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Effects of spectral light quality on the growth, productivity, and elemental ratios in differently pigmented marine phytoplankton species

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Abstract
The recent advancement in LED technology led many incubator manufacturers and research labs to switch to these more efficient, yet spectrally restricted, light sources. Potential effects of commercially available broad range "white" light systems on phytoplankton growth, productivity, light absorption spectra, and cellular composition have not yet been characterized but could affect our interpretation of lab-based projections on responses to environmental changes. In this study, we investigated such effects using cultures of *Prochlorococcus marinus*, *Synechococcus* sp., and *Thalassiosira weissflogii* grown under three different commercially available LED lights as well as one fluorescent growth light. Photosynthetically active radiation was equal for each species, while photosynthetically usable radiation differed among the combinations of species and treatments. Growth rate was unaffected across species, yet all species displayed changes in cellular carbon, nitrogen, and chlorophyll *a* quotas as a direct response to the different light spectra. ^{14}C-based primary productivity was also affected in *P. marinus* and *T. weissflogii.* Analysis of pigment ratios and photophysiological data indicated changes in the photoacclimation state between different light environments. The results of this study show that these species undergo changes in underlying cellular metabolism which in turn affect cellular composition while keeping specific growth constant. The data presented here illustrate ecophysiological responses of differently pigmented species when grown under different artificial growth light spectra. These cellular acclimation responses should be considered when designing laboratory-based incubation experiments, especially when comparing responses to specific changes in environmental conditions, or when implementing physiological parameters, derived from laboratory experiments, into numerical models.

Keywords Phytoplankton · Photosynthesis · Photoacclimation · Light spectra · Phytoplankton culturing · Ecophysiology

Introduction

Marine phytoplankton are mainly photoautotrophic organisms with the ability to efficiently convert light energy into biochemical energy via the process of photosynthesis. Thus, light availability is a key environmental factor affecting phytoplankton growth, productivity, and niche distribution (Six et al. 2007; Boyd et al. 2010). Numerous studies have been conducted investigating the effect of light intensity, light duration, and more recently effects of dynamically changing light on phytoplankton physiology (Falkowski and Owens 1978; Brand and Guillard 1981; Falkowski 1984; Glover et al. 1987; Rost et al. 2006; Hessen et al. 2008; Hoppe et al. 2015; Lehmuskero et al. 2018; White et al. 2020; Li et al. 2020). The ambient light spectrum has also been shown to play an important role in phytoplankton ecophysiology, because it is a determining factor of the ecological success of a species in different environments (Nielsen and Sakshaug 1993; Stomp et al. 2007; Cardol et al. 2008; Esposito et al. 2009; Partensky and Garczarek 2010; Hickman et al. 2010; Bhaya 2016; Luimstra et al. 2020). Furthermore, when other environmental parameters, such as temperature, CO_2, salinity, and/or nutrient concentrations, are varied, light interacts with

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the ecophysiological responses of the phytoplankton communities or cultures (Rhee and Gotham 1981; Redalje and Laws 1983; Healey 1985; Rost et al. 2006; Dickman et al. 2006; Finkel et al. 2006; Ivanikova et al. 2007; Feng et al. 2008; Kranz et al. 2010; Gao et al. 2012; Boatman et al. 2017; Li et al. 2020). Incubation studies which aim to identify or even separate the complex correlations between cellular responses and environmental parameters often follow best practice guides (e.g., Riebesell et al. 2011) to guarantee controlled laboratory environments. These unifying protocols allow for comparison of data between labs and its subsequent use to predict phytoplankton responses to environmental changes. Especially in the laboratory setup, we, however, often accept that the light spectrum (light quality) is seldomly measured and hardly ever mimics that of the natural environment in which different phytoplankton groups thrive. This can have important implications for the interpretation of the data as well as the intercomparison of studies.

To efficiently capture light energy throughout the photosynthetically active light spectrum and to dissipate excess energy which would lead to metabolically expensive damage to the photosynthetic machinery (Han et al. 2000; Katayama et al. 2017), phytoplankton species contain specific sets of pigments. These photosynthetic pigments contain so-called chromophores, tetrapyrroles and derivatives, chlorins and porphyrins, as well as carotenoids (Falkowski and Raven 2007). Closed tetrapyrroles can be split into two basic types, the chlorins, such as chlorophyll *a* (chl *a*) and *b*, and the porphyrins, such as chl *c* (Falkowski and Raven 2007). Chlorophylls all contain two main absorption bands for blue or blue-green and red light, and are the main light-harvesting pigments in the majority of marine phytoplankton, such as the prochlorophytes like *Prochlococcus marinus* (Chisholm et al. 1992; Goericke and Repeta 1992), along with dinoflagellates, chrysophytes, and diatoms, such as *Thalassiosira weissflogii* (Goericke and Welschmeyer 1992a). Generally, chl *a* is the main light-harvesting pigment which donates electrons to PSII and the photosynthetic electron chain while other chlorophylls, like chl *b* and *c*, act as accessory pigments capable of transferring excitation energy to chl *a* (Trees et al. 2000). Open tetrapyrroles (such as phycoerythrin (PE) found in *Synechococcus* sp. WH7803 (Gantt 1981)) are the chromophores found in the phycobilisomes of cyanobacteria and can absorb blue-green, green, yellow, or orange light. In these organisms, energy absorbed by phycobilisomes is transferred directly to photosystem II (PSII) or photosystem I (PSI) and used for energy generation (Gantt 1981). Carotenoids, some of which, like fucoxanthin found in *T. weissflogii*, are also photoactive (Goericke and Welschmeyer 1992b), while others such as diadinoxanthin, are photoprotective and function to dissipate excess energy away from PSII reaction centers. Energy dissipation occurs via conformational changes (e.g., diadinoxanthin to diaxanthin) which allow the xanthophylls to absorb energy from overexcited chl *a* triplets or neutralize reactive oxygen species, protecting the cell from PSII damage (Krinsky 1978; Siefermann-Harms 1985; Wilson et al. 2008). The combination of pigments in a specific phytoplankton determines the spectrum of light an organism can absorb for photosynthesis while the cellular concentration of these pigments is also tightly regulated in response to environmental signals (Beardall and Morris 1976; Prézelin 1976; Dubinsky and Stambler 2009). In order to better understand the wavelength-specific responses of phytoplankton, a process directly linked to the light spectrum available to the organisms, both in nature as well as in the laboratory, multiple studies have been performed using LEDs to quantify photosynthetic responses to distinct wavelengths (Wang et al. 2007; Stadnichuk et al. 2011; Miao et al. 2012; Rendon et al. 2013; Schellenberger Costa et al. 2013a, b; Kim et al. 2013; Marchetti et al. 2013; Xu et al. 2013; Abiusi et al. 2014; Jungandreas et al. 2014). These studies have demonstrated strong wavelength dependence for the activation and regulation of photoacclimation via photoreceptors as well as the influence of discrete light colors on cellular composition, which would be expected from photoautotrophic organisms. However, these studies have typically focused on either the addition or removal of monochromatic light from the growth light provided, which is not representative of light quality of often used phytoplankton culturing light sources.

Historically, laboratory studies investigating the physiological responses of phytoplankton species to environmental change have utilized "daylight" or "growth light" fluorescent bulbs to supply light. These specific fluorescent bulbs have an emission spectrum that supposedly resembles that of the natural solar light experienced at the surface of the ocean (e.g., GE Daylight Ecolux T12). A disadvantage of fluorescent bulbs is that they cannot easily replicate the dynamic and occasionally extreme high light intensity experienced by phytoplankton in nature, nor can their emission spectra be easily modified. These lights also have some very pronounced spikes throughout the photosynthetically active radiation (PAR) spectrum which is unlike any natural spectrum. Recently, light-emitting diode (LED) equipped incubators and stand-alone lights have become readily available for plant and phytoplankton growth and are increasingly used in phytoplankton studies. One of the characteristics of LEDs is that their spectra are typically restricted to narrow emission peaks and hence a mixture of two or more LEDs are used to cover the major light spectra needed for growth. As LED systems have become more flexible and powerful, LED incubators with simple, non-environmentally relevant emission spectra have become more commonly operated in culture studies of phytoplankton (see Schulze et al. 2014 for a review). Unfortunately, more complex LED systems, designed to mimic natural spectra (Göritz et al. 2017), are

not commercially available and hence not utilized in laboratories to date. Consequently, laboratory incubations show a limited capacity to simulate ecologically relevant light regimes which phytoplankton would experience in their natural habitat. These natural variations can be caused, e.g., by mixing up and down the water column, transient cloud cover, waves, or suspended matter, and are experienced by phytoplankton on both short- and long-term timescales. The use of different LED systems between different labs might affect the comparability of data on the responses of species to specific environmental conditions. The goal of this study is to evaluate responses of three uniquely pigmented phytoplankton species to commercially available growth lights which might be used in culture studies. The light systems in our study were chosen to represent both common incubators setups, which include fluorescent bulbs and Bright White LED strips, as well as low-cost commercially available LEDs of differing spectral composition designed to mimic an aquatic light environment. Our hypothesis for this experiment is that the unique emission spectra of the growth lights, despite being broad range "white" light, and the species-specific pigmentation of the individual phytoplankton species will alter photosynthetic machinery and metabolic regulation differently despite similar PAR. To answer this hypothesis, we provide an understanding of the physiological responses including growth rate, primary productivity, elemental composition, chl *a* content, relative pigment composition, and photophysiological properties. Information from this study could help to clarify differences in results from studies using similar environmental treatments, yet different light sources clarify responses of phytoplankton from bottle incubations of a natural community acclimated under artificial light conditions and provide insights for choosing an appropriate growth light for lab-based studies.

Materials and methods

Culture conditions

Prochlorococcus marinus (CCMP1986), *Synechococcus* sp. (CCMP1334), and *Thalassiosira weissflogii* (CCMP1336) obtained from the National Center for Marine Algae and Microbiota were acclimated to four different light sources using a semi-continuous batch culture approach. All cultures were maintained at 22°C in a walk-in temperature-controlled room and grown in modified artificial seawater based on Aquil media (Price et al. 1989) with 25 µM Na_2HPO_4 as the phosphorus source as well as 400 µM $NaNO_3$ as the nitrogen source for *Synechococcus* sp. and *T. weissflogii* and 400 µM NH_4Cl as the nitrogen source for *P. marinus*. Additionally, *P. marinus* only received B_{12} for vitamins and $1/10^{th}$ of the typical Aquil metal mix added. *T. weissflogii* was supplemented with 50 µM Si for growth. *T. weissflogii* and *P. marinus* were maintained at 100 μmol photons·m^{-2}·s^{-1} while *Synechococcus* sp. was maintained at 50 μmol photons·m^{-2}·s^{-1}. Light was on a 12:12 h light:dark cycle and illumination intensity remained constant during the photoperiod. Cultures were grown in 250 mL square polycarbonate bottles (5.7 cm pathlength) and lighting was provided from the side. Cultures were grown and tested in triplicate and given at least 7 generations (approximately 2–4 weeks) to adapt to the different light sources before being used for experiments. The different irradiances in our cultures were chosen by analyzing best growth under a range of light intensities during the pre-acclimation phase. The highest irradiance (PAR) at which consistent growth was observed in our lab across growth lights was subsequently used for all light sources. Cells were kept in low- to mid-exponential growth throughout pre-acclimation, and all experiments were performed in mid-exponential phase of each growth cycle at similar cell number densities within each species and therefore similar optical conditions across light sources. Cultures were diluted to around 9.5×10^6, 5.0×10^6, and 500 cells mL^{-1} and harvested around $2.0–3.0\times10^7$, $2.0–3.0\times10^7$, and 3000–4000 cells mL^{-1} for *P. marinus*, *Synechococcus* sp., and *T. weissflogii*, respectively. Keeping the cells in optically dilute densities with similar concentrations between the different light acclimations within one species and in identical setups ensured that differences observed in this study were the result of disparities in the light spectra provided instead of from different levels of self-shading or light scattering at different wavelength.

Lights used for culture growth include a Fluorescent bulb (GE Daylight Ecolux T12), a Bright White LED (Bright White LED Strip Lights, Cool White), an Aquarium LED (NICREW ClassicLED Plus LED Aquarium Light), and a phytoplankton growth light (Kyocera Aqua light). The photon emission spectra for wavelengths in the photosynthetically active radiation spectrum (PAR, 400–700 nm) of the chosen growth lights are shown in Figure 1a–d. Values shown are normalized so that $\sum_{400}^{700} E_\lambda = 100$ µmol photons·m^{-2}·s^{-1} for comparison between light sources. The specifics of the light emission spectra are roughly described below: the Kyocera LED (Fig. 1a) has a main emission peak around 500 nm with significant light emission between 450 and 600 nm. Between 600 and 700 nm, the emission is strongly reduced. The emission ratio (ER) of red (675nm) to blue (450nm) light was 0.41. This light mimics a natural light spectrum as seen in 5–10 m water depth of clear ocean waters relatively well. A comparison of the Kyocera LED spectrum with natural solar and theoretical spectrum calculated for a 7.5 m water depth is shown in Online Resource, Figure S4. The Bright White LED (Fig. 1b) has a main emission peak at 570 nm and a secondary peak at around 450 nm and an ER of 0.29. A significant dip in the emission

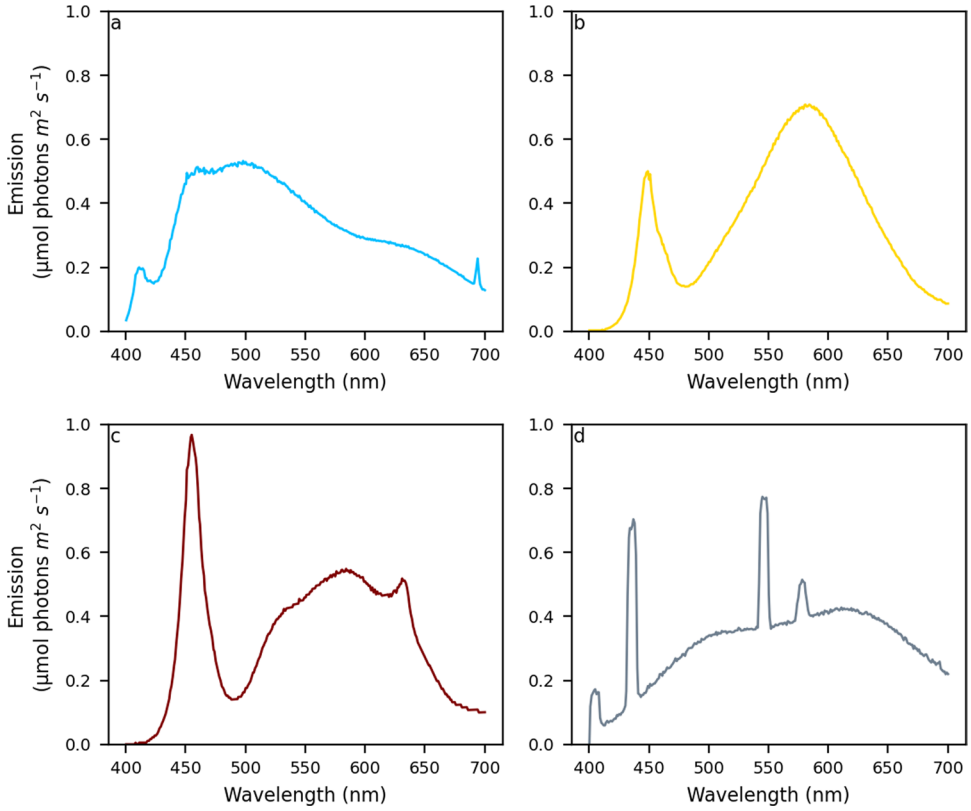


Fig. 1 **a–d** Emission spectra in for the growth lights used in this study normalized to 100 µmol photons·m^{-2}·s^{-1} for comparison between light sources

spectrum with a minimum at around 480 nm is characteristic for this kind of "off the shelf white LED" light. The Aquarium LED (Fig. 1c) has a narrow peak around 450 nm and a broad peak spanning 525–650 nm, due to multiple differently colored LEDs embedded in the array, with an ER of 0.17. The Fluorescent bulb (Fig. 1d) has a main broad peak spanning 500–650 nm, with high spikes at approximately 400, 430, 550, and 575 nm, and an ER of 1.65, the only light providing more red than blue light.

Growth, Chl a, elemental composition, absorbance

Specific growth rates were measured via cell count using a flow-cytometer (CytoFLEX, Beckman, USA). The specific growth rate was estimated by an exponential fit through the data during exponential growth. All experiments and analytical samplings were performed during mid-exponential growth. Samples for cellular chl *a* concentration were taken using gravity filtration onto a GF/F filter during mid-exponential growth. The filter was stored at −20°C until processing. Chl *a* was extracted in 90% acetone for 24 h in the dark at −20°C, sonicated for a brief period and subsequentially measured using a UV/VIS spectrophotometer (Evolution 220, ThermoFisher, USA). Chl *a* concentration was calculated following Eq. 1, adapted from the JGOFs protocol:

$$A(664)–A(750) \times V_A/87.67 \times l \times V_S \quad (1)$$

where $A(664)$ and $A(750)$ are the absorbance at 664 and 750 nm, V_A is the volume of acetone used for extraction in L, 87.67 is the extinction coefficient for chl *a* in 90% acetone, l is the cuvette length in cm, and V_S is the volume of sample filtered. Particulate organic carbon and nitrogen (POC and PON) samples were taken in the same manner. For POC and PON, precombusted GF/F filters (400°C, 12h) were used, followed by an acidification and drying step before sending the compressed filters to the Stable Isotope Facility at University of California, Davis for analysis via a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., UK).

Cellular light absorbance spectra were obtained by measuring the absorbance of a mid-exponential culture sample in artificial seawater media between 400 and 800 nm at 1 nm increments in a UV/VIS spectrophotometer using a 10 cm quartz cuvette (Evolution 220, ThermoFisher). In order to determine the contribution of individual pigments to the absorption spectra, a spectral deconvolution method based on Thrane et al. (2015) was applied. It is important to note that within this deconvolution method, a background spectra which accounts for light attenuation not attributable to pigment absorption (e.g., light scatter) is accounted for (see Online Resource, Fig. S1–S3). *In vivo* pigment absorption spectra were used as described in Bidigare et al. (1990) and

adjusted for absorbance peak shifts which occur due to protein-pigment complexes which form in vivo (Prézelin 1981). Despite the spectrum correction, we would like the reader to note that differences in methods (absorptance of a cell suspension (our study) vs. absorptance of pigments dissolved in ethanol (Thrane et al. 2015)) could result in an intrinsic bias in pigment deconvolution. Parameterization used for our study are given for each species and the respective pigments in Online Resource, Table S1. Additional information on the model used is given in the Online Resource.

Relative absorption coefficients for each culture were obtained from the background corrected-absorption data using Eq. 2 following Kirk (2010):

$$a_\lambda = 2.303\, D_\lambda / r \tag{2}$$

where 2.303 is the factor for converting base *e* to base 10 logarithms, D_λ is the raw measured value for light absorption at each wavelength, and *r* is the pathlength through the cuvette in m. Please note that absorption coefficients are declared "relative" since we did not have a integrating sphere; hence, absolute values would be underestimated despite scatter correction. Values for the chl *a* specific absorption coefficient, a^*_λ, were then calculated by dividing a_λ by the chl *a* concentration of the cultures in units of mg chl $a{\cdot}m^{-3}$. Determination of photosynthetically usable radiation (PUR) was calculated using Eq. 3:

$$PUR = \sum_{400}^{700} E_\lambda \times a^*{}_\lambda \tag{3}$$

where E_λ is the quantity of photons emitted at each wavelength λ normalized so that $\sum_{400}^{700} E_\lambda = 100$ or 50 µmol photons$\cdot m^{-2}\cdot s^{-1}$ for comparison between light sources and $a^*{}_\lambda$ is the chl *a* specific absorption coefficient for each culture at wavelength λ (Morel 1978). Emission spectra for the different growth lights were measured using a calibrated FLAME-S-VIS-NIR-ES Spectrometer (Ocean Insight). Light emission at each wavelength (given in $W{\cdot}m^{-2}{\cdot}nm^{-1}$) was further converted into photon flux density at each wavelength. Details on these calculations as well as the spectrometer calibration can be found in the Online Resource. Due to the relative nature of our measurements of a_λ, data can only be compared between acclimations of the same species and would be unreliable between species.

^{14}C primary productivity

Rates of primary productivity (PP) were determined using ^{14}C-labeled bicarbonate ($NaH^{14}CO_3$) (Nielsen 1952). Cultures in mid-exponential phase were placed in 20 mL borosilicate glass reaction vials and spiked with 0.5 µCi of $NaH^{14}CO_3$. Cultures were then placed in their respective growth chambers. Measurements started at the beginning of the dark period to allow for bottle acclimation to occur in the dark. Based on this setup, estimates of productivity (further referred to as PP) have to be assumed to be between net and gross primary production (NPP, GPP), as they did not include respiration after ^{14}C uptake (Marra 2009). Over the duration of the light phase, vials were inverted regularly to avoid settling. A dark and *t*=0 control were performed for reference. Incubations were stopped after 24 h at the beginning of the following dark period by filtration with gentle pressure onto either GF/F (*T. weissflogii*) or 0.22 µM PES filters (*P. marinus and Synechococcus* sp.). Filters were placed into 20 mL scintillation vials and 600 µL of 6N HCl was added to remove all remaining $^{14}CO_2$. After 24 h of degassing, 10 mL of scintillation cocktail was added to each filter. Samples were counted in a Liquid Scintillation Counter (TriCarb 5110 TR, PerkinElmer, USA) to obtain disintegrations per minute (DPM). The total ^{14}C spike was determined using an aliquot of each sample at the time of incubation termination, transferred into 50 µL of ethanolamine, and 7 mL of scintillation cocktail was immediately added. Rates of PP were then calculated according to Eq. 4:

$$\mathrm{PP} = \frac{\mathrm{SDPM}}{V} \times \mathrm{W} \times \frac{0.2\mathrm{x}10^{-3}}{TDPM} \times 1.05 \times \frac{1}{T} \tag{4}$$

where *SDPM* is the sample DPM, *V* is the volume of the sample in L, *W* is the concentration of dissolved inorganic carbon in the incubations (around 2300 µM), $0.2{\times}10^{-3}$ is the volume of the total count aliquot in L, *TDPM* is the sample's total DPM count, and 1.05 represents the isotope discrimination factor between $^{12}C/^{14}C$. *T* is time in hours. Rates of PP were normalized to both the cell concentration and the cellular chl *a* content using chl *a* $cell^{-1}$ values measured in this study. Productivity data were additionally compared to electron-based productivity data (JVPII; µmol electrons $cell^{-1}$ s^{-1}; see "Photophysiological parameters") to determine the electron to C ratios (K_c) using the following equation:

$$K_c = \mathrm{JVPII}_{acc}/\mathrm{PP} \tag{5}$$

where $JVPII_{acc}$ is the electron-based primary productivity at each species' respective acclimation light level, calculated as described in Eq. 7, and *PP* is the productivity rate calculated according to Eq. 4.

Photophysiological parameters

Rapid fluorescence induction light curves (FLC) were measured using a fast repetition rate fluorometer (FRRf, FastOcean PTX, Chelsea Technologies, UK) along with a FastAct Laboratory system (Chelsea Technologies). FLCs for each species were measured within 2 h in the middle of the photoperiod (5–7 h after onset of the light). The

FastOcean was set to deliver single turnover induction protocols which varied between the species, with these settings listed in Online Resource, Table S3. Cells were dark acclimated for 5 min before the start of each FLC and each of the 10 light steps lasted 1 min each. Excitation flashlets had a peak excitation at 450 nm, and thus the reported measurements of PSII absorption are specifically weighted to 450 nm for *P. marinus* and *T. weissflogii*. For *Synechococcus* sp., data from excitation flashlets with peak excitations at 450 and 530 nm was used as PE is the main photoactive pigment in this species. Measured fluorescence parameters included the dark-adapted minimum (F_0) and maximum fluorescence (F_m), the light-adapted fluorescence at the zeroth flashlet (F'), and the light-adapted maximum fluorescence (F_m'). Estimations of the dark-adapted functional absorption cross-section area of PSII (σ) and the acclimation light intensity non-photochemical quenching using the normalized Stern-Volmer quenching coefficient (NSV) were obtained from the Act2Run software (Oxborough et al. 2012). Electron-based primary productivity (JVPII; µmol electrons cell^{-1} s^{-1}), used to fit the photosynthesis vs irradiance (P vs. I) curve parameters, light saturation point (E_K) and the slope for light limited photosynthesis (α) (Webb et al. 1974), was obtained from the Act2Run software, which calculates JVPII based on the following equation:

$$JVPII = \frac{F_m * F_0}{F_m - F_0} \times \frac{F'_q}{F'_m} \times \frac{K_R}{E_{LED}} \times E \quad (6)$$

where $F_q' = F_m' - F$, K_R is an instrument specific constant, E_{LED} is the photon output from the FRRf measuring LEDs, and E is the incident PAR (Oxborough et al. 2012). To account for any differences in biomass between samples at the time of FRRf measurement, JVPII data was normalized to the cell concentration at the time of measurement. Rapid FLCs require different interpretation compared to growth responses under increasing irradiances or steady state P vs I measurements. In a rapid FLCs, E_K values depict the irradiance at which PSII becomes light saturated under the current photoacclimation state.

A spectral correction was applied to correct for the differences in light spectrum between the actinic light in the FRRf and the growth lights (according to Suggett et al. (2001)):

$$\text{Spectrally corrected light intensity} = \frac{\sum_{400}^{700} E_\lambda * a^*{}_\lambda}{\sum_{400}^{700} E_{FRRf,\lambda} * a^*{}_\lambda} \times E_{FRRf} \quad (7)$$

where E_λ and $E_{FRRf,\lambda}$ are the spectral distributions of the growth lights and the FRRf actinic light, respectively, $a^*{}_\lambda$ is the chl a specific absorption coefficient for each culture at wavelength λ, and E_{FRRf} is the light intensity at each light step of the FLC in µmol photons·m^{-2}·s^{-1} (Suggett et al. 2001). Biomass normalized JVPII was subsequentially plotted against these spectrally corrected light intensities and fit using the Scipy package functions in python to obtain light saturation point (E_K) and the slope for light limited photosynthesis (α) (Webb et al. 1974).

Statistical analysis

Analysis of variance (ANOVA) and Tukey's tests were performed at $\alpha = 0.05$ using the MATLAB and Statistics and Machine Learning Toolbox (2018). Data for ANOVA was grouped by light source for each species with replicates for each acclimation to test for overall differences between groups. ANOVA result parameters such as the significance level (p), the F-statistic (F), degrees of freedom (df), sum of squares (SS), and mean squares (MS) for these groupings are reported in Online Resource, Tables S6–8. Post hoc Tukey's tests were used to determine which groups were different. Data presented are means and standard deviation of triplicate biological samples unless noted otherwise.

Results

Spectral analysis, PUR, growth, elemental composition

Absorption spectra for *P. marinus* did not vary significantly between the differently acclimated cultures, with all but the Kyocera LED cultures being indistinguishable (Fig. 2a). Characteristic peaks for chl a were observed at approximately 450 and 676 nm and a peak likely representing beta-carotene in the 500 nm region. The most notable difference was seen in the Kyocera LED which had higher a* values between 400–500 nm and 660–680 nm ranges. PUR was identified to be highest for the Kyocera cultures, while the Bright White light provided significantly less PUR (roughly 50% of PUR calculated for Kyocera) (Fig. 2b). Estimates of the relative amounts of chl a and b as well as photoprotective carotenoids (PPC), as derived from the model fits, are shown in Online Resource, Table S2 and indicate that around 65% of the light absorption originates from photosynthetically active pigments and 45% from non-photosynthetically active pigments. Despite the seemingly similar absorption scans, a slightly, yet significantly lower ratio of PPC/photoactive pigments was found in the Bright White culture compared to the other light sources (Fig. 2c, Online Resource, Table S2). The Chl a content in *P. marinus* was significantly higher in the Kyocera compared to the Bright White and Aquarium cultures (Table 1).

In *Synechococcus* sp., characteristic peaks for chl a, PE (at 550 nm), and a carotenoid, most likely zeaxanthin (500 nm), were observed in the absorption scans. Throughout the measured light spectrum, a^* was highest for the cells

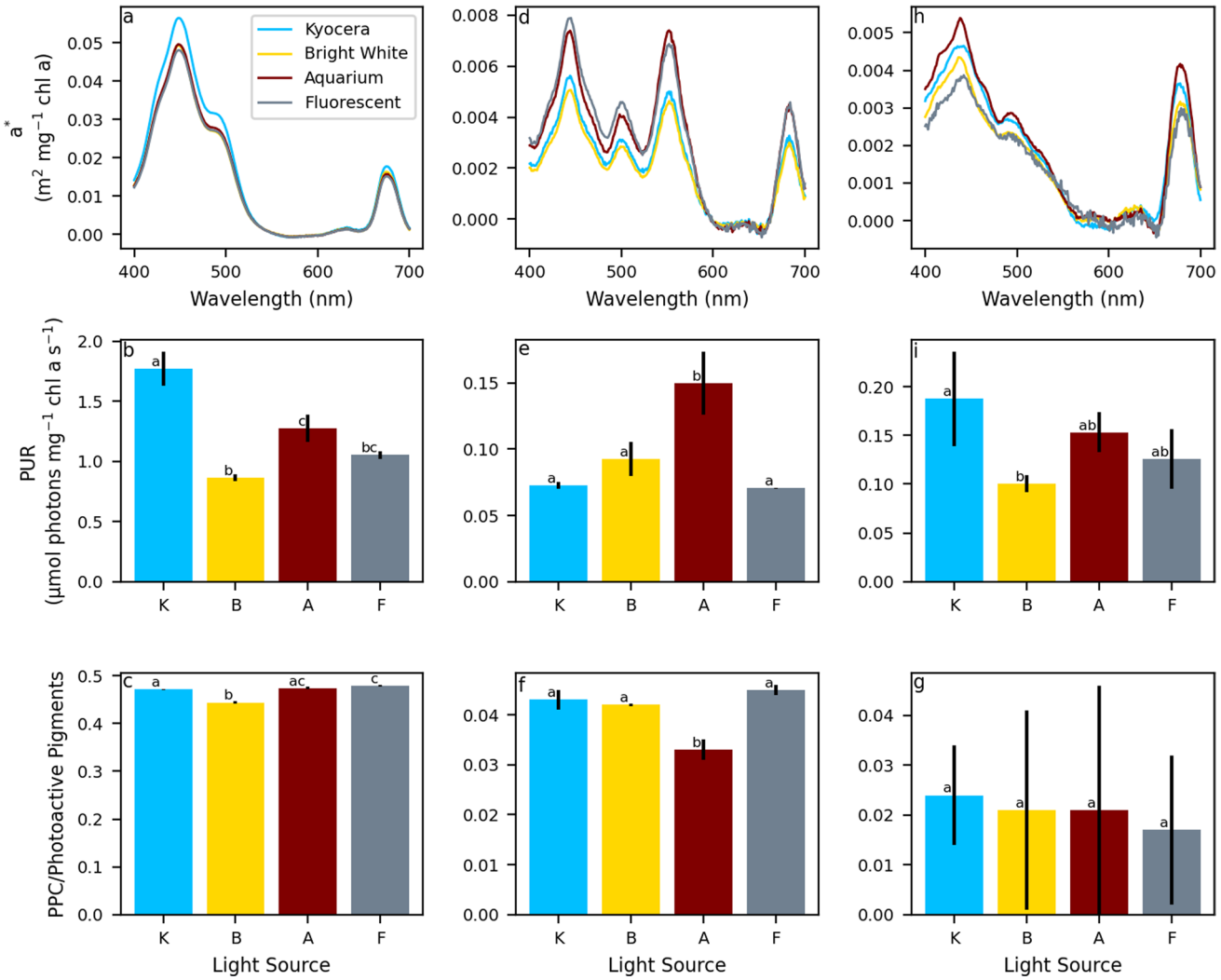


Fig. 2 Cellular light absorption with subtracted background spectrum for *Prochlorococcus marinus* (**a**), *Synechococcus* sp. (**d**), and *Thalassiosira weissflogii* (**h**); calculated PUR for *Prochlorococcus marinus* (**b**), *Synechococcus* sp. (**e**), and *Thalassiosira weissflogii* (**i**); and photo-protective-carotenoid (PPC)/photoactive ratios obtained from the spectral deconvolution for *Prochlorococcus marinus* (**c**), *Synechococcus* sp. (**f**), and *Thalassiosira weissflogii* (**g**). Values shown are mean values for biological replicates ± s.d, $n \geq 2$

grown under Fluorescent and Aquarium light (Fig. 2d). The cultures acclimated to the Aquarium LED displayed highest absorbance around 550 nm where PE absorbs, while the Fluorescent cultures showed higher values between 425 and 525 nm. PUR was highest for the Aquarium cultures, while no significant differences were seen between the other acclimations (Fig. 2e). Spectral deconvolution estimates of the relative amounts of chl *a*, PE, as well as PPC (Online Resource, Table S2) indicate that PE was around 3.5 times the amount of chlorophyll and that 3 to 4% of the total pigments are non-photosynthetically active pigments. The Aquarium light cultures showed a slightly, yet, statistically significant higher PE/chl *a* ratio (Online Resource, Table S2) as well as a slightly lower PPC/photoactive pigment ratio (Fig. 2f) than the rest of the acclimations. Cells grown under the Fluorescent light exhibited significantly higher cellular chl *a* concentration compared to the Aquarium cultures (Table 1).

In *T. weissflogii*, peaks for chl *a* and c along with peaks for photosynthetically active carotenoids (PSC) and PPC were observed. The Aquarium cultures had the highest a^* values across the 400–525 nm range as well as the 660–680 nm range, with the Fluorescent cultures having the lowest values (Fig. 2h). In *T. weissflogii*, PUR was higher in the Kyocera compared to the Bright White LED, while the Aquarium and Fluorescent lights were not significantly different from any other light source (Fig. 2i). Spectral deconvolution indicated no changes in pigment ratios between the light source acclimations. About 2% of the total pigments were calculated to be PPC (Fig. 2g, Online Resource, Table S2). A higher chl

Table 1 Growth rates (μ day^{-1}), POC and PON (fg·cell^{-1} for *Prochlorococcus marinus* and *Synechococcus* sp., pg·cell^{-1} for *Thalassiosira weissflogii*), C:N (mol:mol), chl *a*·cell^{-1} (fg chl *a*·cell^{-1} for *P. marinus and Synechococcus* sp., pg chl *a*·cell^{-1} for *T. weissflogii*), and C:chl *a* (µg:µg). Values shown are mean values for biological replicates ± s.d. Stars represent samples which have n=2 instead of n=3. Letters represent significant groupings from one-way ANOVA and HSD post hoc tests ($p < 0.05$), and boldface indicates a parameter with significant difference between groups

		Kyocera	Bright White	Aquarium	Fluorescent
Prochlorococcus marinus	Growth rate	0.25 ± 0.04^{a}	0.24 ± 0.04^{a}	0.25 ± 0.04^{a}	0.25 ± 0.04^{a}
	POC	**99.2 ± 6.2^{a}**	**55.5 ± 0.8^{b}**	**73.9 ± 4.1^{c}**	**79.8 ± 6.9^{c}**
	PON	**21.0 ± 1.1^{a}**	**12.0 ± 0.4^{b}**	**16.0 ± 1.0^{c}**	**16.7 ± 0.9^{c}**
	C:N	5.52 ± 0.38^{a}	5.38 ± 0.09^{a}	5.38 ± 0.05^{a}	5.56 ± 0.19^{a}
	chl *a*	**3.14 ± 0.10^{a}**	**2.48 ± 0.03^{b}**	**2.54 ± 0.23^{b}**	**2.77 ± 0.16^{ab}**
	C:chl *a*	**33.8 ± 1.9^{a}**	**25.9 ± 0.3^{b}**	**30.8 ± 1.3^{a}**	**32.3 ± 0.8^{a}**
Synechococcus sp.	Growth rate	0.33 ± 0.07^{a}	0.31 ± 0.04^{a}	0.32 ± 0.02^{a}	0.31± 0.02^{a}
	POC	**308.1 ± 10.0^{a}**	**289.7 ± 13.0^{a}**	**258.6 ± 3.7*^{b}**	**304.9 ± 7.0^{a}**
	PON	**60.5 ± 1.9^{a}**	**57.3 ± 2.5^{a}**	**49.8 ± 1.6*^{b}**	**57.9 ± 1.7^{a}**
	C:N	5.95 ± 0.21^{a}	5.89 ± 0.18^{a}	6.07 ± 0.28*^{a}	6.15 ± 0.15^{a}
	chl *a*	**5.06 ± 0.28^{ab}***	**3.61 ± 0.71^{ab}**	**2.82 ± 0.62^{a}***	**5.20 ± 0.67^{b}***
	C:chl *a*	**63.5 ± 4.3^{ac}**	**85.5 ± 11.8^{ab}**	**89.9 ± 10.1^{b}***	**61.8 ± 6.7^{c}**
Thalassiosira weissflogii	Growth rate	0.86 ± 0.05^{a}	0.83 ± 0.04^{a}	0.86 ± 0.03^{a}	0.84 ± 0.03^{a}
	POC	**93.7 ± 7.0^{a}**	**86.2 ± 11.3^{ab}**	**67.7 ± 2.2^{b}**	**81.8 ± 11.7^{ab}**
	PON	18.2 ± 2.3^{a}	19.3 ± 1.2^{a}	15.1 ± 1.0^{a}	19.5 ± 2.4^{a}
	C:N	**6.04 ± 0.32^{a}**	**5.21 ± 0.39^{ab}**	**5.26 ± 0.43^{ab}**	**4.89 ± 0.22^{b}**
	chl *a*	**5.74 ± 0.23^{a}**	**6.08 ± 0.16^{ab}**	**6.42 ± 0.42^{bc}**	**6.97 ± 0.13^{c}**
	C:chl *a*	**20.7 ± 1.7^{a}**	**19.7 ± 2.0^{ab}**	**14.4 ± 0.9^{c}**	**15.9 ± 1.2^{bc}**

a cell^{-1} in the Fluorescent and Aquarium compared to the Kyocera cultures was observed (Table 1).

Pigment ratio data obtained for *P. marinus* matches values reported in Moore et al. (1995), *Synechococcus* sp. values are similar to those reported in Barlow and Alberte (1985) and Kana et al. (1988), and *T. weissflogii* values align with van de Poll et al. (2007) and Goericke and Welschmeyer (1992a). Please note, while the absorbance spectra, measured in vivo in culture suspensions, contain some inherent bias, we believe that the data obtained from the spectral deconvolution is reliable, especially as the data fit well with previously mentioned published data.

Growth rates of all species were independent of the light source (Table 1). For *P. marinus*, cellular POC and PON contents were significantly different, being highest for the Kyocera and lowest for the Bright White with no changes between the Aquarium and Fluorescent cultures (Table 1). C:N ratios did not change significantly between light source acclimations (Table 1). C:chl *a* ratios were 23% lower in the Bright White compared to the Kyocera cultures (Table 1).

Synechococcus sp. cells grown under the Aquarium LED had the lowest cellular POC and PON (Table 1). C:N ratios showed no significant changes (Table 1) and C:chl *a* ratios were highest in the Aquarium and 30% lower in the Kyocera and Fluorescent cultures (Table 1).

Thalassiosira. weissflogii cells significantly changed POC but not PON across light source acclimations (Table 1) resulting in changes to C:N ratios with Kyocera being highest and Fluorescent being lowest (Table 1). The Aquarium and Fluorescent cultures showed 30 and 23% lower values for C:chl *a* compared to the Kyocera culture (Table 1).

Primary productivity

Cell-normalized ^{14}C derived PP rates for *P. marinus* were significantly lower (31–41%) in the Bright White cultures compared to all other acclimations, with the Kyocera culture additionally showing significantly lower rates (12.5%) compared to the Fluorescent culture (Fig. 3a, Online Resource, Table S4). In *Synechococcus* sp., there were no significant differences in cell-normalized ^{14}C derived PP rates (Fig. 3c, Table Online Resource, S4). In *T. weissflogii*, cell-normalized ^{14}C derived PP rates were significantly lower (31%) in the Bright White cultures compared to the Fluorescent cultures (Fig. 3e, Online Resource, Table S4).

In *P. marinus*, K_c, or the electron to carbon ratios, calculated from JVPII data at acclimation light and ^{14}C derived PP were roughly 30% higher in the Bright White LED treatment compared to all other treatments (Fig. 3b, Online Resource, Table S4). No significant differences in K_c between light sources were found for *Synechococcus* sp. (Fig. 3d, Online Resource, Table S4) nor *T. weissflogii* (Fig. 3f, Online Resource, Table S4).

Overall, the largest differences in productivity between the different normalizations are shown in *Prochlorococcus*. Here, the productivity normalized to the absorbed light showed a clear reduction under the Kyocera light source compared to the cell-normalized rates. Additionally, despite having the lowest cell-normalized rates, the electron requirement was highest under the Bright White LED. Please note that rates of C-fixation, while defined here as net productivity, are biased by the fact that ^{14}C PP estimates represent rates between net and gross

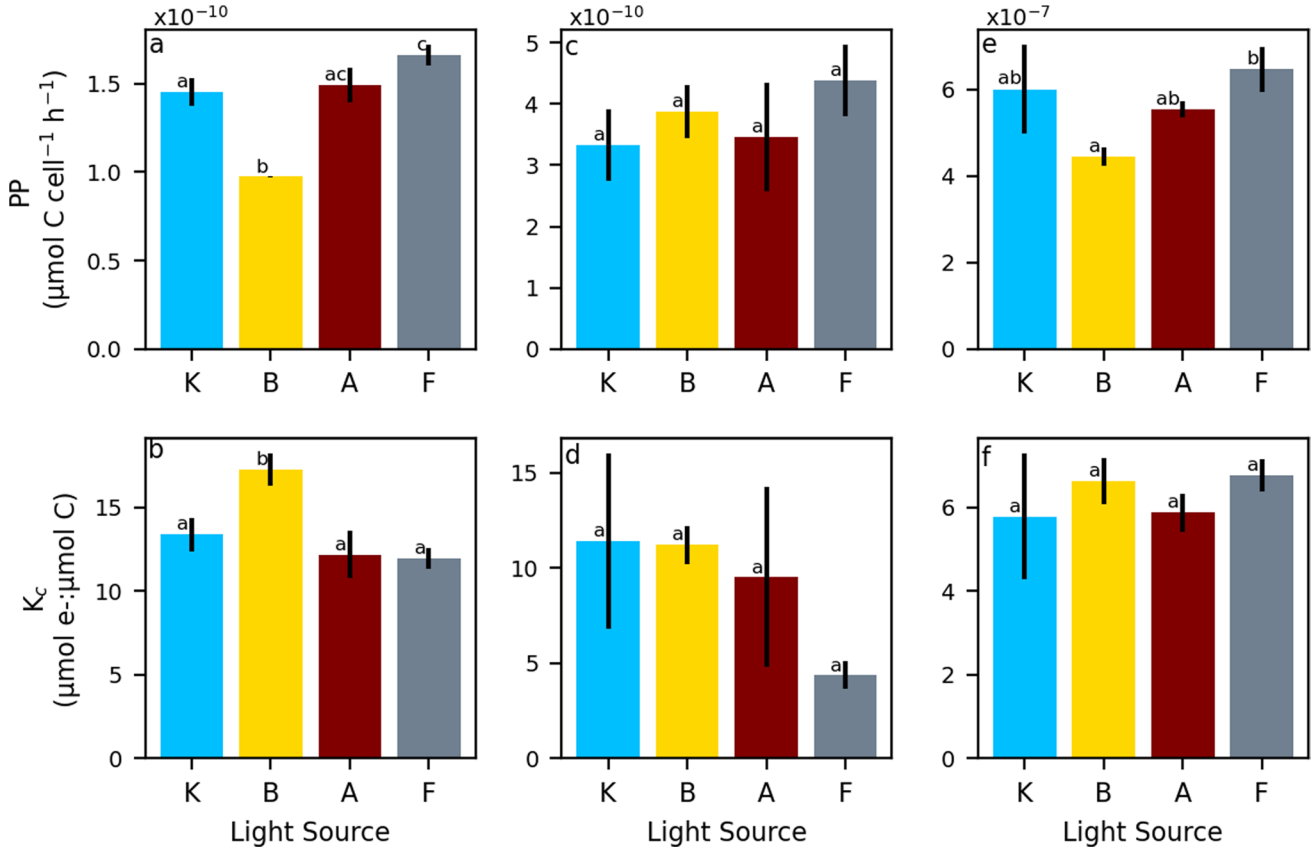


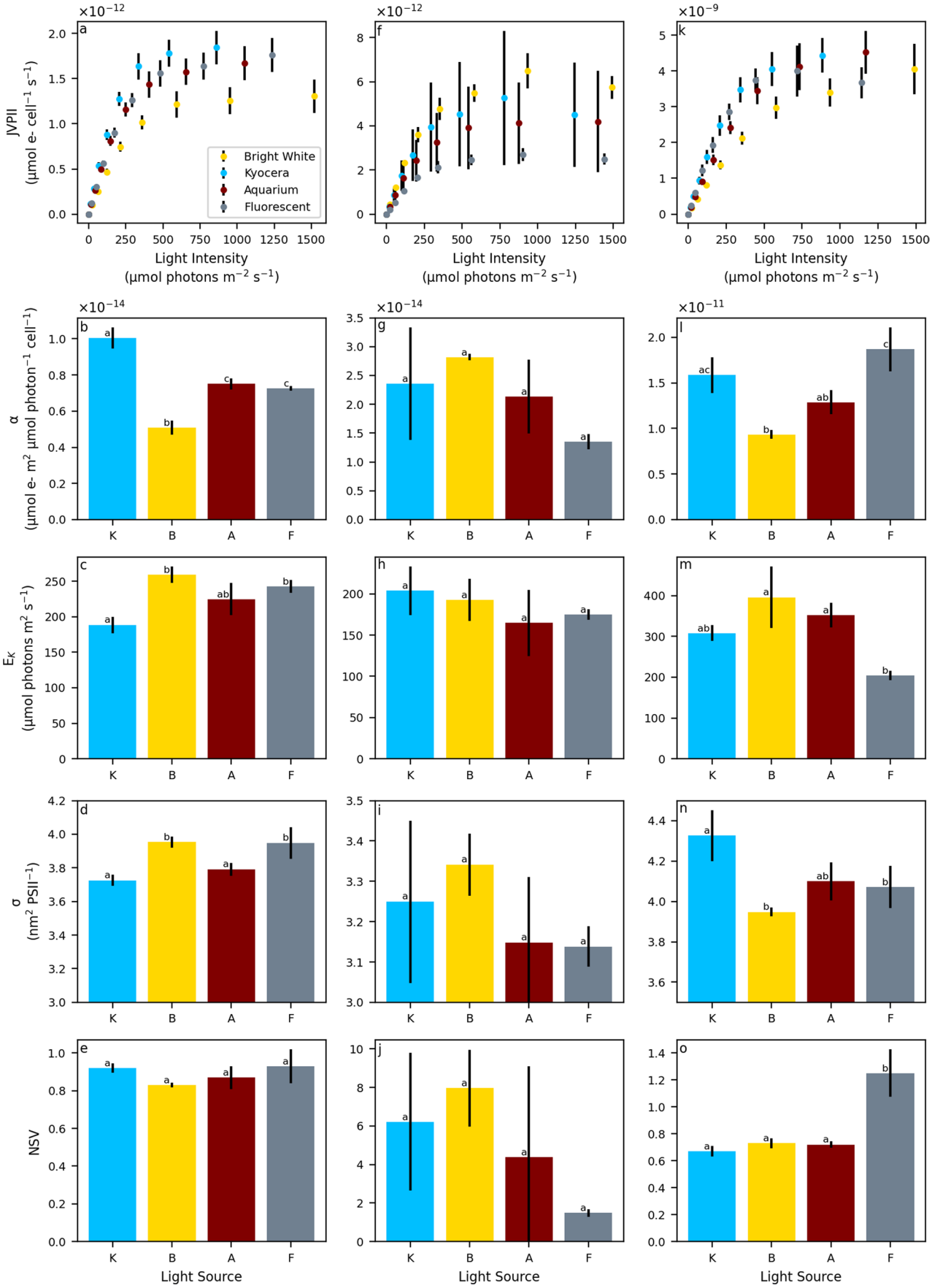
Fig. 3 Primary productivity (PP) estimates from ^{14}C incubations normalized to cell concentration for *Prochlorococcus marinus* (**a**), *Synechococcus* sp. (**c**), and *Thalassiosira weissflogii* (**e**); electron to carbon (K_c) estimates from ^{14}C incubations and JVPII data for *Prochlorococcus marinus* (**b**), *Synechococcus sp.* (**d**), and *Thalassiosira weissflogii* (**e**). Cell-normalized rates are $\times 10^{-10}$ for *P. marinus* and *Synechococcus* sp. and $\times 10^{-7}$ for *T. weissflogii*. Values shown are mean values for biological replicates ± s.d, $n \geq 2$. Letters represent significant groupings from one-way ANOVA and HSD post hoc tests ($p < 0.05$)

productivity, especially since we spiked the radiolabel at the start of a dark phase, prior to the light phase, and harvested cells at the onset of the following dark phase. Furthermore, electron-based productivity estimates, JVPII, are a measure of gross photosynthesis, most closely related to gross O_2 evolution, and therefore gross productivity (Genty et al. 1989; Edwards and Baker 1993). This results in our K_c estimates more closely representing gross efficiency, rather than net efficiency (Lawrenz et al. 2013).

Comparing the carbon production estimates from our ^{14}C-based PP estimates (cell-normalized) with those derived from the daily growth rate and cellular carbon quotas, ratios varying between 0.91 and 2.18 are found. For *P. marinus*, estimates varied between 1.59 and 2.18, for *Synechococcus* sp., values ranged between 0.91 and 1.27, and in *T. weissflogii*, values ranged between 1.29 and 2.01 (Online Resource, Table S4). It is important to note that our ^{14}C measurements do not account for respiration in the dark and only partially for respiration in the light and that the productivity estimate based on POC×µ describes the "true" 24h net productivity while the ^{14}C-PP data depict a mix between net and gross productivity only during the light period.

Photophysiology

Photophysiology was measured to acquire additional parameters on photoacclimation and productivity (Fig. 4, Online Resource, Table S5). Photosynthesis vs. irradiance (P v I) curves fit against the spectrally corrected light intensities are shown in Fig. 4a, f, and k. The α values for *P. marinus* were lowest in the Bright White, and highest in the Kyocera cultures (Fig. 4b, Online Resource, Table S5). E_K values were lower in the Kyocera compared to the Bright White and Fluorescent cultures (Fig. 4c, Online Resource, Table S5). Values for dark-adapted σ in *P. marinus* in the Bright White and Fluorescent acclimations were significantly higher (5.75%) than in the Kyocera acclimation (Fig. 4d). Non-photochemical quenching (NSV) did not significantly differ between light source acclimations (Fig. 4e, Online Resource, Table S5). No significant changes were seen in any FRRf-derived photophysiological parameters for *Synechococcus*


a
f
k
JVPII
(µmol e- cell^{-1} s^{-1})
×10^{-12}
×10^{-12}
×10^{-9}
Bright White
Kyocera
Aquarium
Fluorescent
Light Intensity
(µmol photons m^{-2} s^{-1})
b
g
l
α
(µmol e- m^{2} µmol photon^{-1} cell^{-1})
×10^{-14}
×10^{-14}
×10^{-11}
c
h
m
E_K
(µmol photons m^{2} s^{-1})
d
i
n
σ
(nm^{2} PSII^{-1})
e
j
o
NSV
K
B
A
F
Light Source

◂**Fig. 4** Photophysiological data derived from FRRf. JVPII normalized to cell concentration for *Prochlorococcus marinus* (**a**), *Synechococcus* sp. (**f**), and *Thalassiosira weissflogii* (**k**). α, E_K, σ, as well as values for non-photochemical quenching estimated as the normalized Stern-Volmer quenching coefficient (NSV) at acclimation light intensity for *P. marinus* (**b–e**), *Synechococcus* sp. (**g–j**), and *T. weissflogii* (**l–o**). Cell-normalized JVPII and α values are $\times 10^{-12}$ and $\times 10^{-14}$ for *P. marinus* and *Synechococcus* sp. and $\times 10^{-9}$ and $\times 10^{-11}$ for *T. weissflogii*, respectively. Values shown are mean values for biological replicates ± s.d, $n \geq 2$. Letters represent significant groupings from one-way ANOVA and HSD post hoc tests ($p < 0.05$)

sp. (Fig. 4g, h, i, j; Online Resource, Table S5). In *T. weissflogii*, α values were lowest in the Bright White cultures (Fig. 4l, Online Resource, Table S5). E_K values were significantly higher in the Bright White and Aquarium cultures compared to the Fluorescent cultures (Fig. 4m, Online Resource, Table S5). In *T. weissflogii*, dark-adapted σ was significantly higher in the Kyocera acclimation compared to the Bright White (8.75%) and Fluorescent (6%) acclimations (Fig. 4n). At acclimation light intensity, the Fluorescent cultures showed significantly higher non-photochemical quenching (Fig. 4o, Online Resource, Table S5).

Discussion

Light availability for photosynthesis is commonly regarded as photosynthetically active at wavelengths between 400 and 700 nm, yet, phytoplankton cannot utilize each light wavelength equally (hence, PAR ≠ PUR). With the advent of inexpensive, readily accessible, and even customizable LED systems for scientific experiments, we found it to be important to investigate and describe the influence of different phytoplankton growth lights, containing different light spectra on ecologically and physiologically relevant cellular parameters. A comparison like this is critical as we often attempt to predict how phytoplankton will respond to changes in environmental conditions (e.g., climate change) by using laboratory-based experimental setups in which phytoplankton cultures are grown in different kinds of light incubators.

In our tested species, we determined that the Kyocera light supplied higher usable photons over the absorbance range for our species which use chlorophylls as their main light-harvesting pigments, *P. marinus* and *T. weissflogii*, while the Aquarium light provided the highest usable photons for *Synechococcus* sp. which mainly uses phycobiliproteins for light-harvesting (Fig. 2b, e, i). Despite the difference in PUR, growth rates were independent from the examined light sources for each of the distinct cultures (Table 1). While our growth rates for *P. marinus* and *Synechococcus* sp. were relatively similar to Fu et al. (2007) at similar PAR, growth was mostly lower than reported in literature (e.g., 0.25 vs 0.55–0.70 in (Moore and Chisholm (1999)). Our results suggest that despite the different amounts of PUR supplied, each of the species utilized a relatively similar amount of the emitted light energy to support growth. Similar data on constant growth rates under different spectral quality with apparent similar light intensities have been previously reported (Rivkin 1989; Schellenberger Costa et al. 2013a; Marchetti et al. 2013; Vadiveloo et al. 2015). The surplus of absorbed light energy must consequently be utilized by other metabolic processes or dissipated. For example, cells can optimize the usage of the generated ATP and NADPH from the light reactions in order to balance cellular division and nutrient acquisition by switching between carbohydrate and amino acid synthesis (Behrenfeld et al. 2008), pathways we however did not investigate further.

The ability for *P. marinus* to maintain constant growth rates (Table 1) between light environments while conducting differing daytime primary productivity (Fig. 3a) and altering the cellular composition of POC and PON is indicative of a reallocation of cellular energy and changes in the demand for energy by the different metabolic processes (Table 1)(Halsey et al. 2013; Halsey and Jones 2015). *Prochlorochoccus*, which uses divinyl chl *a* and *b* as its main light-harvesting pigments, had lower cellular chl *a*, POC, and PON (Table 1) when grown under the light sources with the lowest 675:450 nm emission ratios (ER <0.3), the Bright White and Aquarium LEDs, compared to the Kyocera LED culture, which had the most balanced proportions (ER: 0.41). The culture grown under Fluorescent light, which provides more red than blue light (ER: 1.65) had lower cellular POC and PON (Table 1) when compared to the Kyocera LED culture (ER: 0.41). These data suggest that photosynthetic energy was spent in maintaining growth at the expense of cellular components (Rost et al. 2006; Halsey and Jones 2015). Furthermore, under the Bright White LED, which has most of its emission between roughly 550 and 650nm where *P. marinus* pigments exhibit limited absorption, cultures sustained the lowest C:chl *a* and PPC/photoactive pigment ratios (Fig. 2c, Table 1, Online Resource, Table S2). The highest electron to C ratio, K_c, was also seen in this culture, which could be caused by the need to disperse more electrons due to the reduced C:chl *a* measured (Fig. 3b, Table 1). The change in K_c suggests a decoupling between electron transport and carbon fixation, with PSII electrons being diverted to a number of alternative pathways, which either do not directly result in the C-fixation, such as nutrient reduction, the Mehler reaction, or photorespiration (Lawrenz et al. 2013; Hughes et al. 2021) The decreased ratio of carotenoids (PPC) relative to chl would also increase the density of photoactive pigments in the antenna system, and thus explain the increase in σ, a measure of the light-harvesting area in PSII, relative to the Kyocera cultures (Fig. 4d, Online Resource, Table S5) (Dubinsky et al. 1986). These correlations indicate an

acclimation to a perceived lower light environment despite the constant PAR between the different light sources. Similar acclimation responses were found by Hamada et al. (2017) where pigment ratios of chlorophylls and carotenoids were found to change under different light spectra at the same light intensity in *P. marinus*. Lower α and higher E_K were derived from *P* v *I* curve parameters from Bright White LED cultures (lowest PUR), compared to the Kyocera LED cultures (Fig. 4b, c, Online Resource, Table S5). These data indicate that the Bright White light acclimated cells require overall higher irradiance under the Bright White LED to reach the same photosynthetic electron flux compared to the Kyocera LED (Hawes et al. 2003; Ralph and Gademann 2005).

Some of the largest differences between light acclimations were seen in the *Synechococcus* sp. cultures which mainly contain phycobiliproteins in their antenna complexes, with chl *a* being less abundant. Here, the Aquarium light, which has a large emission peak around 450 nm and a broad peak between 500 and 600nm and the lowest ER (675:450nm, 0.17), provided the highest amount of PUR (Fig. 2e). Some of the cellular responses (Table 1) are consistent with what would be expected for cells growing under a higher irradiance (e.g., reduced chl *a*/cell, reduced PPC/PA) (Kana and Glibert 1987). Decreases in the cellular POC and PON quotas found in *Synechococcus* sp. under the Aquarium light (Table 1) furthermore indicate that a reduced fraction of photosynthetic production is directed into net carbon production, a trend opposite to that seen in *P. marinus* and *T. weissflogii*. In general, excitation energy absorbed by phycobilisomes can be directed to either primarily PSII (state I) when the electron chain is oxidized under low light conditions, or direct light energy to PSI under higher light conditions (state II) (Campbell et al. 1998; Falkowski and Raven 2007). The redox state of the electron transport chain has been known to drive state transition shifts in red algae and cyanobacteria (Murata 1969; Ried and Reinhardt 1980; Mullineaux and Allen 1988, 1990; Mullineaux 1992; Campbell and Oquist 1996). One explanation for the changes in cellular POC and PON is that *Synechococcus* sp. grown under the Aquarium light might be locked in the photosynthetic state II, which allows for efficient electron transport through the photosystem without many losses, leading to reduced net carbon acquisition and changes in the photosynthetic efficiency (Bonaventura and Myers 1969). As the photosynthetic and respiratory electron transport share central proteins on the thylakoid membranes (Campbell et al. 1998), it is possible that the changes in the state transitions between light sources resulted in a change in the production of different metabolites, leading to changes observed in cellular POC and PON (Campbell et al. 1998 and references therein). Overall, cultures of the *Synechococcus* strain used in this experiment showed a strong response in cellular composition under one specific kind of growth light, the light with a very low ER (0.17) and an additional broad spectrum in the absorbance spectrum of phycobiliproteins. Hence, the choice of an appropriate culture lighting system for cells containing a significant amount of phycobiliprotein seems to be important in order to best translate data from lab experiments to the field.

In *T. weissflogii*, which uses chlorophylls and fucoxanthin to capture light, the different light environments provided varying amounts of PUR (Fig. 2i). The changes in the cellular POC, chl *a* quota, and C:N ratios of *T. weissflogii* between the Kyocera and the Aquarium and Fluorescent lights, which had similar PUR, (Table 1) indicate that the light quality influenced some of the cellular composition, a response previously observed in the marine diatom *Phaeodactylum tricornutum* where light quality induced a shift in carbon allocation and protein synthesis in the cells (Jungandreas et al. 2014). As indicated by Geider and La Roche (2002), changes to cellular carbon and nitrogen quotas can be caused by changes of relative amounts of pigments, carbohydrates, lipids, proteins, etc. in a cell and previous work has demonstrated that light quality can significantly affect the relative amounts of these cellular components (Rivkin 1989; del Pilar Sánchez-Saavedra and Voltolina 1994; Marchetti et al. 2013; Jungandreas et al. 2014; Gorai et al. 2014; Vadiveloo et al. 2015). In addition to these physiological changes, the photoacclimation state of the cells also varied between acclimations. While the similar C:chl *a* ratios (Table 1) in the Kyocera (highest PUR) and Bright White (lowest PUR) cultures might suggest similar photoacclimation states, the α values point to a comparatively high light acclimation in the Bright White cultures and low light acclimation in the Kyocera cultures (Fig. 4l, m, Online Resource, Table S5). Differences between the suggested light acclimation state from our C:chl a ratio and the FRRf-derived photophysiology data (α and E_K) could be caused by differences in the amount of light absorbed by carotenoids which can affect FRRf analysis as it is specific to an excitation wavelength of 450 nm and ignores light absorbed by photoprotective pigments (Johnsen and Sakshaug 2007; Oxborough et al. 2012). Measured changes in the photoacclimation state between these two lights indicate how spectral quality of growth light can affect the capacity of *Thalassiosira* to harvest light. Importantly, cells seem to have the ability to cope better with higher PAR intensities under a Bright White lighting environment (standard LED) compared to the Kyocera light (shallow surface ocean spectrum). Known photoreceptors in *T. weissflogii* such as cryptochrome-, rhodopsin-, phytochrome-based sensing systems, which typically respond to specific light colors by setting off signal cascades, could have played a role in photoacclimation and responses observed as has been previously demonstrated in marine diatoms (Leblanc et al. 1999),

whereas the investigated cyanobacteria are known to either have limited or no demonstrated photoreceptors (Waterbury et al. 1986; Palenik 2001; Steglich et al. 2005, 2006). Additional blue light photoreceptors, known as aureochromes, have been demonstrated to affect photoacclimation in a number of marine diatoms by acting as transcription factors to induce or enhance high light acclimation (Mercado et al. 2004; Mouget et al. 2004; Wu et al. 2011; Schellenberger Costa et al. 2013a, b). As such, it would be surprising to not find photophysiological adjustments in this study. Overall, *T. weissflogii* showed the smallest response regarding productivity and growth, yet cellular composition was affected, emphasizing again that differences in growth light spectra in laboratory approaches affect the cellular metabolism which can result in changes in the ecophysiological response of phytoplankton and might affect the cells' sensitivity to other environmental stressors.

In general, responses of phytoplankton to both light quantity and quality are complex. When focusing on light quality, a brief discussion on photoreceptors and their role in ecophysiology is warranted. A reduction in perceived light by the blue light receptors between the different light acclimations for *P. marinus* could help to partially explain the reduced PPC/Photoactive pigment ratio mentioned above, as the sensing of high light in *P. marinus* is likely mediated through a blue light receptor (Steglich et al. 2006). Additionally, sigma factors, which play a key role in transcription initiation, have been found to be regulated differently in response to light, which could potentially help to explain the reduced cellular chl *a*, POC, and PON quotas (Steglich et al. 2006). Sensing the amount of blue light likely provides *P. marinus* with cues on how to tune their photosystem as blue light penetrates deepest into the water column. Previous work by Steglich et al. (2006) and this study demonstrate that changes to blue light perception affect the photoacclimation in *P. marinus*. Related to our main message, understanding the spectral emission in growth light is particularly important as a simple high light, low light setup using Bright White LEDs would not only provide a less than optimal blue light component compared to a natural analog, but additionally fail to account for spectral differences in the light field at the surface and at depth. This could potentially lead to obscuring of cellular processes which are regulated both by sensing light quality and quantity. In addition, some marine *P. marinus* and *Synechococcus* strains have been shown to chromatically adapt in order to best match the emission spectra of the light they are exposed to throughout the water column (Palenik 2001; Croce and van Amerongen 2014; Hamada et al. 2017; Grébert et al. 2018). The ability to chromatically adapt their pigment composition provides a distinct competitive advantage. A sensing of red light by phytochromes in *T. weissflogii* in the Fluorescent acclimation, leading to an upregulation of non-photochemical quenching mechanisms, could explain the relatively high NSV measured in this acclimation (Fig. 4o) (Kianianmomeni and Hallmann 2014). Such an upregulation of NSV in response to the perception of red light would provide an advantage for *T. weissflogii* in the natural environment, as increased red light perception, which would occur at shallower depths in the water column where overall intensity is also higher, would allow this species to dissipate excess absorbed light energy more effectively.

Conclusions

The results from this study confirmed our hypothesis that the light quality provided to phytoplankton using commercially available broad range "white" light sources for growth influences their cellular composition as well as photoacclimation state despite receiving equal amounts of PAR. While spectral sensitivity has been tested previously in several studies, an analysis of commercially available broad range "white" growth lights has not been conducted. As we compared intraspecies specific responses where PAR was consistent within each species, any differences in measured cellular parameters directly reflect metabolic changes in response to the varied broad range "white" light spectra. From the changes in physiology seen in our tested species, along with our understanding of phytoplankton light sensing, a pattern of cellular responses to changes in the spectral distribution of light, mediated by photoreceptors, is apparent, and unique to the differently pigmented species.

Our measured responses seemed to be minor in some ways and significant in others, and while we cannot provide a full picture of underlying processes causing these changes and often speculate on the causes, our data clearly show that light quality in phytoplankton laboratory studies should be a factor to be considered in future studies. This will be especially important once experiments which investigate diurnal cycles under variable light intensities (sinusoidal shape day night cycles, variable fluctuating light conditions), using commercially sold LED incubators which might not have an ideal spectrum for the long list of cultured species around the globe.

Paying attention to spectral matching of the growth light emission to the light spectra experienced in the ocean will become pivotal to obtain ecologically relevant results that can be compared across laboratories. Numerical models on the growth of phytoplankton cells have recently started to parametrize models using multi-spectral light availability (Follows et al. 2007; Kettle and Merchant 2008; Hickman et al. 2010; Kim et al. 2015; Gregg and Rousseaux 2016; Moisan and Mitchell 2018), and Dutkiewicz et al. (2015) implemented phytoplankton light absorption properties into global geochemical models. In addition, Kvale and Meissner

(2017) showed that models resolving multiple wavebands and accounting for spectral sensitivity in photosynthesis outperform models with more simplistic assumptions. Other numerical models to determine phytoplankton productivity often use photophysiological parameters for model parametrization, yet data on E_K and α are hard to interpret as not only light quantity but also specific light quality seems to be a controlling factor regulating photophysiological responses. Parametrization of models sometimes rely on laboratory experiments and thus we should be aware of the differences in lighting between the environment and the lab.

While most of our responses to the different acclimations have been rather moderate, the distinct differences found in this study demonstrate that one should keep in mind that distinct spectra of broad range "white" growth lights in combination with specific pigmentation of the individual phytoplankton species can result in changes in ecophysiological relavant cellular parameters (e.g., photoacclimation, changes in cellular ratios) in a laboratory setting. Hence, while fluorescent lights are very affordable, they are, in general, dim and not easily programmable as they are usually built into the incubator and programmed and powered by a relatively simple timer. Bright White LEDs are also very affordable but are highly flexible and easy to exchange as these are often 12 to 24V light strips which can be controlled by various programmable microcontrollers. However, most photosynthetic pigments do not absorb over the wavelength range where these of these Bright White LEDs have their maximum emission. Affordable aquarium style LEDs are usually plug and play, allowing for replication an underwater light spectrum and are generally affordable, but typically lack the ability to be programmed for varying intensity or spectra, making them less flexible compared to Bright White LED strips. Lastly, while more complex lights, like the Kyocera LED, are more expensive, they can provide a realistic underwater light spectrum and can be easily programmed to mimic diurnal changes using various microcontrollers, and simple programming languages including python and Arduino (C-based). These LEDs are also able to emit very high light intensity with relatively low heat emission, making them ideal for incubations where temperature control is an issue, yet high light intensities are required.

Regarding the applicability of the different lighting systems for different culture experiments, we suggest that scientists interested in ecological responses to a diverse range of environmental factors should use a light spectrum as close as possible to what species experience in the water column. This can be obtained by more complex and currently only custom-made LED systems; however, considerations for experimental light spectra should still be made. For species which use accessory pigments and phycobiliproteins, like phycoerythrin and phycocyanin, the use of a broader light spectrum (Aquarium style or Kyocera) rather than a spectrum which lacks emission in the region of phycobiliprotein absorbance (Bright White LEDs) would provide more optimal growth environment. This could reduce any artifacts from chromatic adaptation in phytoplankton, minimizing potential bias in any collected data. For replicating clear surface waters, one should look for a red:blue emission ratio which is ~0.5 to 1 mimicking the partially reduced red light in the surface ocean. When replicating deeper waters, a smaller ratio would be desirable to mimic the nearly full loss of red light in the water column. The results from this study show that changes in the red:blue light emission ratio even in broad range white light sources can impact cellular composition and photoacclimation. Additionally, when studying species known to inhabit coastal and estuarine environments, the absorption of light by suspended particulates and colored dissolved organic matter should be accounted for, with changes to the emission ratios being made. Here a ratio above 1, mimicking the loss of blue light would be desirable. Furthermore, when planning experimental designs for mimicking a cell's turbulent path through the mixed layer, one should take into account both the spectra and the intensity of light which only can be achieved to date with custom-made LED systems. This sort of careful consideration of the light provided in laboratory-based experiments can help to better resolve ecologically relevant responses of phytoplankton which will improve our understanding and model predictions for how phytoplankton will adapt to a changing ocean.

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Declarations

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