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

T. L. Bercel[1*]

tbercel@fsu.edu

S. A. Kranz[1]

skranz@fsu.edu

[1]Department of Earth, Ocean, and Atmospheric Sciences, Florida State University, 1011 Academic Way, Tallahassee, FL, 32306, USA

* Corresponding Author: tbercel@fsu.edu; 602-516-8085

Date of Submission: 04/09/2020

Word Count: 6,154
Number of Figures: 4; All color online only
Number of Tables: 0 Main Text; 4 Supplemental Information

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

Tristyn L. Bercel
Sven A. Kranz

Running Title: Light spectra in cultured phytoplankton matters

Highlight: With light emitting diode-based growth lights becoming available to researchers, it is important to consider the spectral quality of light when designing experiments to understand responses of phytoplankton to environmental conditions.

Abstract

Effects of light quality on the growth, productivity, and cellular composition of three uniquely pigmented marine phytoplankton species were characterized. To accomplish this, cultures of *Prochlorococcus marinus*, *Synechococcus sp.*, and *Thalassiosira weissflogii* were grown under three commercially available LED as well as a fluorescent growth light. Despite having equal photosynthetic active radiation, light quality (light spectrum) and thus photosynthetically usable radiation differed between the treatments. Growth was unaffected in all species tested, and net primary productivity was only affected in *P. marinus* when grown under a "Bright White" LED. Cellular chlorophyll *a* as well as carbon and nitrogen quotas were affected by different light spectra in *Synechococcus sp.* and *T. weissflogii.* Analysis of pigmentation also showed reduced photoprotective to photoactive pigment ratios in some of the cultures under specific lighting environments. Additional photophysiological analysis using fast repetition rate fluorometry indicated changes in the photoacclimation state between different light environments. These results show that while the cells used in our experiment are able to maintain growth and productivity when given lights of varying quality, underlying cellular metabolism and biochemistry is affected. This highlights the importance of carefully choosing spectral quality as well as intensity when designing laboratory-based experiments or setting up bioreactors for biomass generation.

.

Introduction

Marine phytoplankton are mainly photoautotrophic organisms. As such, phytoplankton require 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 (Boyd et al., 2010; Six et al., 2007). Numerous studies have been conducted investigating the effect of light intensity and/or duration on phytoplankton physiology (e.g. Brand and Guillard, 1981; Falkowski, 1984; Falkowski and Owens, 1978; Glover et al., 1987; Hessen et al., 2008; see Lehmuskero et al., 2018 for review). Furthermore when other environmental parameters, such as temperature, CO_2, salinity, and/or nutrient concentrations are varied, the availability of light (both the intensity of the irradiation and the duration) affect the ecophysiological responses of the phytoplankton cultures or communities (Boatman et al., 2017; Dickman et al., 2006; Feng et al., 2008; Finkel et al., 2006; Gao et al., 2012; Healey, 1985; Ivanikova et al., 2007; Kranz et al., 2010; Redalje and Laws, 1983; Rhee and Gotham, 1981; Rost et al., 2006). In addition, it has been shown that a dynamically changing light intensity or simply changes in daylength can affect the cellular response and energetics of phytoplankton (Hoppe et al., 2015; Rost et al., 2006; White et al., 2020).

Therefore, when aiming to better understand and predict phytoplankton responses to environmental changes using quantitative data on cellular response parameters such as growth, productivity, and elemental composition, it is imperative to define the light conditions well. To identify or even separate the complex correlations between cellular responses and environmental parameters, scientists often use controlled laboratory environments, following best practice guides (e.g. Riebesell et al., 2011 and others). We, however, often ignore that the light quality (light spectrum) in the laboratory does not always mimic that of the natural environment in which phytoplankton thrive. Thus, while the laboratory settings provide a controlled environment for the experiments, it only has a limited ability to simulate ecologically relevant light regimes, limiting the accuracy of projecting the findings to the real world.

Historically, laboratory studies investigating the physiological responses of marine phytoplankton species to environmental change have utilized ‘daylight’ or ‘growth light’ fluorescent bulbs to supply light for growth. These specific fluorescent bulbs have an emission spectrum that usually resembles that of the natural solar light experienced at the surface of the

ocean (e.g. GE Daylight Ecolux® T12 fluorescent light bulbs). However, a disadvantage of using 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. Recently, light emitting diode (LED) based light incubators and stand-alone growth lights have become readily available. As LED systems have become more flexible and powerful, LED light incubators have also become more commonly utilized in culture studies of phytoplankton (see Schulze et al., 2014 for a review). One of the disadvantages of LEDs is, however, 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 of photoautotrophic cells. In order to understand wavelength specific responses of phytoplankton, multiple studies have been performed using different LED systems to quantify specific photosynthetic responses to distinct wavelengths (Abiusi et al., 2014; Kim et al., 2013; Marchetti et al., 2013; Miao et al., 2012; Rendon et al., 2013; Schellenberger Costa et al., 2013; Stadnichuk et al., 2011; Wang et al., 2007; Xu et al., 2013). However, the effects of LED systems designed to mimic natural spectra are sparsely investigated (Göritz et al., 2017).

To better understand why growth light spectra matters it is important to recognize that all phytoplankton species contain a specific set of pigments. In general, phytoplankton pigments can be thought of as photoactive or photoprotective. Photoactive pigments' absorption contributes to energy capture which leads to electron transport, and thus carbon fixation, and pigments include chlorophyll *a* (chl *a*) as well as accessory pigments, like those found in cyanobacterial phycobilisomes. Photoprotective pigments however are able to absorb excess light energy trapped by chl *a* and dissipate it as heat or fluorescence, thus avoiding photodamage to the reaction centers in the photosystem. Carotenoids are generally thought of as the main photoprotective pigments found in algae and higher plants (Wilson et al., 2008).

Based on this information it is evident that the growth light choice will affect phytoplankton in many, yet mainly unknown ways. The goal of this study is to understand the effect of using different light systems in phytoplankton culturing on the measured physiological responses in three uniquely pigmented phytoplankton species. To accomplish this, phytoplankton were cultured under the traditional fluorescent light as well under three different LED systems with unique emission spectra. Cellular responses, including growth, productivity, elemental composition, chl *a* content, and photosynthetic properties were analyzed.

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 phosphorus source as well as 400 µM $NaNO_3$ as nitrogen source for *Synechococcus sp.* and *T. weissflogii* and 400 µM NH_4Cl as nitrogen source for *P. marinus*. Additionally, *P. marinus* only received Thiamine for vitamins with a $1/10^{th}$ 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}. 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.

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). Each light source has a unique light emission spectrum, which is shown in Figure 1 A-D.

Growth, Chl *a*, Elemental composition, Absorbance: Specific growth rates were measured via cell count using a flow-cytometer (CytoFLEX (Beckman, Indiana, USA)) and chl *a* fluorescence using a fluorometer (Trilogy, Turner Design, California, USA). The specific growth rate was calculated by fitting an exponential fit through the data. Experiments were performed during mid exponential growth phase. Samples for cellular chl *a* concentration were taken using gravity filtration onto a GF/F filter. The filter was stored at -20°C until processing. Chl *a* was extracted in 90% acetone for 24 hours in the dark at -20°C, sonicated for a brief period and subsequentially measured using a UV/VIS spectrophotometer (Evolution 220, ThermoFisher, Massachusetts, USA). Chl *a* concentration was calculated following Eq. 1, adapted from the JGOFs protocol:

$$A(664) - A(750) * V_A / 87.67 * l * V_S \qquad \text{(Eq. 1)}$$

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, but using precombusted GF/F filters (400°C, 12hr), which were subsequently sent to the Stable Isotope Facility at UC Davis for analysis via a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

Cellular light absorbance spectra were obtained by measuring the absorbance of a culture sample in artificial seawater media between 400-800 nm at 1 nm increments using a UV/VIS spectrophotometer (Evolution 220, ThermoFisher, Massachusetts, USA). The absorbance value at 750 nm, where phytoplankton pigment absorption should not occur, was subtracted to correct for turbidity, and spectra were subsequently normalized to their 667 nm peak for comparison. In order to determine the contribution of individual pigments to the total absorption spectra, a spectral deconvolution method based on Thrane et al. (2015) was employed. Normalized absorption spectra were fed into the R-based pigment fitting program from Thrane et al. (2015) with individualized pigment databases unique to each species as references. While the original program was written for use with absorption scans done on culture extracts in solvents, our absorption scans were obtained *in vivo* from cultures in suspension. In order to compensate for the differences in absorption of pigments in extract vs *in vivo*, our absorption spectra were blue shifted by 10 nm (Bidigare et al., 1990.) Photosynthetic pigments measured *in vivo* demonstrate shifts of 4-40 nm toward the red region of the spectrum compared to the extracts of the pigments in organic solvents (Prezelin, 1981). After fitting our spectra, the pigments given by Thrane et al. (2015) were further classified into either photoactive or photoprotective pigment categories for use to describe light absorption. For purposes of this analysis, photoactive pigments included chl *a* and phycoerythrin, while photoprotective pigments included photoprotectant carotenoids modeled by β-carotene. From here, a photoprotective:photoactive (PP/PA) pigment ratio was determined for each treatment by dividing the contributions of the known photoprotective pigments by the contribution of the known photoactive pigments.

Determination of photosynthetically usable radiation (PUR) was done according to Eq. 2:

$$\text{PUR} = \sum_{400}^{700} E_\lambda * a_\lambda \qquad \text{(Eq. 2)}$$

where E_λ is the emission of the specific growth light at wavelength λ and a_λ is the absorption of the corresponding culture at wavelength λ. To further determine PUR attributed to photoactive pigments, the following equation was used:

$$PUR_{PA} = PUR * PA \qquad \text{(Eq. 3)}$$

where PUR was the value determined in Eq. 2 and PA was the percent absorption determined to be from photoactive pigments as determined in our spectral deconvolution.

^{14}C NPP: Rates of net primary productivity (NPP) 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 front of their respective growth lights at the beginning of the dark period. 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 24hr 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 vial. Samples were counted in a Liquid Scintillation Counter (PerkinElmer TriCarb 5110 TR) 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 net primary production (NPP) were then calculated according to Eq. 4:

$$(SDPM/V)*W*(0.2x10^{-3}/TDPM)*1.05*(1/T) \qquad \text{(Eq. 4)}$$

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), $0.2x10^{-3}$ 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 NPP were subsequently normalized to the cellular chl *a* content measured for the cultures.

Oxygen Evolution: Rates of photosynthetic oxygen evolution were measured using a FirestingO2 optical oxygen meter and respiration vials (Pyro Science, Germany). Cultures in

mid-exponential phase were added into the vials and placed in front of their respective light source at acclimation light intensity. Care was taken that no headspace was left, and a thin syringe needle was injected to allow for potential pressure adjustment. The cultures were continuously mixed using magnetic stir bars. Oxygen evolution was measured in the cultures for 24 hours undisturbed in front of their growth lights. An abiotic control containing fresh sterile, filtered seawater was also measured for corrections. Rates of net oxygen evolution were determined with linear regressions of the data during the light phase, while rates of respiration (Data not shown) were determined using the nighttime O_2 drawdown, with both rates corrected for the signal measured in the abiotic control. O_2 evolution was subsequently normalized to a per chl *a* basis.

Photophysiological parameters: Rapid fluorescence induction light curves (FLC) were measured using a Fast Repetition Rate Fluorometer (FRRf, FastOcean PTX, Chelsea Technologies Group) along with a FastAct Laboratory system (Chelsea Technologies). Cells were dark acclimated for 5 min before the start of each FLC and each of the 10 light steps lasted 1 min each. FLCs were measured during the middle of the photoperiod. Measured fluorescence parameters (Fo, Fm, F', Fm'), along with estimations of the functional absorption cross section area of PSII (σ), non-photochemical quenching using the normalized Stern-Volmer quenching coefficient (NSV), and primary productivity, JVPII, were obtained from the Act2Run software and their derivation can be found in (Oxborough et al., 2012). To account for differences in biomass between samples at the time of FRRf measurement, JVPII data was normalized according to the following equation:

$$JVPII_b = JVPII / Fo/\sigma \qquad \text{(Eq. } \mathbf{5}\text{)}$$

Biomass normalized $JVPII_b$ was then fit using the Scipy package functions in python to obtain the descriptive Photosynthesis vs Irradiance (P vs I) curve parameters: light saturation point (E_K), maximum electron transport rates (Pmax), and the slope for the light limited photosynthesis (α).

<u>Results</u>

PUR, Growth, Elemental Composition, Chl *a* Content

The relative emission spectra for wavelengths in the photosynthetically active radiation spectrum (PAR, 400-700 nm) of the chosen growth lights are shown in Figure 1 A-D. The

Kyocera LED (Fig 1A) has a main emission peak around 500 nm with significant light emission between 500 and 600nm. Between 600 and 700nm the emission is strongly reduced. This light was designed to mimic a natural light spectrum as seen in 5-10m water depth. The Bright White LED (Fig 1B) has a main emission peak at 570 nm and a secondary peak at around 450 nm. A significant dip in the emission spectrum with a minimum at around 480nm is characteristic of this growth light. The Aquarium LED (Fig 1C) has a narrow peak around 450 nm and a broad peak spanning 525 until 650 nm, due to multiple differently colored LEDs. 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.

Normalized absorbance scans for *P. marinus* showed relative similar shapes (Fig. 1E). All but the Bright White LEDs were indistinguishable, with Bright White LED acclimated cells having a slightly reduced absorbance in the blue light (400-500nm) wavelength. Characteristic peaks for chl *a* were observed at approximately 450 and 667nm. A peak in the 500 nm region, which likely represents beta-carotene was observed additionally for all acclimations. The spectral deconvolution identified chl *a* as contributing roughly 58% and beta-carotene as contributing roughly 42% to the total absorption spectra across all light acclimations. Consequently, photoprotective:photoactive pigment (PP/PA) ratios values were between 0.666 and 0.718 for all treatments (Fig 1G, Table S1). The Bright White treatment had a statistically significantly lower ratio compared to the other treatments (One Way ANOVA, $p < 0.000009$).

Similar to *P. marinus*, no major differences in absorption spectra were seen in *Synechococcus sp.*, yet, in this species the Aquarium light treatment showed the lowest absorbance in the blue light absorbance spectrum (400-500 nm) (Fig. 1H). Characteristic peaks for chl *a*, phycoerythrin (at 550 nm), and a carotenoid, most likely zeaxanthin (500 nm) were observed. Furthermore, the PP/PA ratio was lower in the Aquarium treatment (Fig 1J, Table S1). Spectral deconvolution was found to be problematic in this species and we are less confident in the data (please see discussion).

In *T. weissflogii*, the Bright White and Aquarium acclimations showed a slightly higher relative chl *a* peak around 450 nm compared to the Kyocera and Fluorescence light (Fig. 1L). This is reflected in the spectra deconvolution data which shows chl *a* contributing roughly 79 and 78% in the Kyocera and Fluorescent acclimations while it contributed 82 and 81% in the Bright White and Aquarium acclimations. For the carotenoids contributing to the spectra, beta-

carotene and fucoxanthin were found to contribute between 18 and 22% across acclimations, with highest values being in the Kyocera (21% beta-carotene contributions) and Fluorescent acclimation (22% beta-carotene). For PP/PA ratios, values ranged between 0.21 and 0.28 for each treatment (Fig 1M, Table S1). No significant statistical differences were found between treatments (One Way ANOVA, $p > 0.05$).

Based on the emission spectrum of the growth light and the cellular light absorbance, photosynthetically usable radiation **(**PUR) showed differences. Since we were more interested in the PUR for photoactive pigments such as chlorophyll and phycoerythrin, we calculated the data accordingly (Eq. 3). In *P. marinus*, with the Kyocera acclimation showed highest PUR_{PA} while the Bright white acclimation showed strongly reduced PUR rates (51% less compared to Kyocera) (Fig. 1F). In *Synecochcoccus sp.*, PUR_{PA} values were highest for the Aquarium treatment and substantially lower for the Kyocera light (58% less compared to Aquarium) (Fig. 1I). In *T. weissflogii*, PUR_{PA} was roughly similar for the Kyocera and Fluorescence treatments, but the PUR_{PA} in the Bright White treatment was substantially lower (55% less compared to Fluorescent) (Fig. 1L).

Growth rates in *P. marinus* were not significantly different across light treatments with values of 0.25 ± 0.04, 0.24 ± 0.04, 0.25 ± 0.04, and 0.25 ± 0.04 d^{-1} for the Kyocera, Bright White, Aquarium, and Fluorescent, respectively (One Way ANOVA, $p > 0.05$) (Fig. 2A, Table S2). Growth rates were also unaffected in *Synechococcus sp* with rates of 0.33 ± 0.07, 0.31 ± 0.04, 0.32 ± 0.02, and 0.31 ± 0.02 d^{-1} for the four treatments Kyocera, Bright White, Aquarium, and Fluorescent, respectively (One Way ANOVA, $p > 0.05$) (Fig. 2E, Table S2). *T. weissflogii* did not show a significant response in growth with rates of 0.86 ± 0.05, 0.83 ± 0.04, 0.86 ± 0.03, and 0.84 ± 0.03 d^{-1} in the four light treatments, respectively (One Way ANOVA, $p > 0.05$) (Fig. 2I, Table S2).

Cellular chl *a* content in *P. marinus* (Fig. 2B, Table S2) did not significantly change between light treatments 2.88 ± 0.32, 2.43 ± 0.07, 2.63 ± 0.15, and 2.76 ± 0.08 fg chl *a* $cell^{-1}$ for the Kyocera, Bright White, Aquarium, and Fluorescent treatments respectively) (One Way ANOVA, $p > 0.05$). *Synechococcus sp.* cells (Fig. 2F, Table S2) did have significant changes in cellular chl *a* (5.06 ± 0.28, 3.61 ± 0.71, 2.82 ± 0.62, and 5.20 ± 0.67 fg chl *a* $cell^{-1}$ for the Kyocera, Bright White, Aquarium, and Fluorescent treatments, respectively). Here the Kyocera and Aquarium acclimated cells exhibited significant higher cellular chl *a* compared to the Bright

White and Aquarium acclimated cells (One Way ANOVA, p = 0.041). Significant changes in chl *a* cell^{-1} between light treatments Kyocera, Bright White, Aquarium, and Fluorescent treatments were also seen in *T. weissflogii* (Fig. 2J, Table S2) (6.85 ± 0. 28, 6.12 ± 0.49, 5.19 ± 0.75, and 7.11 ± 0.57 pg chl *a* cell^{-1}, respectively (One Way ANOVA, p = 0.0311).

Cellular POC and PON values (Fig. 2C , Table S2) for *P. marinus* changed across light treatments. POC and PON were statically different, being highest for the Kyocera light (99.2 ± 6.2 µg C cell^{-1}, 21.0 ± 1.1 µg N cell^{-1}) and lowest for the Bright White (55.5 ± 0.8 µg C cell^{-1}, 12.0 ± 0.4 µg N cell^{-1}) with no change seen between the Aquarium and Fluorescent treatment (average approximately 75 µg C cell^{-1} and 16.5 µg N cell^{-1}) (One Way ANOVA, p = 0.00004, p = 0.00001). C:N ratios (mol:mol) for *P. marinus* were relatively constant (Fig. 2D, Table S2), 5.52 ± 0.38, 5.38 ± 0.09, 5.38 ± 0.05, and 5.56 ± 0.19 for the four light treatments, Kyocera, Bright White, Aquarium, and Fluorescent, respectively (One Way ANOVA, p > 0.05). *Synechococcus sp.* grown under the Aquarium treatment had the lowest cellular POC and PON (258.6 ± 3.7 µg C cell^{-1}, and 49.8 ± 1.6 fg N cell^{-1}) while the other treatments were relatively constant (Fig. 2G, Table S2) (One Way ANOVA, p = 0.0033, p = 0.0040). C:N ratios for *Synechoccocus sp.* showed no significant change (Fig. 2H, Table S2) (5.95 ± 0.21, 5.89 ± 0.18, 6.07 ± 0.28, and 6.15 ± 0.15 for the Kyocera, Bright White, Aquarium, and Fluorescent light treatments) (One Way ANOVA, p > 0.05). *T. weissflogii* showed significant changes in POC but not PON across light treatments (Fig. 2K, Table S2) (One Way ANOVA, p = 0.0396). *T. weissflogii* did exhibit significant changes to C:N ratios across light treatments with Kyocera being highest and Fluorescent being lowest (Fig. 2L, Table S2) (6.04 ± 0.32, 5.21 ± 0.39, 5.26 ± 0.43, and 4.89 ± 0.22 for the Kyocera, Bright White, Aquarium, and Fluorescent treatments, respectively) (One Way ANOVA, p = 0.0212).

Primary Productivity

Rates of chlorophyll normalized NPP are presented in Figure 3 and in Table S3. Changes in rates of NPP were observed across light treatments in *P. marinus* in both oxygen and ^{14}C derived estimates, with NPP being highest in the Aquarium and Fluorescent treatments (averages approximately 56.5 and 72 μmol C mg chl a^{-1} hr^{-1} for ^{14}C and O_2 based estimates) and lowest in the Kyocera and Bright White treatments (Fig. 3A, Table S3) (averages approximately 40 and 68 μmol C mg chl a^{-1} hr^{-1} for ^{14}C and O_2 based estimates) (One Way ANOVA, p = 0.0068, p =

0.0031). In *Synechococcus sp.*, no significant differences between treatments in ^{14}C NPP measurements were measured (Fig. 3B, Table S3) (average approximately 96 μmol C mg chl a^{-1} hr^{-1}). In the O_2 derived NPP measurements cells acclimated to Aquarium and Fluorescent light did, however, show higher rates compared to Kyocera and Bright white (132.01 ± 33.83 and 90.07 ± 15.64 μmol C mg chl a^{-1} hr^{-1} vs. 54.96 ± 5.17 and 73.59 ± 5.53 μmol C mg chl a^{-1} hr^{-1}, respectively), (One Way ANOVA, $p > 0.05$, $p = 0.0002$). In *T. weissflogii*, NPP rates did not significantly change among light treatments for either ^{14}C or O_2 based estimates (Fig. 3C, Table S3) (averages approximately 90.5 and 97.5 μmol C mg chl a^{-1} hr^{-1} for ^{14}C and O_2 based estimates) (One Way ANOVA, $p > 0.05$, $p > 0.05$).

Photophysiology

Photophysiology was measured to get an additional parameter on productivity and photoacclimation (Fig. 4). Please note that the spectrum and intensities of light in the FRRF differ from the spectrum of light in the acclimation as well as the light used to measure ^{14}C and O_2 NPP. P v I curves for each species using JVPII (mol electron m^{-3} d^{-1}) data from the FRRf are plotted in Fig. 4 A, F, and K. Photophysiological data differed across species and light treatments. The α values for *P. marinus* were lower in the Kyocera and Aquarium treatment compared to the Bright White treatment while the Fluorescent treatment did not show significant differences to all other treatments (Fig. 4B, Table S4). (One Way ANOVA, $p = 0.0332$). E_k and P_{max} values were significantly lower in the Kyocera treatment than the Bright White and Aquarium treatment, but no group was significantly different from the Fluorescent acclimation (Fig. 4C, D, Table S4) (One Way ANOVA, $p = 0.0092$, $p = 0.0199$). Non photochemical quenching (NSV) did not significantly differ between treatments (Fig. 4E, Table S4) (One Way ANOVA, $p > 0.05$). No significant changes were seen in any of the fit or FRRf derived photophysiological parameters for *Synechococcus sp.* (Fig. 4G, H, I, J, Table S4) (One Way ANOVA, $p > 0.05$). Similarly, no significant changes were seen in fit P v I curve statistics for *T. weissflogii* (Fig. 4L. M, N Table S4) (One Way ANOVA, $p > 0.05$), however, at acclimation light, the F treatment showed significantly higher NSV (Fig. 4O, Table S4) (One Way ANOVA, $p = 0.0001738$).

<u>Discussion</u>

With the advent of cheap, readily accessible, and even customizable LED systems for scientific experiments, it is important to examine how the choice of growth light can influence ecologically and physiologically relevant cellular parameters. This is especially 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 kind of temperature-controlled light-incubators. In this study we aimed to understand if different commercially available growth lights with differing light qualities affect phytoplankton growth, pigment content, elemental composition and productivity.

While light availability for photosynthesis is commonly regarded as photosynthetically active radiation (PAR) at wavelengths between 400 and 700 nm, phytoplankton cannot utilize each light wavelength equally (hence, PAR ≠ PUR). In our tested species, we found no changes in growth rate between the examined light sources (Fig. 2, Table S1) which suggests that despite having different amounts of PUR, cells utilized a relative similar amount of the absorbed light energy across spectra to fuel growth while surplus energy will be utilized by other metabolic processes. Phytoplankton cells were not light saturated in our acclimations, as indicated by the up to 2x higher E_K values compared to the acclimation light intensities (see methods, Fig. 4, Table S4). Although we might have expected a growth response under light limited conditions, previous studies have demonstrated that marine phytoplankton maintain constant growth rates under different spectral quality with seemingly similar PAR light intensities (Marchetti et al., 2013; Rivkin, 1989; Schellenberger Costa et al., 2013; Vadiveloo et al., 2015). While cells were maintaining their growth rates, the responses measured on cellular chl *a*, carbon and/or nitrogen content indicate that light sensing and harvesting as well as metabolic processes must have been affected by the changes in light spectrum. Some of the largest differences between light acclimations was seen in the *Synechococcus sp.* cultures. Here cellular chl *a* content and POC was significantly reduced under the Aquarium light (Fig. 2, Table S2). In addition, a higher E_K and lower α was measured (Fig. 4, Table S4) compared to the Kyocera light. We attribute this change to the higher PUR_{PA} in the Aquarium light where more light was emitted in the in the blue 450-470 nm region as well as the yellow to red region of the spectra where chl *a* and phycoerythrin (PE) strongly absorb light (Fig. 1). Hence, it is possible that cells grown under the Aquarium light downregulate their chl *a* and change photophysiology to a “high light” adapted state while still keeping photoactive light absorption for growth and production relative constant.

A potential enrichment of the antenna complex with PE in exchange for chl *a* antenna complexes could on the other hand allow for the cells to balance photosynthetically usable light absorption.

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. While macromolecular composition (e.g. protein, lipid content) was not measured in this study, previous work has demonstrated that light quality can significantly affect the relative amounts of these cellular components (e.g. Gorai et al., 2014; Marchetti et al., 2013; Rivkin, 1989; Sánchez-Saavedra and Voltolina, 1994; Vadiveloo et al., 2015 and others). Changes in the C:N ratios of *T. weissflogii* between the Kyocera and Fluorescent light indicate a potential for those cellular adjustments to have occurred (Figure 2, Table S1). However, changes to cellular macromolecule composition are not the only way these differences in elemental composition could have arose. In *Synechococcus sp.* and *T. weissflogii*, it is possible that a small decrease in cell size could have caused changes of cellular chl *a* and POC/PON. For *Synechococcus* the strong decrease in chl *a* between Kyocera and Aquarium light could be caused by a 25% decrease in cell diameter assuming a cell volume (spherical) based chl *a* correlation. Spectral depended changes in cell size have been found for the green algae *Chlorella kessleri* (Koc et al. 2013) and *Chlorella vulgaris* (Lee and Palsson, 1996). It is possible that *Synechoccocus sp.* and *T. weissflogii* cell size decreased under the Aquarium light where the relative contribution of red light was higher (1.4-fold higher emission at 635nm for Aquarium compared to Kyocera), but here we were unable to resolve these potentially small changes in cell diameter using the flow cytometer.

To better understand potential changes in cellular energetics under the different light emissions, accessory pigmentation and photophysiology of the cells was analyzed. In general, phytoplankton pigments can be separated into photoactive or photoprotective pigments. Photoactive pigments' absorption contributes to energy capture which leads to electron transport, ATP and NADPH production, carbon fixation and energy for other metabolic processes. Those pigments include chlorophylls as well as accessory pigments such as xanthophylls or cyanobacterial phycobili proteins. Photoprotective pigments such as carotenoids are able to absorb light energy trapped by chl *a* and dissipate it as heat or fluorescence, thus avoiding photodamage to the reaction centers in the photosystem. The amounts and ratios of these pigments have been found to be adjusted in order to adapt to various light conditions (MacIntyre

et al., 2002). In our investigated species, both *P. marinus* and *T. weissflogii* showed the lowest ratios of photoprotective:photoactive pigments under the Bright White LED light (Fig. 1, Table S1). While we did grow the cells under non-light stressed conditions (sub saturating light), changes in the photoprotective:photoactive ratio could indicate a general readiness to cope with rapid changes to higher light intensities which we would expect in turbulent waters or shallow mixed layers of highly stratified tropical waters (Giovagnetti et al., 2014; Lewis et al., 1984; MacIntyre et al., 2002). The change in the ratio could also simply be a response to the emission intensity at the xanthophyll specific absorbance wavelength. Bright White LEDs, which have the lowest emission in the 450-500 nm region where carotenoid but also chl *a* absorbance is dominant could thus have played a role in regulation of these pigments. We consequently believe that cells growing under a light spectrum with low emission in the region where photoactive pigments absorb "sense" that they are growing in a low light environment and may thus not be producing abundant carotenoids. These findings could be important as several commercially sold LED incubators use bright white LED systems. Under these light qualities experiments which investigate diurnal cycles under variable light (sinus shape day night cycles, variable fluctuating light condition) could result in phytoplankton being high-light stressed under lower PAR intensities compared to cells which produce more photoprotective pigments acclimated under a different spectrum. In addition to the changes in pigmentation, the cellular photophysiology indicated a similar "low light adaptation" responses. As already discussed earlier for *Synechococcus*, we also found that *P. marinus* cultures had an α value under Bright White acclimations that was significantly higher than the Kyocera and Aquarium light grown cells (Fig. 4, Table S4). The E_K and Pmax values were also lower than in the Kyocera treatment (Fig. 4, Table S4). These photophysiological adjustments are usually expected for low light adapted cells (Fig. 4, Table S4). In *T. weissflogii*, this trend did not manifest with the Bright White LED, yet, the Fluorescent treatment had a significantly higher photoprotective:photoactive pigment ratio and did exhibit higher α values alongside lower E_K and Pmax values (Fig. 1, 4, Table S1, S4).

As shown, patterns of light acclimation are inconsistent between species, but our data demonstrate that the cells are sensing and responding to changes in the spectral quality. Indeed, it has been demonstrated in the diatom *P. tricornutum* that light spectra, in specific the perception of blue light, can affect photoacclimation (Schellenberger Costa et al., 2013) and red and far red light have found to stimulate carotenoid production in *Dunaliella salina* and *D. bardawil*,

respectively (Sánchez-Saavedra et al., 1996; Xu et al., 2013). As such, it would be surprising to not find similar adjustments in this study. The change in photoprotective:photoactive pigment ratio was not well resolved in *Synechococcus sp.*. It is possible that PE remained constant, as was seen in *Spirulina platensis* when comparing red and white light acclimation (Chen et al. 2010), or potentially increased, which was seen in *S. platensis* cultures grown under red light in Walter et al. (2011). However, due to the issues with the spectral deconvolution method used in this study, we could not resolve the spectral overlap between carotenoids (450-550 nm) and phycoerythrin absorption (PE; 500-650 nm) (Carvalho et al., 2011) and therefore data were found to be unreliable. Photophysiological parameter from the acclimated cells showed larger differences for *Synechococcus sp*. compared to the relative unaltered data for *P. marinus* and T. *weissflogii*. However, no statistically significant differences were found due to large uncertainties in our measurements.

Since net growth rates of our cultures did not change no significant change in net productivity was expected. Based on our ^{14}C data and O_2 and FRRF measurements, rates did not significantly change in *Synechococcus sp.* and *T. weissflogii* (Fig. 3). We think that it is likely that the light quality influenced the biochemical composition of these cells, without affecting their growth and productivity, which has been seen in previous studies on marine phytoplankton (Marchetti et al., 2013). On the other hand, productivity rates measured for *P. marinus* (with both O_2 and ^{14}C based methods) under the Bright White treatment showed significantly reduced rates (Fig. 3A). This can be attributed to the low PUR for photochemistry for *P. marinus* under this light treatment. For each species, the chosen growth light intensity was below the measured E_K, so it is possible that larger changes in productivity would emerge under light saturation and even under conditions in which light could become supersaturating. For example, Schellenberger Costa et al., (2013) found no changes in productivity in *P. tricornutum* between white, red, and blue light when the intensity was low, but saw differences under higher light.

Conclusions

The results from this study show that the light quality, not just quantity, provided to phytoplankton for growth can influence their physiology. While spectral sensitivity has been tested previously in several studies, an analysis of commercially available growth lights has not been conducted. The responses to the different growth lights used in this study were minimal in

growth and productivity, however, responses in cellular composition, pigmentation, and estimated P vs I curve parameters were all unique. In this study, distinct changes in POC, PON, C:N ratios and pigments were observed for each species. This is notable as it demonstrates the influence of growth light spectra on cell composition, which is important to keep in mind when performing laboratory experiments to constrain the biochemical composition of phytoplankton and their impact on biogeochemical cycles. Paying attention to spectral matching of emission and absorbance spectra can also prove valuable in photobioreactors cultivation, particularly when used for the production of a desired cellular product (e.g. Abiusi et al., 2014; Baer et al., 2016; Chen et al., 2010; Walter et al., 2011). Additionally, photophysiological parameters, such as E_K, Pmax, and α were impacted, which has significance for the prediction of future ocean scenarios, as models often use these parameters as inputs to determine phytoplankton productivity and distribution. Overall, this study demonstrates that when setting up efficient photobioreactors, one must take into account the spectra of the growth lights as well as the pigmentation of the individual phytoplankton species, not just the light intensity. A simple “blue light, red light” combination of LEDs does not necessarily improve productivity, yet if specified to the absorbance to the cultured species it might. When designing laboratory experiments to mimic natural conditions one should also focus on the “true” spectrum in the water-column which can be obtained by more complex custom-made LED systems.

Supplementary Data

Table S1: Photoprotectice:Photoactive Pigment Ratios for *P. marinus, Synechoccoccus sp.,* and *T. weissflogii*. Phycoerthrine:Chlorophyll a ratios are also shown for *Synechococcus sp*

Table S2: Growth rates, POC and PON cell^{-1}, C:N. mol:mol ratios, and Chl *a* cell^{-1} values for *P. marinus, Synechoccoccus sp.,* and *T. weissflogii*.

Table S3: Carbon based-NPP estimates from ^{14}C and O_2 incubations for *Prochlorococcus marinus*, *Synechococcus sp.*, and *Thalassiosira weissflogii* normalized to Chl *a* content

Table S4: Values for Photosynthesis vs Irradiance curve fits according to Webb et al 1974

Acknowledgements

We would like to thank Douglas Bruce for providing his insights on improving the *in vivo* absorbance scans obtained in this study. This research did not receive monetary funding from third party agencies in the public, commercial, or not-for-profit sections, yet we received the Kyocera light module from Kyocera (USA). Declarations of interest: none.

Figure 1: Emission spectra for the light treatments used in this study (A-D). Peaks shown in the fluorescent spectrum (D) are cut off. Whole cell light absorption normalized to mg Chl *a* L^{-1}. PUR estimates shown in arbitrary units, and Photoprotective:Photoactive pigment ratios obtained from spectral fitting for *Prochlorococcus marinus* (E-G), *Synechococcus sp.* (H-J), and *Thalassiosira weissflogii* (K-M). Values shown are mean values for biological replicates ± s.d, n ≥ 2. Data for J were defined unreliable.

Figure 2: Physiological results for specific growth rate (μ), Chl a and POC $cell^{-1}$ content, as well as mol:mol C:N ratios for *Prochlorococcus marinus* (A-D), *Synechococcus sp.* (E-H), and *Thalassiosira weissflogii* (I-L). Values shown are mean values for biological replicates ± s.d, n ≥ 2. Letters represent significant groupings from one-way ANOVA and HSD post hoc tests ($p < 0.05$).

Figure 3: NPP estimates from ^{14}C and O_2 incubations in units of μmol C mg Chl a^{-1} hr^{-1} for *Prochlorococcus marinus* (A), *Synechococcus sp.* (B), and *Thalassiosira weissflogii* (C) normalized to Chl *a* content. O_2 values were generated by applying a PQ of 1.4 for nitrate or 1 for ammonium usage. Values shown are mean values for biological replicates ± s.d, n ≥ 2. Letters represent significant groupings from one-way ANOVA and HSD post hoc tests ($p < 0.05$).

Figure 4: Photophysiological data derived from FRRf. JVPII (mol electron m^{-3} d^{-1}) for *Prochlorococcus marinus* (A), *Synechococcus sp.* (F), and *Thalassiosira weissflogii* (K). α (mol electron µmol $photons^{-1}$ m^{-2}) , E_K (µmol photons m^{-2} s^{-1}), Pmax (mol electron m^{-3} d^{-1}), as well as values for nonphotochemical quenching estimated as the normalized Stern-Volmer quenching coefficient (NSV) at acclimation light intensity for *Prochlorococcus marinus* (B-E), *Synechococcus sp.* (G-J), and *Thalassiosira weissflogii* (L-O). Values shown are mean values for biological replicates ± s.d, n ≥ 2. Letters represent significant groupings from one-way ANOVA and HSD post hoc tests ($p < 0.05$).

References

Abiusi, F., Sampietro, G., Marturano, G., Biondi, N., Rodolfi, L., D'Ottavio, M., Tredici, M.R., 2014. Growth, photosynthetic efficiency, and biochemical composition of *Tetraselmis suecica* F&M-M33 grown with LEDs of different colors: Growth of *Tetraselmis* With Different LED Colors. Biotechnol. Bioeng. 111, 956–964. https://doi.org/10.1002/bit.25014

Baer, S., Heining, M., Schwerna, P., Buchholz, R., Hübner, H., 2016. Optimization of spectral light quality for growth and product formation in different microalgae using a continuous photobioreactor. Algal Res. 14, 109–115. https://doi.org/10.1016/j.algal.2016.01.011

Bidigare, R.R., Ondrusek, M.E., Morrow, J.H., Kiefer, D.A., 1990. In-vivo absorption properties of algal pigments, in: Spinrad, R.W. (Ed.), . Presented at the Orlando '90, 16-20 April, Orlando, FL, United States, p. 290. https://doi.org/10.1117/12.21451

Boatman, T.G., Lawson, T., Geider, R.J., 2017. A Key Marine Diazotroph in a Changing Ocean: The Interacting Effects of Temperature, CO2 and Light on the Growth of Trichodesmium erythraeum IMS101. PLOS ONE 12, e0168796. https://doi.org/10.1371/journal.pone.0168796

Boyd, P.W., Strzepek, R., Fu, F., Hutchins, D.A., 2010. Environmental control of open-ocean phytoplankton groups: Now and in the future. Limnol. Oceanogr. 55, 1353–1376. https://doi.org/10.4319/lo.2010.55.3.1353

Brand, L.E., Guillard, R.R.L., 1981. The effects of continuous light and light intensity on the reproduction rates of twenty-two species of marine phytoplankton. J. Exp. Mar. Biol. Ecol. 50, 119–132. https://doi.org/10.1016/0022-0981(81)90045-9

Carvalho, A.P., Silva, S.O., Baptista, J.M., Malcata, F.X., 2011. Light requirements in microalgal photobioreactors: an overview of biophotonic aspects. Appl. Microbiol. Biotechnol. 89, 1275–1288. https://doi.org/10.1007/s00253-010-3047-8

Chen, H.-B., Wu, J.-Y., Wang, C.-F., Fu, C.-C., Shieh, C.-J., Chen, C.-I., Wang, C.-Y., Liu, Y.-C., 2010. Modeling on chlorophyll a and phycocyanin production by Spirulina platensis under various light-emitting diodes. Biochem. Eng. J. 53, 52–56. https://doi.org/10.1016/j.bej.2010.09.004

Dickman, E.M., Vanni, M.J., Horgan, M.J., 2006. Interactive effects of light and nutrients on phytoplankton stoichiometry. Oecologia 149, 676–689. https://doi.org/10.1007/s00442-006-0473-5

Falkowski, P.G., 1984. Physiological responses of phytoplankton to natural light regimes. J. Plankton Res. 6, 295–307. https://doi.org/10.1093/plankt/6.2.295

Falkowski, P.G., Owens, T.G., 1978. Effects of light intensity on photosynthesis and dark respiration in six species of marine phytoplankton. Mar. Biol. 45, 289–295. https://doi.org/10.1007/BF00391815

Feng, Y., Warner, M.E., Zhang, Y., Sun, J., Fu, F.-X., Rose, J.M., Hutchins, D.A., 2008. Interactive effects of increased pCO_2, temperature and irradiance on the marine coccolithophore ***Emiliania huxleyi*** (Prymnesiophyceae). Eur. J. Phycol. 43, 87–98. https://doi.org/10.1080/09670260701664674

Finkel, Z.V., Quigg, A., Raven, J.A., Reinfelder, J.R., Schofield, O.E., Falkowski, P.G., 2006. Irradiance and the elemental stoichiometry of marine phytoplankton. Limnol. Oceanogr. 51, 2690–2701. https://doi.org/10.4319/lo.2006.51.6.2690

Gao, K., Xu, J., Gao, G., Li, Y., Hutchins, D.A., Huang, B., Wang, L., Zheng, Y., Jin, P., Cai, X., Häder, D.-P., Li, W., Xu, K., Liu, N., Riebesell, U., 2012. Rising CO_2 and increased light exposure synergistically reduce marine primary productivity. Nat. Clim. Change. https://doi.org/10.1038/nclimate1507

Geider, R., La Roche, J., 2002. Redfield revisited: variability of C:N:P in marine microalgae and its biochemical basis. Eur. J. Phycol. 37, 1–17. https://doi.org/10.1017/S0967026201003456

Giovagnetti, V., Flori, S., Tramontano, F., Lavaud, J., Brunet, C., 2014. The Velocity of Light Intensity Increase Modulates the Photoprotective Response in Coastal Diatoms. PLoS ONE 9, e103782. https://doi.org/10.1371/journal.pone.0103782

Glover, H.E., Keller, M.D., Spinrad, R.W., 1987. The effects of light quality and intensity on photosynthesis and growth of marine eukaryotic and prokaryotic phytoplankton clones. J. Exp. Mar. Biol. Ecol. 105, 137–159. https://doi.org/10.1016/0022-0981(87)90168-7

Gorai, T., Katayama, T., Obata, M., Murata, A., Taguchi, S., 2014. Low blue light enhances growth rate, light absorption, and photosynthetic characteristics of four marine

phytoplankton species. J. Exp. Mar. Biol. Ecol. 459, 87–95. https://doi.org/10.1016/j.jembe.2014.05.013

Göritz, A., von Hoesslin, S., Hundhausen, F., Gege, P., 2017. Envilab: Measuring phytoplankton in-vivo absorption and scattering properties under tunable environmental conditions. Opt. Express 25, 25267. https://doi.org/10.1364/OE.25.025267

Healey, F.P., 1985. Interacting effects of light and nutrient limitation on the growth rate of Synechococcus linearis (Cyanophyceae)1. J. Phycol. 21, 134–146. https://doi.org/10.1111/j.0022-3646.1985.00134.x

Hessen, D.O., Leu, E., Færøvig, P.J., Falk Petersen, S., 2008. Light and spectral properties as determinants of C:N:P-ratios in phytoplankton. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 2169–2175. https://doi.org/10.1016/j.dsr2.2008.05.013

Hoppe, C.J.M., Holtz, L.-M., Trimborn, S., Rost, B., 2015. Ocean acidification decreases the light-use efficiency in an Antarctic diatom under dynamic but not constant light. New Phytol. 207, 159–171. https://doi.org/10.1111/nph.13334

Ivanikova, N.V., McKay, R.M.L., Bullerjahn, G.S., Sterner, R.W., 2007. Nitrate utilization by phytoplankton in Lake Superior is impaired by low nutrient (P, Fe) availability and seasonal light limitation - a cyanobacterial bioreporter study. J. Phycol. 43, 475–484. https://doi.org/10.1111/j.1529-8817.2007.00348.x

Kim, T.-H., Lee, Y., Han, S.-H., Hwang, S.-J., 2013. The effects of wavelength and wavelength mixing ratios on microalgae growth and nitrogen, phosphorus removal using Scenedesmus sp. for wastewater treatment. Bioresour. Technol. 130, 75–80. https://doi.org/10.1016/j.biortech.2012.11.134

Koc, C., Anderson, G.A., Kommareddy, A., 2013. Use of red and blue light-emitting diodes (LED) and fluorescent lamps to grow microalgae in a photobioreactor.

Kranz, S.A., Levitan, O., Richter, K.U., Prasil, O., Berman-Frank, I., Rost, B., 2010. Combined Effects of CO_2 and Light on the N_2-Fixing Cyanobacterium Trichodesmium IMS101: Physiological Responses. Plant Physiol. 154, 334–345.

Lee, C.-G., Palsson, B.Ø., 1996. Photoacclimation of Chlorella vulgaris to red light from light-emitting diodes leads to autospore release following each cellular division. Biotechnol. Prog. 12, 249–256.

Lehmuskero, A., Skogen Chauton, M., Boström, T., 2018. Light and photosynthetic microalgae: A review of cellular- and molecular-scale optical processes. Prog. Oceanogr. 168, 43–56. https://doi.org/10.1016/j.pocean.2018.09.002

Lewis, M., Horne, E., Cullen, J., Oakey, N., Platt, T., 1984. Turbulent motions may control phytoplankton photosynthesis in the upper ocean. Nature 311, 49–50.

MacIntyre, H.L., Kana, T.M., Anning, T., Geider, R.J., 2002. Photoacclimation of photosynthesis irradiance response curves and photosynthetic pigments in microalgae and cyanobacteria 1. J. Phycol. 38, 17–38.

Marchetti, J., Bougaran, G., Jauffrais, T., Lefebvre, S., Rouxel, C., Saint-Jean, B., Lukomska, E., Robert, R., Cadoret, J.P., 2013. Effects of blue light on the biochemical composition and photosynthetic activity of Isochrysis sp. (T-iso). J. Appl. Phycol. 25, 109–119. https://doi.org/10.1007/s10811-012-9844-y

Miao, H., Sun, L., Tian, Q., Wang, S., Wang, J., 2012. Study on the Effect of Monochromatic Light on the Growth of the Red Tide Diatom Skeletonema Costatum. Opt. Photonics J. 02, 152–156. https://doi.org/10.4236/opj.2012.23022

Nielsen, E.S., 1952. The Use of Radio-active Carbon (C14) for Measuring Organic Production in the Sea. ICES J. Mar. Sci. 18, 117–140. https://doi.org/10.1093/icesjms/18.2.117

Oxborough, K., Moore, C.M., Suggett, D.J., Lawson, T., Chan, H.G., Geider, R.J., 2012. Direct estimation of functional PSII reaction center concentration and PSII electron flux on a volume basis: a new approach to the analysis of Fast Repetition Rate fluorometry (FRRf) data: Analysis of FRRf data: a new approach. Limnol. Oceanogr. Methods 10, 142–154. https://doi.org/10.4319/lom.2012.10.142

Price, N.M., Harrison, G.I., Hering, J.G., Hudson, R.J., Nirel, P.M.V., Palenik, B., Morel, F.M.M., 1989. Preparation and Chemistry of the Artificial Algal Culture Medium Aquil. Biol. Oceanogr. 6, 443–461. https://doi.org/10.1080/01965581.1988.10749544

Redalje, D.G., Laws, E.A., 1983. The effects of environmental factors on growth and the chemical and biochemical composition of marine diatoms. I. Light and temperature effects. J. Exp. Mar. Biol. Ecol. 68, 59–79. https://doi.org/10.1016/0022-0981(83)90013-8

Rendon, S.M., Roldan, G.J.C., Voroney, R.P., 2013. Effect of carbon dioxide concentration on the growth response of Chlorella vulgaris under four different LED illumination. Int. J. Biotechnol. Wellness Ind. 2, 125–131.

Rhee, G.--ull, Gotham, I.J., 1981. The effect of environmental factors on phytoplankton growth: Light and the interactions of light with nitrate limitation1: Light-nutrient interactions. Limnol. Oceanogr. 26, 649–659. https://doi.org/10.4319/lo.1981.26.4.0649

Riebesell, U., Fabry, V.J., Hansson, L., Gattuso, J.-P., 2011. Guide to best practices for ocean acidification research and data reporting. Office for Official Publications of the European Communities.

Rivkin, R.B., 1989. Influence of irradiance and spectral quality on the carbon metabolism of phytoplankton. I. Photosynthesis, chemical composition and growth. Mar. Ecol. Prog. Ser. Oldendorf 55, 291–304.

Rost, B., Riebesell, U., Sültemeyer, D., 2006. Carbon acquisition of marine phytoplankton: effect of photoperiod length. Limnol. Oceanogr. 51, 12–20.

Sánchez-Saavedra, M. del P., Voltolina, D., 1994. The chemical composition of Chaetoceros sp. (Bacillariophyceae) under different light conditions. Comp. Biochem. Physiol. Part B Comp. Biochem. 107, 39–44. https://doi.org/10.1016/0305-0491(94)90222-4

Sánchez-Saavedra, M., Jiménez, C., Figueroa, F., 1996. Far-red light inhibits growth but promotes carotenoid accumulation in the green microalga Dunaliella bardawil. Physiol. Plant. 98, 419–423.

Schellenberger Costa, B., Jungandreas, A., Jakob, T., Weisheit, W., Mittag, M., Wilhelm, C., 2013. Blue light is essential for high light acclimation and photoprotection in the diatom Phaeodactylum tricornutum. J. Exp. Bot. 64, 483–493. https://doi.org/10.1093/jxb/ers340

Schulze, P.S.C., Barreira, L.A., Pereira, H.G.C., Perales, J.A., Varela, J.C.S., 2014. Light emitting diodes (LEDs) applied to microalgal production. Trends Biotechnol. 32, 422–430. https://doi.org/10.1016/j.tibtech.2014.06.001

Six, C., Finkel, Z.V., Irwin, A.J., Campbell, D.A., 2007. Light Variability Illuminates Niche-Partitioning among Marine Picocyanobacteria. PLoS ONE 2, e1341. https://doi.org/10.1371/journal.pone.0001341

Stadnichuk, I.N., Bulychev, A.A., Lukashev, E.P., Sinetova, M.P., Khristin, M.S., Johnson, M.P., Ruban, A.V., 2011. Far-red light-regulated efficient energy transfer from

phycobilisomes to photosystem I in the red microalga Galdieria sulphuraria and photosystems-related heterogeneity of phycobilisome population. Biochim. Biophys. Acta BBA - Bioenerg. 1807, 227–235. https://doi.org/10.1016/j.bbabio.2010.10.018

Vadiveloo, A., Moheimani, N.R., Cosgrove, J.J., Bahri, P.A., Parlevliet, D., 2015. Effect of different light spectra on the growth and productivity of acclimated Nannochloropsis sp.(Eustigmatophyceae). Algal Res. 8, 121–127.

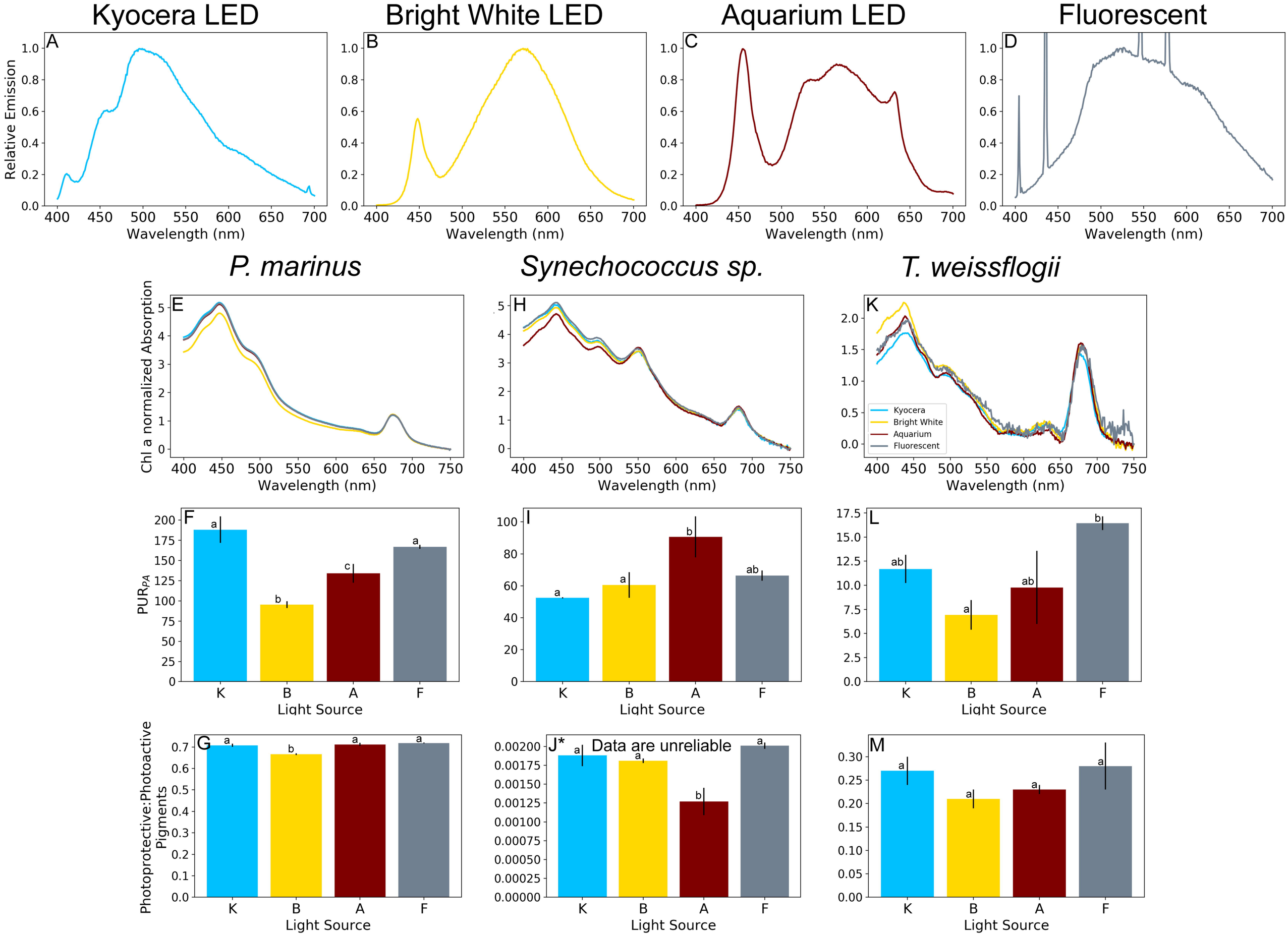
Walter, A., Carvalho, J.C. de, Soccol, V.T., Faria, A.B.B. de, Ghiggi, V., Soccol, C.R., 2011. Study of phycocyanin production from Spirulina platensis under different light spectra. Braz. Arch. Biol. Technol. 54, 675–682. https://doi.org/10.1590/S1516-89132011000400005

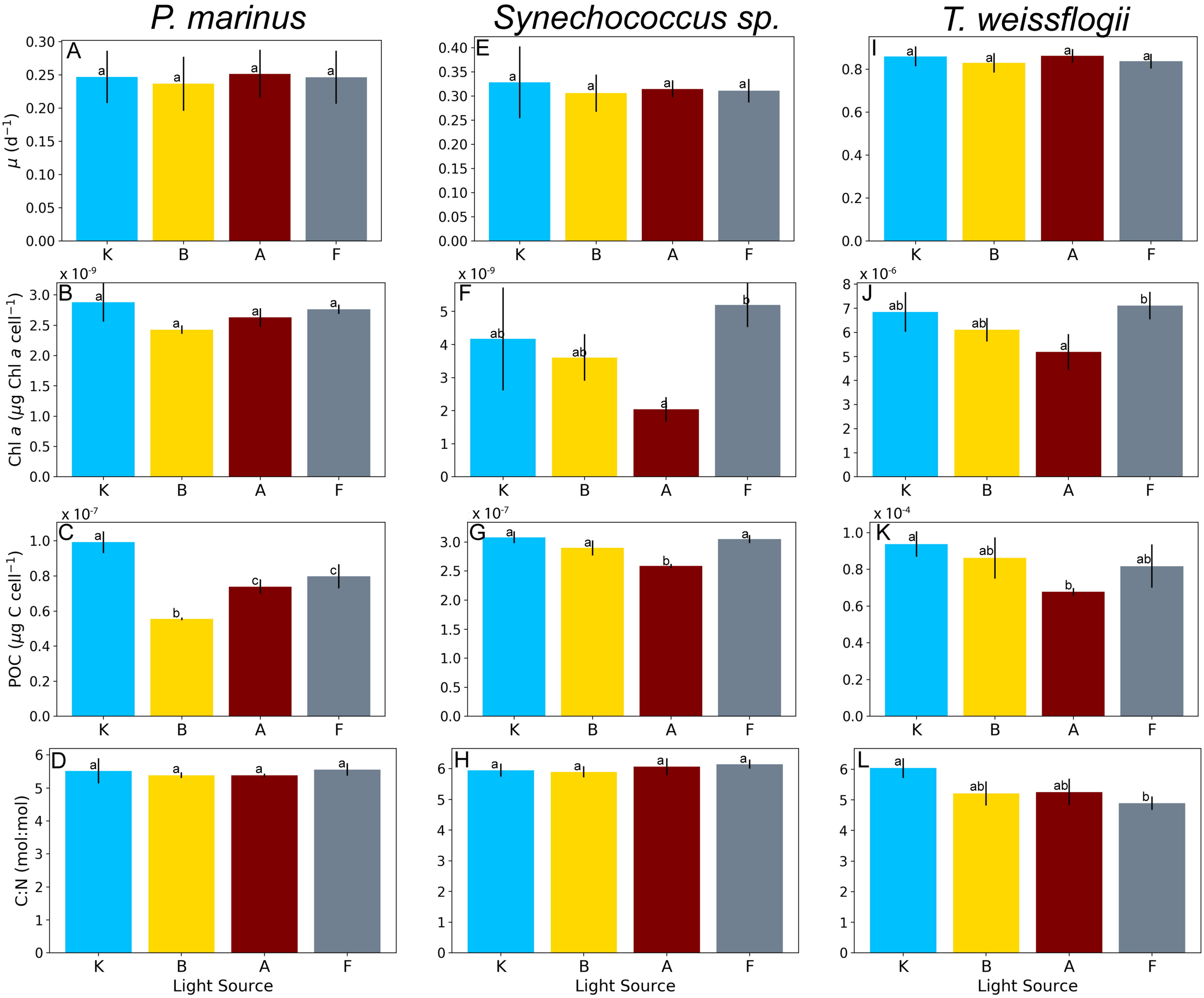
Wang, C.-Y., Fu, C.-C., Liu, Y.-C., 2007. Effects of using light-emitting diodes on the cultivation of Spirulina platensis. Biochem. Eng. J. 37, 21–25. https://doi.org/10.1016/j.bej.2007.03.004

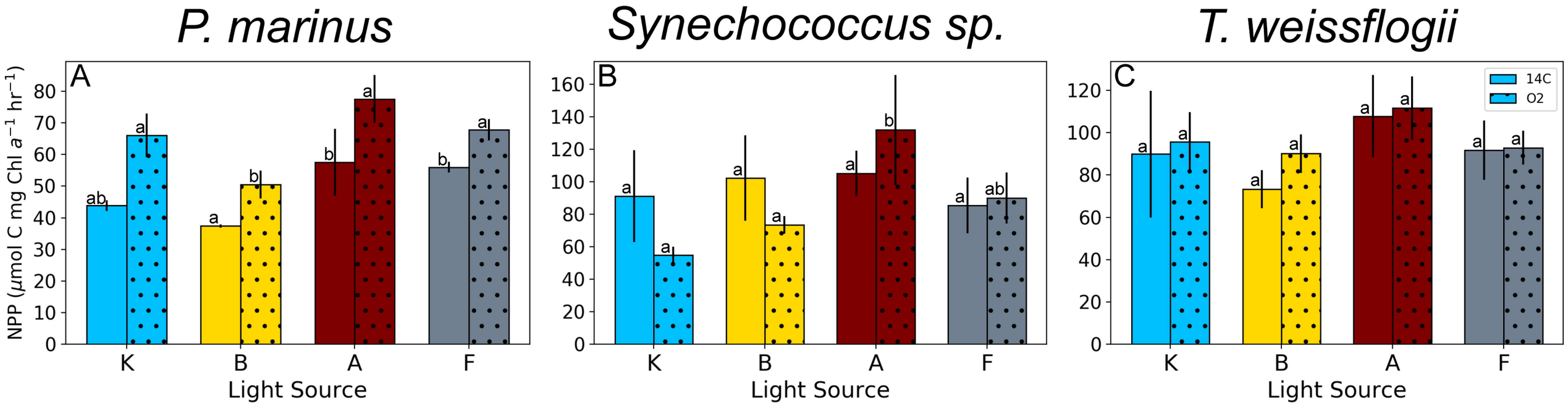
White, E., Hoppe, C.J.M., Rost, B., 2020. The Arctic picoeukaryote Micromonas pusilla benefits from ocean acidification under constant and dynamic light. Biogeosciences 17, 635–647. https://doi.org/10.5194/bg-17-635-2020

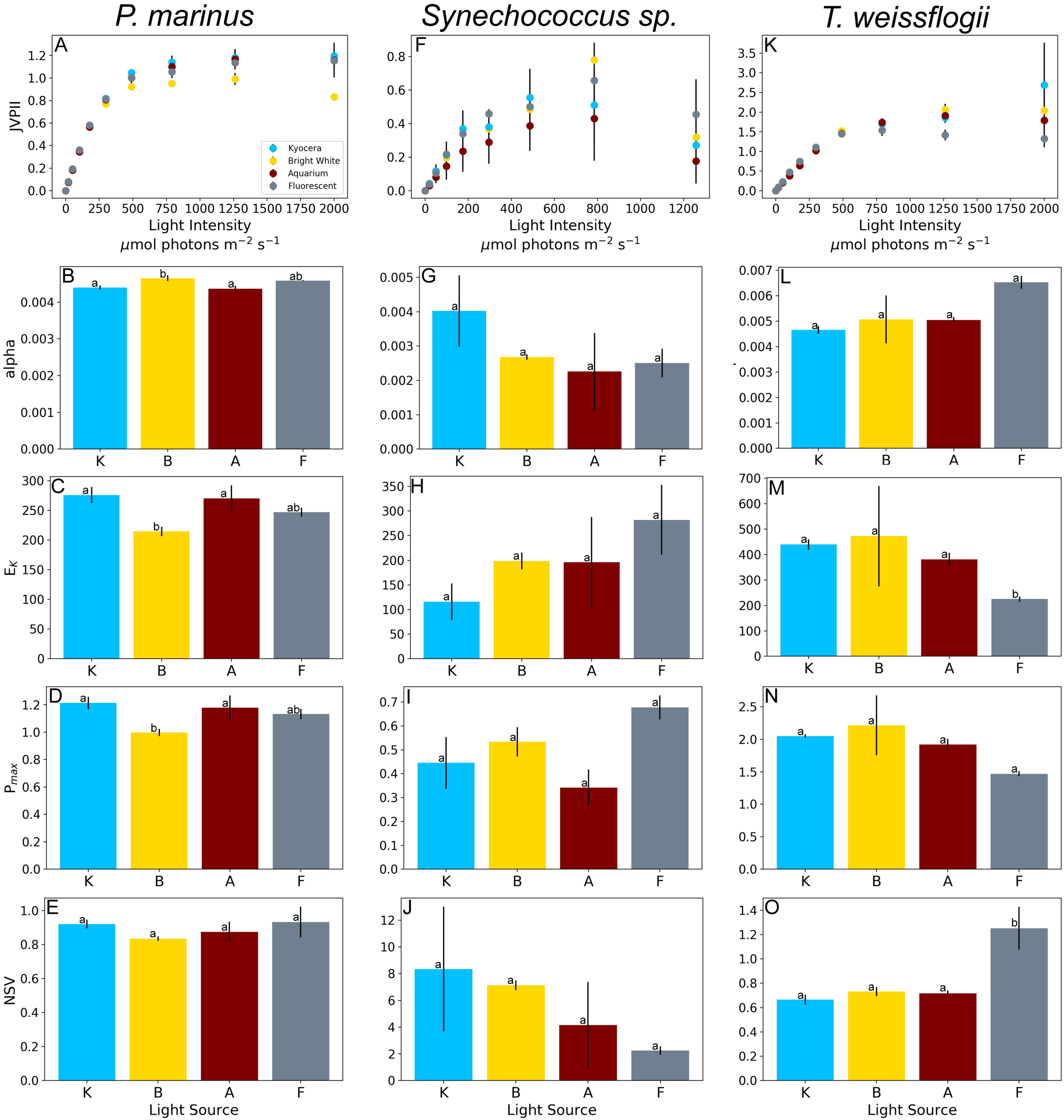
Wilson, A., Punginelli, C., Gall, A., Bonetti, C., Alexandre, M., Routaboul, J.-M., Kerfeld, C.A., Van Grondelle, R., Robert, B., Kennis, J.T., others, 2008. A photoactive carotenoid protein acting as light intensity sensor. Proc. Natl. Acad. Sci. 105, 12075–12080.

Xu, B., Cheng, P., Yan, C., Pei, H., Hu, W., 2013. The effect of varying LED light sources and influent carbon/nitrogen ratios on treatment of synthetic sanitary sewage using Chlorella vulgaris. World J. Microbiol. Biotechnol. 29, 1289–1300. https://doi.org/10.1007/s11274-013-1292-6


Kyocera LED
Bright White LED
Aquarium LED
Fluorescent
A
B
C
D
Relative Emission
Wavelength (nm)
P. marinus
Synechococcus sp.
T. weissflogii
E
H
K
Chl a normalized Absorption
Kyocera
Bright White
Aquarium
Fluorescent
F
I
L
PUR$_{PA}$
G
J*
Data are unreliable
M
Photoprotective:Photoactive Pigments
Light Source
K
B
A
F


P. marinus
Synechococcus sp.
T. weissflogii
A
E
I
B
F
J
C
G
K
D
H
L
μ (d⁻¹)
Chl a (μg Chl a cell⁻¹)
POC (μg C cell⁻¹)
C:N (mol:mol)
x 10⁻⁹
x 10⁻⁷
x 10⁻⁶
x 10⁻⁴
K
B
A
F
Light Source


P. marinus
Synechococcus sp.
T. weissflogii
A
B
C
NPP (μmol C mg Chl a⁻¹ hr⁻¹)
14C
O2
K
B
A
F
Light Source


P. marinus
Synechococcus sp.
T. weissflogii
A
F
K
JVPII
Light Intensity
μmol photons m⁻² s⁻¹
Kyocera
Bright White
Aquarium
Fluorescent
B
G
L
alpha
C
H
M
E_K
D
I
N
P_max
E
J
O
NSV
Light Source