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Photosynthetic pigments of co-occurring Northeast Atlantic Laminaria spp. are unaffected by decomposition

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1 Note

2 Title: **Photosynthetic pigments of co-occurring Northeast Atlantic *Laminaria* spp. are**
3 **unaffected by decomposition**

4 Running page head: *Laminaria* spp. pigments

5

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10

11 **Abstract**

12 Along Northeast Atlantic coasts, the genus *Laminaria* dominates kelp forests. Two species,
13 *L. digitata* and *L. hyperborea*, are cold temperate whilst the third, *L. ochroleuca*, is warm
14 temperate. In northern France and the southern British Isles, all three species now co-
15 occur, with a gradual rise in predominance of *L. ochroleuca* evident over recent decades
16 due to climate-driven range shifts. Despite recent focus on the export of
17 photosynthetically viable macroalgal detritus, the effect of decomposition on detrital
18 pigment concentration remains unknown for northern hemisphere kelps. Furthermore,
19 notwithstanding its importance in determining habitat suitability, the photosynthetic
20 pigments of all three species have not yet been assessed comparatively within the same
21 forest. Here we present results of a field experiment aimed to test potential changes in the
22 pigments of decomposing kelp blade fragments. Using spectrophotometry and Gaussian
23 peak spectral deconvolution to quantify pigments, we found that shallow benthic
24 decomposition over one month does not affect major photosynthetic pigment
25 concentrations in any of the examined species. Moreover, the two boreal species were
26 similar in their sporophyte pigment stoichiometry and had more chlorophyll *a*,
27 chlorophyll *c*, fucoxanthin and minor carotenoids (β,β -carotene and zeaxanthin) than *L.*
28 *ochroleuca*. This resulted in total pigment content that was 82% and 74% higher in *L.*
29 *digitata* and *L. hyperborea* than *L. ochroleuca*. These differences correspond
30 approximately to each species' latitudinal distribution and photosynthetic performance.

31

32 **Key words**

33 climate change; biogeography; brown algae; marine macrophytes; marine vegetated
34 habitats; decay; degradation; litter bag experiment

35

36 **1. Introduction**

37 The chlorophylls *a* (Chl *a*), *c* (Chl *c*) and the major carotenoid fucoxanthin (Fuco) are at
38 the root of the photosynthetic apparatus of Phaeophyceae (Caron et al. 2001). These main

1 photosynthetic pigments are situated in the light harvesting complex; Chl *a* is also found
2 in reaction centres I and II where it is responsible for charge separation. The so-called
3 antenna pigments Chl *c* and Fuco enhance the light gathering efficiency of the
4 photosystems by passing harvested light energy to Chl *a* via resonance transfer. Their
5 concentration relative to Chl *a* is an indication of antenna size (Caron et al. 2001,
6 Delebecq et al. 2012). Minor photoprotective carotenoids of brown algae include β,β -
7 carotene ($\beta\beta$ -Car) along with the xanthophylls violaxanthin (Viola), antheraxanthin
8 (Anth) and zeaxanthin (Zea).

9

10 Photosynthetic pigments vary considerably between species, predominantly driven by
11 light availability: when less light is available, more pigments need to be produced to
12 harvest enough energy from scarce photons. For instance, pigments of kelps are generally
13 more concentrated in deeper or more turbid water (Koch et al. 2016, Desmond et al.
14 2019) and during darker months (Marins et al. 2014, Varela et al. 2018). Similarly, brown
15 algal antenna size is larger in species that are distributed lower down on rocky shores and
16 consequently receive less light (Caron et al. 2001). Conversely, if kelps are exposed to
17 higher natural (Rothäusler et al. 2011a, 2018) or artificial (Rothäusler et al. 2011b)
18 irradiance, they exhibit reduced pigmentation.

19

20 Recent research revealed the sustained capacity of kelp detritus (defined as any portion of
21 the thallus detached from the substrate) to maintain positive net carbon uptake over
22 several months (de Bettignies et al. 2020, Frontier et al. 2021), leading to potentially
23 enhanced contribution to detrital food webs and carbon sequestration. The characteristics
24 of detrital photosynthetic pigments and their change or constancy during microbial and
25 macrofaunal decomposition will be instrumental in determining the fate of specific
26 macroalgal autotrophic production and hence specific contribution to these carbon flows.
27 However, studies on pigment concentrations in macroalgal detritus have been restricted
28 the southern hemisphere (Rothäusler et al. 2018, Hees et al. 2019, Tala et al. 2019). With
29 the exception of Hees et al. (2019), past research has also focused solely on floating
30 detritus which occupies a markedly different photoenvironment to benthic detritus of
31 boreal kelps which lack pneumatocysts or buoyant porous tissues.

32

33 The main kelps in the Northeast Atlantic are *Laminaria* spp., represented by cold
34 temperate *L. digitata* and *L. hyperborea* along with their warm temperate congener *L.*
35 *ochroleuca* (Lüning 1990) (**Fig. 1**). Sporophytes of the latter species can withstand
36 temperatures up to 25°C (Franco et al. 2018) and increasingly dominate temperate kelp
37 forests in the face of climate change (Pessarrodona et al. 2019). In addition to thermal
38 tolerance, adaptability of the photosynthetic apparatus to prevailing light regimes may

1 facilitate biogeographic shifts (Rothäusler et al. 2018, Tala et al. 2019). *L. ochroleuca*
2 displays a characteristic light ochre colouration across its range (Franco et al. 2018),
3 begging the question whether or not *L. ochroleuca* has a lower photosynthetic
4 pigmentation than its congeners, potentially constraining its distribution. Sporophyte
5 pigment concentrations are available for these species (Dring 1986, Delebecq et al. 2012,
6 Fernandes et al. 2016) but, with the exception of Hellebust & Haug (1972), no study has
7 attempted an interspecific comparison.

8

9 Here we report the first data on detrital pigment concentrations in any northern
10 hemisphere kelp over the first month post-excision, using a benthic litter bag experiment.
11 Moreover, we present the first interspecific comparison of photosynthetic pigment
12 composition between all Northeast Atlantic *Laminaria* spp. from the same kelp forest. We
13 tested the null hypotheses that *Laminaria* spp. photosynthetic pigmentation (1) is
14 unaffected by decomposition and (2) is similar between species.

15

16 **2. Materials and methods**

17 **2.1. Sampling**

18 All species were sampled from within Plymouth Sound in southern England (**Fig. 1**). Nine
19 mature sporophytes each of *L. digitata*, *L. hyperborea* and *L. ochroleuca* were collected
20 within a ~2-m depth range from the mixed kelp forest occurring in a ~20-m band around
21 lowest astronomical tide at West Hoe (50.363629°N, 4.144978°W) on 17th May 2019.

22

23 **2.2. Field experiment**

24 Three fronds were removed from each sporophyte *in situ* and trimmed to a standardised
25 sample mass of 20 ± 1 g. Frond samples were taken from the central part of the current
26 year's lamina growth, avoiding the meristematic basal and eroding apical regions. For
27 each species, one sample from each sporophyte was placed within each of three
28 rectangular, galvanised steel mesh enclosures (62.4×34.4 cm, 13-mm mesh \varnothing). The nine
29 mesh cages were then chained together, closed with cable ties and deployed at ~2 m
30 below lowest astronomical tide in the mixed kelp forest from which the specimens were
31 collected. A temperature and light logger (HOBO Pendant[®], Onset, Massachusetts, USA)
32 was secured to one end of the chain facing the surface and the chain was deployed
33 parallel to the shoreline to control for depth. Samples were retrieved on 30th May, 11th
34 June and 18th June (i.e. after 13, 25 and 32 d). On each retrieval date, three randomly
35 selected frond samples were removed from each litter bag. After detaching any
36 conspicuous epibiota, these samples were frozen at -20°C and immediately lyophilised
37 prior to pigment extraction (see Fig. S1 for a comparison of lyophilised and fresh tissue
38 extract concentrations).

1

2 **2.3. Pigment extraction**

3 Frozen subsamples were lyophilised (Lablyo, Frozen in Time Ltd, York, UK) and
4 subsequently ground to 250- μ m powder. Pigments were then extracted from 100 ± 1 mg
5 (Fisherbrand™ Analytical Balances, Thermo Fisher Scientific, Massachusetts, USA)
6 powder through five serial elutions with 5 ml of 100% room temperature acetone,
7 resulting in a 0.4% (w/v) solution.

8

9 **2.4. Spectrophotometry and spectral deconvolution**

10 The five serial elutions from each sample were amalgamated and made up to 25 ml with
11 solvent, the solution was then decanted into 2-ml microtubes and centrifuged (Sigma 1–
12 14, Osterode am Harz, Germany) for 5 min at 4722 x *g*. The supernatant was pipetted into
13 a crystal cuvette (1-cm path length). Using a Jenway 7315 spectrophotometer (Cole-
14 Palmer, Staffordshire, UK), absorbance spectra were recorded between 400 and 750 nm
15 (1-nm resolution) with 100% acetone blanks after every five samples. The resulting
16 spectra were translated into individual relative pigment concentrations (μ g g^{-1}) by fitting
17 a series of Gaussian peaks using non-negative least squares (**Fig. S2**) using R code modified
18 from Thrane et al. (2015), who also provide a validation of the technique against the more
19 exhaustive HPLC-based approach. Maximum absorbances (λ_{max}) and absorption
20 coefficients (α) obtained from acetone extractions of Chl *a*, phaeophytin *a* (Phytin *a*), Chl
21 c_1 , Chl c_2 , $\beta\beta$ -Car and the xanthophylls Fuco, Viola and Zea were collated from the
22 scientific literature (**Table S2**). Unfortunately, α and λ_{max} for Anth were not available for
23 acetone extractions and therefore we did not estimate this pigment. In addition, $\beta\beta$ -Car
24 and Zea have effectively identical absorption spectra. These trace pigments were
25 therefore grouped into a category which we refer to as minor carotenoids, as opposed to
26 the major carotenoid Fuco (**Table 1**). Chl *c* was calculated as Chl c_1 + Chl c_2 and the
27 antenna pigment to Chl *a* ratio was calculated as (Fuco + Chl *c*)/Chl *a* (Delebecq et al.
28 2012).

29

30 **2.5. Data analysis and visualisation**

31 Data analysis and visualisation were performed in R v4.0.2 (R Core Team 2020); R
32 packages used are cited in **Table S3**. Interspecific differences in relative pigment
33 stoichiometry were analysed using permutational multivariate analysis of variance
34 (Anderson 2001) based on Euclidian distances. Linear models were built with individual
35 pigment concentrations as the response variable with species (categorical) and detrital age
36 (continuous) as explanatory variables. Model fitting was performed using graphical
37 techniques and heterogeneity was modelled as a function of explanatory variables using
38 generalised least squares (Zuur et al. 2009). The resulting type II and III sums of squares

1 hypothesis tests and pairwise contrasts are reported in **Table S4**. Multivariate data were
2 visualised using nonmetric multidimensional scaling. Data and code available at
3 github.com/lukaseamus/pigments.

4

5 **3. Results**

6 Analysis of environmental data revealed that seawater temperature increased in an
7 oscillating pattern at a linear rate of $0.04^{\circ}\text{C d}^{-1}$ over the experiment (**Fig. S3**). Ambient
8 irradiance was low (daytime mean \pm standard error: $1.68 \pm 0.07 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) but
9 comparable to other studies in the locality (N. Frontier et al. unpubl. data). Under these
10 environmental conditions, *L. digitata*, *L. hyperborea* and *L. ochroleuca* wet mass declined
11 at rates of 0.2 ± 0.04 , 0.16 ± 0.05 and $0.36 \pm 0.07 \text{ g d}^{-1}$. Of our target pigments, Phytin *a*
12 and Viola were not recorded in any of the *Laminaria* spp. While Chl *a*, Chl *c* and Fuco
13 were measured in all samples, $\beta\beta$ -Car and Zea were absent from 78% and 26% of samples,
14 respectively.

15

16 Multivariate analysis revealed that photosynthetic pigment stoichiometry was unaffected
17 by detrital age (Pseudo $F_{1,75} = 0.99$, $p = 0.32$) but 43% of the variance in overall pigment
18 composition is explained by the distinction between species (Pseudo $F_{2,75} = 28.4$, $p <$
19 0.001) (**Fig. 2**). More specifically, the 95% confidence ellipses of *L. digitata* and *L.*
20 *hyperborea* overlap, indicating that these boreal species have a similar pigment
21 composition (**Fig. 2**). In contrast, the ellipse of warm temperate *L. ochroleuca* is far
22 removed in ordination space from those of its cold temperate congeners, suggesting a
23 markedly different pigment stoichiometry.

24

25 The age of detritus had no effect on total pigment content of any species (**Table S4**).
26 Neither the chlorophylls *a* and *c*, nor the major xanthophyll Fuco were affected by
27 decomposition in any of the species. While also showing no change with age in *L.*
28 *hyperborea* and *L. ochroleuca*, the minor carotenoids decreased at a rate of $2.1 \mu\text{g g}^{-1} \text{d}^{-1}$
29 in *L. digitata* (**Table S4, Fig. S4**). The antenna pigment to Chl *a* ratio remained unchanged
30 in *L. hyperborea* but increased at rates of 0.008 and 0.005 d^{-1} in *L. digitata* and *L.*
31 *ochroleuca* (**Table S4, Fig. S5**). Across detrital ages, *L. digitata*, *L. hyperborea* and *L.*
32 *ochroleuca* had mean antenna pigment to Chl *a* ratios of 0.8 ± 0.02 , 0.75 ± 0.01 and $0.73 \pm$
33 0.02 . Overall, time since the start of the experiment had little effect on any aspect of
34 pigment stoichiometry with minor changes mostly noticeable in *L. digitata*. Hence, we
35 cannot reject our first null hypothesis.

36

37 In contrast to the lack of change with detrital age, interspecific differences in total
38 photosynthetic pigment content were large (**Table S4**). While being similar in their total

1 pigment concentration, the boreal species *L. digitata* and *L. hyperborea* contained 82%
2 and 74% more pigment than their warm temperate congener (Table 1, Table S4). This
3 difference was also evident in all individually analysed pigments (Table S4). Chl *a*, Chl *c*,
4 Fuco and minor carotenoids were 75% and 68%, 32% and 35%, 95% and 73% and 2.94
5 times and 4.86 times more concentrated in *L. digitata* and *L. hyperborea* than *L.*
6 *ochroleuca* respectively (Table 1). We can therefore reject our second null hypothesis.

8 4. Discussion

9 Our results indicate that a one-month period in the benthos does not affect gross laminar
10 pigment concentration or pigment stoichiometry in benthic detritus of any *Laminaria*
11 spp. Interspecific contrasts, on the other hand, were clearly defined by a higher
12 concentration of all pigments in the two cold temperate species than warm temperate *L.*
13 *ochroleuca*.

14
15 Our first major result, the lack of a temporal effect, is in line with recently published data
16 on the maintenance of photosynthesis in *L. hyperborea* and *L. ochroleuca* detritus (de
17 Bettignies et al. 2020, Frontier et al. 2021) as well as similar Chl *a* content in old and new
18 blade parts of *L. digitata* and *L. hyperborea* (Hellebust & Haug 1972). Although Chl *a*
19 increases and decreases in floating *Macrocystis pyrifera* detritus over a 14-d period, this
20 was attributed to decreases and increases in irradiance (Rothäusler et al. 2018). Over the
21 same time period, Fuco and Chl *a* of floating and benthic *Sargassum spinuligerum* remains
22 unchanged (Hees et al. 2019). However, Chl *a* in floating *Durvillaea antarctica* detritus
23 can decrease at rates up to 2% d⁻¹ regardless of irradiance regime (Tala et al. 2019). This
24 may be attributed to the longer experimental duration (20–203 d) of this study or to the
25 high irradiances experienced by floating detritus. Further research is required to show
26 whether *Laminaria* spp. detritus also displays signs of reduced pigmentation over longer
27 timescales than the 32-d period reported here. Our relatively short experimental period
28 may also be the reason for the absence of Phytin *a*, which is found in algal detritus
29 (Jeffrey et al. 1997).

30
31 Our second major result, the large interspecific difference in pigment content, cannot be
32 explained by the local light regime since all species were sampled from a single kelp forest
33 within the same ~2-m depth range. Therefore, this finding is perhaps best explained by
34 species distribution: *L. digitata*, *L. hyperborea* and *L. ochroleuca* have their approximate
35 range centres in southern Norway, northern Scotland and northern Portugal (Fig. 1).
36 Annual irradiance decreases with increasing latitude, wherefore pigments are more
37 concentrated at higher latitudes (Rothäusler et al. 2011a, 2018). Accordingly, *L. digitata*
38 has the highest photosynthetic pigment content and antenna size of all Northeast Atlantic

1 *Laminaria* spp., followed by *L. hyperborea* and *L. ochroleuca*. *L. digitata* was also
2 previously found to have somewhat more Chl *a* than *L. hyperborea* (Hellebust & Haug
3 1972). Our hypothesis is further supported by the higher Chl *a* content of *Laminaria*
4 *solidungula* (1140–1340 $\mu\text{g g}^{-1}$, cf. **Table 1**), an arctic congener of the species studied here
5 (Scheschonk et al. 2019). The observed difference in pigmentation between cold and
6 warm temperate *Laminaria* spp. may also explain the significantly higher photosynthetic
7 performance of *L. digitata* and *L. hyperborea* than *L. ochroleuca* (Frontier et al 2021; L. S.
8 Wright unpubl. data), which in turn may explain their slower decomposition. This
9 conjecture is supported by similar Chl *a* content and photosynthetic performance
10 between *L. digitata* and *L. hyperborea* from a forest in Norway (Hellebust & Haug 1972).

11

12 In the face of climate change, the rearrangement of Northeast Atlantic macrophyte
13 communities is becoming a reality. The process of assemblage shift has primary abiotic
14 (e.g. thermal regime, photo-environment) and secondary biotic (e.g. competition) drivers,
15 both of which are likely to implicate photosynthetic capacity and adaptability. The
16 photosynthetic characteristics of existing and future dominant primary producers will
17 shape the flux of carbon within the coastal system, altering the patterns of export and
18 subsidy that link this carbon source to other, often distant organisms, ecosystems and
19 carbon sinks. With photosynthetic viability of detrital matter also influencing these
20 carbon flows to an as yet undetermined extent, understanding differences in
21 photosynthetic pigments and their behaviour in the detrital phase of species with
22 different thermal affinities can help us make informed predictions about their likely
23 contributions to future carbon cycling in the coastal and shelf seas.

24

25 **Data and code availability**

26 We provide unrestricted access to all data and annotated R scripts necessary to reproduce
27 our analysis and visualisation. These resources reside in the project repository at
28 github.com/lukaseamus/pigments.

29

30 **Acknowledgements**

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33

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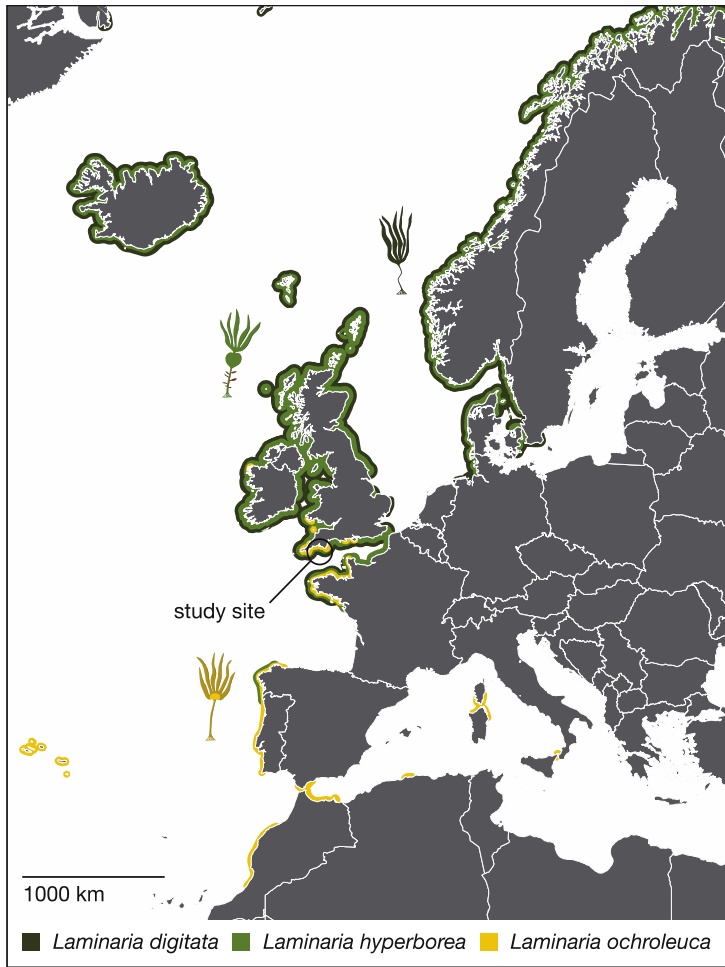
Tables

Table 1. Relative photosynthetic pigment concentrations of the three Northeast Atlantic *Laminaria* spp. at West Hoe. All concentrations are means \pm standard errors (n = 27) across three detrital ages and given in $\mu\text{g g}^{-1}$ dry mass.

Pigment	<i>L. digitata</i>	<i>L. hyperborea</i>	<i>L. ochroleuca</i>
Chlorophyll <i>a</i>	1110.23 \pm 40.31	1069.61 \pm 58.54	636.03 \pm 49.87
Chlorophyll <i>c</i>	99.07 \pm 4.08	101.43 \pm 8.19	74.97 \pm 7.06
Fucoxanthin	784.26 \pm 32.12	694.8 \pm 33.55	402.27 \pm 38.12
Minor carotenoids	63.03 \pm 5.91	93.79 \pm 7.16	16.01 \pm 3.06
Total	2056.59 \pm 69.89	1959.63 \pm 101.26	1129.27 \pm 95.45

1

2 **Figures**

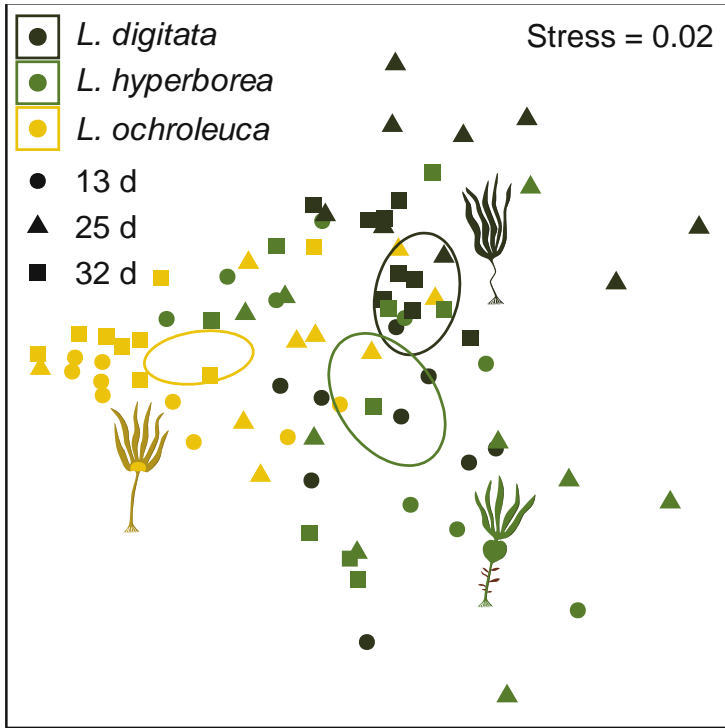


3

4 **Figure 1.** Present species distributions of the three Northeast Atlantic *Laminaria* spp. Kelp icons denote the
5 approximate range centre of each species. All three species co-occur at the study site in Plymouth.

6 Biogeographical data sources are available in **Table S1**.

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Figure 2. Photosynthetic pigment composition of the three Northeast Atlantic *Laminaria* spp. at West Hoe. Colour represents species, while shape indicates detrital age. Ellipses are 95% confidence intervals around group centroids. Overlapping ellipses indicate compositional similarity at the 95% confidence level.