herbivorous

562 gastropods in the former. Meanwhile, Pessarrodona *et al.* (2018b) found a similar herbivore

563 preference for *L. ochroleuca* over *L. hyperborea*, recording a faster degradation of the former. If

564 detritivore preference for the more palatable *L. ochroleuca* mirrors that of grazers, then the

565 reconciliation of the slower degradation of *L. ochroleuca* in the earlier stages of the present study

566 with the faster *in situ* degradation of *L. ochroleuca* observed by Pessarrodona *et al.* (2018b) could be

567 attributed to mechanical effects, especially of saprovores aiding conversion of frond tissue into

568 coarse particulate organic matter and facilitating ingress by saprophytic micro-organisms. Future

569 study should therefore aim to evaluate the importance of the ecological consequences of

570 environmentally realistic deposits of macroalgal detritus with their attendant bacterial and

571 detritivorous assemblages and also continue to compare the detrital compositions from species at risk

572 of local extinction from a variety of range-expanding or invasive algae (Sorte *et al.* 2010), taking into

573 account different environmental contexts in which kelp degradation may occur, testing the

574 degradation response *in situ* across a gradient of turbulence, and explicitly focusing on detritivores as

575 a driver of tissue fragmentation and a facilitator of micro-organismal colonization. These questions

576 have indeed been addressed in other contexts spanning from shallow shorelines to the deep sea

577 whilst the shallow subtidal has often been considered as a mere transitional deposition area.

578 However, we argue that detrital accumulations can exert measurable impacts on ecosystem

579 functioning and deserve enhanced attention.

580

581 **5. CONCLUSION**

582   Kelp fragments remained physiologically competent for 56 days and possibly reproductively

583   active for up to 108 days after they were cut from the thallus. The fragments' photosynthetic

584   apparatus continued to function adequately to allow short-term (~ 56 days in *L. ochroleuca*)

585   net gains in biomass which was sustained under ambient light levels. Light availability was

586   the greatest determinant of photosynthetic performance, and net and gross primary

587   production, whilst light and interspecific differences dominated the response of respiration.

588   The range-expanding *L. ochroleuca* broke down more slowly under attenuated illumination,

589   challenging previous findings. We believe that a re-evaluation of recently formed macroalgal

590   detritus as 'living material' is due and should certainly be considered when evaluating the

591   functional integrity and spatial subsidies afforded by kelp forests. The predicted expansion of

592   the thermally tolerant species, *L. ochroleuca*, and replacement of the less tolerant *L.*

593   *hyperborea* across extensive areas is likely to alter the cycling of organic matter. Overall,

594   these findings demonstrate the indispensable need to consider detritus as an important

595   autotrophic resource, even after exportation, depending on the environmental conditions.

596

597   **DATA AVAILABILITY**

598   Data will be archived in GitHub repository: https://github.com/nadiafrontier/The-degradation-

599   of-kelp-detritus.git

604   **SUPPLEMENTARY INFORMATION**

605   Supplementary tables 1-4 contain abridged statistical tables following permanova, linear

606   mixed effect models and generalised last squares analysis to support the summary statistics

607   quoted in the manuscript.

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SUPPLEMENTARY MATERIAL

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

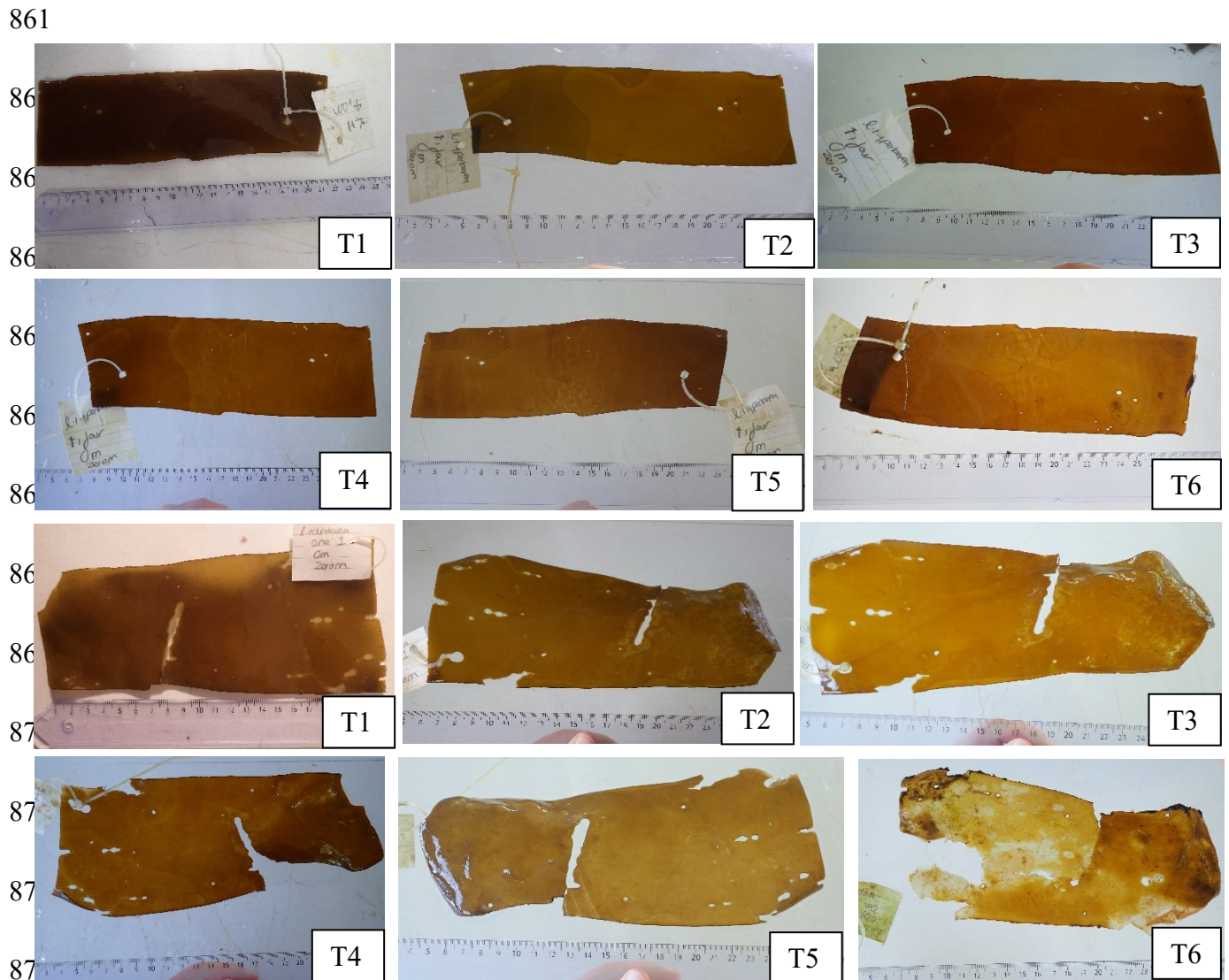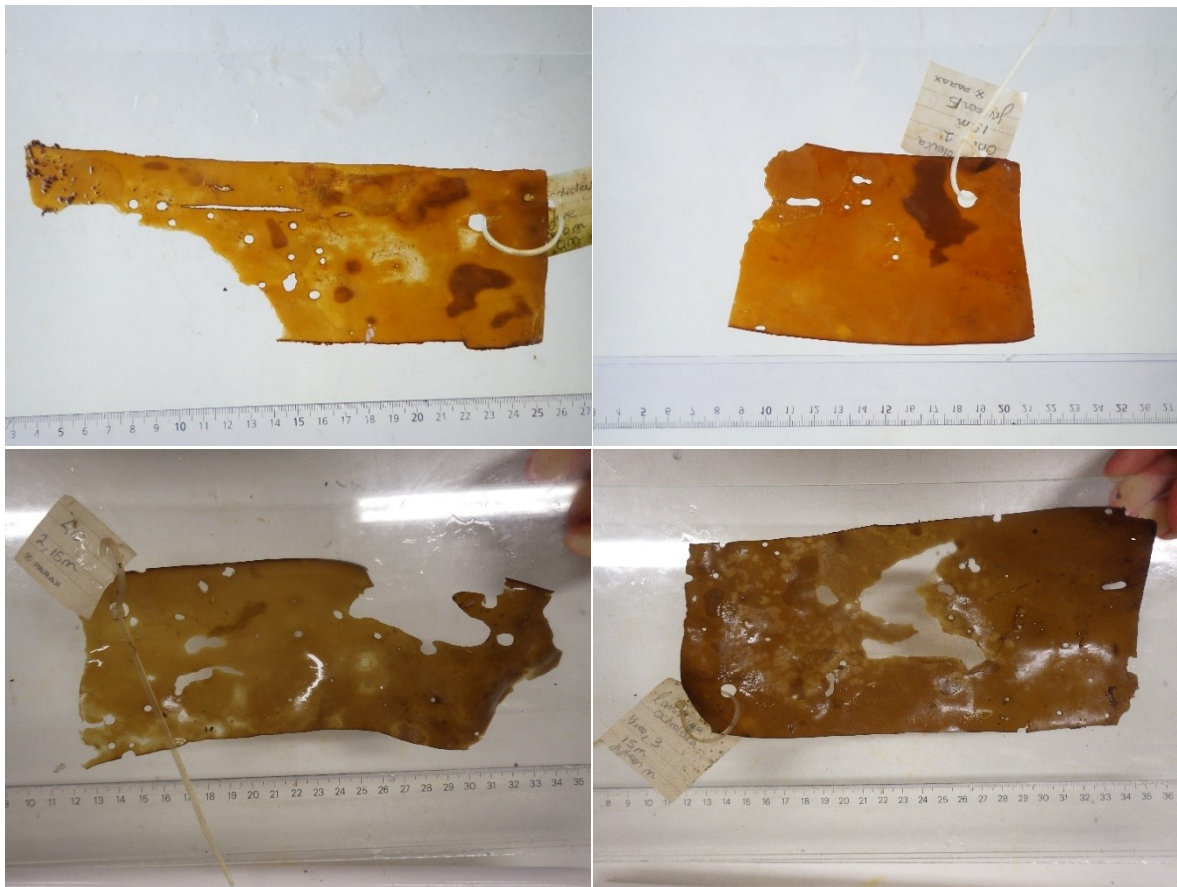Nadia Frontier, Florian de Bettignies, Andy Foggo, Dominique Davoult

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

880   **Figure S2:** Moving clockwise from top left: Sorus material (dark patches) from *Laminaria*

881   *ochroleuca* fragments at 0 m and 15 m at Time 6, 56 days into the degradation period. Sorus

882   material from two different *Laminaria ochroleuca* fragments at 15 m, 108 days post fragment

883   detachment when the experiment terminated.

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