Varying photosynthetic quotients strongly influence net kelp primary production and seasonal differences increase under warming

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Reliable net primary production (NPP) estimations of kelp forests are important to evaluate their C-fixation potential. Photosynthetic oxygen measurements can be converted to C-fixation using photosynthetic quotients (PQs). Although there is a known high variability in PQs, the extent and the consequences for NPP is understudied in kelp species. Thus, the present study aimed (i) to quantify the variability of PQs, (ii) to model NPP and (iii) to assess the impact of warming on both. The kelp, *Laminaria hyperborea*, was studied near the island of Helgoland (North Sea, Germany) along a depth gradient (2, 4, 6 m below mean low water spring tide) across all four seasons. Blade discs were cultivated during at least 6 days per season under simulated ambient photosynthetic photon flux density (PPFD) and temperature conditions and, in parallel, in a warming scenario (+ 4°C). PQs were calculated from parallel oxygen production and ^{14}C-fixation measurements at saturating PPFD at the end of the incubation period. Seasonal PQs varied between 1.7 and 4.4, with highest values in summer due to increased oxygen production. The warming scenario stimulated C-fixation in most seasons, lowering the PQ in comparison to ambient temperature conditions, while collection depth had no significant effect on PQs. The seasonal PQs were used to model daily NPP rates for kelp standing stock at 4 m depth. These daily NPP rates were compared between temperature treatments and with daily NPP rates based on fixed PQs. The warming scenario had a stimulating effect on daily NPP rates in the high-light season spring. In the low-light season autumn, warming resulted in negative daily NPP rates, as the high respiration rates could not be compensated by gross photosynthesis. Overall, annual NPP rate under warming conditions (347 g C m^{-2} yr^{-1}) was 14% higher than the annual NPP rate under ambient conditions (303 g C m^{-2} yr^{-1}). Modelling daily NPP with fixed PQs, which neglects the seasonal variation of the

PQs, led to a high overestimation of up to 255%. We, therefore, recommend modelling NPP rates not with a fixed PQ, but with seasonal PQs determined under different temperature scenarios in order to obtain reliable future predictions.

1 Introduction

By definition, net primary production (NPP) is the total light-dependent carbon assimilated by a given area or biomass in a given period, minus carbon losses (e.g. respiration). Global NPP takes place approximately equally in marine and terrestrial ecosystems, representing a main driver of the biospheric carbon cycle (Kaiser et al., 2020). Phytoplankton contributes approximately 90% of the oceanic NPP, while other communities (e.g. coral reefs, macroalgal forests, seagrass beds and mangroves) make up 10% (Duarte and Cebrián, 1996). Rough estimations indicate that the marine coastal vegetation is responsible for about half of the carbon burial in the ocean (coastal and global), although they only cover about 2% of the ocean surface (Duarte and Cebrián, 1996; Duarte et al., 2005). Lately, attention has focused on the contribution of coastal marine habitats, especially kelp forests, to the global carbon budget (e.g. Duarte et al., 2005; Duarte, 2017). The impact of warming on the photosynthetic activity (Burdett et al., 2019; Smale et al., 2020; Franke et al., 2024), the carbon sequestration potential (Pessarrodona et al., 2018; Wright et al., 2022), and distribution ranges (Smale, 2020) of kelps has been extensively studied. However, it is difficult to predict annual NPP estimates of kelps because the seasonal pattern of photosynthetic activity in general and under warming scenarios is not well studied.

Kelp forests and seaweed beds are highly productive coastal ecosystems with an estimated NPP between 197 and 1711 g C m^{-2} yr^{-1} (Smale et al., 2020; Pessarrodona et al., 2022a). Most studies estimate NPP of kelps indirectly from standing stock or biomass accumulation (Smale et al., 2020), while photo-respirometry in terms of oxygen production and isotopic carbon assimilation (e.g. O_2 and ^{13}C: Miller et al., 2009; O_2 and ^{14}C: Iñiguez et al., 2016a, b) provides a direct way to physiologically estimate "true" NPP (Pessarrodona et al., 2022b). NPP in units of fixed carbon can be measured directly or converted from units of released oxygen using a known photosynthetic quotient (PQ). The PQ is a molar ratio to convert gross oxygen photosynthesis into assimilated carbon during photosynthesis (Iñiguez et al., 2016a). While PQ values for many algal species are largely unknown, the few available data show high species-specific variability (Buesa, 1980), or even differ within the same species, due to differences in environmental factors such as temperature (Hatcher et al.,

1977; Iñiguez et al., 2016b), nutrient availability (Trentman et al., 2023), depth (Miller et al., 2009), and light availability (Hatcher et al., 1977; Weykam et al., 1997). In most studies that deal with macroalgal PQ values, samples were either collected only in one season and experiments were conducted under different levels of abiotic factors (e.g. Iñiguez et al., 2016a, b), or samples were collected at different seasons and experiments were performed only under current environmental conditions (e.g. Hatcher et al., 1977; Weykam et al., 1997). The setup for direct carbon assimilation measurements is expensive and time consuming, in addition to the risks associated with radioisotopic methods. Therefore, to date, conversions of O_2 production rates to NPP rates have mostly been performed with a theoretical PQ of around 1 (e.g. Fairhead and Cheshire, 2004; Miller et al., 2011; Rodgers and Shears, 2016), which is insufficient to describe the complex relationship between O_2 release and C-fixation (Trentman et al., 2023). The O_2 signal derives from the early steps in the photosynthesis process, i.e. cleavage of water at photosystem II, while the C-fixation signal originates from the late carboxylation in the Calvin cycle (Taiz and Zeiger, 2002). Many enzymatic steps are involved in both processes, and their susceptibility to environmental stressors can shift the ratio between oxygen production and carbon fixation. PQ values mainly depend on the photosynthetic end products (Norici et al., 2011; Palmucci et al., 2011), photorespiration (Stewart, 1974; Pokorny et al., 1989), and nitrate or ammonium assimilation (Williams et al., 1979; Bell and Kuparinen, 1984; Smith et al., 2012).

The kelp that contributes most biomass in the rocky mid-sublittoral along the European coastline is *Laminaria hyperborea* (Gunnerus) Foslie (Smale et al., 2020). This species forms extensive forests from northern Portugal (Araujo et al., 2005) to northern Norway (Kylin, 1947; Lüning, 1990). Climate change is already threatening this unique ecosystem, leading to biomass and range contractions and even to local extinctions at its southern distribution edge (Voerman et al., 2013; Piñeiro-Corbeira et al., 2016; Casado-Amezúa et al., 2019). In the German Bight, the rocky shore off the island of Helgoland is covered by a dense *L. hyperborea* forest along a depth gradient between 1 and 6 m with a maximum depth of occurrence of single individuals of down to 12.5 m (Pehlke and Bartsch, 2008). Helgolandic *L. hyperborea* is exposed to a wide range of monthly mean sea surface temperatures between 4.3°C and

19.0°C annually (Bio-ORACLE v.3.0: Tyberghein et al., 2012; Assis et al., 2024). This temperature range corresponds to the temperature requirements of *L. hyperborea* over most of its distribution range (e.g. Lauksletta, Norway: 3.8° – 11.5°C; Vila Praia de Âncora, Portugal: 12.6° – 17.9°C; Bio-ORACLE v.3.0: Tyberghein et al., 2012; Assis et al., 2024). Future predictions for Helgoland assume a maximum monthly sea surface temperature of 19.9° and 22.5°C for 2050 and 2100, respectively (SSP585; Bio-ORACLE v.3.0: Tyberghein et al., 2012; Assis et al., 2024). Although this scenario is the most extreme and rather unlikely (Burgess et al., 2023), it exceeds the two-week lethal limit temperature for Helgolandic *L. hyperborea* (20-21°C; tom Dieck, 1992). However, no study has yet been conducted in which temperature was manipulated during all four seasons in order to assess the consequences of warming on seasonal photosynthetic activity. The Helgolandic *L. hyperborea* forest provides a well-suited model ecosystem to study the year-round variation of PQ values under ambient and warming scenarios.

The main objectives of the present study were (i) to quantify the seasonal variability of PQ values and (ii) its influence in NPP modelling; and (iii) to assess the effect of a warming scenario on future NPP. We hypothesise that (1) in summer, the excess of photosynthetic photon flux density (PPFD) maximises PQ values; (2) along the depth gradient, decreasing PPFD availability leads to lower PQ values as most of the photosynthetic energy produced will be invested in carbon fixation; (3) warming increases NPP and decreases PQ values, especially in spring when PPFD already saturates O_2 production and temperature rise promotes enhanced carbon fixation rates.

2 Materials and methods

2.1 Study site and algal material

Adult *Laminaria hyperborea* sporophytes were collected along a depth gradient measured at the holdfast (2, 4, 6 m below mean low water spring tide [MLWS]) near the island of Helgoland (North Sea, Germany; 54.1881° N, 7.8699° E) in all four seasons between spring 2021 and winter 2022 (Figure 1, Supplementary Table S1). For logistical reasons, no 2-m algae could be sampled in summer. For details on sampling criteria and material transport, see Franke et al. (2024).

In the laboratory (Dummermuth et al., 2023), blade discs were cut from the meristem and incubated in two temperature scenarios before oxygen and carbon fixation were measured after six days (Supplementary Figure S1).

To measure oxygen production and carbon fixation, blade discs (Ø 2 cm) and rectangular blade pieces (1.5×0.8 cm) were cut out using custom-made cork borers (see Supplementary Figure S1). In spring, summer and autumn, material was cut at a 5 cm distance above the stipe-blade transition zone (vital meristematic tissue) as only one blade was present (Supplementary Figure S2A). In winter, algal material was cut from the old blade at a distance of 5 cm above the isthmus zone, as the new blades were not yet large enough for our sampling procedure. Franke et al. (2023) showed that photosynthesis did not change along the thallus of *L. hyperborea* if data were referred to blade area; therefore, the meristem is representative for most of the thallus. In total, 18 individuals were pooled into six replicates (n=6 per temperature treatment and depth; Franke et al., 2024). From three
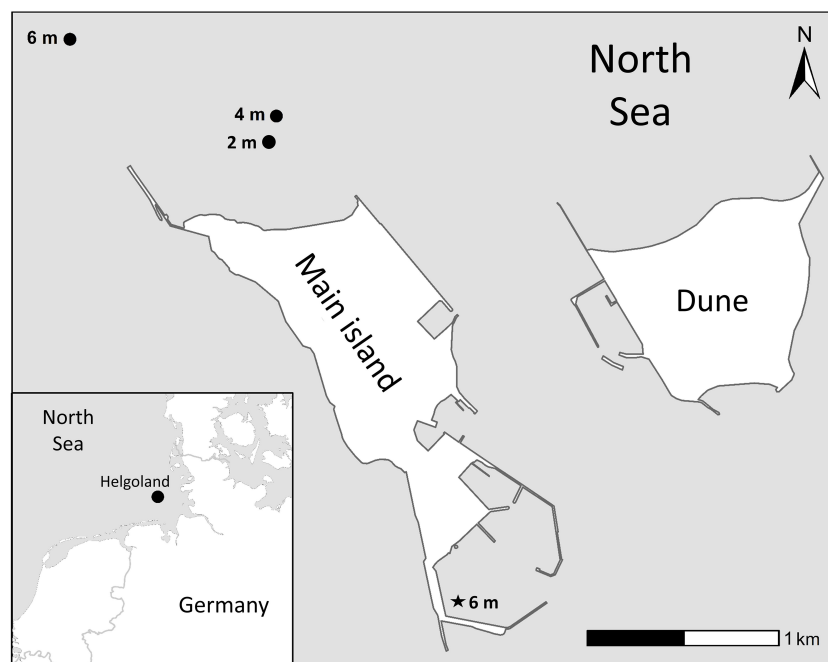

FIGURE 1
Study site in the north-western rocky sublittoral of the main island off Helgoland (North Sea, Germany; 54.1881° N, 7.8699° E). Black circles: locations of the *Laminaria hyperborea* station (depths in mean low water spring tide); Black star: 6 m station during winter due to harsh weather conditions. More information is provided in Supplementary Table S1.

individuals, blade discs (four discs per individual) and rectangular blade pieces (one piece per individual) were cut and evenly distributed between the two temperature treatments (ambient and a warming scenario of + 4°C for each season).

2.1.1 *Laminaria hyperborea* areal coverage survey

A concomitant vegetation survey of *L. hyperborea* areal coverage was conducted in July 2021, in order to relate productivity rates to kelp leaf area. Kelp individuals were harvested by SCUBA divers in 1 m² quadrats at three different depths measured at the holdfast (2, 4, 6 m below MLWS; n=5 in 2 and 4 m, n=10 in 6 m), resulting in a total of 20 quadrats (Table 1).

2.2 Experimental setup

The discs and rectangular pieces were cultivated for six days (Supplementary Figure S1). In spring, 6 m algae were cultivated for 7 days and in summer for 13 days for logistical reasons. The values from longer cultivation periods were taken into account because they were in the same range as other values determined in the same season. Algae were cultivated in aerated natural North Sea water (0.2 μm filtered) in plastic beakers (1.6 L) without the addition of nutrients. The seawater was changed after one night of wound healing and thereafter every three days. The seasonal ambient temperature conditions were averaged as *in situ* water temperature data measured at 10 m depth (MLWS) between 2016 and 2020 (Data Publisher for Earth & Environmental Science; Fischer et al., 2021a, b, c, d, 2022). For the warming treatment, the ambient temperature was elevated by + 4°C over two days in 2°C steps per day for each season according to Franke et al. (2024, Table 2). The warming treatment was chosen based on the SSP3-7.0 scenario presented in the IPCC report 2023 which estimated an increase by 4°C by the end of the century relative to 1850-1900 (Lee et al., 2023). Both temperatures were maintained at ±0.02°C in water baths fitted with thermostats (DC10 and D3, Thermo Haake) in a constant-temperature room. Light:dark photoperiods and PPFD were adjusted to the respective season and depth (LED Mitras lightbar daylight 150 controlled by ProfiLux 3, GHL Advanced Technology). Daily mean PPFD was calculated based on incoming photon flux density (PFD) measurements at Helgoland between 2014 and 2017 performed by the Helmholtz-Zentrum Hereon (https://codm.hzg.de/codm/) and vertical

attenuation coefficients from the water column around Helgoland (Lüning and Dring, 1979) for each depth separately (2, 4 and 6 m MLWS) according to Franke et al. 2024, Table 2).

2.3 Chlorophyll *a* fluorescence

The maximum quantum yield of *in vivo* chlorophyll *a* fluorescence of photosystem II (F_v/F_m) of dark-acclimated (5 min) *L. hyperborea* discs was measured using pulse amplitude modulated (PAM) fluorometry (PAM 2000, Walz) as described by Schreiber et al. (1986). These measurements were performed prior to the oxygen production incubations to verify that the discs were in a vital physiological state (brown algae: 0.7–0.8; Hanelt, 2018). The duration of the dark acclimation was tested previously and no significant difference in F_v/F_m values was observed between 5, 10, 15 and 20 min (data not shown).

2.4 Oxygen production

On the 6th day (except: 6 m in spring at day 7 and in summer at day 13), net photosynthetic rates under saturating PPFD levels (Supplementary Table S2), along with dark respiration rates, were measured using an oxygen optode system (Fibox 3, PreSens) following the set-up and method of Franke et al. (2023). The saturating PPFD levels were derived from photosynthesis versus irradiance (P-I) curves performed in each season on day 0 using a custom-made light bar with white LEDs (LUXEON Rebel, Model: LXML-PWN1-0100, Philips) in combination with Schott neutral grey filters (data presented in Franke et al., 2024; Supplementary Table S2). Oxygen production rates were measured in a constantly stirred circular airtight acrylic glass chamber in a constant-temperature room at the respective cultivation temperature according to Franke et al. (2023, Table 2; Supplementary Figures S2B, C). First, the discs were acclimated to darkness for 20 mins and the dark respiration rate was measured during 10 min in the dark. This was followed by the determination of the net photosynthetic rate during a 10-minute exposure to the respective seasonal, depth-

TABLE 1   Kelp lamina cover information.

Holdfast depth (m)	LAI (m² lamina m⁻² seafloor)	No. of replicates	Latitude	Longitude
2	5.78 ± 3.61	5	54.19107	7.86578
4	6.70 ± 0.98	5	54.19545	7.85983
6	4.33 ± 1.37	10	54.19678	7.85797

Holdfast depth below mean low water spring tide and Leaf Area Index (LAI) of *Laminaria hyperborea* individuals are shown. Mean ± SD.

TABLE 2   Experimental set-up.

	Depth (m)	Spring	Summer	Autumn	Winter
Photoperiod (L:D; h)		14:10	16:8	10.5:13.5	8.5:15.5
PPFD (μmol photons m⁻² s⁻¹)	2	233	290	114	62
	4	86	114	37	18
	6	50	62	19	8
Ambient (°C)		7	16	14	6
+ 4°C (°C)		11	20	18	10

Light: Dark (L:D) photoperiod, mean photosynthetic photon flux density (PPFD) and temperature treatments that were applied during the six days of incubation. The ambient temperature was averaged between 2016 and 2020. Mean PPFD was adjusted along the respective depth (2, 4, 6 m below mean low water spring tide) and season (spring, summer, autumn, winter).

dependent, saturating PPFD value to measure maximum photosynthetic activity (Supplementary Table S2). Oxygen concentration was logged by the OxyView software (Presens) and corrected for air pressure, salinity and logged temperature according to Tengberg et al. (2006). During post-processing, the oxygen production rate was normalised to disc area (unit: μmol O_2 cm^{-2} h^{-1}). Disc area was determined after the oxygen measurements via image analysis (Image J: Rasband, W.S., U. S. National Institutes of Health, Bethesda, 1997–2023).

2.5 Inorganic ^{14}C-fixation

On the 6th day (except: 6 m in spring at day 7 and in summer at day 13), the algal samples were transferred to 8-mL septum-sealed glass vials filled with sterile autoclaved seawater (pre-aerated for approximately 24 h). The glass vials were placed in a custom-made transparent acrylic water bath connected to a thermostat (DC10 and V26, Thermo Haake) keeping the incubation temperature (Table 2). The medium in the glass vials was stirred continuously to reach homogenisation. The six replicates were distributed into four light (C_{light} fixation; n=4) and two dark (C_{dark} fixation; n=2) samples. A pre-acclimation period of 15 min in light for reaching steady-state photosynthesis or 15 min in darkness for the dark controls was applied before injecting the $H^{14}CO_3^-$ spiked medium (Perkin Elmer). From the $H^{14}CO_3^-$ stock solution, 30 μl (~3 μCi ml^{-1}) were injected into each 8-mL septum-sealed glass vial. After injection of the $H^{14}CO_3^-$ solution, the *L. hyperborea* tissue pieces were either incubated at seasonal, depth-dependent, saturating PPFD to achieve maximum photosynthetic rates (Supplementary Table S2) or in darkness (as a control of light-independent C-fixation) for 20 min. Incident PPFD was provided by a custom-made light bar with white LEDs (CREE white light LED: CXA1304/C00A20E8, CreeLED, Inc.; Supplementary Figures S2D, E). After the incubation period, algae were immediately rinsed in unlabelled medium, blotted dry, submersed in liquid nitrogen to stop reactions and settled in 20-ml scintillation vials containing 400 μL of 68% HNO_3 (Roth). After 10 min in a mini oven (BG 950, Rommelsbacher) at 50°C, vials were left on an orbital shaker inside a fume hood for approximately 24 h. The procedure was based on the protocol of Iñiguez et al. (2016a).

The next day, after the addition of 15 ml of scintillation cocktail (Insta-gel Plus, Perkin Elmer) and 4 mL MiliQ water, the equivalent C-fixation rates were determined by measuring acid-stable ^{14}C-fixation using a liquid scintillation counter (TriCarb 2910, Perkin Elmer). Additionally, the automatic quench and colour correction of the scintillation counter was used. The C-fixation rates were related to the dissolved inorganic carbon content of the incubation medium. Total alkalinity was determined by potentiometric titrations according to Gran (1952) and for details see Supplementary Materials. Activity levels of dark controls (light-independent C-fixation = C_{dark} fixation) were subtracted from light C-fixation (C_{light} fixation) measurements (Supplementary Table S3) to gain the light-dependent gross C-fixation (C_{gross} fixation) rate. For the calculation of the C-fixation rate, it was further assumed that the uptake of ^{14}C is 5% slower than of ^{12}C (based on Steeman-Nielsen, 1952).

2.6 Photosynthetic quotient

The photosynthetic quotient (PQ) is the molar ratio of the rate of gross oxygen production (O_{gross} production) to the rate of light-dependent C_{gross} fixation. Both rates were calculated as follows:

$$\mathbf{O_{gross}\ production = O_{net}\ production - Dark\ respiration} \quad (1)$$

$$\mathbf{C_{gross}\ fixation = C_{light}\ fixation - C_{dark}\ fixation} \quad (2)$$

where O_{gross} production is calculated by subtracting negative dark respiration from net oxygen production under saturating PPFD (O_{net} production), and light-dependent C_{gross} fixation is calculated by subtracting light-independent C-fixation measured in darkness (C_{dark} fixation) from C-fixation under saturating PPFD (C_{light} fixation). PQ values were calculated as mean and standard deviation according to:

$$PQ = \frac{\mathbf{O_{gross}\ production}}{\mathbf{C_{gross}\ fixation}} \quad (3)$$

2.7 Leaf area index

Leaf Area Index (LAI) was determined for *L. hyperborea* by taking digital photographs (Nikon Coolpix L110) of each individual with a calibration area. Subsequently, the blade area was quantified via image analysis (ImageJ: Version 1.53k, 2021) and LAI was calculated. The summer LAI was used for the following annual NPP modelling. Jupp and Drew (1974) found no difference between LAI in Scottish *L. hyperborea* from different seasons, while Lüning (1971) obtained a peak in blade area in single individuals of Helgolandic *L. hyperborea* in May-July. Therefore, the NPP rates were presumably modelled with the maximum possible LAI for this location.

2.8 Modelling of net primary production

Annual NPP rates were calculated for *L. hyperborea* lamina standing stock per m² at 4 m depth as *L. hyperborea* off Helgoland has the highest LAI at this depth (Pehlke and Bartsch, 2008; present study). Following the approach of Deregibus et al. (2016), daily O_{gross} production of 4-m *L. hyperborea* was calculated by correlating the P-I curve parameters obtained *in vitro* (presented in Franke et al., 2024) with continuous *in situ* PPFD data at 4 m calculated from incoming solar PFD data between 01.01.2020 00:00 and 31.12.2020 23:50 (measured in 10 min intervals; unit: J cm^{-2}; Helgoland; DWD station-ID: 2115, https://cdc.dwd.de). Data were converted to PPFD (unit: μmol photons m^{-2} s^{-1}) as follows:

$$\mathbf{PPFD = \frac{solar\ incoming\ PFD}{600} \times 10000 \times \frac{4.6}{2}} \quad (4)$$

The unit Joule is converted into μmol photon with the conversion factor 4.6 (Lange et al., 1981) and only half of the available PFD is usable for PPFD (Kirk, 1994). PPFD available at the

holdfast depths I_d(4 m) was estimated, including the monthly vertical attenuation coefficient K_d(PPFD) in m^{-1} for the water column above 4 m around Helgoland (Lüning and Dring, 1979). The PPFD at 4 m depth was averaged per hour. Daily oxygen production rates were calculated with P-I parameters, PPFD at 4 m and the model proposed by Jassby and Platt (1976):

$$P = P_{max} \times \tanh\left(\frac{\alpha \times I}{P_{max}}\right) + R \qquad (5)$$

where P is the O_{gross} production rate (µmol O_2 cm^{-2} h^{-1}), at a given I (PPFD, µmol photons m^{-2} s^{-1}). The maximum oxygen production rate is P_{max} (µmol O_2 cm^{-2} h^{-1}), α (µmol O_2 cm^{-2} h^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$) is the light utilisation coefficient, and R (µmol O_2 cm^{-2} h^{-1}) is the initial dark respiration rate. Gross oxygen production rate (µmol O_2 cm^{-2} h^{-1}) was converted into mol O_2 cm^{-2} h^{-1}, and then, into C-fixation rates using the molar weight of carbon of 12.011 g mol^{-1} and the seasonal PQ values of 4-m *L. hyperborea* according to Franke et al. (2023).

Next, the hourly NPP was summed over a 24-h period to calculate daily NPP (g C cm^{-2} d^{-1}). Finally, the daily NPP per m² seafloor (g C m^{-2} seafloor d^{-1}) was estimated by multiplying the production rate per cm² by the mean *in situ* LAI determined in July 2021 (Table 1). The seasonal NPP rates were calculated by summing the daily NPP rates for each season (each three months) and annual NPP rates were calculated by summing the daily NPP rates for each temperature treatment. For comparative purposes, seasonal NPP rates were calculated using the P-I curve parameters (Supplementary Table S5) and PQ values obtained from samples exposed to ambient and warming conditions, expressed as NPP_ambient and NPP_warming, respectively. For comparative purposes, seasonal NPP rates were also calculated using a literature PQ of 1.18 determined by Miller et al. (2009) for *L. hyperborea* and a mean PQ of 3.24 (mean of the four seasonal PQ values for 4-m sampled *L. hyperborea*), expressed as NPP_Miller and NPP_mean, respectively.

2.9 Statistical analysis

Data were analysed using the open-source statistical program R (R Core Team, 2023).

Chlorophyll a fluorescence, oxygen production (O_{net} & O_{gross} production & respiration rate), C_{gross} fixation and PQ values: First, technical outliers were excluded from data using the R package 'performance' (version 0.10.5; Lüdecke et al., 2021). The Shapiro-Wilk-Test (normality) and Levene's test (homogeneity of variance) were applied. If the assumptions were met, analyses of variance (ANOVAs) were applied with depth, temperature (categories: ambient and warming) and season as fixed factors; if the assumption of homogeneity was not met the significance level was lowered (alpha <0.01) to reduce the probability of false positive reports (Curran-Everett, 2017). Tukey HSD *post-hoc* tests were performed when significant differences were found. For the statistical analysis of C_{gross} fixation and PQ values, a data set was generated in R (R-script in Supplementary Material) based on the mean, standard deviation and replicate size.

Leaf area index: For LAI, a non-parametric Kruskal-Wallis ANOVA and a Dunn's test with Bonferroni-correction (alpha <0.0125) for comparison between different depths were applied.

Net primary production: <u>Intra-seasonal comparison:</u> Daily NPP rates (NPP_warming, NPP_Miller, NPP_mean) were compared to the daily NPP_ambient rate in separate, non-parametric Wilcoxon tests for each season and over all seasons. <u>Inter-seasonal comparison:</u> Seasonal effects within each daily NPP rate category (NPP_warming, NPP_Miller, NPP_mean, NPP_ambient) were tested with non-parametric Kruskal-Wallis ANOVAs and pairwise Wilcoxon tests with Bonferroni-correction (alpha <0.0083).

3 Results

3.1 Chlorophyll *a* fluorescence

After six days of culture, spring, autumn and winter samples of *Laminaria hyperborea* showed F_v/F_m values of 0.76 ± 0.07, reflecting a physiologically healthy state with no significant difference (Figure 2). In summer, the F_v/F_m values exhibited a wide range from 0.19 to 0.81, on average 12% lower than the average of all other seasons, resulting in a significant seasonal effect (Tukey test: p<0.001; Table 3). However, there were neither significant effects of the single factors temperature and depth nor interactions of all three fixed factors depth, temperature and season (Table 3).

3.2 Oxygen evolution, carbon fixation and PQ

Oxygen evolution: The main factor season had a significant effect on all measured parameters (Table 3). In summer, net oxygen production was significantly higher (0.51 ± 0.27 µmol O_2 cm^{-2} h^{-1}) than in autumn (0.25 ± 0.27 µmol O_2 cm^{-2} h^{-1}) and winter (0.30 ± 0.19 µmol O_2 cm^{-2} h^{-1}), while O_{net} production was intermediate in spring across all depths and temperature treatments (Figure 3A, Supplementary Table S4). Respiration was comparable in spring, summer and autumn (average over three seasons: -0.41 ± 0.24 µmol O_2 cm^{-2} h^{-1}), but was significantly lower in winter (-0.17 ± 0.09 µmol O_2 cm^{-2} h^{-1}; Figure 3B, Table 3; Tukey test: p<0.001). The pattern of oxygen production in the different seasons was reflected by high O_{gross} production in spring and summer (average over both seasons: 0.87 ± 0.27 µmol O_2 cm^{-2} h^{-1}) and significantly lower rates in autumn (0.65 ± 0.21 µmol O_2 cm^{-2} h^{-1}) and winter (0.47 ± 0.20 µmol O_2 cm^{-2} h^{-1}) across all depths and temperature treatments (Table 3, Tukey test: p<0.001; Figure 4A). The opposing effects of the single factor temperature on O_{net} production and respiration resulted in a compensation of the calculated O_{gross} production, and the single factors temperature and depth had no effect on O_{gross} production (Table 3). Net oxygen production was 31% higher under warming than under ambient conditions (0.31 ± 0.21 µmol O_2 cm^{-2} h^{-1}) in all seasons and depths (Table 3; Tukey test: p<0.004), while respiration was significantly decreased to -0.30 ± 0.14 µmol O_2 cm^{-2} h^{-1} under warming (ambient: -0.37 ± 0.20 µmol O_2 cm^{-2} h^{-1};
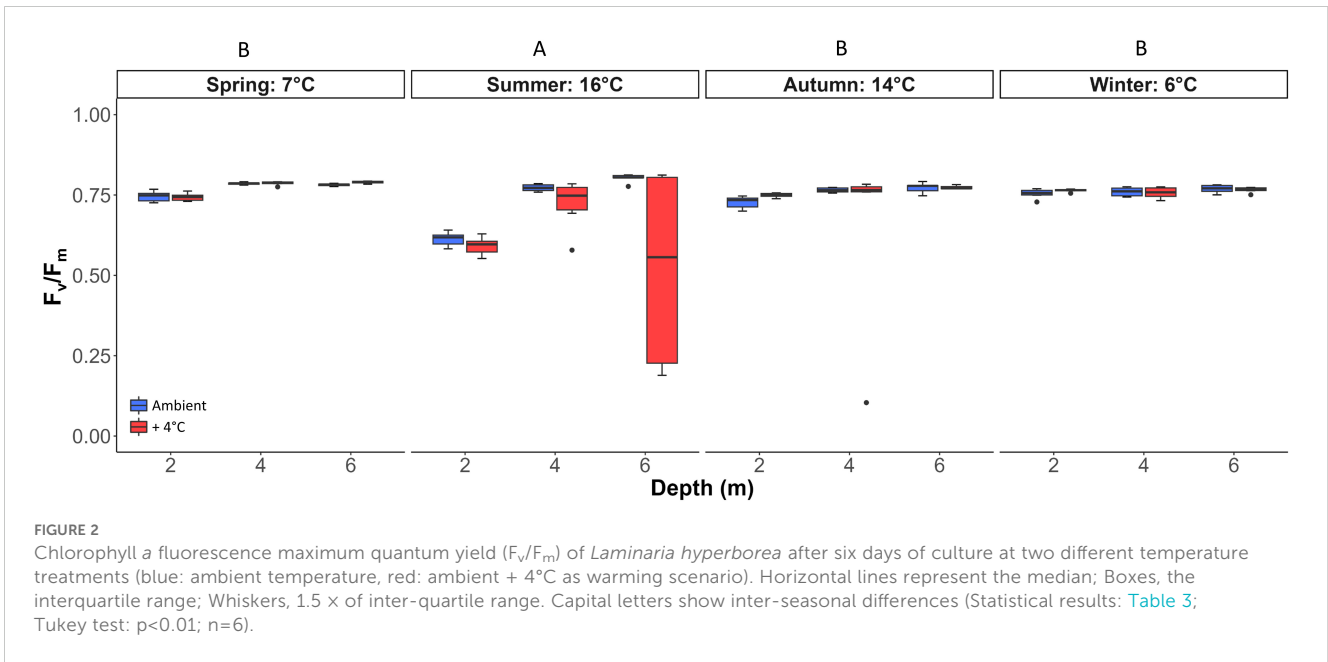
FIGURE 2

Chlorophyll *a* fluorescence maximum quantum yield (F_v/F_m) of *Laminaria hyperborea* after six days of culture at two different temperature treatments (blue: ambient temperature, red: ambient + 4°C as warming scenario). Horizontal lines represent the median; Boxes, the interquartile range; Whiskers, 1.5 × of inter-quartile range. Capital letters show inter-seasonal differences (Statistical results: Table 3; Tukey test: p<0.01; n=6).

Table 3; Tukey test: p<0.003). Sampling depth significantly affected respiration rates, as 6-m algae had 21% lower respiration (-0.29 ± 0.14 µmol O_2 cm^{-2} h^{-1}) than 4-m algae (-0.37 ± 0.19 µmol O_2 cm^{-2} h^{-1}), while respiration of 2-m algae was comparable to that of 4-m algae (-0.37 ± 0.19 µmol O_2 cm^{-2} h^{-1}; Figure 3B; Table 3; Tukey test: p<0.004).

The only significant interaction was the temperature×season interaction for the respiration rate, as the respiration rate at ambient temperature was 165% higher at all depths in spring than under warming conditions (-0.31 ± 0.09 µmol O_2 cm^{-2} h^{-1}; Tukey test: p<0.001; Figure 3B). In all other seasons, algae revealed comparable respiration rates between the two treatments across all depths (Table 3).

Carbon fixation: The pattern of oxygen production in the different seasons was also present in the C_{gross} fixation (Tables 3;

Supplementary Table S4; Tukey test: p<0.001; Figure 4B). In spring, C_{gross} fixation was significantly higher with 0.32 ± 0.07 µmol C cm^{-2} h^{-1} than in autumn (0.28 ± 0.11 µmol C cm^{-2} h^{-1}) and winter (0.22 ± 0.05 µmol C cm^{-2} h^{-1}; Table 3; Tukey test: p<0.001). Warming significantly increased C_{gross} fixation (0.32 ± 0.06 µmol C cm^{-2} h^{-1}) compared to ambient temperature conditions (0.25 ± 0.05 µmol C cm^{-2} h^{-1}; Table 3; Tukey test: p<0.001). The single factor depth also affected C_{gross} fixation, as 2-m algae with 0.33 ± 0.07 µmol C cm^{-2} h^{-1} had significantly higher C_{gross} fixation than algae from other depths with 0.27 ± 0.05 µmol C cm^{-2} h^{-1} (average over both depths) across all seasons and temperature treatments (Table 3; Tukey test: p<0.001). Only the depth×season interaction was significant for C_{gross} fixation, as rates were -60% lower in 2-m algae in winter than for 2-m algae in spring, for both treatments (Figure 4B; Tukey test: p<0.01).

TABLE 3 Results of three-way ANOVAs.

Effect	F_v/F_m			O_{net} production			Respiration			O_{gross} production			C_{gross} fixation			PQ		
	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Depth	2	3.0	0.053	2	0.6	0.533	2	5.8	**0.004**	2	2.6	0.083	2	6.9	**<0.001**	2	2.9	0.057
Temp	1	6.0	0.016	1	8.9	**0.004**	1	9.4	**0.003**	1	0.5	0.499	1	21.6	**<0.001**	1	11.0	**<0.001**
Seas	3	9.9	**<0.001**	3	10.4	**<0.001**	3	36.7	**<0.001**	3	30.6	**<0.001**	3	5.9	**<0.001**	3	8.8	**<0.001**
Depth×Temp	2	2.0	0.140	2	0.9	0.408	2	0.9	0.914	2	0.1	0.892	2	2.2	0.122	2	1.7	0.197
Depth×Seas	6	2.6	0.023	5	0.6	0.741	5	1.9	0.095	6	1.0	0.411	5	3.3	**0.009**	5	2.3	0.054
Temp×Seas	3	3.8	0.012	3	0.3	0.829	3	4.6	**0.004**	3	2.3	0.081	3	1.6	0.197	3	2.1	0.104
Depth×Temp×Seas	6	2.6	0.020	5	0.2	0.977	5	2.4	0.040	6	0.4	0.839	5	1.1	0.352	5	0.8	0.538
Residuals	120			104			109			110			105			105		

The effects of depth, temperature (Temp) and season (Seas) on chlorophyll *a* fluorescence maximum quantum yield (F_v/F_m), photosynthetic and respiration rates measured as oxygen evolution (O_{net} & O_{gross} production, Respiration), photosynthetic rate measured as light-dependent ^{14}C fixation (C_{gross} fixation) and photosynthetic quotient (PQ) of *Laminaria hyperborea*. Significant differences in bold: alpha <0.05 for O_{net} and O_{gross} production, alpha <0.01 for F_v/F_m, respiration, C_{gross} fixation and PQ due to partially inhomogeneous data. n=6.
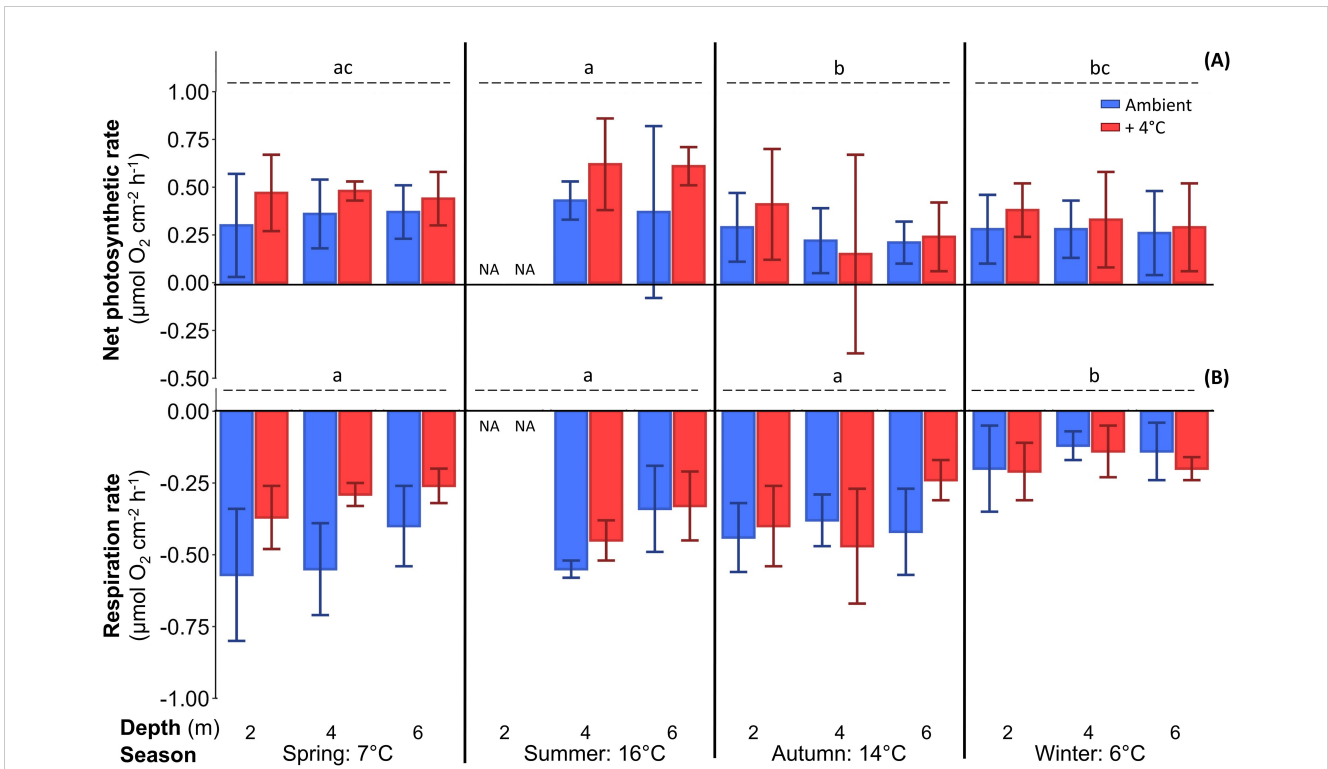
FIGURE 3

Net photosynthetic rate under saturating light for photosynthesis **(A)** and respiration rate **(B)**, measured as oxygen evolution, of *Laminaria hyperborea* after at least six days of cultivation at two temperatures (blue: ambient, red: ambient + 4°C as warming scenario). Lower case letters indicate inter-seasonal differences (further statistical results: Table 3; mean $\pm$ SD; n=6).

Photosynthetic quotient: The seasonal variation in oxygen production and C_{gross} fixation resulted in a seasonal pattern in PQ values with significantly highest values in summer (3.5 ± 1.1) compared to all other seasons (average over all other seasons: 2.3 ± 1.0) across all depths and temperature treatments (Figure 4C, Tables 3, Supplementary Table S4; Tukey test: p<0.001). Under warming conditions PQ values decreased significantly. Samples under warming revealed a PQ of 2.3 ± 1.0 across all depths and seasons, which was 22% lower than under ambient conditions (PQ of 2.9 ± 1.1; Table 3; Tukey test: p<0.001). Along the depth gradient PQ values showed no significant differences, although 4-m discs from the ambient treatment exhibited a trend toward 21% higher PQ values compared to discs from 2 and 6 m across all seasons. For PQ values no significant interactions of the three main factors were present (Table 3).

3.3 Leaf area index

The LAI had a peak at 4 m with 6.70 ± 0.98 m^2 lamina m^{-2} seafloor. This was 14% higher than the LAI at 2 m and 36% higher than the LAI at 6 m (Table 1). However, depth had no significant effect on LAI (Kruskal-Wallis ANOVA: $\chi^2 = 5.97$, df=3, p=0.051). At 2 m, LAI of *L. hyperborea* varied greatly between replicates (1.02 to 10.07; raw data not shown).

3.4 Modelled net primary production

Comparison of modelled NPP under ambient and warming conditions at 4 m depth: Seasonal variation was evident in the daily $NPP_{ambient}$ and the daily $NPP_{warming}$ rates (Tables 4, 5; Figure 5B). Daily $NPP_{ambient}$ rates were significantly higher in spring and summer than in the other seasons and only negative in winter. Daily $NPP_{warming}$ was significantly different in all seasons, with the highest rates in spring and lowest in autumn, while rates were negative in autumn and winter (Table 4). No significant difference was observed between the annual $NPP_{ambient}$ rate and the annual $NPP_{warming}$ rate, although the annual $NPP_{warming}$ rate was 14% higher (Tables 4, 5).

The seasonal NPP rates of both scenarios differed significantly in spring, autumn, and winter (Table 5). In spring, the daily $NPP_{warming}$ rate was twice as high as the daily $NPP_{ambient}$ rate, which is due to lower C-fixation at ambient temperature (Table 4; Figure 5). In autumn, daily $NPP_{ambient}$ rates were positive, but under warming they turned into significantly lower, negative daily $NPP_{warming}$ rates (Table 4). In winter, daily $NPP_{warming}$ rates were 35% lower than daily $NPP_{ambient}$ rates (Tables 4, 5; Figure 5B).

Comparison of modelled NPP with different PQ approaches: As we have also shown for daily $NPP_{warming}$ rates, the daily NPP_{Miller} and NPP_{mean} rates differed significantly between seasons. Both
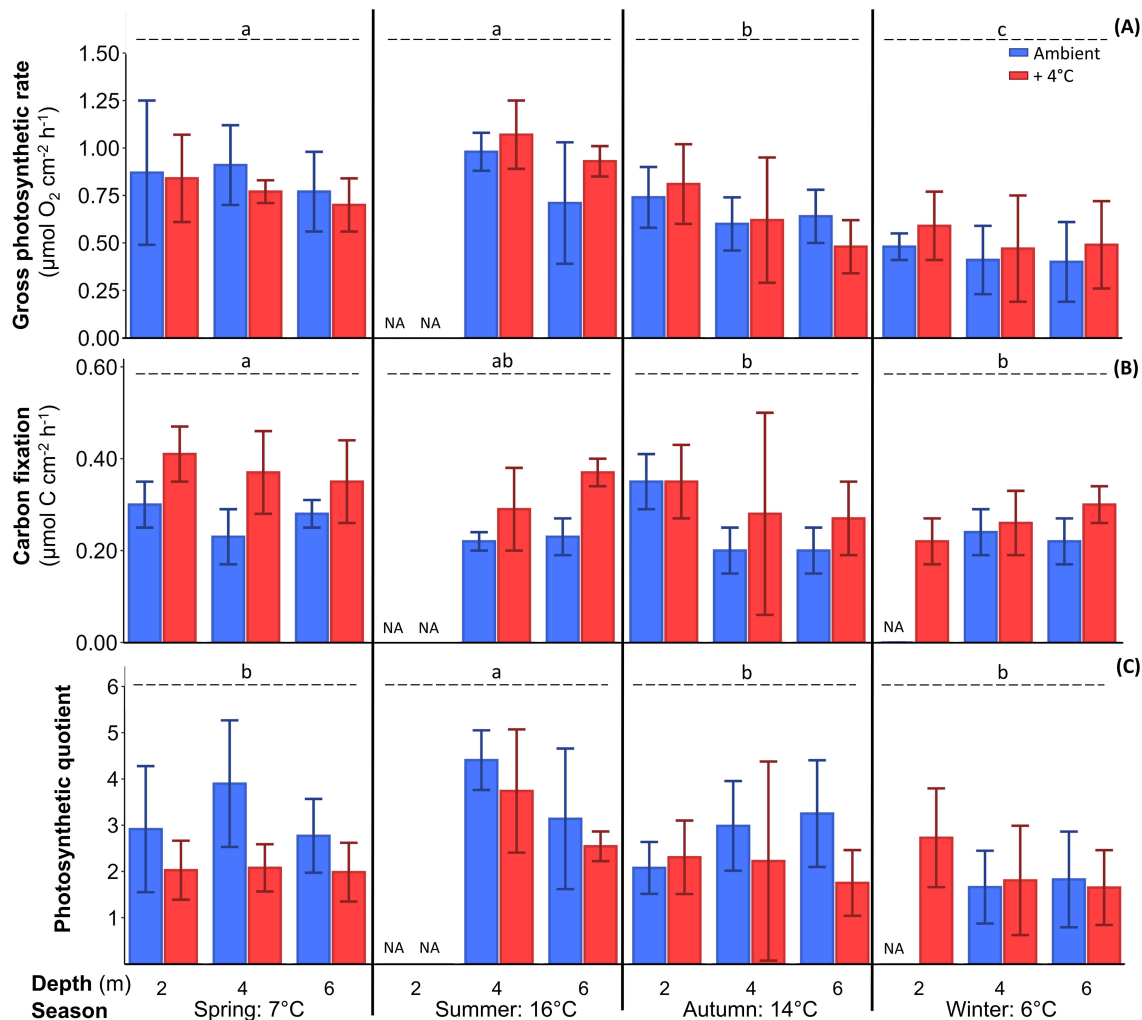
FIGURE 4
Gross photosynthetic rate **(A)** measured as oxygen production, gross carbon fixation rate **(B)** measured as light-dependent ^{14}C fixation, and photosynthetic quotient **(C)** of *Laminaria hyperborea* after at least six days of cultivation at two temperatures (blue: ambient, red: ambient + 4°C as warming scenario). C-fixation and oxygen production were measured under saturating light for photosynthesis. Lower case letters indicate inter-seasonal differences (further statistical results: Table 3; Tukey test: p<0.01; mean ± SD; n=6).

rates were significantly higher in summer and lowest in winter (Table 4; Figure 5C). The daily $NPP_{PQ-Miller}$ rates and the daily NPP_{mean} rates were significantly different from $NPP_{ambient}$ rates in spring, summer and winter, but were comparable to $NPP_{ambient}$ rates in autumn (Table 5; Tukey test: p<0.001). In spring and summer, the Miller PQ and mean PQ values were lower than the seasonal PQ values, resulting in a 330–373% higher NPP_{Miller} and a 20–36% higher NPP_{mean} compared to $NPP_{ambient}$ (Figure 5C). In winter, $NPP_{ambient}$ was calculated with a PQ of 1.66, which was higher than the Miller PQ of 1.18, but lower than the mean PQ of 3.24, resulting in a significantly lower NPP_{Miller} (41%) and a significantly higher NPP_{mean} (49%; Tables 4, 5; Tukey test: p<0.001). Both modelled annual NPP rates based on fixed PQs were significantly higher than the annual $NPP_{ambient}$ rate (Table 5).

4 Discussion

The importance of kelps in the coastal carbon cycle has been known for decades (e.g. Smith, 1981; Duarte, 2017). In most studies, net primary production (NPP) rates were derived from biomass surveys that included the total standing stock, or oxygen production rates that were converted to NPP rates using a fixed, theoretical PQ (Pessarrodona et al., 2022a). However, direct measurements of seasonal C-fixation rates of kelps are missing and using a fixed PQ is unable to reflect dynamic aspects in primary productivity (Wright et al., 2022; Trentman et al., 2023). Our study for the first time highlights the variability of PQ values over the course of the investigated seasons ranging from 1.7 to 4.4 within one important kelp species and evaluates its impact on modelling kelp NPP rates. This aspect has been neglected in other

TABLE 4 Modelled daily net primary production (NPP) rates of the *Laminaria hyperborea* forest at 4 m water depth.

Season	n	NPP$_{ambient}$	NPP$_{warming}$	NPP$_{Miller}$	NPP$_{mean}$
		(g C m^{-2} seafloor d^{-1})			
Spring	92	1.60 ± 0.61[a]	3.26 ± 1.39[a]	5.29 ± 2.02[a]	1.93 ± 0.74[a]
Summer	92	1.59 ± 0.64[a]	1.65 ± 0.72[b]	5.93 ± 2.40[b]	2.16 ± 0.87[b]
Autumn	91	0.31 ± 0.65[b]	-0.88 ± 0.96[c]	0.77 ± 1.65[c]	0.28 ± 0.60[c]
Winter	91	-0.20 ± 0.62[c]	-0.28 ± 0.76[d]	-0.29 ± 0.88[d]	-0.11 ± 0.32[d]
		(g C m^{-2} seafloor yr^{-1})			
Annual		303.10	346.88	1077.19	376.98

Daily NPP rates were calculated with different photosynthetic quotients (PQs). NPP$_{ambient}$: using PQ under ambient temperatures; NPP$_{warming}$: using PQ under warming (ambient + 4°C as warming scenario); NPP$_{Miller}$: using PQ of 1.18 according to Miller et al. (2009); NPP$_{mean}$: using average PQ of 3.24 over all seasons under ambient temperatures. For annual NPP rates, daily NPP rates were summed up. Letters indicate significant differences within each NPP rate category between seasons (pairwise Wilcoxon rank test, Bonferroni corrected alpha <0.0083). Mean ± SD.

studies. Overall, measured PQ values were highest in high-light season summer, when oxygen production was maximised. While depth effects could be neglected, warming resulted in overall significantly lower PQ values, but seasonally this effect was most prominent in spring and summer.

Modelled daily NPP rates over the year were highly variable and followed the seasonally changing PPFD (Figure 5), revealing highest rates in high-light seasons spring and summer under ambient conditions. Warming intensified the effect of PPFD especially in spring, while caused a switch to negative NPP rates in the low-light season autumn in contrast to positive NPP rates at ambient temperatures due to increased respiration rate at 4 m depth under warming condition (Franke et al., 2024). The potentially higher NPP rates resulting from the lowered PQ during warming were however only apparent in spring, while PQ values were lower under warming conditions also in summer and winter without an effect on NPP rates. Interestingly, daily NPP rates modelled under ambient conditions with a fixed PQ value of 1.18 (Miller et al., 2009 for *L. hyperborea*), resulted in

TABLE 5 Results of non-parametric Wilcoxon tests for the modelled daily net primary production (NPP) rates of *Laminaria hyperborea* collected at 4 m depth, calculated with different photosynthetic quotients (PQs).

Season	NPP$_{warming}$		NPP$_{Miller}$		NPP$_{mean}$	
	W	p	W	p	W	p
Spring	1183	**<0.001**	619	**<0.001**	2848	**<0.001**
Summer	3786	0.217	609	**<0.001**	2319	**<0.001**
Autumn	6879	**<0.001**	3707	0.223	4198	0.872
Winter	4990	**0.003**	5165	**<0.001**	2447	**<0.001**
All seasons	67732	0.601	48098	**<0.001**	57217	**0.001**

NPP$_{ambient}$ was calculated using the seasonal PQs measured at ambient temperatures and were compared to: NPP$_{warming}$: using PQ under warming; NPP$_{Miller}$: using PQ of 1.18 according to Miller et al. (2009); NPP$_{mean}$: using mean PQ of 3.24 over all seasonal PQs measured at ambient temperature. NPP$_{ambient}$ was compared with each NPP category within each season (n=92 for spring & summer; n=91 for autumn & winter), but average values were also compared for all the year around (all seasons, n=366). alpha <0.05, significant results in bold.
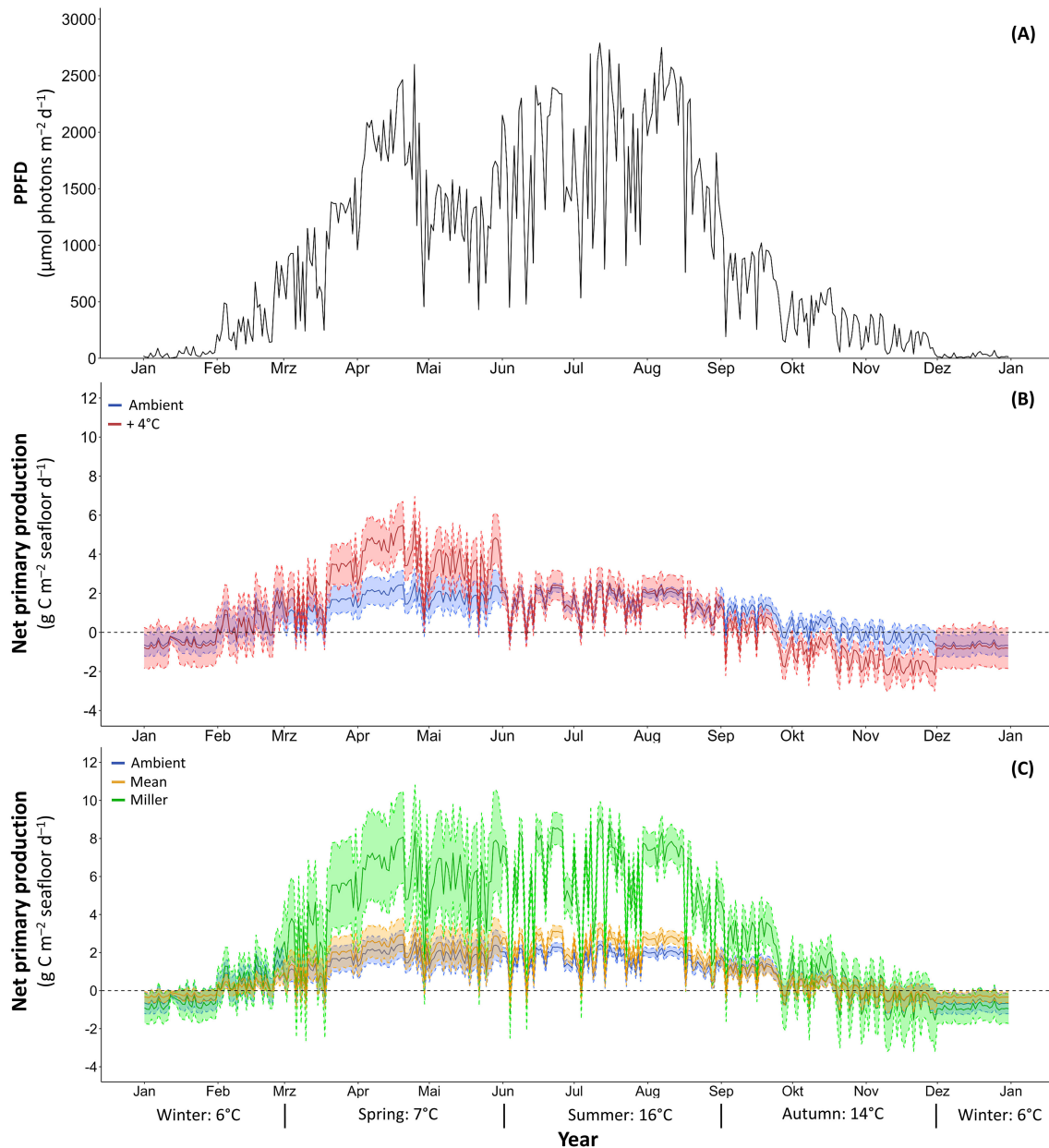
annual NPP rates three times higher than using seasonally changing PQ values, reflecting a large overestimation. In contrast, daily NPP rates modelled under ambient conditions with a mean PQ for the whole year, based on the seasonal PQ values derived from our measurements, only resulted in a slightly higher annual NPP rate compared to the annual NPP rate using seasonally changing PQ values. We thus suggest to consider this approach as a direct method to measure so-called "true" C-fixation (Arnold and Littler, 1985; Kaiser et al., 2020), in addition to the usual standing stock surveys, or at least to include variable PQ values in NPP predictions.

The physiological and ecological consequences of a sub-lethal year-round global warming on *L. hyperborea* and kelps in general are unknown. Our study provides a first insight about possible negative and positive effects of warming in *L. hyperborea* over the seasons. In summer, higher temperatures increased the variance in maximum quantum yield which indicating onset of sub-lethal heat stress (Graiff et al., 2015). This may become lethal depending on the duration of the heat stress, as juvenile *L. hyperborea* has a two-week lethal temperature limit of 20°C (tom Dieck, 1992). In autumn, negative C-fixation rates as indicated by our model, may however lead to the incorporation of less carbon reserves (Schiener et al., 2015) which are crucial for winter survival in low light conditions (Scheschonk et al., 2019) and for nourishing the newly emerging blade via translocation from old to new blade (Lüning et al., 1972). Although the removal of the old blade does not prevent formation of a new blade in spring (Lüning, 1969), the new blade will become much smaller. This situation may also be the case if carbon reserves become diminished due to autumn warming in an elongated negative carbon balance situation. The situation changes again from mid-winter onwards when blade growth is initiated (Schaffelke and Lüning, 1994) and will profit from increased temperatures as optimum growth temperatures of *L. hyperborea* are at 10-17°C (tom Dieck, 1992). As we could show that higher temperatures in spring substantially increased the primary production rates, this, in combination with increased growth rates, may potentially result in larger and more vigorous thalli entering summer. As a consequence, NPP may possibly even increase with warming over the year, under the condition

FIGURE 5
Daily photosynthetic photon flux density (PPFD) **(A)** used to model net primary production of *Laminaria hyperborea* collected at 4 m with different photosynthetic quotients (PQs). Blue: using PQ under ambient temperatures & Red: using PQ under warming (ambient + 4°C) **(B)**; Green: using PQ of 1.18 according to Miller et al. (2009) & Orange: using average PQ of 3.24 over all seasons under ambient temperatures **(C)**. Continuous line: mean, dashed line: ± SD; n=6.

that temperatures do not surpass critical high limits over extended periods.

4.1 Oxygen production, carbon fixation and the photosynthetic quotient

By definition, the PQ describes the molar ratio of oxygen released during the assimilation of carbon into organic matter (Kaiser et al., 2020). The methods used in the present study provide reliable estimates of photosynthetic activities in terms of moles of oxygen produced per mol of fixed carbon (Hurd et al., 2014). In the present study, Helgolandic *L. hyperborea* exhibited PQ values ranging from 1.65 ± 0.81 to 4.41 ± 0.64. The comparison of PQ values in literature is quite difficult because of the different methodologies used (relative atomic compositions: e.g. Ryther, 1956 used data from Brandt and Raben, 1919; C:N ratios: Gerard, 1988; combination of oxygen production measurements and isotopic C-fixation: Hatcher et al., 1977; Miller et al., 2009; Iñiguez et al., 2016b). Therefore, the PQ values reported for macroalgae vary widely from 0.67 to 5.20 (Ryther, 1956 used data from Brandt and Raben, 1919: *Saccharina latissima*; Hatcher et al., 1977: *Laminaria*

longicruris; Gerard, 1988: *S. latissima*; Weykam et al., 1997: *Iridaea cordata*; Iñiguez et al., 2016b: *S. latissima, Laminaria solidungula*). Compared to Norwegian *L. hyperborea*, our PQ values were considerably higher (1.18 and 1.3; Miller et al., 2009). While the oxygen production rates were comparable to those of our study, the higher ^{13}C-fixation rates at saturated PPFD could be caused by differences in the methodology, as the high background level of ^{13}C, while ^{14}C signal is almost completely added throughout the experiment (Miller et al., 2009; Beer et al., 2014). Miller et al. (2009) used ^{13}C, a stable isotope that is more common in nature and requires significant ^{13}C enrichment to produce measurable uptake signals in kelp tissue. In contrast, ^{14}C only occurs in low abundance in nature, making detection very sensitive, even with short incubation times (Miller and Dunton, 2007; Beer et al., 2014; Kaiser et al., 2020). Our ^{14}C-fixation rates under saturating light conditions ranged from 1.2 to 3.4 μmol C g^{-1} FM h^{-1} (corresponding to 0.25 to 0.42 μmol C cm^{-2} h^{-1}) and were comparable to ^{14}C-fixation rates presented in Wiencke and Bischof (2012: summarised from Kremer, 1981: 2.1 μmol C g^{-1} FM h^{-1}) measured under saturating PPFD for Helgolandic *L. hyperborea*.

Laminaria hyperborea revealed a strong seasonality in its photosynthetic activity as measured by both oxygen production and ^{14}C-fixation, with peak values in spring and summer, which is confirmed by other studies on this kelp (Drew, 1983; White et al., 2021; Franke et al., 2024) and other Laminariales (Blain and Shears, 2019). In summer, an enhanced activity of the light-dependent reactions provides more photosynthetic energy, but C-fixation rates were not significantly increased (Kirk, 1994; Wiencke and Bischof, 2012), leading to the highest PQ values. The photosynthetic energy is distributed between C-uptake and fixation on the one hand, and other nutrient assimilation mechanisms (such as essential enzymes and transporters involved in nitrate and phosphate uptake and assimilation) on the other (Gordillo et al., 2002). Although nutrient levels are low in summer, kelps accumulate mainly carbohydrates such as mannitol and laminarin as storage compounds for being used during the growth period in late winter and early spring (Kain and Jones, 1976; Küppers and Weidner, 1980; Kirk, 1994; Schaffelke and Lüning, 1994), but also expend more photosynthetic energy in maintaining active inorganic carbon acquisition mechanisms under saturating light conditions. In spring, the combination of high PPFD and elevated nutrient availability resulted in higher C-fixation rates (Kirk, 1994). In summer, higher PQ values were measured when nutrients were low and the assimilation of nitrate was the main source of nitrogen, which also increases PQ (Beer et al., 2014; Trentman et al., 2023). The high impact of the nitrogen source on PQ values was also demonstrated in studies using nitrate instead of ammonium, which determined 50% higher PQ values due to lower C-fixation as more energy was required to reduce nitrate to ammonium (Beer et al., 2014; Hurd et al., 2014; Kaiser et al., 2020).

Along the depth gradient, gross oxygen production and PQ values did not differ significantly, indicating a high acclimatisation

potential to the different PPFD conditions of the photosynthetic processes of *L. hyperborea*, which has already been discussed by Franke et al. (2023, 2024). However, ^{14}C-fixation was significantly higher in 2-m kelps compared to other depths across all seasons and temperature treatments, confirming the previously observed increase in C-fixation rates in Norwegian *L. hyperborea* sampled at mean low water (= 0 m) compared to 10 m depth (below mean low water; Miller et al., 2009). Although gross oxygen production was not significantly higher in 2-m kelps, it was 8–25% higher than at other depths, most likely due to higher PPFD availability.

Warming resulted in increased F_v/F_m variances and a partial decrease in F_v/F_m values only in summer, indicating a moderate stress response. Burdett et al. (2019) exposed *L. hyperborea* from Plymouth Sound, UK, to short-term warming events (+ 4°C) and observed an insensitive photo-physiological response with no significant change in net oxygen production during the cultivation period of three days. Nevertheless, kelp studies in which temperature was manipulated during all four seasons in an experimental setup with simultaneous measurements of oxygen production and C-fixation are missing. In the present study, warming had no significant impact on gross oxygen production measured under saturating PPFD, while ^{14}C-fixation was stimulated in all seasons, which was also observed in *L. solidungula* under increased temperature (Iñiguez et al., 2016b). In the present study, short-term warming may have increased enzyme activity, including carbon assimilation, which is supported by the study of Küppers and Weidner (1980), who showed an increase in RubisCO activity of *L. hyperborea* in response to seasonally increasing temperatures. As a result, the higher ^{14}C-fixation at elevated temperatures resulted in lower PQ values.

4.2 Net primary production

Our study modelled daily NPP rates with seasonally changing PQ values as well as P-I curve parameters (Franke et al., 2024), hourly PPFD data and a fixed LAI. The LAI was obtained during the summer campaign as Lüning (1971) measured a peak in blade area during early summer. The daily NPP rate of our blade disc was up scaled with this fixed LAI in a linear equation. A lower LAI would directly led to reduced daily NPP rates, indicating that negative rates become less negative and positive rates are less positive, resulting in an overall lower NPP rate. In the present study, these potential differences in LAI were neglected. However, variable LAI should be taken into account in future studies to get a more reliable NPP. Nevertheless, the highest variability in daily NPP rates is driven by the PPFD. Franke et al. (2023) evaluated the impact of changing underwater PPFD on kelp daily NPP rates during one summer, which can lead to negative rates already in >3-4 m during a storm period leading to enhanced turbidity with low PPFD.

The annual NPP rate presented was comparable to annual NPP rates based on a biomass survey conducted by Smale et al. (2020) in *L. hyperborea* forests in Great Britain. They investigated the

productivity based on biomass at two sites with different temperatures and revealed a decrease in productivity at the warmer site (Smale et al., 2020). Our temperature manipulation experiment was conducted on a kelp population at one site and revealed a trend towards a higher annual NPP rate under warming and highlighted significant differences in seasonal NPP rates in spring, autumn and winter. Warming had an intensifying effect on the seasonal variability of NPP rates due to higher C-fixation and therefore lower PQ values under warming conditions. The overall shape of the daily NPP curve is driven by PPFD (Deregibus et al., 2016; Franke et al., 2023, 2024). In both temperature scenarios, NPP rates were highest in spring compared to the other seasons, which may be a consequence of the annual growth rhythm of *L. hyperborea* (Kain and Jones, 1976; Schaffelke and Lüning, 1994). Due to lower PPFD in autumn and winter, NPP rates (ambient and warming) were up to 127% lower than the NPP rates in spring. This seasonality in NPP rates was also observed for *Ecklonia radiata* (Rodgers and Shears, 2016) and *Macrocystis pyrifera* (Miller et al., 2011), which were modelled using biomass surveys and theoretical fixed PQ values, respectively, resulting in highest production rates in spring and summer. We also observed a change from positive NPP rates under ambient conditions to negative NPP rates under warming conditions in autumn, which is attributed to a three-time higher respiration rate and the typical low PPFD of this season.

The Helgolandic *L. hyperborea* forest exhibits LAI values comparable to other *L. hyperborea* populations along the NE-Atlantic coastline ranging from 1-12.7 m^2 lamina m^{-2} seafloor pointing to a highly productive ecosystem (Jupp and Drew, 1974; Kain and Jones, 1977; Pehlke and Bartsch, 2008). White et al. (2021) modelled daily NPP rates between 3.9 and 24.5 g C m^{-2} d^{-1} in sub-canopy and canopy blades, respectively, in summer and between -10.1 and 1.5 g C m^{-2} d^{-1} in canopy and sub-canopy blades, respectively, in autumn with a fixed PQ (1.2), *in situ* P-I curves and PPFD data for a *L. hyperborea* forest at 4 m depth in France. Daily NPP rates for these two seasons in the present study were at the lower end of the above-mentioned ranges. Our seasonal PQ values were up to three times higher than the theoretical PQ value used by White et al. (2021). Thus, low PQ values result in higher NPP rates and a possible overestimation of the C-fixation of kelps. Estimations of kelp NPP based on oxygen measurements combined with a single theoretical PQ value (Fairhead and Cheshire, 2004; White et al., 2021; Franke et al., 2023) neglect seasonal differences in PQ values and their impact on NPP rates. This became apparent when we compared modelled annual NPP rates with the PQ value of 1.18 from Miller et al. (2009) with NPP rates resulting from our seasonal PQ values. The approach of Miller et al. (2009) resulted in three-time higher annual NPP rate, as the PQ value was much lower than our seasonal PQ values. As it is common knowledge that *Laminaria* species have a pronounced seasonality in a series of parameters such as growth (Kain and Jones, 1976; Schaffelke and Lüning, 1994), carbon storage (Schiener et al., 2015; Scheschonk et al., 2019), photosynthesis (Franke et al., 2024) or enzyme activity (Küppers and Weidner, 1980), we assume that the seasonal difference in PQs which we identified, is a general feature of kelps, although this may need verification at least in one or two

other kelps species from other locations. In the end, the high variability in PQ values directly affected NPP rates and was neglected in former models. Therefore, we recommend modelling NPP rates not with a fixed PQ, but with variable PQ values to obtain reliable future predictions.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

Funding

Acknowledgments

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1455706/full#supplementary-material

References

Araujo, R., Bárbara, I., Sousa-Pinto, I., and Quintino, V. (2005). Spatial variability of intertidal rocky shore assemblages in the northwest coast of Portugal. *Estuar. Coast. Shelf Sci.* 64, 658–670. doi: 10.1016/j.ecss.2005.03.020

Arnold, K. E., and Littler, M. M. (1985). "The carbon-14 method for measuring primary productivity," in *Handbook of phycological methods, ecological field methods: macroalgae*. Eds. M. M. Littler and D. S. Littler (Cambridge, UK: Cambridge University Press), 377–396.

Assis, J., Fernández Bejarano, S. J., Salazar, V. W., Schepers, L., Gouvêa, L., Fragkopoulou, E., et al. (2024). Bio-ORACLE v3.0. Pushing marine data layers to the CMIP6 Earth system models of climate change research. *Global Ecol. Biogeogr.* 33, e13813. doi: 10.1111/geb.13813

Beer, S., Björk, M., and Beardall, J. (2014). *Photosynthesis in the marine environment* (New Jersey: John Wiley & Sons).

Bell, R. T., and Kuparinen, J. (1984). Assessing phytoplankton and bacterioplankton production during early spring in Lake Erken. *Sweden. Appl. Environ. Microbiol.* 48, 12211230. doi: 10.1128/aem.48.6.1221-1230.1984

Blain, C. O., and Shears, N. T. (2019). Seasonal and spatial variation in photosynthetic response of the kelp *Ecklonia radiata* across a turbidity gradient. *Photosynth. Res.* 140, 21–38. doi: 10.1007/s11120-019-00636-7

Brandt, K., and Raben, E. (1919). Zur Kenntnis der chemischen Zusammensetzung des Planktons und einiger Bodenorganismen. *Wiss. Meeresuntersuch.* 19, 175–209.

Buesa, R. J. (1980). Photosynthetic quotient of marine plants. *Photosynthetica* 14, 337–342.

Burdett, H. L., Wright, H., and Smale, D. A. (2019). Photophysiological responses of canopy-forming kelp species to short-term acute warming. *Front. Mar. Sci.* 6. doi: 10.3389/fmars.2019.00516

Burgess, M. G., Becker, S. L., Langendorf, R. E., Fredston, A., and Brooks, C. M. (2023). Climate change scenarios in fisheries and aquatic conservation research. *ICES J. Mar. Sci.* 80, 1163–1178. doi: 10.1093/icesjms/fsad045

Casado-Amezúa, P., Araujo, R., Criado, I. B., Bermejo, R., Borja, A., Díez, I., et al. (2019). Distributional shifts of canopy-forming seaweeds from the Atlantic coast of Southern. *Europe. Biodivers. Conserv.* 28, 1151–1172. doi: 10.1007/s10531-019-01716-9

Curran-Everett, D. (2017). CORP: Minimizing the chances of false positives and false negatives. *J. Appl. Physiol.* 122, 91–95. doi: 10.1152/japplphysiol.00937.2016

Deregibus, D., Quartino, M. L., Campana, G. L., Momo, F. R., Wiencke, C., and Zacher, K. (2016). Photosynthetic light requirements and vertical distribution of macroalgae in newly ice-free areas in Potter Cove, South Shetland Islands, Antarctica. *Polar Biol.* 39, 153–166. doi: 10.1007/s00300-015-1679-y

Drew, E. A. (1983). Physiology of *Laminaria. Mar. Ecol.* 4, 227–250. doi: 10.1111/j.1439-0485.1983.tb00298.x

Duarte, C. M. (2017). Reviews and syntheses: Hidden forests, the role of vegetated coastal habitats in the ocean carbon budget. *Biogeosciences* 14, 301–310. doi: 10.5194/bg-14-301-2017

Duarte, C. M., and Cebrián, J. (1996). The fate of marine autotrophic production. *Limnol. Oceanogr.* 41, 1758–1766. doi: 10.4319/lo.1996.41.8.1758

Duarte, C. M., Middelburg, J. J., and Caraco, N. (2005). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* 2, 1–8. doi: 10.5194/bg-2-1-2005

Dummermuth, A., Wiltshire, K. H., Kirstein, I., Brodte, E. M., Wichels, A., Shama, L., et al. (2023). Marine Stations Helgoland and Sylt operated by the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research. *J. Large Scale Res. Facil.* 8, A184. doi: 10.17815/jlsrf-8-184

Fairhead, V. A., and Cheshire, A. C. (2004). Rates of primary productivity and growth in *Ecklonia radiata* measured at different depths, over an annual cycle, at West Island, South Australia. *Mar. Biol.* 145, 41–50. doi: 10.1007/s00227-004-1308-8

Fischer, P., Brand, M., Friedrich, M., Eickelmann, L., Lienkämper, M., Spotowitz, L., et al. (2021b). *Hydrographical time series data of Helgoland, Southern North Sea 2018* (PANGAEA). doi: 10.1594/PANGAEA.934740

Fischer, P., Brand, M., Friedrich, M., Eickelmann, L., Lienkämper, M., Spotowitz, L., et al. (2021c). *Hydrographical time series data of Helgoland, Southern North Sea 2019* (PANGAEA). doi: 10.1594/PANGAEA.927379

Fischer, P., Brand, M., Friedrich, M., Eickelmann, L., Lienkämper, M., Spotowitz, L., et al. (2021d). *Hydrographical time series data of Helgoland, Southern North Sea 2020* (PANGAEA). doi: 10.1594/PANGAEA.933714

Fischer, P., Happel, L., Anselm, N., Bussmann, I., Lienkämper, M., Brand, M., et al. (2022). *Hydrographical time series data of Helgoland, Southern North Sea 2016* (PANGAEA). doi: 10.1594/PANGAEA.942188

Fischer, P., Happel, L., Brand, M., Eikelmann, L., Lienkämper, M., Spotowitz, L., et al. (2021a). *Hydrographical time series data of Helgoland, Southern North Sea 2017* (PANGAEA). doi: 10.1594/PANGAEA.935808

Franke, K., Bartsch, I., Karsten, U., and Graiff, A. (2024). Seasonality influences the effect of warming on kelp photosynthesis. *MEPS* 739, 15–29. Available at: https://www.int-res.com/prepress/m14623.html.

Franke, K., Matthes, L. C., Graiff, A., Karsten, U., and Bartsch, I. (2023). The challenge of estimating kelp production in a turbid marine environment. *J. Phycol.* 59, 518–537. doi: 10.1111/jpy.13327

Gerard, V. A. (1988). Ecotypic differentiation in light-related traits of the kelp *Laminaria saccharina. Mar. Biol.* 97, 25–36. doi: 10.1007/BF00391242

Gordillo, F. J., Dring, M. J., and Savidge, G. (2002). Nitrate and phosphate uptake characteristics of three species of brown algae cultured at low salinity. *Mar. Ecol. Prog. Ser.* 234, 111–118. doi: 10.3354/meps234111

Graiff, A., Liesner, D., Karsten, U., and Bartsch, I. (2015). Temperature tolerance of western Baltic Sea *Fucus vesiculosus*–growth, photosynthesis and survival. *J. Exp. Mar. Biol. Ecol.* 471, 8–16. doi: 10.1016/j.jembe.2015.05.009

Gran, G. (1952). Determination of the equivalence point in potentiometric titrations. *Part II. Anal.* 77, 661–671. doi: 10.1039/AN9527700661

Hanelt, D. (2018). "Photosynthesis assessed by chlorophyll fluorescence," in *Bioassays, advanced Methods and Applications*. Eds. D. P. Häder and G. S. Erzinger (Elsevier, The Netherlands), 169–198.

Hatcher, B. G., Chapman, A. O., and Mann, K. H. (1977). An annual carbon budget for the kelp *Laminaria longicruris. Mar. Biol.* 44, 85–96. doi: 10.1007/BF00386909

Hurd, C. L., Harrison, P. J., Bischof, K., and Lobban, C. S. (2014). *Seaweed ecology and physiology. 2nd* (GB: Cambridge University Press).

Iñiguez, C., Carmona, R., Lorenzo, M. R., Niell, F. X., Wiencke, C., and Gordillo, F. J. (2016a). Increased CO_2 modifies the carbon balance and the photosynthetic yield of two common Arctic brown seaweeds: *Desmarestia aculeata* and *Alaria esculenta. Polar Biol.* 39, 1979–1991. doi: 10.1007/s00300-015-1724-x

Iñiguez, C., Carmona, R., Lorenzo, M. R., Niell, F. X., Wiencke, C., and Gordillo, F. J. (2016b). Increased temperature, rather than elevated CO_2, modulates the carbon assimilation of the Arctic kelps *Saccharina latissima* and *Laminaria solidungula. Mar. Biol.* 163, 1–18. doi: 10.1007/s00227-016-3024-6

Jassby, A. D., and Platt, T. (1976). Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnol. Oceanogr.* 21, 540–547. doi: 10.4319/lo.1976.21.4.0540

Jupp, B. P., and Drew, E. A. (1974). Studies on the growth of *Laminaria hyperborea* (Gunn.) Fosl. I. Biomass and productivity. *J. Exp. Mar. Biol. Ecol.* 15, 185–196. doi: 10.1016/0022-0981(74)90044-6

Kain, J. M., and Jones, N. S. (1976). The biology of *Laminaria hyperborea* IX. Growth pattern of fronds. *J. Mar. Biol. Assoc. U. K.* 56, 603–628. doi: 10.1017/S0025315400020683

Kain, J. M., and Jones, N. S. (1977). The biology of *Laminaria hyperborea* X. The effect of depth on some populations. *J. Mar. Biol. Assoc. U. K.* 57, 587–607. doi: 10.1017/S0025315400025054

Kaiser, M. J., Attrill, M. J., Jennings, S., Thomas, D. N., Barnes, D. K. A., Brierley, A. S., et al. (2020). *Marine ecology: Processes, systems, and impacts. 3rd* (New York: Oxford University Press).

Kirk, J. T. (1994). *Light and photosynthesis in aquatic ecosystems. 2nd* (GB: Cambridge University Press).

Kremer, B. P. (1981). Metabolic implications of non-photosynthetic carbon fixation in brown macroalgae. *Phycologia* 20, 242–250. doi: 10.2216/i0031-8884-20-3-242.1

Küppers, U., and Weidner, M. (1980). Seasonal variation of enzyme activities in *Laminaria hyperborea. Planta* 148, 222–230. doi: 10.1007/BF00380031

Kylin, H. (1947). Die Phaeophyceen der schwedischen Westküste. *Lunds Univ. Årsskr. (Avd. 2)* (Lund, Sweden: C.W.K. Gleerup) 43, 1–99.

Lange, O. L., Nobel, P. S., Osmond, C. B., and Ziegler, H. (1981). *Physiological Plant Ecology I* (Berlin: Springer Verlag).

Lee, H., Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P., et al. (2023). *IPCC 2023: Climate Change 2023: Synthesis Report, Summary for Policymakers. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.* Eds. H. Lee and J. Romero (Geneva, Switzerland: IPCC). doi: 10.59327/IPCC/AR6-9789291691647.001

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., and Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *J. Open source. Software* 6, 3139. doi: 10.21105/joss.03139

Lüning, K. (1969). Growth of amputated and dark-exposed individuals of the brown alga *Laminaria hyperborea. Mar. Biol.* 2, 218–223. doi: 10.1007/BF00351143

Lüning, K. (1971). "Seasonal growth of *Laminaria hyperborea* under recorded underwater light conditions near Helgoland," in *Fourth Europ. Mar. Biol. symp*, vol. 4. (University Press, Cambridge), 347–361.

Lüning, K. (1990). *Seaweeds: their environment, biogeography, and ecophysiology* (New Jersey: John Wiley & Sons).

Lüning, K., and Dring, M. J. (1979). Continuous underwater light measurement near Helgoland (North Sea) and its significance for characteristic light limits in the sublittoral region. *Helgol. Wiss. Meeresunters* 32, 403–424. doi: 10.1007/BF02277985

Lüning, K., Schmitz, K., and Willenbring, J. (1972). Translocation of ^{14}C-labeled assimilates in two *Laminaria* species. *Proc. Int. Seaweed Symp.* 7, 420–425.

Miller, H. L.III, and Dunton, K. H. (2007). Stable isotope (^{13}C) and O_2 micro-optode alternatives for measuring photosynthesis in seaweeds. *Mar. Ecol. Prog. Ser.* 329, 85–97. doi: 10.3354/meps329085

Miller, H. L.III, Neale, P. J., and Dunton, K. H. (2009). Biological weighting functions for UV inhibition of photosynthesis in kelp *Laminaria hyperborea* (Phaeophyceae). *J. Phycol.* 45, 571–584. doi: 10.1111/j.1529-8817.2009.00694.x

Miller, R. J., Reed, D. C., and Brzezinski, M. A. (2011). Partitioning of primary production among giant kelp (*Macrocystis pyrifera*), understory macroalgae, and phytoplankton on a temperate reef. *Limnol. Oceanogr.* 56, 119–132. doi: 10.4319/lo.2011.56.1.0119

Norici, A., Bazzoni, A. M., Pugnetti, A., Raven, J. A., and Giordano, M. (2011). Impact of irradiance on the C allocation in the coastal marine diatom *Skeletonema marinoi* Sarno and Zingone. *Plant Cell Environ.* 34, 1666–1677. doi: 10.1111/j.1365-3040.2011.02362.x

Palmucci, M., Ratti, S., and Giordano, M. (2011). Ecological and evolutionary implications of carbon allocation in marine phytoplankton as a function of nitrogen availability: A Fourier transform infrared spectroscopy approach. *J. Phycol.* 47, 313–323. doi: 10.1111/j.1529-8817.2011.00963.x

Pehlke, C., and Bartsch, I. (2008). Changes in depth distribution and biomass of sublittoral seaweeds at Helgoland (North Sea) between 1970 and 2005. *Clim. Res.* 37, 135–147. doi: 10.3354/cr00767

Pessarrodona, A., Assis, J., Filbee-Dexter, K., Burrows, M. T., Gattuso, J. P., Duarte, C. M., et al. (2022a). Global seaweed productivity. *Sci. Adv.* 8, eabn2465. doi: 10.1126/sciadv.abn2465

Pessarrodona, A., Filbee-Dexter, K., Krumhansl, K. A., Pedersen, K. A., Moore, P. J., and Wernberg, T. (2022b). A global dataset of seaweed net primary productivity. *Sci. Data* 9, 484. doi: 10.1038/s41597-022-01554-5

Pessarrodona, A., Moore, P. J., Sayer, M. D., and Smale, D. A. (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. doi: 10.1111/gcb.14303

Piñeiro-Corbeira, C., Barreiro, R., and Cremades, J. (2016). Decadal changes in the distribution of common intertidal seaweeds in Galicia (NW Iberia). *Mar. Environ. Res.* 113, 106–115. doi: 10.1016/j.marenvres.2015.11.012

Pokorny, J., Orr, P., Ondok, J., and Denny, P. (1989). Photosynthetic quotients of some aquatic macrophyte species. *Photosynthetica* 23, 494–506.

Rodgers, K. L., and Shears, N. T. (2016). Modelling kelp forest primary production using *in situ* photosynthesis, biomass and light measurements. *Mar. Ecol. Prog. Ser.* 553, 67–79. doi: 10.3354/meps11801

Ryther, J. H. (1956). The Measurement of Primary Production. *Limnol. Oceanogr.* 1, 72–84. doi: 10.4319/lo.1956.1.2.0072

Schaffelke, B., and 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. doi: 10.1080/09670269400650471

Scheschonk, L., Becker, S., Hehemann, J. H., Diehl, N., Karsten, U., and Bischof, K. (2019). Arctic kelp eco-physiology during the polar night in the face of global warming: a crucial role for laminarin. *Mar. Ecol. Prog. Ser.* 611, 59–74. doi: 10.3354/meps12860

Schiener, P., Black, K. D., Stanley, M. S., and Green, D. H. (2015). The seasonal variation in the chemical composition of the kelp species *Laminaria digitata, Laminaria hyperborea, Saccharina latissima* and *Alaria esculenta. J. Appl. Phycol.* 27, 363–373. doi: 10.1007/s10811-014-0327-1

Schreiber, U., Schliwa, U., and Bilger, W. (1986). Continuous recording of photochemical and non-photochemical chlorophyll fluorescence quenching with a new type of modulation fluorometer. *Photosynth. Res.* 10, 51–62. doi: 10.1007/BF00024185

Smale, D. A. (2020). Impacts of ocean warming on kelp forest ecosystems. *New Phytol.* 225, 1447–1454. doi: 10.1111/nph.16107

Smale, D. A., Pessarrodona, A., King, N., Burrows, M. T., Yunnie, A., Vance, T., et al. (2020). Environmental factors influencing primary productivity of the forest-forming kelp *Laminaria hyperborea* in the northeast Atlantic. *Sci. Rep.* 10, 12161. doi: 10.1038/s41598-020-69238-x

Smith, S. V. (1981). Marine macrophytes as a global carbon sink. *Science* 211, 838–840. doi: 10.1126/science.211.4484.83

Smith, L. M., Silver, C. M., and Oviatt, C. A. (2012). Quantifying variation in water column photosynthetic quotient with changing field conditions in Narragansett Bay, RI, USA. *J. Plankton Res.* 34, 437–442. doi: 10.1093/plankt/fbs011

Steeman-Nielsen, E. (1952). The use of radioactive carbon (^{14}C) for measuring organic production in the sea. *J. Cons. Int. Explor. Mer.* 18, 117–140. doi: 10.1093/icesjms/18.2.117

Stewart, W. D. P. (1974). *Algal physiology and biochemistry* (California: University of California Press).

Taiz, L., and Zeiger, E. (2002). *Plant physiology. 3rd* (Massachusetts: Sinauer Associates).

Tengberg, A., Hovdenes, J., Andersson, H. J., Brocandel, O., Diaz, R., Hebert, D., et al. (2006). Evaluation of a lifetime-based optode to measure oxygen in aquatic systems. *Limnol. Oceanogr.: Methods* 4, 7–17. doi: 10.4319/lom.2006.4.7

tom Dieck, I. (1992). North Pacific and North Atlantic digitate *Laminaria* species (Phaeophyta): hybridization experiments and temperature responses. *Phycologia* 31, 147–163. doi: 10.2216/i0031-8884-31-2-147.1

Trentman, M. T., Hall, R. O. Jr., and Valett, H. M. (2023). Exploring the mismatch between the theory and application of photosynthetic quotients in aquatic ecosystems. *Limnol. Oceanogr.: Lett.* 8, 565–579. doi: 10.1002/lol2.10326

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., and De Clerck, O. (2012). Bio-ORACLE: A global environmental dataset for marine species distribution modelling. *Glob. Ecol. Biogeogr.* 21, 272–281. doi: 10.1111/j.1466-8238.2011.00656.x

Voerman, S. E., Llera, E., and Rico, J. M. (2013). Climate driven changes in subtidal kelp forest communities in NW Spain. *Mar. Environ. Res.* 90, 119–127. doi: 10.1016/j.marenvres.2013.06.006

Weykam, G., Thomas, D. N., and Wiencke, C. (1997). Growth and photosynthesis of the Antarctic red algae *Palmaria decipiens* (Palmariales) and *Iridaea cordata* (Gigartinales) during and following extended periods of darkness. *Phycologia* 36, 395–405. doi: 10.2216/i0031-8884-36-5-395.1

White, L., Loisel, S., Sevin, L., and Davoult, D. (2021). *In situ* estimates of kelp forest productivity in macro-tidal environments. *Limnol. Oceanogr.* 66, 4227–4239. doi: 10.1002/lno.11955

Wiencke, C., and Bischof, K. (2012). *Seaweed biology. Ecological studies* (Heidelberg: Springer Verlag).

Williams, P. J. B., Raine, R. C. T., and Bryan, J. R. (1979). Agreement between ^{14}C and oxygen methods of measuring phytoplankton production: Reassessment of the photosynthetic quotient. *Oceanol. Acta* 2, 411–416.

Wright, L. S., Pessarrodona, A., and Foggo, A. (2022). Climate-driven shifts in kelp forest composition reduce carbon sequestration potential. *Glob. Change Biol.* 28, 5514–5531. doi: 10.1111/gcb.16299