



# Photosynthetic capacity of co-occurring kelp species revealed by *in situ* measurements

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**ABSTRACT:** Accurate estimates of productivity of marine macrophytes are crucial to predict the consequences of invasive species expansions and climate-related range shifts on coastal ecosystem functioning and carbon cycling. We examined the potential impacts of climate-driven shifts in the relative abundances of foundation species within a temperate reef system on net primary productivity. Specifically, we estimated productivity rates of 3 co-occurring kelp species (*Laminaria hyperborea*, *L. ochroleuca* and *Undaria pinnatifida*) in contrasting regions of their ranges (centre, leading-edge and invasive, respectively) via *in situ* photorespirometry methods in Brittany, France. Lamina tissues of cold-temperate *L. hyperborea* and warm-temperate *L. ochroleuca* had similar rates of net productivity. The stipes of *L. hyperborea*, however, displayed much higher rates of productivity and respiration than *L. ochroleuca*, likely due to the dense macroalgal epiphytes colonising their surface. Our results suggest that replacement of *L. hyperborea* by *L. ochroleuca* in the NE Atlantic due to increased dominance or further range expansion of this warm-temperate species might lead to reduced net rates of productivity as a result of increased lamina respiration and reduced photosynthetic capacity of stipes. The invasive kelp *U. pinnatifida* had high rates of net productivity at saturating light levels (294  $\mu\text{mol O}_2 \text{ g}^{-1} \text{ dry weight h}^{-1}$ ), 3 times higher than any kelp species ever incubated *in situ*, helping to explain its high success as an invader. We show that shifts in the distributions and relative abundances of seemingly similar foundation species may lead to subsequent changes in net metabolic balance.

**KEY WORDS:** Primary productivity · Respiration · Metabolic balance · Kelp forest · Coastal ecosystem · Subtidal rocky reef

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## 1. INTRODUCTION

Kelps represent key components of multiple food web pathways and subsequently mediate numerous ecosystem processes (Fredriksen 2003, Norderhaug et al. 2003, Miller & Page 2012, Leclerc et al. 2013, Duggins et al. 2016). Studies estimate that intertidal and subtidal macrophytes contribute 45% of total primary production in coastal waters (Mann 1973, 2009). The majority of this production comes from kelps, which make significant contributions to carbon draw-down via carbon fixation, hold substantial quantities

of carbon as above-ground biomass (Chung et al. 2011, Krumhansl & Scheibling 2012, Krause-Jensen & Duarte 2016, Smale et al. 2016, Pessarrodona et al. 2018) and represent an important trophic subsidy in the form of detritus (Walton et al. 2022). Although herbivores can remove substantial portions of kelp primary productivity *in situ* (Ling et al. 2015), most of the production (>80%) enters the food web through detrital pathways following erosion and fragmentation of fronds or dislodgement of entire sporophytes (Krumhansl & Scheibling 2011, de Bettignies et al. 2013). This detritus constitutes an important carbon

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flux leaving the forest that can be exported to surrounding habitats (Smale et al. 2021), creating strong linkages to both adjacent (e.g. seagrass meadows, rocky shores and sandy beaches) and distant (e.g. the deep sea) habitats (Thrush 1986, Bustamante & Branch 1996, Gómez et al. 2013, Filbee-Dexter & Scheibling 2016, Gilson et al. 2021a).

Global declines have been observed in numerous marine habitat-forming species (Pandolfi et al. 2003, Waycott et al. 2009), with climate change driving the redistribution of species at a global scale. Species distributions, however, are not moving in unison, shifting instead at different rates due to differential tolerances and responses to thermal stress (Sorte et al. 2010, Pinsky et al. 2013, Sunday et al. 2015). Populations of several warm-adapted species have expanded polewards at their leading range edge, driving new competitive shifts and resulting in altered interactions and species replacements (Vergés et al. 2014, Wernberg et al. 2016); conversely, several cold-adapted species have contracted at their trailing range edge (Raybaud et al. 2013, Smale et al. 2013, Wernberg et al. 2019). Kelps are considered useful sentinels of change because they are highly sensitive to climate change (Wernberg et al. 2013, Bell et al. 2015, Thomsen et al. 2019) and are commonly exposed to many anthropogenic activities that occur near coastal habitats (Bennett et al. 2016). Recent analysis has shown that kelp populations have declined in 38% of the ecoregions examined and either increased or remained stable in 62% of ecoregions, with regional differences in the drivers of this change (Krumhansl et al. 2016). Given that warm- and cold-water species differ in both their phenology and functional traits, there is a need for comparative studies on their relative contributions to key ecological processes in order to better predict potential impacts of species replacements (Pessarrodona et al. 2019, Gilson et al. 2021b).

Coincident with warming trends, decreased abundance, local extinctions and range contractions of *Laminaria hyperborea*, the dominant forest-building kelp in the NE Atlantic, have been reported along the Iberian Peninsula, where many kelp species persist at their thermal maxima (Smale 2020). Warming has also led to range expansions of kelps, such as in southwest England and western Ireland, where the warm-temperate Lusitanian kelp *L. ochroleuca* has significantly increased in abundance and extended its distribution in recent decades and now coexists with the assemblage-dominant *L. hyperborea* (Smale et al. 2015, Hargrave et al. 2017, King et al. 2018, Schoenrock et al. 2019), which is at the centre of its

range. Although morphologically similar to *L. ochroleuca*, *L. hyperborea* differs in many critical functional traits (Pessarrodona et al. 2019). This cold-temperate kelp requires cold (<18°C), nutrient-rich waters for growth, with peak growth observed during winter and early spring (Sheppard et al. 1978, Wiencke et al. 1994) before shedding of the old lamina tissue occurs in spring. In contrast, *L. ochroleuca* displays more continuous growth peaking in late spring/early summer, with erosion of the lamina highest during late summer/early autumn (Pessarrodona et al. 2019). Furthermore, *L. ochroleuca* has been shown to be almost twice as productive, generating twice as much detritus via lamina erosion and resulting in a larger pool of organic matter entering detrital food webs, with lamina tissue degrading much faster (~6×) relative to the cold-water *L. hyperborea* (Pessarrodona et al. 2019). *L. hyperborea* stipes are well known for supporting highly abundant and diverse epiphyte communities (Leclerc et al. 2016, King et al. 2021), whereas the stipes of *L. ochroleuca* are relatively devoid of epiphytes (Teagle & Smale 2018), providing reduced secondary habitat and supporting impoverished faunal communities (Smale et al. 2022). Local substitutions of *L. hyperborea*, or significant shifts in their abundance, will likely have knock-on consequences for ecosystem functioning and coastal carbon budgets (Krumhansl & Scheibling 2012, Hargrave et al. 2017, Pessarrodona et al. 2019, Gilson et al. 2021b).

Alongside long-lived perennial *Laminaria* species, other annual or pseudo-annual species, e.g. *Undaria pinnatifida* and *Saccorhiza polyschides*, respectively, are patchily distributed throughout subtidal kelp forests due to their opportunistic nature (Smale et al. 2013). The invasive pacific kelp *U. pinnatifida* (Epstein & Smale 2017) is farmed in some areas of the NE Atlantic where it has proliferated in urban coastal areas, specifically across harbours, with subsequent spillovers into natural rocky reef communities (Epstein & Smale 2018, Salamon et al. 2020). Its widespread invasion has been attributed to long-distance dispersal via fouling and ballast water (Wallentinus 1999, Silva et al. 2002), its resistance to large changes in temperature (Henkel & Hofmann 2008, James et al. 2015) and its ability to colonise a broad range of artificial and natural substrates (Castric-Fey et al. 1999, Russell et al. 2008, Salamon et al. 2020). *U. pinnatifida* is known to colonise a range of different niches, bringing it into competition with native forest-forming kelp species (Farrell & Fletcher 2006). In parts of the NE Atlantic (Castric-Fey et al. 1993, Antoine et al. 2012) and Australasia (Valentine &

Johnson 2004, Russell et al. 2008), active management practises are in place to prevent potential ecological impacts and further spread, with the aim of inhibiting range expansion.

Using recently developed photorespirometry methods (Rodgers et al. 2015, White et al. 2021), we performed *in situ* incubations on the cold-water kelp *L. hyperborea*, the warm-temperate species *L. ochroleuca* and the invasive kelp *U. pinnatifida* in order to calculate photosynthesis–irradiance ( $P-I$ ) curves. We (1) provide  $P-I$  curves for these 3 common kelp species calculated from *in situ* estimates of light and photosynthetic parameters during early summer in Brittany, France. The high diversity of kelp species in the region makes Brittany an ideal location to study shifting species distributions and their interactions, allowing us to compare sympatric kelp species occurring in contrasting regions of their ranges (centre, leading-edge, invasive). We (2) hypothesised that the invasive kelp *U. pinnatifida* would have the highest capacity for photosynthesis due to its shallower habitat and thin lamina tissue, potentially aiding its competitive ability. Because of the differing growing seasons of *L. hyperborea* vs. *L. ochroleuca*, we (3) hypothesised that *L. ochroleuca* individuals would have higher productivity rates than *L. hyperborea*, as the sampling period coincided with their peak biomass accumulation rates (Pessarrodona et al. 2019). Due to the contrasting stipes of these 2 *Laminaria* species (Leclerc et al. 2016, Teagle & Smale 2018), we also (4) compared estimates of stipe community metabolism. We discuss photosynthetic parameters with respect to the ecology and morphology of the different kelp species and implications for current and future carbon cycling.

## 2. MATERIALS AND METHODS

### 2.1. Sites and study species

Field measurements were carried out at 2 sites in northwestern Brittany: Blosson marina (48° 24' 37" N, 3° 32' 24" E), a newly built marina heavily colonised by the invasive kelp *Undaria pinnatifida*, and Ar Chaden, a nearby natural rocky reef (48° 43' 94" N, 3° 58' 26" E) which supports mixed kelp canopies primarily comprising *Laminaria hyperborea* and *L. ochroleuca* (Fig. 1). Photosynthetic measurements were carried out on *U. pinnatifida* individuals growing at 1 m depth on a floating breakwater at Blosson, and on *L. hyperborea* and *L. ochroleuca* sporophytes at Ar Chaden growing at depths of approximately 4 m (below chart datum).

*In situ* photosynthetic and respiration rates of adult *L. hyperborea*, *L. ochroleuca* and *U. pinnatifida* sporophytes were measured using photorespirometry chambers (see White et al. 2021 for full description of the chambers and methodology). In brief, flexible polyethylene bags of a fixed volume were used to incubate sections of (or entire) sporophytes *in situ* in the light and then in the dark. Continuous oxygen and light loggers within the chamber allowed calculation of net photosynthetic rates for each given light intensity as well as respiration rates for dark incubations. Kelp were incubated during summer 2020 (June–July) at either high or low tide to minimize strong tidal movements, characteristic of the area. Thus, incubations of *U. pinnatifida* were carried at a constant depth of 1 m due to the floating nature of the pontoon, whereas *L. hyperborea* and *L. ochroleuca* were incubated at a range of water depths (5–12 m).

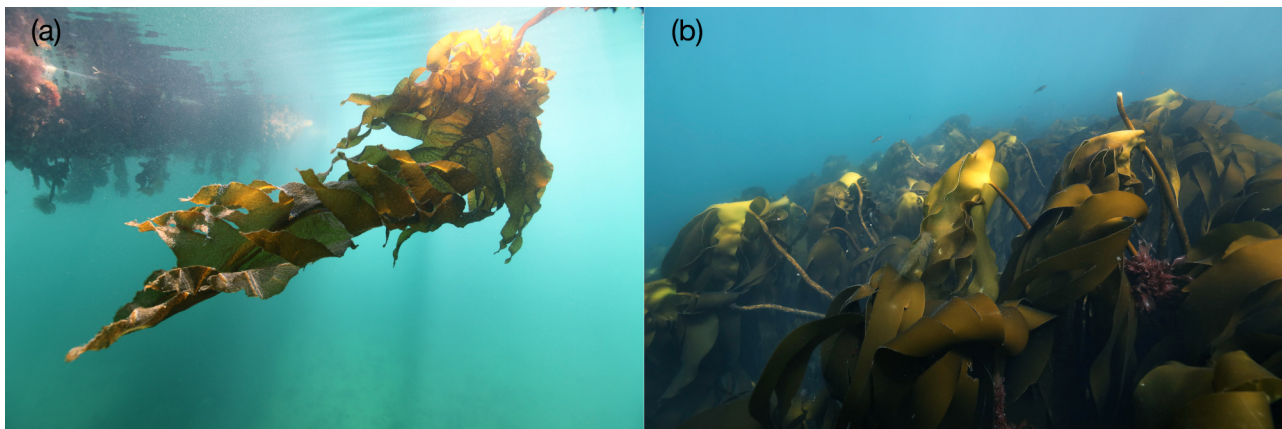


Fig. 1. (a) *Undaria pinnatifida* individual growing on artificial structures at a marina in the Bay of Morlaix and (b) mixed stands of *Laminaria hyperborea* and *L. ochroleuca* growing at 4 m depth at Ar Chaden, both in Brittany, France. Photos taken by Wilfried Thomas, Service Mer & Plongée, Station Biologique Roscoff, CNRS-Sorbonne Université

As such, all kelp species experienced a range of natural light conditions (between 0 and  $>700 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ).

## 2.2. Incubation procedure

Adult kelp individuals were randomly selected for chamber incubations (stipe  $>50 \text{ cm}$  for both species of *Laminaria*, *L. hyperborea* with a typical stipe community comprising  $>80\%$  cover of algal species interspersed with invertebrate epibionts [White et al. 2021]; *U. pinnatifida* total length:  $>40 \text{ cm}$ ). Large *L. ochroleuca* individuals were not incubated to avoid any effects of self-shading from excessive constriction of the laminae, and any individuals with a high density of epibionts growing on the lamina were avoided. During a single dive, up to 3 chambers were deployed simultaneously.

Chambers were positioned over the fronds and stipe of *U. pinnatifida* plants and sealed firmly around the base of the stipe with cable ties. At this stage of the growing season, *U. pinnatifida* individuals are sexually mature with frilled sporophylls surrounding the stipes and are therefore less morphologically distinct from the lamina. Because of their larger size and

the distinct morphological and ecological differences between lamina and stipe, chambers were positioned over the fronds of *L. hyperborea* and *L. ochroleuca* and sealed firmly around the top of the stipe (Fig. 2). Additional smaller chambers were used to incubate the mid-section of stipes of *L. hyperborea* and *L. ochroleuca*. Bags were sealed at a pre-marked position, approximately 10 cm above the holdfast, and then filled using a battery-powered pump and valves until the bag was full (White et al. 2021), ensuring consistent volume for all incubations (mean  $\pm$  SE: large chamber:  $56.8 \pm 0.55 \text{ l}$ ; stipe chamber:  $12.1 \pm 0.14 \text{ l}$ ;  $n = 6$  for both).

Each sporophyte was incubated under natural light conditions for 15 min, followed by a partial flush of the chamber (replacement of  $\geq 50\%$  total volume) before being covered by 2 layers of black plastic simulating night-time conditions (reducing photosynthetically active radiation [PAR] to  $<1 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) for a further 15 min incubation. Due to consistently high light levels during *U. pinnatifida* incubations, a subset of the plants ( $n = 6$ ) were incubated a third time with just one layer of black plastic to ensure that there were some incubations at low light levels (Rodgers et al. 2015). For *Laminaria* sporophytes, separate stipe incubations

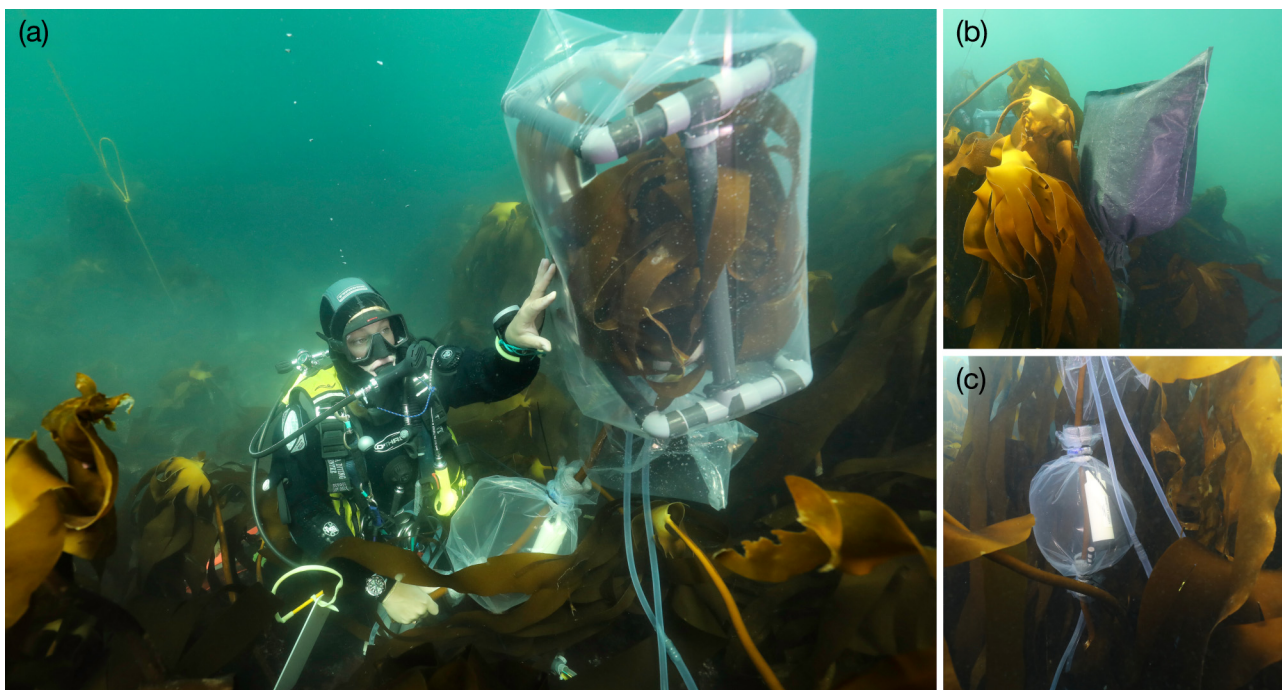


Fig. 2. Photorespirometry chamber system deployed *in situ* on (a) lamina and stipe sections of a *Laminaria ochroleuca* individual; (b) the large chamber is covered by 2 layers of black plastic during a dark incubation of *L. hyperborea* and (c) a smaller chamber deployed on the mid-section of a stipe of *L. ochroleuca*, all at Ar Chaden, Brittany, France. Photos taken by Wilfried Thomas, Service Mer & Plongée, Station Biologique Roscoff, CNRS-Sorbonne Université

were carried out simultaneously with lamina incubations, i.e. under similar light conditions, but lasting just 10 min due to the smaller size of the chamber. Due to time constraints, stipes of 5 of the 27 *Laminaria* sporophytes were not incubated (i.e. only lamina sections were incubated). Dissolved oxygen concentration and temperature inside the chamber were logged at a frequency of once per minute by a miniDOT logger (PME), an optode that measures dissolved oxygen concentration in water via fluorescence methods. MiniDOT loggers automatically corrected for temperature and salinity effects on dissolved oxygen. Irradiance (measured as photon flux density PAR 400–700 nm) was measured at 1 min intervals using loggers with planar cosine-corrected PAR sensors (DEFI2-L, JFE Advantech). PAR sensors were mounted at the top of the frame inside the chamber, ensuring they were not obscured by kelp lamina (Rodgers et al. 2015, White et al. 2021). The relatively short time periods minimized fluctuations in light intensity during each incubation. After incubation, plants were harvested and length, wet weight and dry weight (DW) (following 72 h dried at 60°C) were measured.

### 2.3. Data analysis

Rates of photosynthesis and respiration were calculated from the linear slope of oxygen concentration during light and dark periods of each field incubation, respectively. Linearity of slopes was maintained during incubations, suggesting that water was not super-saturated with oxygen or limited by either nutrients or carbon dioxide (Noël et al. 2010; Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m697p031\\_supp.pdf](http://www.int-res.com/articles/suppl/m697p031_supp.pdf)). Slopes of oxygen concentration during stipe incubations were more variable than during lamina incubations, which was attributed to the more variable light environment beneath the canopy and/or the mixed assemblage that inhabited *L. hyperborea* stipes. Slopes were calculated based on at least 15 min of data for each *U. pinnatifida* or *Laminaria* lamina incubation and at least 10 min of data for *Laminaria* stipe incubations, and mean irradiance was calculated from the same 15 or 10 min period. Photosynthesis and respiration rates were standardized per unit of dry biomass per hour ( $\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ ).  $P-I$  curves were plotted separately for *U. pinnatifida* sporophytes and laminas and stipes of each *Laminaria* species, with each individual representing 2 points (one light, one dark) on the curve, or 3

points for a subset of *U. pinnatifida* (one light, one medium, one dark;  $n = 6$ ). Curves were fitted using non-linear regression in R version 4.1.2 (R Core Team 2021), following Webb et al. (1974):

$$P = P_{\max} \times (1 - e^{-\alpha I / P_{\max}}) \quad (1)$$

where  $P$  is the net photosynthetic rate at any photon flux ( $I$ ),  $P_{\max}$  is the maximum net rate of photosynthesis recorded at or near saturating irradiances,  $\alpha$  is the photosynthetic efficiency (i.e. the slope of the linear light-limited part of the curve) and  $I$  is incident irradiance. Additional parameters calculated were  $R_d$  (mean rate of respiration i.e. net photosynthesis recorded during dark incubations),  $I_k$  (the onset of light saturation estimated as modelled  $P_{\max} / \alpha$ ) and  $I_c$  (the compensation irradiance at which photosynthesis is balanced by respiration, estimated as  $R_d / \alpha$ ). Values of net productivity were transformed to gross productivity by correcting for mean respiration rates (i.e. adding the absolute mean respiration rates across replicates; see Figs. S2 & S3; Gevaert et al. 2011, White et al. 2021) before fitting the models.

Lamina and stipe  $P-I$  curves were combined for each *Laminaria* species and scaled up to sporophyte level, based on mean species-specific biomass, to compare estimated photosynthetic capacity of entire *L. hyperborea*, *L. ochroleuca* and *U. pinnatifida* individuals.

### 2.4. Literature review

We reviewed literature of *in situ* estimates of macroalgal productivity via photorespirometry methods. The photorespirometry research community is reasonably limited, so we used recent reviews and databases (Dolliver & O'Connor 2022, Gallagher et al. 2022, Pessarrodona et al. 2022) combined with expert knowledge to find relevant literature that would allow us to explore trends of macroalgal net productivity. Studies were included if they performed *in situ* incubations on entire lamina or sporophytes of a single macroalgal species under a range of light intensities to produce a  $P-I$  curve and expressed rates of oxygen evolution standardised by biomass (fresh or dry) rather than per unit surface area. We extracted  $\alpha$ ,  $P_{\max}$ ,  $I_k$ ,  $I_c$  and  $R_d$ . When values were not stated but presented only in figures, data were digitally extracted using the 'metaDigitise' R package (Pick et al. 2019). Studies of *L. digitata* that expressed productivity in grams of fresh weight were converted to DW using a conversion factor of 0.16 (Migné et al. 2021).

### 3. RESULTS

We generated  $P$ – $I$  curves for *Undaria pinnatifida*, *Laminaria hyperborea* and *L. ochroleuca* individuals *in situ* (Fig. 3). Photosynthetic rates measured along the range of irradiances across the course of incubations meant that saturating irradiance was achieved for *L. ochroleuca* and for the stipes of *L. hyperborea* and that  $P_{\max}$  could be modelled (Fig. 3a, Table 1). The  $P$ – $I$  curves for *U. pinnatifida* individuals and *L. hyperborea* fronds and their corresponding photosynthetic parameters (Table 1) were estimated using  $P_{\max}$  values of the highest photosynthetic rates recorded during incubations. The resulting  $P$ – $I$  curve for *U. pinnatifida* individuals had a pseudo- $R^2$  value of 0.94, an  $\alpha$  of 0.43 and reached  $P_{\max}$  of 294  $\mu\text{mol O}_2 \text{g}^{-1} \text{DW h}^{-1}$ . Photosynthesis of *U. pinnatifida* individ-

uals reached  $I_k$  at irradiance levels of 685  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  and  $I_c$  at 107  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . Mean  $R_d$  rates were 45.93  $\mu\text{mol O}_2 \text{g}^{-1} \text{DW h}^{-1}$ .

$P$ – $I$  curves for lamina sections of *L. hyperborea* and *L. ochroleuca* were similar (Fig. 3b, Table 1), with pseudo  $R^2$  values of 0.95 and 0.88 and  $\alpha$  values of 0.23 and 0.35, respectively. *L. hyperborea* lamina displayed greater  $P_{\max}$  (68  $\mu\text{mol O}_2 \text{g}^{-1} \text{DW h}^{-1}$ ) and lower  $R_d$  (8.32  $\mu\text{mol O}_2 \text{g}^{-1} \text{DW h}^{-1}$ ), than *L. ochroleuca* ( $P_{\max} = 62 \mu\text{mol O}_2 \text{g}^{-1} \text{DW h}^{-1}$ ;  $R_d = 16.34 \mu\text{mol O}_2 \text{g}^{-1} \text{DW h}^{-1}$ ). Photosynthesis of *L. hyperborea* lamina reached  $I_k$  at higher irradiance levels (303  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) than *L. ochroleuca* (175  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) but reached  $I_c$  at lower irradiances (*L. hyperborea*: 37  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; *L. ochroleuca*: 47  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ). Stipes of *L. hyperborea* also displayed higher rates of photosynthesis ( $P_{\max} = 27 \mu\text{mol O}_2 \text{g}^{-1}$

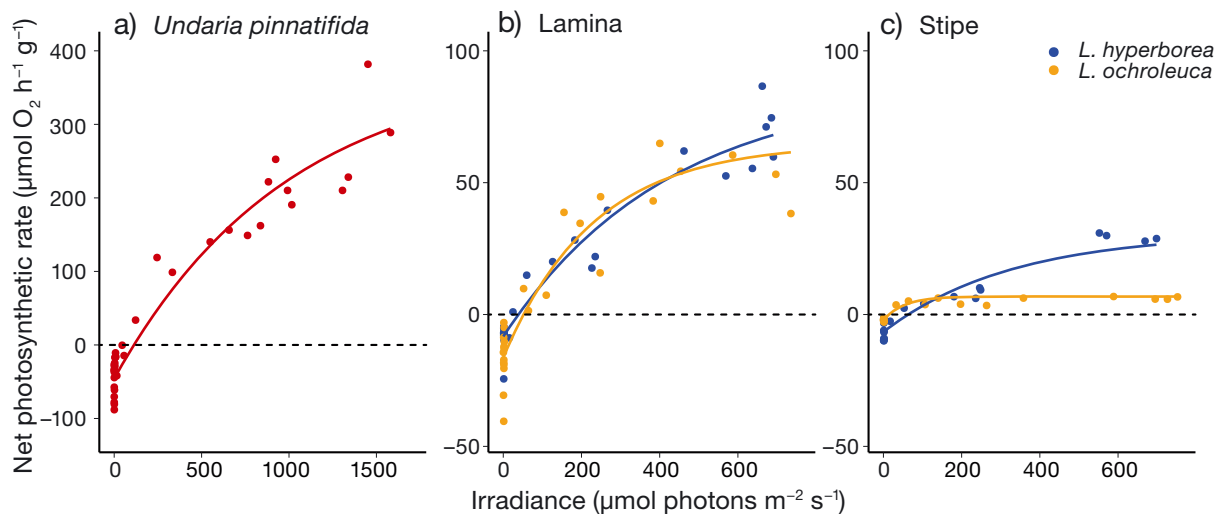


Fig. 3. *In situ* photosynthesis–irradiance curves for (a) *Undaria pinnatifida* sporophytes (red;  $n = 14$  for light and dark incubations,  $n = 6$  for shaded incubations) at Blosson; (b) lamina of *Laminaria hyperborea* (blue,  $n = 15$  for light and dark incubations) and *L. ochroleuca* (orange;  $n = 14$  for light and dark incubations) plants and (c) stipes of *L. hyperborea* (blue,  $n = 11$  for light and dark incubations) and *L. ochroleuca* (orange;  $n = 11$  for light and dark incubations) from populations at Ar Chaden, based on photosynthetic parameters (Table 1). Y-axis scale varies between (a) *U. pinnatifida* and (b,c) *Laminaria* species

Table 1. Mean ( $\pm$ SE) dry weight (DW, g), length ( $L$ , cm), photosynthetic parameters and respiration rates for *Undaria pinnatifida* sporophytes (lamina and stipe combined) and lamina and stipes of *Laminaria hyperborea* and *L. ochroleuca* individuals incubated May–July 2020.  $P_{\max}$ : modelled maximum rate of net photosynthesis ( $\mu\text{mol O}_2 \text{g}^{-1} \text{DW h}^{-1}$ );  $\alpha$ : initial slope of the photosynthesis–irradiance ( $P$ – $I$ ) curve at non-saturating irradiance;  $R_d$ : mean rate of respiration ( $\mu\text{mol O}_2 \text{g}^{-1} \text{DW h}^{-1}$ );  $I_k$ : saturation irradiance ( $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ );  $I_c$ : compensation irradiance ( $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ); pseudo- $R^2$ : fit of  $P$ – $I$  curve

Species	Section	$n$	DW	$L$	$R_d$	$P_{\max}$	$\alpha$	$I_k$	$I_c$	Pseudo- $R^2$
<i>Undaria pinnatifida</i>	Lamina and stipe	15	28.81 $\pm$ 5.07	69.08 $\pm$ 4.56	–45.93 $\pm$ 5.91	294.22	0.43	685.47	107.00	0.94
<i>Laminaria hyperborea</i>	Lamina	14	117.35 $\pm$ 7.78	98.33 $\pm$ 4.28	–8.32 $\pm$ 1.29	68.09	0.23	303.02	37.04	0.95
	Stipe	11	55.99 $\pm$ 6.21	65.25 $\pm$ 3.40	–6.62 $\pm$ 1.00	26.48	0.11	230.68	57.69	0.93
<i>Laminaria ochroleuca</i>	Lamina	13	125.49 $\pm$ 10.56	166.02 $\pm$ 9.46	–16.34 $\pm$ 2.83	61.52	0.35	175.17	46.53	0.88
	Stipe	11	46.35 $\pm$ 4.68	87.64 $\pm$ 4.68	–2.13 $\pm$ 0.13	6.83	0.17	40.14	12.52	0.90

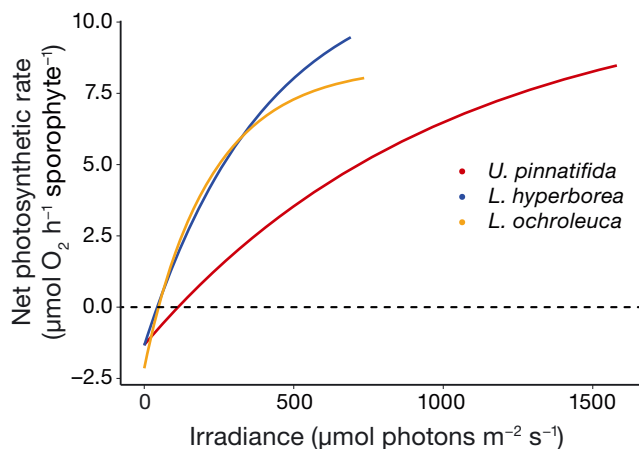


Fig. 4. Scaled up photosynthesis–irradiance curves for *Undaria pinnatifida*, *Laminaria hyperborea* and *L. ochroleuca* sporophytes, calculated using photosynthetic parameters and mean species-specific biomass values (Table 1) from *in situ* incubations at Bloscon and Ar Chaden

DW h<sup>-1</sup>) than *L. ochroleuca* ( $P_{\max} = 7 \mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ ) at saturating irradiances (Fig. 3c), despite having a lower  $\alpha$  value. In contrast to lamina, respiration rates of *L. hyperborea* stipes ( $R_d = 6.62 \mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ ) were 3 times higher than stipes of *L. ochroleuca* ( $R_d = 2.13 \mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ ). *L. hyperborea* stipes had a higher  $I_c$  ( $58 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) and reached saturation at higher  $I_k$  ( $231 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) than *L. ochroleuca* stipes ( $I_c = 13 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ;  $I_k = 40 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ).

Scaling up  $P$ – $I$  curves based on mean species-specific biomass values resulted in similar  $P$ – $I$  curves for both *Laminaria* species (Fig. 4). Curves were characterised by greater respiration rates of *L. ochroleuca*, driven by increased respiration of lamina tissue relative to *L. hyperborea* (Table 1), as well as increased photosynthesis of *L. hyperborea* at high irradiance as a result of increased photosynthetic capacity of *L. hyperborea* stipes relative to *L. ochroleuca* (Fig. 3). Scaled up  $P$ – $I$  curves for *U. pinnatifida* had lower  $\alpha$  (i.e. the slope of the linear light-limited section of the curve) than *Laminaria* species; however, sporophytes could achieve similar maximum rates of oxygen production, albeit at higher irradiances (which it experienced naturally in its shallow habitat), despite having just ~20% the mass of the *Laminaria* species studied (Table 1).

#### 4. DISCUSSION

We present the first *in situ* productivity estimates (including lamina and stipes) of 3 co-occurring kelp species, each found growing in distinctly different

regions of their geographical distributions. Lamina tissues of the cold-water *Laminaria hyperborea* and warm-temperate *L. ochroleuca* generally displayed similar photosynthetic characteristics, although *L. ochroleuca* had higher rates of respiration. In contrast, stipes of these 2 species had markedly different  $P$ – $I$  curves, with *L. hyperborea* exhibiting considerably higher rates of maximum photosynthesis and respiration. Maximum rates of stipe photosynthesis and average respiration rates were 10–40 and 15–80% of lamina rates, respectively, depending on the species in question. Considering the large contribution stipes often make to kelp forest biomass (30% in this study; Kain & Jones 1963, Smale et al. 2016, White et al. 2021), these results highlight the importance of including stipes, a commonly overlooked component, within photorespirometry-based estimates of kelp forest production (Rodgers et al. 2015, Rodgers & Shears 2016, White et al. 2021). Importantly, their inclusion ensures that overall estimates of forest productivity are not over-inflated by lamina-based studies, which could potentially skew estimates of the net metabolic balance of kelp forest ecosystems and their role as carbon sinks or sources (Gallagher et al. 2022). Furthermore, it makes photorespirometry methods more comparable with traditional estimates of kelp forest production (Pessarrodona et al. 2018, Smale et al. 2020).

*Laminaria* species growing at 4 m depth (below chart datum) had a lower compensation point (i.e. the light level at which photosynthesis balances respiration) than *Undaria pinnatifida* which grew at 1 m depth, supporting the idea that light limitation results in a lower compensation point as a result of photoacclimation. Our experimental design, however, did not allow us to disentangle the effects of species from depth, as these species typically inhabit different depth ranges in Brittany (Leclerc et al. 2015, Salamon et al. 2020). However, when reviewing the literature, photoacclimation by kelps appears to be a general pattern whereby compensation point decreases with increased light limitation (Table 2), be it depth (Rodgers et al. 2015), canopy shading (White et al. 2021), onset of autumn/winter (Gevaert et al. 2011, Rodgers & Shears 2016) or increased turbidity (Blain et al. 2020). This is likely driven by increased photosynthetic efficiency with increased light limitation; alpha values are higher for deeper populations of the same species, higher for sub-canopy vs. canopy individuals and higher in autumn/winter vs. summer (Table 2). These increases in efficiency can be accompanied by—and may be explained by—increases in photosynthetic pigments and photoki-

Table 2. Photosynthetic parameters quantified using *in situ* photorespirometry methods; means ( $\pm$ SE). Studies were chosen if they performed *in situ* incubations on entire lamina or sporophytes of a single macroalgal species under a range of light intensities to produce a photosynthesis–irradiance (*P*–*I*) curve and expressed rates of oxygen evolution standardised by biomass (fresh or dry) rather than per unit surface area. Temp: mean temperatures during study period (rounded to nearest degree);  $\alpha$ : initial slope of the *P*–*I* curve at non-saturating irradiance;  $P_{\max}$ : modelled maximum rate of net photosynthesis ( $\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ );  $I_k$ : saturation irradiance ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ );  $I_c$ : compensation irradiance ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ );  $R_d$ : mean rate of respiration ( $\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ )

Species	Location	Latitude	Depth (m)	Season	Temp (°C)	Section	Study	$\alpha$	$P_{\max}$	$I_k$	$I_c$	$R_d$
<i>U. pinnatifida</i>	France	48° 24' N	1	Summer	16	Sporophyte	Present study	0.43	294.22	685.47	107.00	-45.93 $\pm$ 5.91
<i>L. hyperborea</i>	France	48° 44' N	4	Summer	15	Lamina	Present study	0.23	68.09	303.02	37.04	-8.32 $\pm$ 1.29
						Stipe		0.11	26.48	230.68	57.69	-6.62 $\pm$ 1.00
<i>L. ochroleuca</i>	France	48° 43' N	4	Summer	15	Lamina	Present study	0.35	61.52	175.17	46.53	-16.34 $\pm$ 2.83
						Stipe		0.17	6.83	40.14	12.52	-2.13 $\pm$ 0.13
<i>L. hyperborea</i>	France	48° 44' N	5	Autumn	14	Lamina	White et al. (2021)	0.28	82.93	297.12	30.61	-8.54 $\pm$ 1.98
<i>L. hyperborea</i>	France	48° 44' N	5	Autumn	14	Sub-canopy lamina	White et al. (2021)	1.83	38.32	45.29	12.97	-5.45 $\pm$ 1.20
<i>E. radiata</i>	New Zealand	36° 45' S	10	Summer	17	Lamina	Blain et al. (2020) <sup>a</sup>	0.94 $\pm$ 0.12	90.78 $\pm$ 11.78	98.43 $\pm$ 10.50	12.0 $\pm$ 1.67	-10.20 $\pm$ 1.04
						High turbidity						
<i>E. radiata</i>	New Zealand	35° 57' S	10	Summer	18	Lamina	Blain et al. (2020) <sup>a</sup>	0.65 $\pm$ 0.13	113.54 $\pm$ 12.31	234.38 $\pm$ 52.49	17.74 $\pm$ 2.74	-8.92 $\pm$ 4.0
						Low turbidity						
<i>E. radiata</i>	New Zealand	36° 44' S	10	Summer	19	Lamina	Blain & Shears (2019) <sup>a</sup>	1.41 $\pm$ 0.17	73.72 $\pm$ 3.48	56.68 $\pm$ 5.88	14.94 $\pm$ 1.24	-17.48 $\pm$ 0.83
						High turbidity						
<i>E. radiata</i>	New Zealand	35° 57' S	10	Summer	19	Lamina	Blain & Shears (2019) <sup>a</sup>	1.01 $\pm$ 0.08	115.07 $\pm$ 7.73	114.19 $\pm$ 7.41	13.76 $\pm$ 0.61	-12.18 $\pm$ 0.53
						Low turbidity						
<i>E. radiata</i>	New Zealand	36° 17' S	6	Spring	16	Lamina	Rodgers & Shears (2016)	0.88 $\pm$ 0.13	143.2 $\pm$ 10.2	178.4 $\pm$ 14.0	26.5 $\pm$ 3.2	-21.3 $\pm$ 2.9
<i>E. radiata</i>	New Zealand	36° 17' S	6	Summer	21	Lamina	Rodgers & Shears (2016)	0.65 $\pm$ 0.13	56.6 $\pm$ 10.3	104.0 $\pm$ 19.9	28.1 $\pm$ 7.1	-13.0 $\pm$ 0.8
<i>E. radiata</i>	New Zealand	36° 17' S	6	Autumn	18	Lamina	Rodgers & Shears (2016)	0.98 $\pm$ 0.20	71.4 $\pm$ 7.1	87.5 $\pm$ 23.8	10.2 $\pm$ 1.8	-8.9 $\pm$ 1.3
<i>E. radiata</i>	New Zealand	36° 17' S	6	Winter	15	Lamina	Rodgers & Shears (2016)	0.87 $\pm$ 0.08	67.6 $\pm$ 5.4	80.3 $\pm$ 7.8	15.0 $\pm$ 2.8	-13.0 $\pm$ 2.8
<i>E. radiata</i>	New Zealand	36° 17' S	14	Summer	21	Lamina	Rodgers & Shears (2016)	1.01 $\pm$ 0.13	164.4 $\pm$ 29.8	186.6 $\pm$ 19.9	11.2 $\pm$ 1.8	-11.5 $\pm$ 2.6
<i>E. radiata</i>	New Zealand	36° 17' S	14	Winter	15	Lamina	Rodgers & Shears (2016)	1.19 $\pm$ 0.14	102.2 $\pm$ 4.5	91.9 $\pm$ 10.7	5.1 $\pm$ 0.8	-5.7 $\pm$ 2.8
<i>L. digitata</i>	France	50–51° N	1	Autumn	10	Sporophyte	Gevaert et al. (2011) <sup>a</sup>	0.81	26	36.26	4.55	-3.6875
<i>L. digitata</i>	France	50–51° N	1	Summer	15	Sporophyte	Gevaert et al. (2011) <sup>a</sup>	0.50	103.13	224.40	20.62	-10.3125
<i>L. digitata</i>	France	50–51° N	1	Summer	18	Sporophyte	Gevaert et al. (2011) <sup>a</sup>	0.38	86.88	286.27	34.04	-12.9375
<i>L. digitata</i>	France	48° 5' N	0.5	Spring	13	Sporophyte	Delebecq et al. (2011) <sup>ab</sup>	0.38	116.88	306	13.09	-5.92
<i>L. digitata</i>	France	48° 5' N	0.5	Summer	15	Sporophyte	Delebecq et al. (2011) <sup>ab</sup>	0.41	73.75	178	39.22	-7.89

<sup>a</sup>Studies where data were extracted from figures using the R package 'metaDigitise' (Pick et al. 2019)

<sup>b</sup>Studies that were converted from fresh to dry weight (Migné et al. 2021); see Section 2.4 for full details



netic changes in thallus morphology (Blain & Shears 2019), although the time scales over which these responses operate remain unclear. Photoacclimation of kelps to degrading light environments may also be driven by reduced respiration with increasing light limitation; kelps have a tendency for higher respiration in summer compared to winter (Gevaert et al. 2011, Rodgers & Shears 2016) and in shallower populations compared to those at depth (Rodgers et al. 2015).

The invasive *U. pinnatifida* had the highest photosynthetic capacity per gram of tissue of any species measured in our experiments and displayed 2.5–3-fold higher  $P_{\max}$ ,  $R_d$ ,  $I_k$  and  $I_c$  than any other species reported in the literature (Table 2). Sporophytes had a relatively high compensation point of almost 100  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , considerably higher than any other species in the literature, even those inhabiting similar depths (Delebecq et al. 2011, Gevaert et al. 2011). Similarly, *U. pinnatifida* has also displayed superior photosynthetic performance (~2-fold higher) in laboratory settings relative to numerous native perennial macroalgal species in New Zealand (Desmond et al. 2019). But unlike other kelps previously incubated *in situ*, *U. pinnatifida* is an annual species with a short life cycle of just a few months (Murphy et al. 2017) with much thinner, less structurally complex fronds (Castric-Fey et al. 1999). Comparisons against other native species with more similar morphology, e.g. *Alaria esculenta*, would help to reveal if these photosynthetic traits are merely a common feature of faster-growing annuals. In addition, *U. pinnatifida* populations were at a much shallower depth, and, importantly, their depth was constant compared to *Laminaria* reefs as a result of growing on a floating breakwater. Due to time constraints, it was not possible to carry out incubations on any local *Undaria* populations inhabiting natural substrates (therefore exposed to diurnal macrotidal depth changes) before the annual summer die-off occurred (Murphy et al. 2016). These natural populations, however, are limited and patchy in both time and space (Salamon et al. 2020), making measurements challenging. It would be interesting to compare photoacclimation capacities of kelp species inhabiting constant vs. variable water depths whilst controlling for mean depth. Laboratory studies of *Undaria* sporophytes all report compensation points well below 20  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Dean & Hurd 2007, Epstein & Smale 2018), suggesting that this species can efficiently photoacclimate to its surrounding environment—which may explain why it can also invade deeper reefs (Desmond et al. 2019) down to 15 m (Valentine & Johnson 2003) and

supports the idea that a plastic physiology allows *U. pinnatifida* sporophytes to match their physiology to a range of environments (Dean & Hurd 2007).

*Laminaria* species had almost indistinguishable  $P-I$  curves when considering lamina only, despite their differing growth patterns (Pessarrodona et al. 2019). During our summer sampling period, *L. hyperborea* generally displays its lowest growth rates whereas *L. ochroleuca* experiences some of its highest; thus, we assumed that *L. ochroleuca* would show higher photosynthetic efficiency. Therefore, it remains to be explained how *L. ochroleuca* accumulates more biomass than *L. hyperborea* whilst photosynthetic rates are equal. It is likely that *L. hyperborea*, a cold-water kelp, synthesizes and stores reserve products in summer when nutrients can be limiting (Drew 1983) and remobilizes them for growth in winter months when light is limited (Bartsch et al. 2008) but nutrients are abundant. The growth of *L. hyperborea* is controlled by a strategic circannual rhythm (Schafelke & Lüning 1994). Meanwhile, *L. ochroleuca* has growth rates closely correlated with irradiance levels (Kain 1989, Pessarrodona et al. 2019) and can take advantage of high light availability and allocate fixed carbon for a more continuous growth pattern. Quantifying carbon to nitrogen ratios in lamina and stipe tissues alongside photosynthesis and growth parameters would help to confirm the mechanisms facilitating differences in seasonal growth patterns of these 2 species (Gevaert et al. 2011).

If the warm-temperate kelp *L. ochroleuca* continues to expand northwards (Franco et al. 2018) competing with, and increasing in abundance relative to, the cold-water congener *L. hyperborea*, carbon fixation rates during summer may be reduced as a result of increased lamina respiration and reduced photosynthetic capacity of stipes. Our results, however, provide just a single snapshot in time. Photosynthetic parameters of *L. hyperborea* measured the previous autumn from a nearby reef of comparable depth were similar to our results (Table 2, White et al. 2021), although maximum rates of photosynthesis were 20% higher in autumn. Photorespirometry studies on other kelp species have shown that photosynthetic parameters can vary substantially between seasons, with respiration, maximum photosynthetic rates and photosynthetic efficiency varying by a factor of 2–3 (Table 2, Gevaert et al. 2011, Rodgers & Shears 2016), with consequences for annual budgets. Seasonal  $P-I$  curves that can be incorporated into models alongside light and biomass data are required to generate and compare accurate annual estimates of net macroalgal production for these 2 *Laminaria* species.

Studies in SW England show that *L. ochroleuca* can accumulate more biomass over an annual cycle than *L. hyperborea* but releases more biomass, which then degrades at considerably faster rates (Pessarrodona et al. 2019, Frontier et al. 2022, Wright et al. 2022), although *L. hyperborea* degraded more quickly at imitated depths of 15–30 m in laboratory experiments in Brittany (Frontier et al. 2021). In Brittany and SW England, where *L. ochroleuca* is at the leading edge of its distribution, it is generally found in mixed stands with *L. hyperborea* and other kelp species at moderately exposed or sheltered reefs (Pessarrodona et al. 2019, authors' pers. obs.). These mixed kelp stands, however, are not representative of wider, open, wave-exposed coastlines, which remain dominated by *L. hyperborea* (Smale & Moore 2017). *L. ochroleuca* is more susceptible to being dislodged by wave action (Sheppard et al. 1978, Smale & Vance 2016) and therefore seems unlikely to proliferate on exposed reefs where its cold-water congener thrives at highest densities. If *L. ochroleuca* continues to expand in sheltered areas (Smale et al. 2015, 2022), producing greater quantities of detritus (Pessarrodona et al. 2019), the lower residence time of such detritus would mean that, assuming similar transport rates, mixed forests would have lower carbon sequestration potential than current *L. hyperborea* forests (Filbee-Dexter et al. 2018, Wright et al. 2022). Other kelp species within this system expected to benefit from warming, *U. pinnatifida* and *Saccorhiza polyschides*, are relatively short-lived annuals, rapidly fixing carbon for growth and then releasing it back into the system, meanwhile supporting less diverse communities (Arnold et al. 2016, Salland & Smale 2021).

*L. hyperborea* stipes had higher photosynthetic capacity than *L. ochroleuca*, which translated to higher productivity at saturating irradiances when scaled up to the sporophyte level. This difference is likely a consequence of dense algal epiphytic communities (Leclerc et al. 2016, Teagle & Smale 2018, Smale et al. 2022). Stipes typical of the region were chosen for incubations, e.g. comprising >80% cover of algal species interspersed with invertebrate epibionts (Smale et al. 2015, Leclerc et al. 2016), but stipes can sometimes be heavily colonised by heterotrophic communities resulting in much lower photosynthetic capacity (White et al. 2021). In addition, epiphyte communities are not constant along the stipe, but rather have distinct layers (Leclerc et al. 2016). So scaling up mid-section-derived rates of photosynthesis for the entire stipe could potentially over- or underestimate productivity. Our scaled-up  $P-I$  curves of *L. ochroleuca* are likely to be underes-

timates due to biased estimation of mean plant biomass. *L. ochroleuca* are often significantly larger than *L. hyperborea* along the French coast (Sheppard et al. 1978), and individuals with lamina 2–3 m in length were observed at the study site (authors' pers. obs.). As such, we chose to exclude very large *L. ochroleuca* individuals to avoid self-shading within chambers. It is possible that *L. ochroleuca* fronds could have been constricted by the size of the chamber, as it has longer narrower fronds than *L. hyperborea*; however, total biomass was comparable between our sampled populations. We chose to incubate kelp populations in their natural habitat, without artificially manipulating light intensity (Rodgers et al. 2015). As such, photosynthesis did not reach saturation for all species, and some estimates of modelled  $P_{\max}$  and  $I_k$  may be slight underestimates; however, considering the limited exposure these kelps have to such high irradiances, these underestimates are likely to have negligible consequences when scaling up seasonal or annual rates of productivity.

Accurately estimating net productivity of benthic habitats is crucial for better prediction of consequences of changes in biodiversity for net metabolic balance. Our results suggest that any replacement of *L. hyperborea* by *L. ochroleuca* due to further northward expansion or increases in relative abundance might lead to reduced net rates of productivity as a result of increased lamina respiration and reduced photosynthetic capacity of stipes. These results, combined with higher degradation rates of *L. ochroleuca*, imply that shifts in the distributions and abundances of these 2 species could subsequently lead to shifts in net metabolic balance. We highlight the rapid rates of photosynthesis observed for *U. pinnatifida*, undoubtedly contributing to its success as an invader, although less is known about the fate of its detritus. We also show that photoacclimation appears to be a common strategy employed by kelps to cope with light limitation, due to depth, canopy sheltering and turbidity, as evidenced by *in situ* measurements. It remains to be seen, however, how quickly kelps can adapt to abrupt changes in light as a result of extreme climatic events.

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## LITERATURE CITED

- Antoine L, Lemoine M, Boulben S, Kaas R, Laurans M, Viard F, Potin P (2012) Emergence d'une filière de culture de macro-algues en Bretagne et problème relatif à une espèce non indigène, le wakame (*Undaria pinnatifida*). IFREMER, Brest
- Arnold M, Teagle H, Brown MP, Smale DA (2016) The structure of biogenic habitat and epibiotic assemblages associated with the global invasive kelp *Undaria pinnatifida* in comparison to native macroalgae. *Biol Invasions* 18: 661–676
- Bartsch I, Wiencke C, Bischof K, Buchholz CM and others (2008) The genus *Laminaria* sensu lato: recent insights and developments. *Eur J Phycol* 43:1–86
- Bell TW, Cavanaugh KC, Reed DC, Siegel DA (2015) Geographical variability in the controls of giant kelp biomass dynamics. *J Biogeogr* 42:2010–2021
- Bennett S, Wernberg T, Connell SD, Hobday AJ, Johnson CR, Poloczanska ES (2016) The 'Great Southern Reef': social, ecological and economic value of Australia's neglected kelp forests. *Mar Freshw Res* 67:47–56
- Blain CO, Shears NT (2019) Seasonal and spatial variation in photosynthetic response of the kelp *Ecklonia radiata* across a turbidity gradient. *Photosynth Res* 140:21–38
- Blain CO, Rees TAV, Hansen SC, Shears NT (2020) Morphology and photosynthetic response of the kelp *Ecklonia radiata* across a turbidity gradient. *Limnol Oceanogr* 65:529–544
- Bustamante RH, Branch GM (1996) The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. *J Exp Mar Biol Ecol* 196:1–28
- Castric-Fey A, Girard A, Lhardyhalos MT (1993) The distribution of *Undaria pinnatifida* (Phaeophyceae, Laminariales) on the coast of St. Malo (Brittany, France). *Bot Mar* 36: 351–358
- Castric-Fey A, Beauvilain C, Bouchain J, Pradier E, L'Hardy-Halos MT (1999) The introduced alga *Undaria pinnatifida* (Laminariales, Alariaceae) in the rocky shore ecosystem of the St Malo area: morphology and growth of the sporophyte. *Bot Mar* 42:71–82
- Chung IK, Beardall J, Mehta S, Sahoo D, Stojkovic S (2011) Using marine macroalgae for carbon sequestration: a critical appraisal. *J Appl Phycol* 23:877–886
- de Bettignies T, Wernberg T, Lavery PS, Vanderklift MA, Mohring MB (2013) Contrasting mechanisms of dislodgement and erosion contribute to production of kelp detritus. *Limnol Oceanogr* 58:1680–1688
- Dean PR, Hurd CL (2007) Seasonal growth, erosion rates, and nitrogen and photosynthetic ecophysiology of *Undaria pinnatifida* (Heterokontophyta) in southern New Zealand. *J Phycol* 43:1138–1148
- Delebecq G, Davoult D, Menu D, Janquin MA, Migné A, Dauvin JC, Gevaert F (2011) *In situ* photosynthetic performance of *Laminaria digitata* (Phaeophyceae) during spring tides in northern Brittany. *Cah Biol Mar* 52: 405–441
- Desmond MJ, Pritchard DW, Hurd CL, Richards DK, Schweikert K, Wing S, Hepburn CD (2019) Superior photosynthetic performance of the invasive kelp *Undaria pinnatifida* may contribute to continued range expansion in a wave-exposed kelp forest community. *Mar Biol* 166:139
- Dolliver J, O'Connor N (2022) Whole system analysis is required to determine the fate of macroalgal carbon: a systematic review. *J Phycol* 58:364–376
- Drew EA (1983) Physiology of *Laminaria*. *Mar Ecol* 4: 227–250
- Duggins DO, Gómez-Buckley MC, Buckley RM, Lowe AT, Galloway AWE, Dethier MN (2016) Islands in the stream: kelp detritus as faunal magnets. *Mar Biol* 163:17
- Epstein G, Smale DA (2017) *Undaria pinnatifida*: a case study to highlight challenges in marine invasion ecology and management. *Ecol Evol* 7:8624–8642
- Epstein G, Smale DA (2018) Environmental and ecological factors influencing the spillover of the non-native kelp, *Undaria pinnatifida*, from marinas into natural rocky reef communities. *Biol Invasions* 20:1049–1072
- Farrell P, Fletcher RL (2006) An investigation of dispersal of the introduced brown alga *Undaria pinnatifida* (Harvey) Suringar and its competition with some species on the man-made structures of Torquay Marina (Devon, UK). *J Exp Mar Biol Ecol* 334:236–243
- Filbee-Dexter K, Scheibling RE (2016) Spatial patterns and predictors of drift algal subsidy in deep subtidal environments. *Estuaries Coasts* 39:1724–1734
- Filbee-Dexter K, Wernberg T, Norderhaug KM, Ramirez-Llodra E, Pedersen MF (2018) Movement of pulsed resource subsidies from kelp forests to deep fjords. *Oecologia* 187:291–304
- Franco JN, Tuya F, Bertocci I, Rodríguez L, Martínez B, Sousa-Pinto I, Arenas F (2018) The 'golden kelp' *Laminaria ochroleuca* under global change: integrating multiple eco-physiological responses with species distribution models. *J Ecol* 106:47–58
- Fredriksen S (2003) Food web studies in a Norwegian kelp forest based on stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) analysis. *Mar Ecol Prog Ser* 260:71–81
- Frontier N, de Bettignies F, Foggo A, Davoult D (2021) Sustained productivity and respiration of degrading kelp detritus in the shallow benthos: detached or broken, but not dead. *Mar Environ Res* 166:105277
- Frontier N, Mulas M, Foggo A, Smale DA (2022) The influence of light and temperature on detritus degradation rates for kelp species with contrasting thermal affinities. *Mar Environ Res* 173:105529
- Gallagher JB, Shelamoff V, Layton C (2022) Seaweed ecosystems may not mitigate CO<sub>2</sub> emissions. *ICES J Mar Sci* 79:585–592
- Gevaert F, Delebecq G, Menu D, Brutier L (2011) A fully automated system for measurements of photosynthetic oxygen exchange under immersed conditions: an example of its use in *Laminaria digitata* (Heterokontophyta: Phaeophyceae). *Limnol Oceanogr Methods* 9:361–379
- Gilson AR, Smale DA, Burrows MT, O'Connor NE (2021a) Spatio-temporal variability in the deposition of beach-cast kelp (wrack) and inter-specific differences in degradation rates. *Mar Ecol Prog Ser* 674:89–102
- Gilson AR, Smale DA, O'Connor NE (2021b) Ocean warming and species range shifts affect rates of ecosystem functioning by altering consumer–resource interactions. *Ecology* 102:e03341
- Gómez M, Barreiro F, López J, Lastra M, de la Huz R (2013) Deposition patterns of algal wrack species on estuarine beaches. *Aquat Bot* 105:25–33
- Hargrave MS, Foggo A, Pessarrodona A, Smale DA (2017) The effects of warming on the ecophysiology of two co-existing kelp species with contrasting distributions. *Oecologia* 183:531–543
- Henkel SK, Hofmann GE (2008) Thermal ecophysiology of gametophytes cultured from invasive *Undaria pinnati-*

- fida* (Harvey) Suringar in coastal California harbors. *J Exp Mar Biol Ecol* 367:164–173
- ✦ James K, Kibele J, Shears NT (2015) Using satellite-derived sea surface temperature to predict the potential global range and phenology of the invasive kelp *Undaria pinnatifida*. *Biol Invasions* 17:3393–3408
- ✦ Kain JM, Jones NS (1963) Aspects of the biology of *Laminaria hyperborea* II. Age, weight and length. *J Mar Biol Assoc UK* 43:129–151
- ✦ Kain JM (1989) The seasons in the subtidal. *Br Phycol J* 24: 203–215
- ✦ King NG, Wilcockson DC, Webster R, Smale DA, Hoelters LS, Moore PJ (2018) Cumulative stress restricts niche filling potential of habitat-forming kelps in a future climate. *Funct Ecol* 32:288–299
- ✦ King NG, Moore PJ, Wilding C, Jenkins HL, Smale DA (2021) Multiscale spatial variability in epibiont assemblage structure associated with stipes of kelp *Laminaria hyperborea* in the northeast Atlantic. *Mar Ecol Prog Ser* 672:33–44
- ✦ Krause-Jensen D, Duarte CM (2016) Substantial role of macroalgae in marine carbon sequestration. *Nat Geosci* 9:737–742
- ✦ Krumhansl KA, Scheibling RE (2011) Detrital production in Nova Scotian kelp beds: patterns and processes. *Mar Ecol Prog Ser* 421:67–82
- ✦ Krumhansl KA, Scheibling RE (2012) Detrital subsidy from subtidal kelp beds is altered by the invasive green alga *Codium fragile* ssp. *fragile*. *Mar Ecol Prog Ser* 456:73–85
- ✦ Krumhansl KA, Okamoto DK, Rassweiler A, Novak M and others (2016) Global patterns of kelp forest change over the past half-century. *Proc Natl Acad Sci USA* 113: 13785–13790
- ✦ Leclerc JC, Riera P, Leroux C, Lévêque L, Laurans M, Schaal G, Davoult D (2013) Trophic significance of kelps in kelp communities in Brittany (France) inferred from isotopic comparisons. *Mar Biol* 160:3249–3258
- ✦ Leclerc JC, Riera P, Laurans M, Leroux C, Lévêque L, Davoult D (2015) Community, trophic structure and functioning in two contrasting *Laminaria hyperborea* forests. *Estuar Coast Shelf Sci* 152:11–22
- ✦ Leclerc JC, Riera P, Lévêque L, Davoult D (2016) Contrasting temporal variation in habitat complexity and species abundance distributions in four kelp forest strata. *Hydrobiologia* 777:33–54
- ✦ Ling SD, Scheibling RE, Rassweiler A, Johnson CR and others (2015) Global regime shift dynamics of catastrophic sea urchin overgrazing. *Proc R Soc B* 370:20130269
- ✦ Mann KH (1973) Seaweeds: their productivity and strategy for growth. *Science* 182:975–981
- Mann KH (2009) Ecology of coastal waters: with implications for management, 3<sup>rd</sup> edn. John Wiley & Sons, Hoboken, NJ
- Migné A, Delebecq G, Davoult D, Spilmont N, Menu D, Janquin MA, Gevaert F (2021) Photosynthesis of *Laminaria digitata* during the immersion and emersion periods of spring tidal cycles during hot, sunny weather. *Cah Biol Mar* 62:143–155
- ✦ Miller RJ, Page HM (2012) Kelp as a trophic resource for marine suspension feeders: a review of isotope-based evidence. *Mar Biol* 159:1391–1402
- ✦ Murphy JT, Johnson MP, Viard V (2016) A modelling approach to explore the critical environmental parameters influencing the growth and establishment of the invasive seaweed *Undaria pinnatifida* in Europe. *J Theor Biol* 396: 105–115
- ✦ Murphy JT, Johnson MP, Viard F (2017) A theoretical examination of environmental effects on the life cycle schedule and range limits of the invasive seaweed *Undaria pinnatifida*. *Biol Invasions* 19:691–702
- ✦ Noël LMLJ, Griffin JN, Thompson RC, Hawkins SJ, Burrows MT, Crowe TP, Jenkins SR (2010) Assessment of a field incubation method estimating primary productivity in rockpool communities. *Estuar Coast Shelf Sci* 88: 153–159
- ✦ Norderhaug KM, Fredriksen S, Nygaard K (2003) Trophic importance of *Laminaria hyperborea* to kelp forest consumers and the importance of bacterial degradation to food quality. *Mar Ecol Prog Ser* 255:135–144
- ✦ Pandolfi JM, Bradbury RH, Sala E, Hughes TP and others (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958
- ✦ Pessarrodona A, Moore PJ, Sayer MDJ, Smale DA (2018) Carbon assimilation and transfer through kelp forests in the NE Atlantic is diminished under a warmer ocean climate. *Glob Change Biol* 24:4386–4398
- ✦ Pessarrodona A, Foggo A, Smale DA (2019) Can ecosystem functioning be maintained despite climate-driven shifts in species composition? Insights from novel marine forests. *J Ecol* 107:91–104
- ✦ Pessarrodona A, Filbee-Dexter K, Krumhansl KA, Pedersen MF, Moore PJ, Wernberg T (2022) A global data set of seaweed net primary productivity. *Sci Data* 9:484
- ✦ Pick JL, Nakagawa S, Noble DWA (2019) Reproducible, flexible and high-throughput data extraction from primary literature: the metaDigitise R package. *Methods Ecol Evol* 10:426–431
- ✦ Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) Marine taxa track local climate velocities. *Science* 341:1239–1242
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Raybaud V, Beaugrand G, Goberville E, Delebecq G and others (2013) Decline in kelp in West Europe and climate. *PLOS ONE* 8:e66044
- ✦ Rodgers KL, Shears NT (2016) Modelling kelp forest primary production using *in situ* photosynthesis, biomass and light measurements. *Mar Ecol Prog Ser* 553:67–79
- ✦ Rodgers KL, Rees TAV, Shears NT (2015) A novel system for measuring *in situ* rates of photosynthesis and respiration of kelp. *Mar Ecol Prog Ser* 528:101–115
- ✦ Russell LK, Hepburn CD, Hurd CL, Stuart MD (2008) The expanding range of *Undaria pinnatifida* in southern New Zealand: distribution, dispersal mechanisms and the invasion of wave-exposed environments. *Biol Invasions* 10:103–115
- ✦ Salamon M, Lévêque L, Ballenghien M, Viard F (2020) Spill-back events followed by self-sustainment explain the fast colonization of a newly built marina by a notorious invasive seaweed. *Biol Invasions* 22:1411–1429
- ✦ Salland N, Smale D (2021) Spatial variation in the structure of overwintering, remnant *Saccorhiza polyschides* sporophytes and their associated assemblages. *J Mar Biol Assoc UK* 101:639–648
- ✦ Schaffelke B, Lüning K (1994) A circannual rhythm controls seasonal growth in the kelps *Laminaria hyperborea* and *L. digitata* from Helgoland (North Sea). *Eur J Phycol* 29: 49–56
- ✦ Schoenrock KM, O'Callaghan T, O'Callaghan R, Krueger-Hadfield SA (2019) First record of *Laminaria ochroleuca*

- Bachelot de la Pylaie in Ireland in Béal an Mhuirthead, county Mayo. *Mar Biodivers Rec* 12:9
- Sheppard CRC, Jupp BP, Sheppard ALS, Bellamy DJ (1978) Studies on the growth of *Laminaria hyperborea* (Gunn.) Fosl. and *Laminaria ochroleuca* De La Pylaie on the French channel coast. *Bot Mar* 21:109–116
- Silva PC, Woodfield RA, Cohen AN, Harris LH, Goddard JH (2002) First report of the Asian kelp *Undaria pinnatifida* in the northeastern Pacific Ocean. *Biol Invasions* 4:333–338
- Smale DA (2020) Impacts of ocean warming on kelp forest ecosystems. *New Phytol* 225:1447–1454
- Smale DA, Moore PJ (2017) Variability in kelp forest structure along a latitudinal gradient in ocean temperature. *J Exp Mar Biol Ecol* 486:255–264
- Smale DA, Vance T (2016) Climate-driven shifts in species' distributions may exacerbate the impacts of storm disturbances on North-east Atlantic kelp forests. *Mar Freshw Res* 67:65–74
- Smale DA, Burrows MT, Moore P, O'Connor NE, Hawkins SJ (2013) Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecol Evol* 3:4016–4038
- Smale DA, Wernberg T, Yunnice ALE, Vance T (2015) The rise of *Laminaria ochroleuca* in the Western English Channel (UK) and comparisons with its competitor and assemblage dominant *Laminaria hyperborea*. *Mar Ecol* 36:1033–1044
- Smale DA, Burrows MT, Evans AJ, King N, Sayer MDJ, Yunnice ALE, Moore PJ (2016) Linking environmental variables with regional-scale variability in ecological structure and standing stock of carbon within UK kelp forests. *Mar Ecol Prog Ser* 542:79–95
- Smale DA, Pessarrodona A, King N, Burrows MT, Yunnice A, Vance T, Moore P (2020) Environmental factors influencing primary productivity of the forest-forming kelp *Laminaria hyperborea* in the northeast Atlantic. *Sci Rep* 10:12161
- Smale DA, Pessarrodona A, King N, Moore PJ (2021) Examining the production, export, and immediate fate of kelp detritus on open-coast subtidal reefs in the Northeast Atlantic. *Limnol Oceanogr*, doi:10.1002/lno.11970
- Smale DA, Teagle H, Hawkins SJ, Jenkins HL and others (2022) Climate-driven substitution of foundation species causes breakdown of a facilitation cascade with potential implications for higher trophic levels. *J Ecol* 110:2132–2144
- Sorte CJB, Williams SL, Carlton JT (2010) Marine range shifts and species introductions: comparative spread rates and community impacts. *Glob Ecol Biogeogr* 19:303–316
- Sunday JM, Pecl GT, Frusher S, Hobday AJ and others (2015) Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecol Lett* 18:944–953
- Teagle H, Smale DA (2018) Climate-driven substitution of habitat-forming species leads to reduced biodiversity within a temperate marine community. *Divers Distrib* 24:1367–1380
- Thomsen MS, Mondardini L, Alestra T, Gerrity S and others (2019) Local extinction of bull kelp (*Durvillaea* spp.) due to a marine heatwave. *Front Mar Sci* 6:84
- Thrush SF (1986) The sublittoral macrobenthic community structure of an Irish sea-lough: effect of decomposing accumulations of seaweed. *J Exp Mar Biol Ecol* 96:199–212
- Valentine JP, Johnson CR (2003) Establishment of the introduced kelp *Undaria pinnatifida* in Tasmania depends on disturbance to native algal assemblages. *J Exp Mar Biol Ecol* 295:63–90
- Valentine JP, Johnson CR (2004) Establishment of the introduced kelp *Undaria pinnatifida* following dieback of the native macroalga *Phyllospora comosa* in Tasmania, Australia. *Mar Freshw Res* 55:223–230
- Vergés A, Steinberg PD, Hay ME, Poore AGB and others (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proc R Soc B* 281:20140846
- Wallentinus I (1999) Marine brown seaweed: *Undaria pinnatifida* (Harvey) Suringar, Laminariales, Phaeophyceae (Japanese kelp). In: Gollasch S, Minchin D, Rosenthal H, Voight M (eds) Exotics across the ocean. Case histories on introduced species: their general biology, distribution, range expansion and general impact. Department of Fishery Biology, Institute for Marine Science, University of Kiel, p 13–19
- Walton MEM, Browne R, Griffiths JN, Cartwright D, Robins P, Malham SK, Le Vay L (2022) Kelp detritus: Unutilized productivity or an unacknowledged trophic resource? *Sci Total Environ* 820:153191
- Waycott M, Duarte CM, Carruthers TJB, Orth RJ and others (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc Natl Acad Sci USA* 106:12377–12381
- Webb WL, Newton M, Starr D (1974) Carbon dioxide exchange of *Alnus rubra*. *Oecologia* 17:281–291
- Wernberg T, Smale DA, Tuya F, Thomsen MS and others (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nat Clim Chang* 3:78–82
- Wernberg T, Bennett S, Babcock RC, De Bettignies T and others (2016) Climate-driven regime shift of a temperate marine ecosystem. *Science* 353:169–172
- Wernberg T, Krumhansl K, Filbee-Dexter K, Pedersen MF (2019) Status and trends for the world's kelp forests. In: Sheppard C (ed) World seas: an environmental evaluation, 2<sup>nd</sup> edn. Academic Press, Cambridge, MA, p 57–78
- White L, Loisel S, Sevin L, Davoult D (2021) *In situ* estimates of kelp forest productivity in macro-tidal environments. *Limnol Oceanogr* 66:4227–4239
- Wiencke C, Bartsch I, Bischoff K, Peters AF, Breeman AM (1994) Temperature requirements and biogeography of Antarctic, Arctic and amphiequatorial seaweeds. *Bot Mar* 37:247–259
- Wright LS, Pessarrodona A, Foggo A (2022) Climate-driven shifts in kelp forest composition reduce carbon sequestration potential. *Glob Change Biol* 28:5514–5531

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