



NOTE

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

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ABSTRACT: Along Northeast Atlantic coasts, the genus *Laminaria* dominates kelp forests. Two species, *L. digitata* and *L. hyperborea*, are cold temperate whilst the third, *L. ochroleuca*, is warm temperate. In northern France and the southern British Isles, all 3 species now co-occur, with a gradual rise in predominance of *L. ochroleuca* evident over recent decades due to climate-driven range shifts. Despite recent focus on the export of photosynthetically viable macroalgal detritus, the effect of decomposition on detrital pigment concentration remains unknown for northern hemisphere kelps. Furthermore, notwithstanding their importance in determining habitat suitability, the photosynthetic pigments of all 3 species have not yet been assessed comparatively within the same forest. Here, we present results of a field experiment aimed to test potential changes in the pigments of decomposing kelp blade fragments. Using spectrophotometry and Gaussian peak spectral deconvolution to quantify pigments, we found that shallow benthic decomposition over 1 mo did not affect major photosynthetic pigment concentrations in any of the examined species. Moreover, the 2 boreal species were similar in their sporophyte pigment stoichiometry and had more chlorophyll *a*, chlorophyll *c*, fucoxanthin and minor carotenoids (β,β -carotene and zeaxanthin) than *L. ochroleuca*. This resulted in total pigment content that was 82 and 74% higher in *L. digitata* and *L. hyperborea* than in *L. ochroleuca*. These differences correspond approximately to each species' latitudinal distribution and photosynthetic performance. Our results suggest photosynthetic viability of Northeast Atlantic kelp in the initial detrital phase and a potential reduction of forest-scale photosynthetic capacity under continued ocean warming.

KEY WORDS: Climate change · Biogeography · Brown algae · Marine macrophytes · Marine vegetated habitats · Decay · Degradation · Litter bag experiment

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1. INTRODUCTION

The chlorophylls *a* (Chl *a*) and *c* (Chl *c*) and the major carotenoid fucoxanthin (Fuco) are at the root of the photosynthetic apparatus of Phaeophyceae (Caron et al. 2001). These main photosynthetic pigments are situated in the light-harvesting complex, and Chl *a* is also found in reaction centres I and II, where it is responsible for charge separation. The so-called antenna pigments Chl *c* and Fuco enhance the

light-gathering efficiency of the photosystems by passing harvested light energy to Chl *a* via resonance transfer. Their concentration relative to Chl *a* is an indication of antenna size (Caron et al. 2001, Delebecq et al. 2013). Minor photoprotective carotenoids of brown algae include β,β -carotene (β,β -Car) along with the xanthophylls violaxanthin (Viola), antheraxanthin (Anth) and zeaxanthin (Zea).

Photosynthetic pigments vary considerably between species, predominantly driven by light avail-

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

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

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

thetic apparatus to prevailing light regimes may facilitate biogeographic shifts (Rothäusler et al. 2018, Tala et al. 2019). *L. ochroleuca* displays a characteristic light ochre colouration across its range (Franco et al. 2018), begging the question of whether *L. ochroleuca* has a lower photosynthetic pigmentation than its congeners, potentially constraining its distribution. Sporophyte pigment concentrations are available for these species (Delebecq et al. 2013, Schmid & Stengel 2015, Fernandes et al. 2016), but no study has attempted an interspecific comparison between all of them.

Here, we report the first data on detrital pigment concentrations in any northern hemisphere kelp over the first month post-excision, using a benthic litter bag experiment. Moreover, we present the first inter-

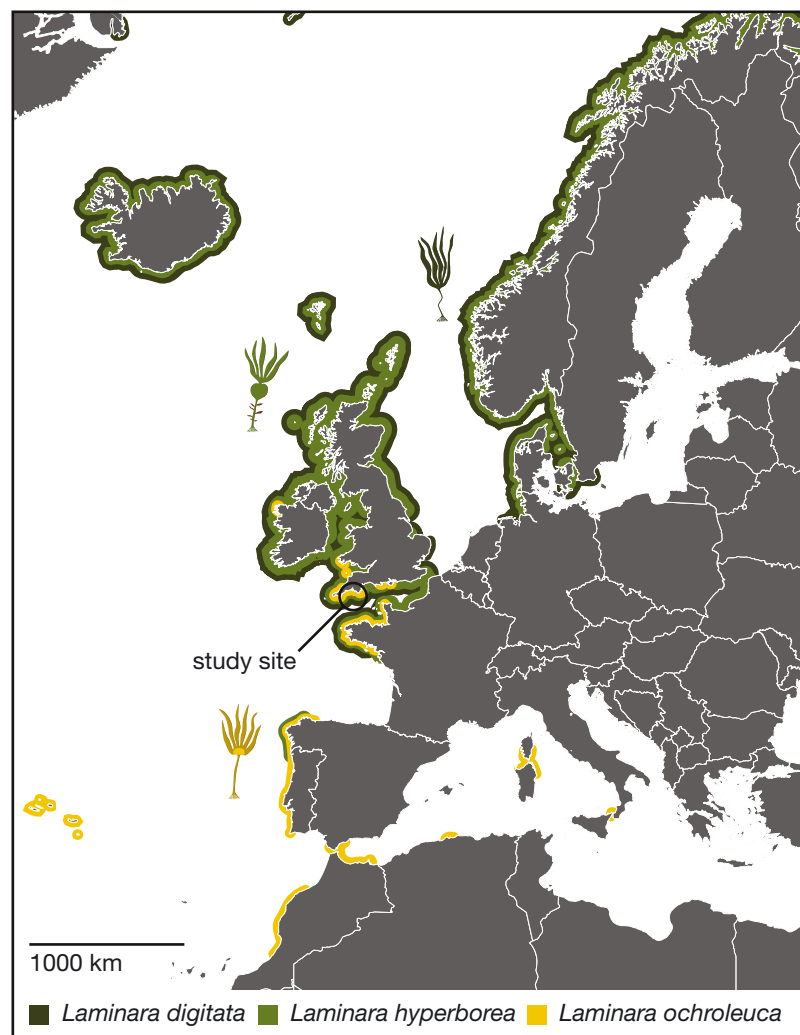


Fig. 1. Present species distributions of the 3 Northeast Atlantic *Laminaria* spp. Kelp icons denote the approximate range centre of each species. All 3 species co-occur at the study site in Plymouth Sound, UK. Biogeographical data sources are available in Table S1

specific comparison of photosynthetic pigment composition between all Northeast Atlantic *Laminaria* spp. from the same kelp forest. We tested the null hypotheses that *Laminaria* spp. photosynthetic pigmentation (1) is unaffected by decomposition and (2) is similar between species.

2. MATERIALS AND METHODS

2.1. Sampling

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

2.2. Field experiment

Three fronds were removed from each sporophyte *in situ* and trimmed to a standardised sample mass of 20 ± 1 g. Frond samples were taken from the central part of the current year's lamina growth, avoiding the meristematic basal and eroding apical regions. For each species, 1 sample from each sporophyte was placed within each of 3 rectangular, galvanised steel mesh enclosures (62.4×34.4 cm, 13-mm mesh diameter). The 9 mesh cages were then chained together, closed with cable ties and deployed at ~2 m below lowest astronomical tide in the mixed kelp forest from which the specimens were collected. A temperature and light logger (HOBO Pendant®, Onset) was secured to one end of the chain facing the surface, and the chain was deployed parallel to the shoreline to control for depth. Samples were retrieved on 30 May, 11 June and 18 June (i.e. after 13, 25 and 32 d). On each retrieval date, 3 randomly selected frond samples were removed from each litter bag. After detaching any conspicuous epibiota, these samples were frozen at -20°C and immediately lyophilised (Lablyo, Frozen in Time Ltd).

2.3. Pigment extraction

Lyophilised samples were ground to 250- μm powder. Pigments were then

extracted from 100 ± 1 mg (Fisherbrand™ Analytical Balances, Thermo Fisher Scientific) of powder through 5 serial elutions with 5 ml of 100% room temperature acetone, resulting in 25 ml of a 0.4% (w/v) solution amalgamated in a volumetric flask. For a comparison of lyophilised and fresh tissue extract concentrations, see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m678p227_supp.pdf.

2.4. Spectrophotometry and spectral deconvolution

The solution was then decanted into 2-ml microtubes and centrifuged (Sigma 1–14) at $4722 \times g$ (5 min). The supernatant was pipetted into a crystal cuvette (1-cm path length). Using a Jenway 7315 spectrophotometer (Cole-Palmer), absorbance spectra were recorded between 400 and 750 nm (1-nm resolution) with 100% acetone blanks after every 5 samples. The resulting spectra were translated into individual relative pigment concentrations ($\mu\text{g g}^{-1}$) by fitting a series of Gaussian peaks using non-negative least squares (Fig. S2). R code was modified from Thrane et al. (2015), who also provided a validation of the technique against the more exhaustive HPLC-based approach. Maximum absorbances (λ_{max}) and absorption coefficients (α) obtained from acetone extractions of Chl *a*, phaeophytin *a* (Phytin *a*), Chl *c*₁, Chl *c*₂, $\beta\beta$ -Car and the xanthophylls Fuco, Viola and Zea were collated from the scientific literature (Table S2). Unfortunately, α and λ_{max} for Anth were not available for acetone extractions and therefore we did not estimate this pigment. In addition, $\beta\beta$ -Car and Zea have effectively identical absorption spectra. These trace pigments were therefore grouped into a category which we refer to as minor carotenoids, as opposed to the major carotenoid Fuco (Table 1). Chl *c* was calculated as Chl *c*₁ + Chl *c*₂ and the antenna pigment to Chl *a* ratio was calculated as (Fuco + Chl *c*)/Chl *a* (Delebecq et al. 2013).

Table 1. Relative photosynthetic pigment concentrations of the 3 Northeast Atlantic *Laminaria* spp. at West Hoe, Plymouth Sound, UK. All concentrations are means \pm SE ($n = 27$) across 3 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

2.5. Data analysis and visualisation

Data analysis and visualisation were performed in R v4.0.2 (R Core Team 2020), and R packages are cited in Table S3. Interspecific differences in relative pigment stoichiometry were analysed using permutational multivariate analysis of variance (Anderson 2001) based on Euclidian distances. Linear models were built with individual pigment concentrations as the response variable and species (categorical) and detrital age (continuous) as explanatory variables. Model fitting was performed using graphical techniques and heterogeneity was modelled as a function of explanatory variables using generalised least squares (Zuur et al. 2009). The resulting type II and III sums of squares hypothesis tests and pairwise contrasts are reported in Table S4. Multivariate data were visualised using nonmetric multidimensional scaling. Data and code are available at <https://github.com/lukaseamus/Laminaria-pigments>.

3. RESULTS

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

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

The age of detritus had no effect on total pigment content of any species (Table S4). Neither the chloro-

phylls *a* and *c*, nor the major xanthophyll Fuco were affected by decomposition in any of the species. While also showing no change with age in *L. hyperborea* and *L. ochroleuca*, the minor carotenoids decreased at a rate of $2.1 \mu\text{g g}^{-1} \text{d}^{-1}$ in *L. digitata* (Table S4, Fig. S4). The antenna pigment to Chl *a* ratio remained unchanged in *L. hyperborea* but increased at rates of 0.008 and 0.005 d^{-1} in *L. digitata* and *L. ochroleuca* (Table S4, Fig. S5). Across detrital ages, *L. digitata*, *L. hyperborea* and *L. ochroleuca* had mean antenna pigment to Chl *a* ratios of 0.8 ± 0.02 , 0.75 ± 0.01 and 0.73 ± 0.02 , respectively. Overall, time since the start of the experiment had little effect on any aspect of pigment stoichiometry with minor changes mostly noticeable in *L. digitata*. Hence, we cannot reject our first null hypothesis.

In contrast to the lack of change with detrital age, interspecific differences in total photosynthetic pigment content were large (Table S4). While being similar in their total pigment concentration, the boreal species *L. digitata* and *L. hyperborea* contained 82 and 74 % more pigment, respectively, than their warm temperate congener (Table 1, Table S4). This difference was also evident in all individually analysed pigments (Table S4). Chl *a*, Chl *c*, Fuco and minor carotenoids were 75 and 68 %, 32 and 35 %, 95 and 73 % and 2.94 and 4.86 times more concentrated

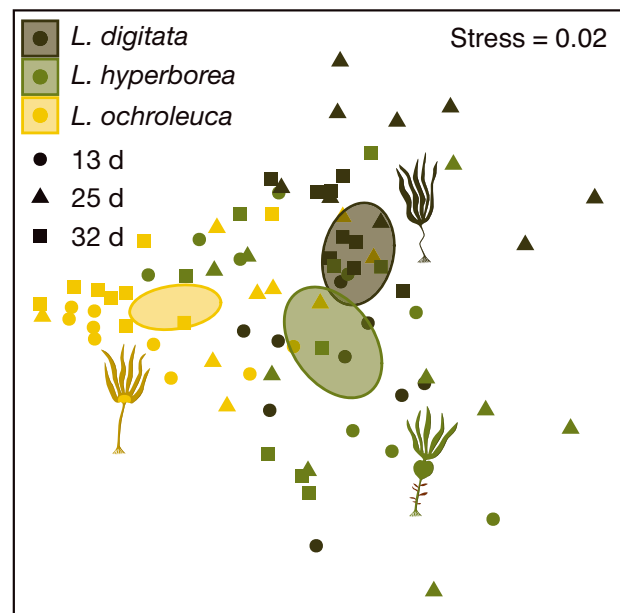


Fig. 2. Photosynthetic pigment composition of the 3 North-east Atlantic *Laminaria* spp. at West Hoe, Plymouth Sound, UK. Colour represents species, while shape indicates detrital age. Ellipses are 95 % confidence intervals around group centroids. Overlapping ellipses indicate compositional similarity at the 95 % confidence level

in *L. digitata* and *L. hyperborea* than *L. ochroleuca*, respectively (Table 1). We can therefore reject our second null hypothesis.

4. DISCUSSION

Our results indicate that a 1-mo period does not affect gross laminar pigment concentration or pigment stoichiometry in benthic detritus of any *Laminaria* spp. Interspecific contrasts, on the other hand, were clearly defined by a higher concentration of all pigments in the 2 cold temperate species than in the warm temperate *L. ochroleuca*.

Our first major result, the lack of a temporal effect, is in line with recently published data on the maintenance of photosynthesis in *L. hyperborea* and *L. ochroleuca* detritus (de Bettignies et al. 2020, Frontier et al. 2021) as well as similar Chl *a* and *c* content in old and new blade parts of *L. digitata* and *L. hyperborea* (Hellebust & Haug 1972, Schmid & Stengel 2015). Although Chl *a* increases and decreases in floating *Macrocystis pyrifera* detritus over a 14-d period, this was attributed to decreases and increases in irradiance (Rothäusler et al. 2018). Over the same time period, Fuco and Chl *a* of floating and benthic *Sargassum spinuligerum* remain unchanged (Hees et al. 2019). However, Chl *a* in floating *Durvillaea antarctica* detritus can decrease at rates up to 2% d⁻¹ regardless of irradiance regime (Tala et al. 2019). This may be attributed to the longer experimental duration (≤203 d) of that study or to the high irradiances experienced by floating detritus. Further research is required to show whether *Laminaria* spp. detritus also displays signs of reduced pigmentation over longer timescales than the 32-d period reported here. Our relatively short experimental period may also be the reason for the absence of Phytin *a*, which is found in algal detritus (Jeffrey et al. 1997).

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

hyperborea and *L. ochroleuca*. *L. digitata* was also previously found to have somewhat more Chl *a* than *L. hyperborea* (Hellebust & Haug 1972, Schmid & Stengel 2015). Our hypothesis is further supported by the higher Chl *a* content of *L. solidungula* (1140–1340 µg g⁻¹, cf. Table 1), an arctic congener of the species studied here (Scheschonk et al. 2019). The observed difference in pigmentation between cold and warm temperate *Laminaria* spp. may also explain the significantly higher photosynthetic performance of *L. digitata* and *L. hyperborea* than *L. ochroleuca* (Frontier et al. 2021, L. S. Wright unpubl. data), which in turn may explain their slower decomposition. This conjecture is supported by similar Chl *a* content and photosynthetic performance between *L. digitata* and *L. hyperborea* from a kelp forest in Norway (Hellebust & Haug 1972).

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

Data and code availability. We provide unrestricted access to all data and annotated R scripts necessary to reproduce our analysis and visualisation. These resources reside in the project repository at <https://github.com/lukaseamus/Laminaria-pigments>.

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