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RESEARCH ARTICLE

Light spectrum matters: Interactive effects of light and nutrients on phytoplankton communities and trophic transfer

Sebastian Neun[1] | **Alexander Wacker**[2] | **Maren Striebel**[1]

[1]Institute for Chemistry and Biology of the Marine Environment (ICBM), School of Mathematics and Science, Carl von Ossietzky Universität Oldenburg, Wilhelmshaven, Lower Saxony, Germany

[2]Zoological Institute and Museum, University of Greifswald, Greifswald, Mecklenburg-Vorpommern, Germany

Correspondence
Sebastian Neun
Email: sebastian.neun@uol.de

Maren Striebel
Email: maren.striebel@uol.de

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Abstract

1. Phytoplankton is highly sensitive to both the quantity (intensity) and quality (spectrum) of available light, due to their wide range of light-absorbing pigments. Light is a major driver of trophic energy transfer, and while the impact of light intensity is well investigated, it is unclear how changes in light spectrum may influence this mechanism. The distribution of light underwater is strongly dependent on the optical properties of the water column, and both the available light intensity and wavelength spectrum change with increasing depth.
2. In this study, we investigated the effect of different light spectra on the community structure and biochemical composition (nutrient stoichiometry and fatty acids) of natural freshwater phytoplankton, additionally including two different levels of water depth and nutrient availability in a full-factorial design. The field experiment was combined with a subsequent laboratory experiment using the lake seston as food to identify potential nutritional constraints for the zooplankton species *Daphnia pulex* in response to the treatments.
3. We found that light spectrum influences phytoplankton species composition and seston biochemistry, with these effects being highly dependent on the available light intensity (through depth) and nutrients. In particular, the spectral quality of light was important when light, but not nutrients, limited primary producers.
4. In addition, we could observe that the growth performance of *D. pulex* differed when grazing on the different seston communities because abiotic factors altered the prevalent growth constraints of *Daphnia*, affecting both mineral and biochemical growth constraints. This indicated that the effects of different light spectra were propagating from the primary producer level to the consumers.
5. *Synthesis*. Overall, our results showed that the spectral quality of light has a significant impact on phytoplankton community dynamics and the biochemical composition of lake seston. Moreover, the results suggest that light intensity, light spectrum, and nutrients interactively act at the base of aquatic food webs with propagating effects to herbivores, particularly under scenarios of light limitation. Thus, we demonstrate that the light spectrum is a significant component of the

abiotic environment that influences plankton dynamics and the trophic transfer in aquatic ecosystems.

KEYWORDS
ecological stoichiometry, fatty acids, light, light spectrum, phytoplankton, pigments, trophic interactions, zooplankton

1 | INTRODUCTION

In many biological systems, autochthonous fluxes of carbon (C) are governed by phototrophic primary producers and heavily rely on energy inputs from solar radiation and its conversion into chemical energy (Wetzel, 2001). These processes are also highly dependent on stratification as the primary physical property that structures underwater light dynamics, water chemistry and biological dynamics in lakes (Wetzel, 2001). Phytoplankton organisms are remarkably efficient in light energy conversion through photosynthetic processes (Agustí et al., 1994; Sand-Jensen & Borum, 1991). Environmental factors, such as light and nutrient elements, including nitrogen (N) or phosphorus (P), strongly influence phytoplankton growth and community development (Karlsson et al., 2009; Schindler, 1978; Urabe & Sterner, 1996). Since both the rate of nutrient uptake and the absorption of light are often species-specific in phytoplankton, both resources have a crucial role in community structuring processes (Burson et al., 2018; Huisman & Weissing, 1995; Klausmeier & Litchman, 2001).

Phytoplankton experiences a complex underwater light field modulated through absorption and scattering of the incoming light beam by water molecules, dissolved and particulate organic matter, including the phytoplankton itself (Kirk, 2011). These processes also affect the wavelength spectrum of *photosynthetically available radiation* (PAR) from 400 to 700 nm, and species have different strategies in light harvesting to mitigate competition for light. For instance, species that absorb in different regions of the PAR spectrum are able to coexist, showing that differing light-harvesting strategies can prevent competitive exclusion (Burson et al., 2019; Stomp et al., 2004). These observations prompt that the range of the available light spectrum and thus the colour of light also impacts phytoplankton community composition (Hintz et al., 2021; Stockenreiter et al., 2021; Wall & Briand, 1979).

Beyond the individual effects of nutrient availability, light intensity and light spectrum on phytoplankton, complex interactions among these factors exist. Increasing light intensity compared to P availability typically increases seston C:P ratios in lakes due to the positive light effect on phytoplankton photosynthetic C fixation (Healey, 1985; Sterner et al., 1997). The strength of this relationship depends, however, on the nutrient background and, for example, weakens with increasing nutrient supply (Dickman et al., 2006). Likewise, the production and availability of more complex biomolecules are interactively affected by light intensity and nutrients. This has been demonstrated for fatty acids, for example (Hill et al., 2011; Piepho et al., 2012; Thompson et al., 1990). Considering light as a resource defined by its intensity *and* spectral quality adds another dimension to these interdependencies. How the shape of the light spectrum might interact here is little understood, although studies indicate that light colour also influences phytoplankton nutrient uptake and fatty acid production (Bercel & Kranz, 2022; Helamieh et al., 2021; Rivkin, 1989).

Interactive effects of light and nutrients on seston stoichiometry and biochemical composition are highly relevant for the trophic dynamics in aquatic systems. In particular, the trophic crossover from phytoplankton to zooplankton is commonly characterised by various mineral (Hessen, 1992; Sterner, 1993; Urabe et al., 2002) and biochemical limitation scenarios (Brett & Müller-Navarra, 1997; Hartwich et al., 2012; Müller-Navarra et al., 2000). Many herbivorous zooplankton, like the cladoceran *Daphnia* species, have, in contrast to phytoplankton, a relatively stable elemental composition and are sensitive to imbalances in nutrient stoichiometry (Andersen & Hessen, 1991; Hessen, 1990; Hessen et al., 1992). Therefore, alterations in seston C:nutrient ratios due to changes in the abiotic light:nutrient supply ultimately translate into altered growth and reproduction of zooplankton (Elser, Fagan, et al., 2000; Elser, Sterner, et al., 2000; Sterner et al., 1998; Striebel et al., 2008; Urabe & Sterner, 1996). Beyond the mineral or elemental content of phytoplankton, it is often also specific biochemicals in phytoplankton that limit zooplankton performance, including sterols (e.g. Martin-Creuzburg & Merkel, 2016) and fatty acids (e.g. Brett & Müller-Navarra, 1997), particularly the polyunsaturated fatty acids (PUFA). Both components are mandatory for zooplankton growth and reproduction (Wacker & Martin-Creuzburg, 2007) and must be acquired from the ingested food. As a consequence, drivers of zooplankton growth limitation in natural systems usually alternate throughout the year between limitation by food quantity, mineral or biochemical constraints, as well as states of complex co-limitation, stressing the complexity of nutritional constraints at the phytoplankton–zooplankton interface (Hartwich et al., 2012; Park et al., 2003; Wacker & von Elert, 2001).

While recent studies addressed the interactive effects of light intensity and nutrients on phytoplankton and their consequences for upper trophic levels, only a few considered the spectral quality of light. This has been considered particularly for its meaning in diversity and distribution patterns of phytoplankton in nature (Holtrop et al., 2021; Stomp et al., 2004), whereas its significance for the biochemistry of phytoplankton and potential bottom-up

effects in aquatic food webs is uncertain. With this study, we elaborate on this issue and address the question of whether the composition of the underwater light spectrum should be considered for phytoplankton productivity and trophic dynamics, especially in freshwaters where shifts in water colour have been documented in recent years and are ascribed to changing temperature and precipitation patterns (Leech et al., 2018; Yang et al., 2022). In a more general sense, we ask: Does the composition of the underwater light spectrum affect trophic relations in aquatic systems by acting at the base of the food webs, that is on phytoplankton? We first assessed the role of environmental light intensity, light quality, and nutrients for a natural freshwater phytoplankton community. We manipulated the environmental factors in a full-factorial design in situ and determined their effects on the community structure and the elemental and biochemical composition of phytoplankton. The available light intensity was determined by the water depth at which phytoplankton was incubated. In addition to the naturally occurring changes in light spectrum with increasing depth, we manipulated the light spectrum at each depth experimentally by using light filter foils.

With this setup, we tested the hypothesis that, besides the well-known effects of nutrient supply and light intensity on seston (see above), the light spectrum also impacts the level of primary producers, that is seston biomass, biochemistry (stoichiometry, fatty acids), and phytoplankton community composition (hypothesis H1). This hypothesis would be supported if multivariate analyses of these responses reveal a significant single or interactive effect of light spectrum. Particularly when phytoplankton grows under low light conditions, different light spectra impact its community characteristics (resulting in an interactive effect of depth and spectrum).

In a second step, we investigated the nutritional quality of the resulting seston communities for a higher trophic level, using freshly isolated individuals of the zooplankton herbivore *Daphnia pulex*. Here, we also expect that, beyond the effects of nutrient supply and depth, the light spectrum has an impact on the trophic transfer from phytoplankton to zooplankton (H2). *Daphnia* growth rates should show indirect treatment effects because of alterations in available food quantity and quality, as well as compositional changes in phytoplankton. This hypothesis will be supported by significant treatment effects (individual or interactive) when comparing the growth rates of *D. pulex*. We assume that *Daphnia* growth rates increase with higher food quantity (seston biomass) and potentially better food quality in terms of increasingly available nutrient elements and fatty acids. In addition, *Daphnia* growth rates should depend on phytoplankton community identity. We used an ordination method (principal component analysis) to reduce the multivariate character of the drivers in trophic relationships and expected that principal components should reveal the potentially decisive food quality parameters in lake seston. *Daphnia* growth should then correlate positively with these principal components.

2 | MATERIALS AND METHODS

2.1 | Study site

The experiment was performed from 27 May to 9 June 2022 in Lake Schortens, a small oligotrophic lake (total P between 4.3 and 9.2 $\mu g L^{-1}$, chlorophyll *a* 6.73 ± 0.39 $\mu g L^{-1}$ (mean ± SD) on 27 May 2022) of 12,000 m^2 with a mean and maximum depth of 6.5 and 10 m, respectively, located in Lower Saxony, Germany (53°33′05.2″ N, 7°56′08.8″ E). No permission for the field work was needed, but it was conducted in consultation with the city of Schortens, Germany and the leaseholder of the lake.

2.2 | Experimental setup

A full-factorial design was conceived that included two incubation depths (0.5 and 2.5 m), two nutrient levels (ambient (−NP) and enriched (+NP)), and four different light spectra (full spectrum (Full), blue (B), green (G), and red (R)). Each treatment combination was replicated fourfold, leading to 64 experimental units in total. Phytoplankton was incubated in situ for 13 days in 650 mL cell culture flasks (T175, SARSTEDT, Nümbrecht, Germany), which were fixed onto a custom incubation setup (Figure 1). The spring phytoplankton community from Lake Schortens was sampled from different depths in the water column (0–5 m, in 1 m steps) in equal amounts with a 2.0 L Ruttner water sampler (HYDRO-BIOS, Kiel, Germany) and subsequently pooled. To reduce the impact of grazing by large zooplankton during incubation, the water was filtered twice through a 53 µm polyamide mesh. The filtration also removed large species from the start community, like the colonial chrysophyte *Dinobryon* sp., species of the desmid *Closterium* spp., and the dinoflagellate *Ceratium* sp. We acknowledge here that the initial removal of larger species might have biased our associated grazing assay with *D. pulex* since phytoplankton size could interact with phytoplankton stoichiometry (DeMott & Van Donk, 2013), fatty acid content (Ravet & Brett, 2006), and a suite of vitamins and macromolecules (Finkel et al., 2010, 2016; Jónasdóttir, 2019), influencing *Daphnia* growth performance. After filtration, the volume of the start community was divided into two, with one half being spiked with nutrients as described below. All culture flasks were filled up to a final volume of 600 mL each.

Two different incubation depths were chosen, at which either light was in excess but without harmful effects from too high intensities and ultraviolet radiation (i.e. 0.5 m depth), and 2.5 m, where 90% of surface light was attenuated (see Figure 1). Background concentrations of N ($NO_2^- + NO_3^-$) and P (soluble reactive P) in Lake Schortens were 15.7 ± 0.2 µM (mean ± SD) or 220.1 ± 2.2 $\mu g L^{-1}$ for N and 0.053 ± 0.011 µM or 1.6 ± 0.3 $\mu g L^{-1}$ for P, measured with a continuous-flow analyser (San++; Skalar Analytical B.V., Breda, the Netherlands). For the nutrient addition treatment (+NP), N and P were added as $NaNO_3$ to obtain molar concentrations of 43.3 µM (606.5 $\mu g L^{-1}$) for N, and as K_2HPO_4 to obtain 3.33 µM (102.2 $\mu g L^{-1}$) for P, respectively. This increased the total quantity of nutrients for phytoplankton and

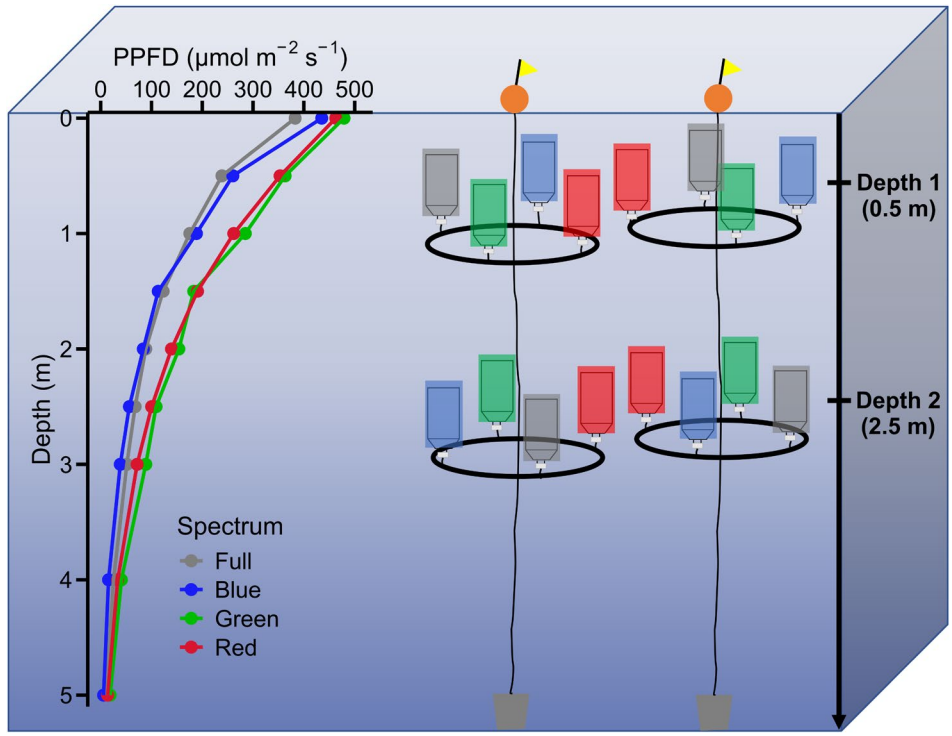

FIGURE 1 Scheme of the setup for the in situ incubation of phytoplankton in the water column. A natural freshwater phytoplankton community was incubated in cell culture flasks that were fixed onto a customised ring widget and aligned vertically in the water column. Flasks were placed at 0.5 m for high light and 2.5 m for low light. For different light spectra, flasks were covered with light filters (grey (intensity reduced full spectrum), blue, green and red), and communities were grown either under ambient or enriched nutrients. All treatments were realised in a full-factorial design and replicated fourfold. The vertical depth profiles shown were measured once during the study period (see Section 2).

reduced the severity of P limitation (N:P ratio of 13). Finally, the available light spectrum was manipulated by covering the flasks with coloured light filter foils: blue (LEE Filter no. 118, Hampshire, UK), green (LEE no. 122), and red (LEE no. 182) (Figure 1; Figure S1). In addition, experimental units that served as controls (full spectrum but with reduced intensity) were covered with a neutral density filter (LEE no. 210) to compensate for the overall reduction in available light intensity but without affecting the spectrum. Vertical depth profiles of photosynthetic photon flux density (PPFD) of reduced full spectrum, blue light, green light and red light were measured once during the study period on a sunny, cloudless day. Measurements were done with a spherical quantum sensor (LI-193; LI-COR, Lincoln, USA) connected to a LI-250A Light Meter from LI-COR, covered with the same light filter foils. Specifically, at 0.5 m depth, measured light intensities (PPFD) among light colour treatments were (in µmol photons $m^{-2}s^{-1}$): 238.7 (Full), 260.1 (B), 363.1 (G), 353.1 (R); and, at 2.5 m: 67.85 (Full), 56.41 (B), 109.05 (G) and 100.32 (R). The light intensity without filter was 1101.3 and 306.2 µmol photons $m^{-2}s^{-1}$ for 0.5 and 2.5 m, respectively. Furthermore, vertical attenuation coefficients were determined to be 0.7544 m^{-1} (Full), 0.8702 m^{-1} (B), 0.5839 m^{-1} (G) and 0.6019 m^{-1} (R).

During incubation, temperature and light conditions in the lake were monitored with continuous data loggers (HOBO Pendant MX2202; Onset, Bourne, MA, USA) in 1-minute intervals, which were employed at the same depths as the experimental units (Figure S2A,B). Temperature during incubation was 17.8 ± 1.3°C (mean ± SD) at 0.5 m and 16.6 ± 0.4°C at 2.5 m depth; thus, temperature effects between depths were expected to be negligible (Figure S2A).

2.3 | Sampling and laboratory analysis

After the 13 days, seston was sampled for the analysis of stoichiometry (particulate organic carbon (POC), nitrogen (PON) and phosphorus (POP)), pigments and fatty acids. For that, the whole setup was removed from the water column, culture flasks were stored in boxes protected from light, transported to the laboratory and then processed immediately.

Samples for particulate nutrient (POC, PON and POP), pigment and fatty acid analyses were filtered onto pre-combusted, acid-washed GF/C glass-fibre filters (Whatman) and frozen at −80°C until further analysis. For POC and PON, filters were dried for at least 1 week, transferred into tin capsules, and measured with an elemental analyser (Flash EA 1112; Thermo Scientific, Waltham, MA, USA). For the analysis of POP, filters were combusted and digested with potassium peroxydisulfate ($K_2S_2O_8$), and the POP was determined photometrically (Synergy H1; BioTek Germany, Bad Friedrichshall, Germany) by molybdate reaction (Wetzel & Likens, 2000).

Bulk phytoplankton pigments were extracted from filters by adding 1.2 mL of 90% ethanol and sonication for 30 min (in an ice

bath). After refrigeration at 4°C overnight, 200 µL of the extracts were pipetted into 96-well flat-bottom microtiter plates and measured photometrically in triplicate (Synergy H1; BioTek Germany). Absorbance spectra of pigments were measured from 300 to 800 nm at 1 nm intervals, and pigment concentrations were calculated via spectral deconvolution following the method from Thrane et al. (2015). Thereby, concentrations of 19 different pigments were obtained, of which 9 could be assigned as marker pigments for specific taxonomic groups of phytoplankton. A full list of the measured pigments is provided in the Supporting Information (Table S1).

Fatty acids were extracted, identified and quantified by gas chromatography (GC 6890N; Network GC System, Agilent Technologies GmbH) from three of the four replicates following Wacker et al. (2016).

2.4 | Zooplankton grazing assay

The nutritional quality of the reared phytoplankton communities (seston) was assessed in a short-term grazing assay with the cladoceran *Daphnia pulex* directly after the experimental units arrived in the laboratory. The experiment did not require ethical approval. Individuals of *D. pulex* were isolated from Lake Schortens three weeks before the grazing assay and synchronised in glass jars at 18°C with the green alga *Tetradesmus obliquus* as food. Filtered (<0.2 µm) water from Lake Schortens was used as medium for *D. pulex*. The food alga *T. obliquus* was grown in full WC medium (Guillard & Lorenzen, 1972) at 100 µmol photons $m^{-2} s^{-1}$ and 18°C, aerated with pre-filtered air (<0.2 µm). To produce enough synchronised experimental animals, it was necessary to conduct the preculturing of the daphnids with *T. obliquus*, which is of moderate food quality. We acknowledge that maternal provisioning effects might lead to an underestimation of experimental treatment effects in our results (Lukas et al., 2013). For the grazing assay, glass jars were filled with 120 mL of the respective experimental units, and three juveniles (age <24 h) of *D. pulex* were added and grown for 4 days in total. To retain spectral light conditions similar to those during the in situ incubation, glass jars were covered with the same light filter foils and illuminated with white light (Econlux, Cologne, Germany) at low intensity (10 µmol photons $m^{-2} s^{-1}$ PPFD) without incorporating different light intensities for the different depths. We chose this low light intensity here because it was observed to be optimal for *Daphnia*. We are aware that we do not cover the full natural complexity with this experimental setup; however, this is a common bias in experiments involving transitioning from complex to more controlled and consequently simplified scenarios (Gerhard et al., 2023). We conducted a near-natural incubation of lake phytoplankton and fed these cultures to *Daphnia* to cover multiple scales of experimental setups and trophic levels. Generally, moving from natural to controlled systems improves mechanistic understanding but compromises ecological realism (Boyd et al., 2018; Petersen et al., 2009).

Somatic growth rate g (day^{-1}) of *D. pulex* was calculated as the increase in dry mass using the equation:

$$g = \frac{\ln M_T - \ln M_0}{T},$$

where T is the duration of the growth experiment (4 days), M_0 the initial dry mass of individuals (5 subsamples of 10 juveniles each), and M_T the final dry mass of animals.

2.5 | Statistical analysis

We first tested whether the different growth conditions led to statistically significant differences in seston biomass production (POC) by applying a three-factorial ANOVA. Nutrient treatments (−NP, +NP), incubation depths (0.5 m, 2.5 m) and light spectra (Full, B, G, R) were included as independent variables. Multivariate analyses were considered to determine treatment effects on pigment composition (as a proxy for changes in phytoplankton community), elemental composition (i.e. N:C and P:C ratio), and fatty acid profiles, respectively. For this, permutational multivariate ANOVAs (PERMANOVA; Anderson (2017)) were performed based on Euclidean distances with 9999 permutations, avoiding assumptions of homoscedasticity and multivariate normality like in classical multivariate ANOVA. Concentrations of marker pigments were divided by the concentration of chlorophyll *a*, while elemental ratios (N:C, P:C) and fatty acids were expressed as mass ratios per carbon (g per g C). As a measure of effect size, partial η^2 was calculated:

$$\text{partial } \eta^2 = \frac{SS_{Effect}}{SS_{Effect} + SS_{Residual}},$$

taking into account the variance explained by the variable (SS_{Effect}) and the residual sum of squares ($SS_{Residual}$). Given a potential autocorrelation of light quantity and quality with depth, we performed all the above analyses with measured PPFDs (cf. Figure 1) instead of depth as well (Tables S2–S4). As this does not correct for changes in the light spectrum (with depth), we continued using depth as a factor throughout the manuscript. To clarify whether treatment-related changes at the primary producer level were strong enough to impact the trophic transfer to *D. pulex*, we tested whether growth responses of *D. pulex* differed significantly among treatments with a three-factorial ANOVA. ANOVA assumptions for normality and homoscedasticity in data were tested with the Shapiro–Wilk test and Levene's test, respectively. Results of ANOVA were interpreted when the data met at least the assumption of homoscedasticity. We expected that significant differences in *Daphnia* growth are caused by changes in available food quantity (POC), phytoplankton community composition, and food quality. We performed a linear model for the relationship between *D. pulex* growth rates and seston carbon to estimate the effect of food quantity. To determine the impact of phytoplankton compositional change on *D. pulex* growth, we applied a principal component analysis (PCA) to the scaled pigment data, extracted the first axis, which explains the most variance (PC1), and calculated a linear model for the relationship between *D. pulex* growth rates and PC1. The same approach was applied to the combined data matrix of elemental ratios and fatty acids to reduce the dimensionality of food quality parameters in lake seston.

All statistical tests and figures were performed with the software R, version 4.3.2 (R Core Team, 2023). Data handling and plots

were carried out using functions from the 'tidyverse' collection, version 2.0.0 (Wickham et al., 2019) and the packages 'ggpubr' (v0.6.0; Kassambara, 2023) and 'ggpmisc' (v0.5.5; Aphalo, 2023). Additional packages included 'vegan' (v2.6-4; Oksanen et al., 2022) and its function adonis2() for PERMANOVA, 'ggfortify' for PCA plots (v0.4.16; Tang et al., 2016) and 'car' (v3.1-2; Fox & Weisberg, 2019) for Levene's test for homoscedasticity. Statistical results were interpreted as significant for a significance level of $\alpha = 0.05$.

3 | RESULTS

3.1 | Effects of nutrients, depth and light spectrum on lake seston and phytoplankton community composition

Seston biomass (POC), stoichiometry (i.e. N:C, P:C) and fatty acid composition were all significantly affected by nutrient availability, depth and light spectrum, showing significant main effects as well as interactive effects (Tables 1 and 2). Generally, nutrient addition (+NP) increased seston biomass as well as the elemental and fatty acid (especially ω3 PUFAs) content per biomass, but the effect was more pronounced at shallow depth (0.5 m) than in the deeper incubation (2.5 m; Figure S3). Differences among light spectra highly depended on nutrient supply and water depth.

Seston biomass was significantly affected by nutrient supply ($p < 0.001$), depth ($p < 0.001$), and marginally by light spectrum ($p = 0.053$; three-way ANOVA, Table 1). In addition, interactive effects between Depth × Nutrients, Nutrients × Spectrum, and Depth × Nutrients × Spectrum were revealed (see Table 1). Largest effect sizes were associated with depth, nutrients and the interaction between these two factors (partial η^2 of 0.859, 0.791 and 0.830, respectively), indicating them as the primary drivers of variation. In contrast, spectrum alone contributed only minor effects (partial η^2 of 0.150), but its influence became more pronounced in combination with nutrients (partial η^2 of 0.249), reflecting a moderate interactive effect (Table 1).

Seston stoichiometry and fatty acid composition showed significant main effects as well as significant interactive terms between all possible treatment combinations except for the three-fold interaction (PERMANOVA, Table 2). Hence, light spectrum, particularly through its effect in the interaction with depth (partial η^2 of 0.423), shaped seston stoichiometry (Table 2), even though nutrients remained the strongest driver (partial η^2 of 0.894) by overall increasing seston nutrient:C ratios (Figure S3B,C). Similarly, nutrient supply was the dominant factor influencing seston fatty acids (partial $\eta^2 = 0.377$). However, light spectrum was revealed to have a strong impact – not only directly (partial $\eta^2 = 0.194$), but also through its interactions with nutrients (partial $\eta^2 = 0.147$) and depth (partial $\eta^2 = 0.174$)—emphasising its multifaceted influence on these variables. Depth alone contributed a moderate effect across these response variables (partial $\eta^2 = 0.292$ and 0.115, respectively), showing a consistent, though for fatty acids a less dominant, role compared to nutrients and light spectrum.

Finally, all treatments had a highly significant impact on pigment composition and thus phytoplankton community structure (significant main and interactive effects, PERMANOVA, Table 2). Again,

TABLE 1 Three-factorial ANOVA of seston carbon testing for the effects of incubation depth (D), nutrient supply (N) and light spectrum (S).

Effect	df	Partial η^2	*F*	*p*
Depth	1	0.859	287.0	<0.001
Nutrients	1	0.791	178.1	<0.001
Spectrum	3	0.150	2.8	NS (0.053)
D×N	1	0.830	230.1	<0.001
D×S	3	0.029	0.5	NS (0.708)
N×S	3	0.249	5.2	<0.01
D×N×S	3	0.222	4.5	<0.01
Residuals	47			

Note: Results are shown as the degrees of freedom (df), partial η^2 as effect size, *F* statistic and *p*-value for each analysis. For non-significant effects (NS), exact *p*-values are given in brackets.

TABLE 2 Results of PERMANOVA of seston stoichiometric ratios (N:C, P:C), fatty acids (11 fatty acids), and phytoplankton community pigments (9 pigments), testing the effects of incubation depth (D), nutrient supply (N), and light spectrum (S).

		Stoichiometry			Fatty acids			Pigments		
Effect	df	Partial η^2	*F*	*p*	Partial η^2	*F*	*p*	Partial η^2	*F*	*p*
Depth	1	0.292	18.9	<0.001	0.115	4.2	<0.01	0.293	19.9	<0.001
Nutrients	1	0.894	386.6	<0.001	0.377	19.3	<0.001	0.453	39.8	<0.001
Spectrum	3	0.170	3.2	<0.05	0.194	2.6	<0.01	0.262	5.7	<0.001
D×N	1	0.100	5.1	<0.05	0.140	5.2	<0.001	0.283	19.0	<0.001
D×S	3	0.423	11.2	<0.001	0.174	2.2	<0.01	0.099	1.8	<0.05
N×S	3	0.187	3.5	<0.05	0.147	1.8	<0.05	0.260	5.6	<0.001
D×N×S	3	0.107	1.8	NS (0.151)	0.088	1.0	NS (0.395)	0.161	3.1	<0.001

Note: Results are shown as the degrees of freedom (df), partial η^2, pseudo *F*, and *p*-value for each analysis. For non-significant effects (NS), exact *p*-values are given in brackets. Residual df for each analysis was 48 for pigments, 46 for stoichiometric ratios, and 32 for fatty acids.

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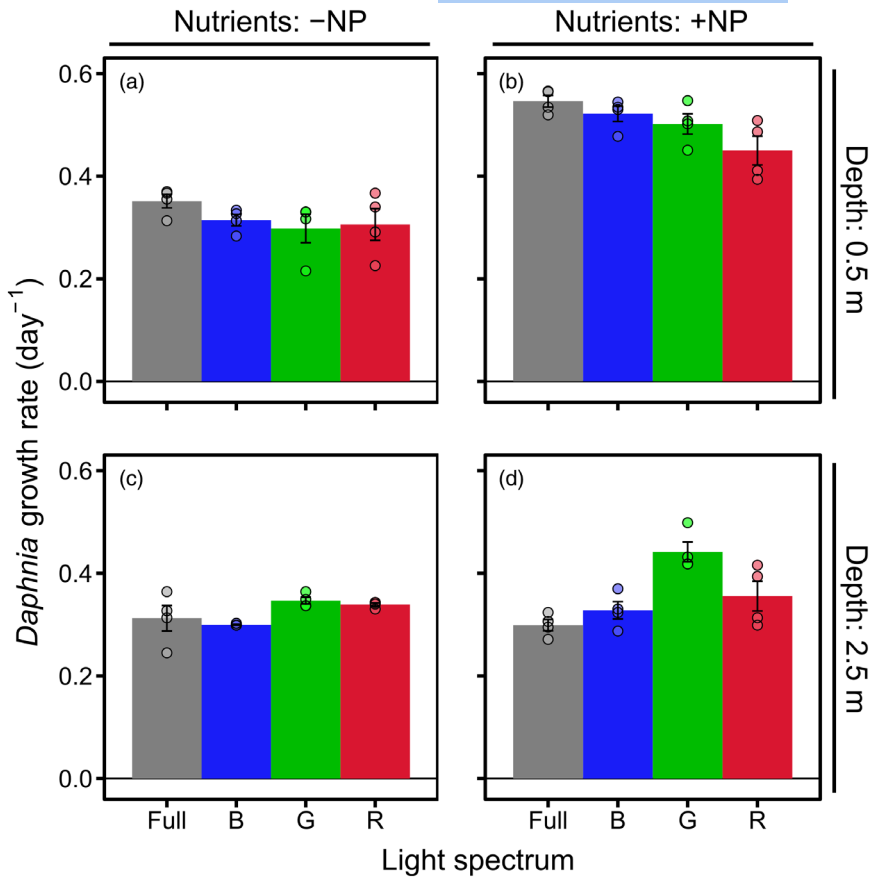

FIGURE 2 Growth rates of the cladoceran *Daphnia pulex* after feeding on lake seston that experienced different levels of nutrient supply, water depth and light spectrum. Seston was grown under (a), (c) ambient (−NP) or (b), (d) replete (+NP) nutrients, shallow (0.5 m, a, b) or deeper (2.5 m, c, d) water depth and under four different light spectra (intensity reduced full spectrum (Full), blue (B), green (G) and red (R)). Filled bars indicate the mean of four replicates (dots) and error bars represent the standard error.

nutrient addition had the strongest impact (partial $\eta^2 = 0.453$) while depth and light spectrum influenced phytoplankton communities similarly (partial η^2 of 0.293 and 0.262, respectively), also in interaction with nutrients (Table 2). Comparing chlorophyll *a*-to-carbon ratios among treatments indicated that nutrient addition was also important for pigment build-up in phytoplankton communities (Figure S4).

3.2 | Indirect effects on *Daphnia* growth

Lake seston from the different treatments resulted in significantly different growth rates of *D. pulex* when provided as food (Figure 2; Table 3). Nutrient supply displayed the highest effect size (partial $\eta^2 = 0.732$), followed by depth (partial $\eta^2 = 0.534$) and the interaction between depth and nutrients (partial $\eta^2 = 0.581$). While light spectrum had a relatively modest main effect and interactive effect with nutrients (partial η^2 of 0.142 and 0.140, respectively), its interaction with depth was more pronounced (partial $\eta^2 = 0.409$), underscoring the importance of spectral composition in modulating depth-related responses. This pattern was reflected in the observed growth rates. *Daphnia* grew better on seston from the high nutrient treatment (+NP, Figure 2b,d), especially at the shallow incubation depth of 0.5 m. Both the main effects of depth and nutrients, as well as their interaction, were significant ($p < 0.001$), whereas the effect of the light spectrum on *D. pulex* growth rates was marginally significant ($p = 0.059$, three-way ANOVA, Table 3). Yet, for the seston from +NP treatments, *D. pulex* growth rates tended to be higher for communities from full spectrum and decreased towards red light at 0.5 m (Figure 2b). The pattern became opposite for 2.5 m, where it was particularly the community from green light that resulted in the highest *Daphnia* growth (Figure 2d and significant Depth × Spectrum effect, three-way ANOVA, Table 3).

TABLE 3 Three-factorial ANOVA including growth rates of *Daphnia pulex* after grazing on seston that was reared under different treatments of incubation depth (D), nutrient supply (N) and light spectrum (S).

Effect	df	Partial η^2	*F*	*p*
Depth	1	0.534	55.1	<0.001
Nutrients	1	0.732	131.0	<0.001
Spectrum	3	0.142	2.7	NS (0.059)
D×N	1	0.581	66.5	<0.001
D×S	3	0.409	11.1	<0.001
N×S	3	0.140	2.6	NS (0.062)
D×N×S	3	0.082	1.4	NS (0.245)
Residuals	48			

Note: Shown are the degrees of freedom (df), partial η^2 as effect size, *F* statistic, and *p*-value for each analysis. For non-significant effects (NS), exact *p*-values are given in brackets.

3.3 | Principal component analyses (PCA)

A PCA on food quality indicators revealed clear treatment-dependent patterns (see Figure 3a). The first principal component (PC1) explained 42.89% of the total variance and was positively correlated with N:C, P:C, α-linolenic acid (C18:3ω3), stearidonic acid (C18:4ω3), eicosapentaenoic acid (C20:5ω3), and docosapentaenoic acid (C22:5ω6). These variables distinguished seston from −NP treatments from those in +NP treatments (Figure 3a; Table S5). Within communities from +NP, those from 0.5 m had generally higher scores on PC1 than those from 2.5 m. In addition, at 2.5 m depth, communities from green and red light treatments tended to differ from those under full and blue light spectrum, showing higher PC1 scores and thus elevated levels of the aforementioned elements and fatty acids. PC2 explained another 13.45% of the variance and was associated with monounsaturated fatty acids (MUFA), eicosatetraenoic acid (C20:4ω3), arachidonic acid (C20:4ω6), docosapentaenoic acid (C22:5ω3), and docosahexaenoic acid (C22:6ω3) (Figure 3a). Along PC2, seston from −NP treatments was separated by incubation depth, but here, no clear pattern emerged among the different light spectra.

A second PCA on phytoplankton pigments revealed shifts in the community due to the treatments (Figure 3b). The first two principal components explained about 55% of the variance in the pigment data. PC1 mainly separated phytoplankton communities with dominance of diatoms and chrysophytes (fucoxanthin + chlorophyll c_1) from communities with cryptophyte (alloxanthin) and green algal (chlorophyll b + lutein) dominance, while PC2 separated dinoflagellate-dominated communities (peridinin) from communities with diatoms and chrysophytes (Figure 3b; Table S6). For example, communities under ambient nutrients (−NP) were different from those under replete nutrients (+NP) due to opposing trends in the number of dinoflagellates versus diatoms, chrysophytes, cryptophytes, and green algae. Communities under +NP also evolved differently depending on the incubation depth and were clearly separated by PC1 and PC2. Here, differences were primarily controlled by diatoms and chrysophytes versus chlorophytes (lutein). Regarding the light spectrum, communities grown under red light seemed to be the most different from communities from other light spectra, especially at 0.5 m (Figure 3b).

3.4 | *Daphnia* growth and seston food quality

Growth rates of *D. pulex* correlated positively with increasing seston biomass (as POC) along the entire range of available carbon

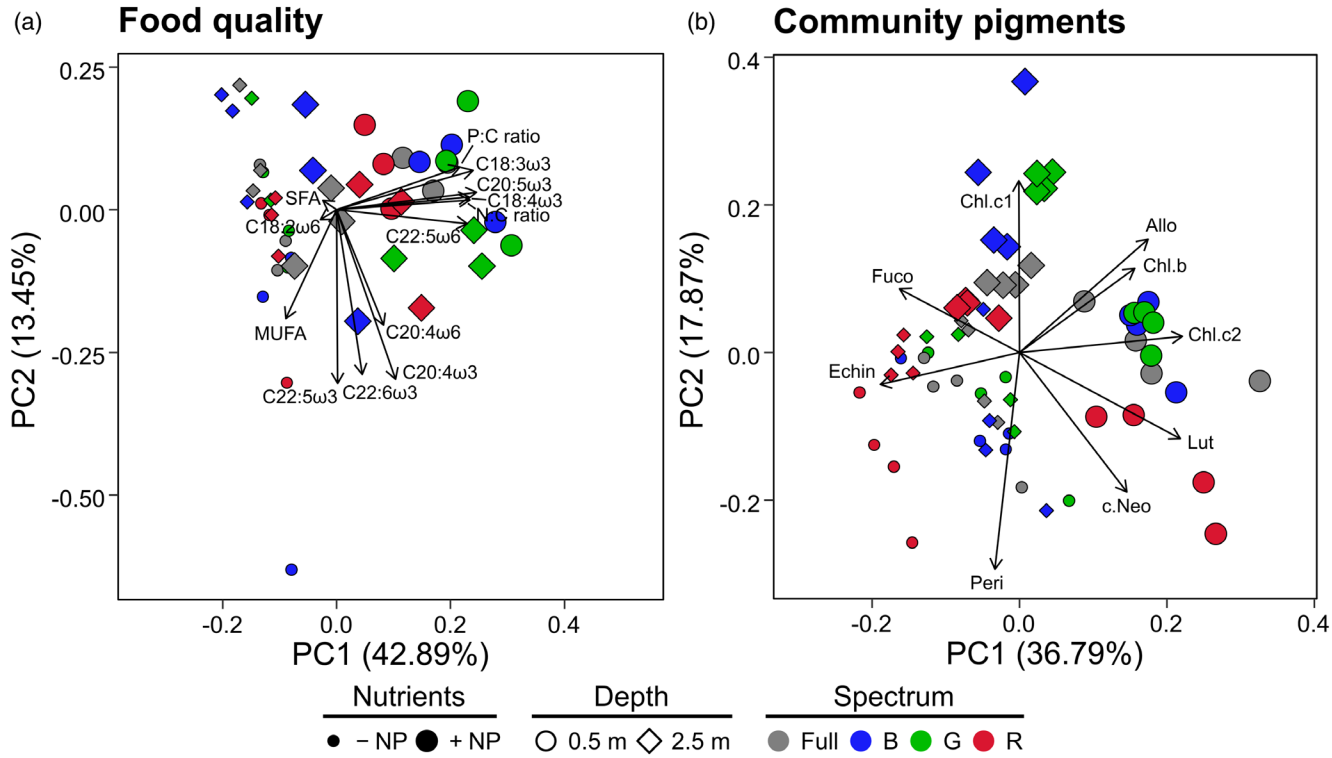

FIGURE 3 Principal component analysis including (a) seston elemental ratios (N:C, P:C) and fatty acids (all as mass ratios per g C) and (b) phytoplankton pigment concentrations (scaled on chlorophyll *a*). Nutrient levels are differentiated by the size of data points, depths of incubation are marked with different symbols and the light spectra (intensity reduced full spectrum (Full), blue (B), green (G), and red (R)) are indicated by different colours (see legend). Abbreviations in (a) are SFA for saturated fatty acids and MUFA for monounsaturated FAs. Included marker pigments in (b) are abbreviated as follows: Alloxanthin (Allo), 9′-*cis*-neoxanthin (c.Neo), chlorophylls *b*, c_1, c_2 (Chl.b, c1, c2, respectively), *trans*-echinenone (Echin), fucoxanthin (Fuco), lutein (Lut), and peridinin (Peri). A full list of all detected pigments can be found in Table S1.

that varied between 0.8 and 3.5 mg L^{-1} ($R^2 = 0.6611$; Figure 4a). Except for seston from +NP and 0.5 m incubations, total food concentration was always <2 mg L^{-1}. Still, *Daphnia* growth rates were higher for +NP treatments (2.5 m, especially green and red spectrum) than for −NP, despite the similar food concentrations (Figure 4a). *Daphnia* growth rates were also highly correlated with the first principal component of the food quality PCA ($R^2 = 0.6615$; Figure 4b), which reflects higher levels of N:C, P:C, C18:3ω3, C18:4ω3, C20:5ω3 and C22:5ω6. Growth rates also showed a substantial correlation with PC1 of the pigment PCA ($R^2 = 0.6016$; Figure 4c), indicating increased *Daphnia* growth in the presence of more cryptophytes and green algae as opposed to diatoms and chrysophytes. Correlations with higher-order principal components were weak ($R^2 < 0.1$; Figure S5).

4 | DISCUSSION

The results of this study demonstrate complex interactive effects of light intensity (through water depth), light spectrum and nutrients and how they act on the performance and biochemical composition of natural lake seston, with propagating effects to the zooplankton level. Beyond nutrient supply and water depth (and thus light intensity), we observed that the light spectrum had a significant impact on the biomass and biochemistry of lake seston, as well as the identity of phytoplankton communities, which is in full agreement with our hypothesis H1. The effect of the light spectrum closely interacted with water depth and nutrients, suggesting a changing sensitivity of phytoplankton to the quality of light, depending on the nutrient content and light intensity underwater. In addition to that, we identified that the resulting changes in lake seston ultimately translated into an altered growth performance of the zooplankton species *D. pulex*. Thus, we can accept our second hypothesis (H2). Overall, treatments with additional nutrient supply improved available food quantity (seston biomass), seston biochemical composition and phytoplankton community composition for *D. pulex*, but the effect highly depended on the background in light conditions. This indicates that both light intensity, as well as the spectral quality of light, influence seston biochemistry under natural circumstances, and that these effects propagate to the next trophic level in aquatic food webs.

4.1 | Light intensity and light spectrum influence lake seston

Total biomass, mineral and biochemical composition of the lake seston were interactively affected by nutrient supply, depth, and light spectrum. Generally, high availability of light (at 0.5 m) and nutrients resulted in the highest seston biomass production. At 2.5 m, the communities responded only weakly to nutrient enrichment (Figure S3A), which suggests that the seston was rather limited by light intensity.

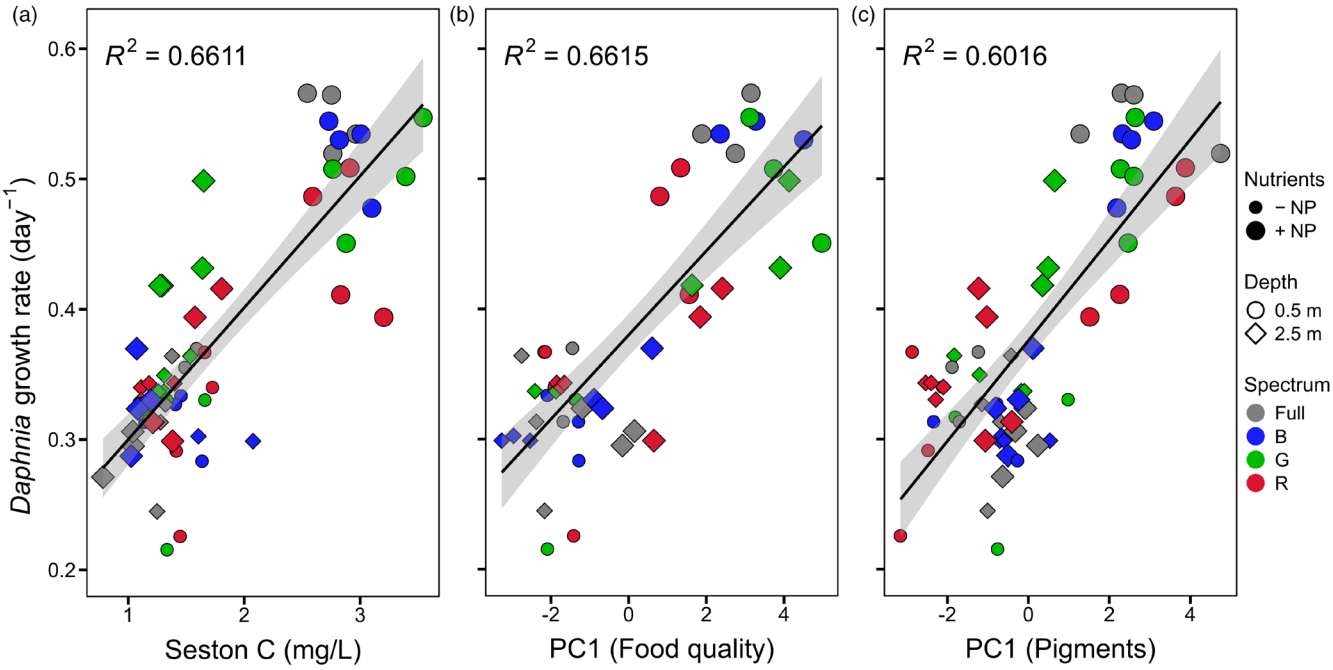

FIGURE 4 Growth rates of *Daphnia pulex* as a function of (a) seston carbon (biomass), (b) PC1 data scores from PCA with elemental ratios and fatty acids in lake seston, and (c) PC1 data scores from PCA with phytoplankton pigments. The size of data points indicates the nutrient treatment of incubated seston, the different symbols distinguish the incubation depths, and the colours represent the different light spectra (full (Full), blue (B), green (G) and red (R)) (see legend). Solid black lines represent linear regression models with their respective R^2 metric denoted on top. Grey shadings represent the 5%–95% quantiles. The number of replicates was $n = 4$ for C and pigments, and $n = 3$ for fatty acid data.

Nutrient addition had a strong effect on seston stoichiometry and behaved in accordance with stoichiometric theory (Sterner & Elser, 2002). Furthermore, the interactive effect of depth and spectrum, as well as depth as a single effect, showed high effect sizes, indicating the (interactive) relevance of light intensity and light spectrum. Our results are consistent with studies that stress the interactive nature of light-nutrient effects on the elemental composition of primary producers (Dickman et al., 2006; Sterner et al., 1997; Striebel et al., 2008), although we provide evidence that the quantity and quality of light both play an important role here. The close interrelation between light intensity and spectrum with increasing depth makes it particularly difficult to disentangle their individual effects in a natural system. Moreover, no consistent patterns in nutrient:C ratios across the different light spectra could be identified (Figure S3B,C). We assume that shifts in the species composition of phytoplankton communities might have superimposed, for example, the light effect on nutrient:C ratios, considering that species have varying cell stoichiometry (see below; e.g. Quigg et al., 2011).

Except for the three-fold interaction, all possible interactive terms between the abiotic factors nutrients, light intensity (through water depth), and light spectrum significantly affected the fatty acid profile of seston communities. This partly fits observations from laboratory studies showing that the intracellular composition of fatty acids in phytoplankton critically depends on nutrient supply and light intensity (Hill et al., 2011; Piepho et al., 2012; Thompson et al., 1990). For example, intracellular processes involved in photosynthetic light acclimation were shown to alter the content of PUFAs in phytoplankton (Wacker et al., 2015, 2016). Beyond intracellular physiological adjustments, shifts in dominant species might have been even more relevant for community fatty acid profiles than the direct (physiological) effects of the abiotic treatments of the experiment.

Under replete nutrients, we observed a clear impact of light spectrum and depth on the amount of essential ω3 PUFAs per biomass in seston (Figure S3G). Although the light spectra that induced higher fatty acid content in seston differed between depths, this suggests that fatty acid production is sensitive to the quality of light. In line with that, laboratory studies revealed that the fatty acid production of individual phytoplankton indeed depends on light quality (e.g. Abiusi et al., 2014; Helamieh et al., 2021; Maltsev et al., 2021). What was particularly striking in our study was that differences in light spectrum resulted in differences in elemental stoichiometry and fatty acid content of a whole seston community and that these were strong enough to translate into different growth responses of the zooplankton species *D. pulex*.

4.2 | Community identity shaped the mineral and biochemical composition of seston: Impact on *Daphnia* growth

Nutrient supply, depth and light spectrum not only affected seston biochemistry but also the community composition of phytoplankton, presumably as a result of shifts in the dominant species due to different resource requirements (Litchman & Klausmeier, 2008). Furthermore, community shifts could be explained by the applied light spectrum treatments because the wavelength spectrum of PAR provides space for niche differentiation (Burson et al., 2019; Holtrop et al., 2021; Stomp et al., 2004). Phytoplankton species are known to have broad preferences for different wavelengths of light (Glover et al., 1987; Stomp et al., 2004), but it has rather recently been shown that shifts in underwater light spectrum affect the community composition of natural phytoplankton (Hintz et al., 2021; Lebret et al., 2018). The results of this study contribute to these findings, although clear patterns were difficult to distinguish, largely due to the concurrent community changes with altered nutrients and light intensities. Conspicuous, however, was the distinctiveness of evolved communities under red light spectrum, particularly at 0.5 m water depth.

Changes in the community composition of phytoplankton might be an additional factor that influenced seston food quality for *Daphnia*, as has been observed for nutrient stoichiometry (Hall et al., 2007; Mette et al., 2011; Striebel et al., 2009) and can be expected for community fatty acids (Ahlgren et al., 1992; Marzetz et al., 2017). For example, the experimental increase in nutrient availability favoured the growth of green algae and cryptophytes at 0.5 m and diatoms at 2.5 m over taxa adapted to low nutrient conditions, such as dinoflagellates and chrysophytes. These shifts in the community might have also contributed to the observed higher contents of ω3 PUFAs such as α-linolenic acid (ALA) and eicosapentaenoic acid (EPA) per biomass in the high nutrient treatments. Cryptophytes and diatoms are both known to have high cellular EPA content, whereas chlorophytes are rich in ALA (Ahlgren et al., 1992; Brett & Müller-Navarra, 1997). Hence, phytoplankton communities clearly differed between depths at high nutrients but only little in terms of their food quality for *Daphnia* (Figure 3). This emphasises that community changes in natural systems can be of particular relevance for the trophic transfer between phytoplankton and zooplankton (Brett et al., 2000; Hartwich et al., 2012; Striebel et al., 2012).

Trophic interactions between phytoplankton and zooplankton in oligotrophic environments typically show high responsiveness to alterations in the light:nutrient supply ratios (Diehl, 2007; Striebel et al., 2008; Urabe et al., 2002). We observed that individuals of *D. pulex* showed the lowest growth when fed with seston reared under the ambient, nutrient-deficient conditions of the oligotrophic lake. In contrast, seston from high nutrient supply clearly augmented *D. pulex* growth, depending on the relative light supply. Since observed changes in food quantity for *D. pulex* were between 1 and 3 mg C L^{-1}, C limitation of *Daphnia* was less likely (Hessen et al., 2002; Striebel et al., 2008) and therefore, individuals were more sensitive to the quality of food. Studies showed that nutrient addition to nutrient-limited phytoplankton, especially P, can have a direct positive effect on *Daphnia* growth rates (Elser et al., 2001; Plath & Boersma, 2001), corresponding to the results here. Besides P limitation, biochemical limitations (e.g. fatty acids) could also be present in our system as PC1 of the food quality PCA highly correlated with ω3 PUFAs

(ALA, EPA), which were described to be potentially limiting in laboratory and field experiments (Hartwich et al., 2012; Müller-Navarra et al., 2000; Wacker & von Elert, 2001). Yet, we could not distinguish mineral from biochemical limitations in our study since the availability of elements (i.e., N:C, P:C) and fatty acids was closely related (PCA in Figure 3a). For this, additional supplementation experiments would be needed, which were out of the scope of this study (but see Hartwich et al., 2012; Ravet & Brett, 2006).

In conclusion, our study revealed clear shifts in the community composition of natural phytoplankton as well as significant interactive effects of nutrients and light on the elemental and biochemical composition of freshwater seston, with both the intensity and the spectral quality of light being relevant. The shape of the underwater light spectrum was most important when light (but not nutrients) was the growth-limiting resource for primary producers. Moreover, changes in seston stoichiometry and fatty acid composition had a direct impact on the growth performance of *Daphnia pulex*. Changes at the base of the aquatic food web induced by alterations in the abiotic environment of nutrients and light, including its spectral composition, were thus directly propagated to the next trophic level. As a consequence, we argue that it is not only the amount of light but also its spectral composition that has an important role in the trophic transfer dynamics in aquatic systems.

AUTHOR CONTRIBUTIONS

Sebastian Neun, Alexander Wacker, and Maren Striebel designed the study. Alexander Wacker and Maren Striebel acquired funding. Sebastian Neun conducted the experiment and collected the data. Sebastian Neun and Alexander Wacker performed the chemical analyses. Sebastian Neun, Alexander Wacker, and Maren Striebel analysed the data. Sebastian Neun created the figures and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data and code are publicly available at the Zenodo repository https://doi.org/10.5281/zenodo.17054695 (Neun et al., 2025).

ORCID

Sebastian Neun https://orcid.org/0000-0003-0578-8928
Alexander Wacker https://orcid.org/0000-0001-9687-6477
Maren Striebel https://orcid.org/0000-0003-2061-2154

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Phytoplankton community composition was approximated based on the occurrence and relative contribution of different marker pigments. Pigments were measured according to the method of Thrane et al. (2015) and scaled on the concentration of chlorophyll *a* in each sample. Pigments that were excluded from the dataset were those involved in photoprotective mechanisms like the xanthophyll cycle or those with a chlorophyll *a*-based concentration below 0.01 which was the case for *trans*-canthaxanthin and myxoxanthophyll, respectively. The literature that was consulted for taxonomic group assignments is indicated with footnotes.

Table S2. Three-factorial ANOVA of seston carbon testing for the effects of available photosynthetic photon flux density (PPFD, 400–700 nm), nutrient supply (N) and light spectrum (S). Results are shown as the degrees of freedom (Df), partial η^2, *F* statistic and *p*-value for each analysis. For non-significant effects (NS), exact *p*-values are given in brackets.

Table S3. Results of PERMANOVA of phytoplankton community pigments (9 pigments), seston stoichiometric ratios (N:C, P:C), and seston fatty acids (11 fatty acids) testing the effects of available photosynthetic photon flux density (PPFD, 400–700 nm), nutrient supply (N) and light spectrum (S). Results are shown as the degrees of freedom (df), R^2, partial η^2, pseudo *F* and *p*-value for each analysis. For non-significant effects (NS), exact *p*-values are given in brackets. Residual df for each analysis were 48 for pigments, 46 for stoichiometric ratios, and 32 for fatty acids.

Table S4. Three-factorial ANOVA including growth rates of *Daphnia pulex* after grazing on phytoplankton that was reared under different treatments of light intensity (PPFD; 400–700 nm), nutrient supply (N), and light spectrum (S). Shown are the degrees of freedom (df), partial η^2, *F* statistic and *p*-value for each analysis. For non-significant effects (NS), exact *p*-values are given in brackets.

Table S5. Variable loadings of principal component analysis (PCA) using parameters of elemental (N:C, P:C ratio) and biochemical (fatty acids) food quality in lake seston. MUFA, monounsaturated fatty acids; SFA, saturated fatty acids.

Table S6. Variable loadings of principal component analysis (PCA) using concentrations of different phytoplankton pigments. Pigments are: alloxanthin (Allo), 9′-cis-neoxanthin (c.Neo), chlorophylls b, c1, c2 (Chl.b, c1, c2, respectively), trans-echinenone (Echin), fucoxanthin (Fuco), lutein (Lut), and peridinin (Peri).

Figure S1. Wavelength spectra of light transmission of the applied coloured light filters that were used to manipulate the underwater light spectrum experienced by incubated phytoplankton communities. The respective light filters from LEE (Hampshire, UK) are indicated by their colour of maximum light transmission. The black line shows the wavelength spectrum of solar light. Note that the different spectra were measured in air and not in water. All spectra were measured with the LI-180 spectrometer from LICOR.

Figure S2. Overview of environmental parameters monitored during the study period in the water of Lake Schortens. (A) Logging data of temperature in°C measured every minute at a water depth of 0.5 m and 2.5 m indicated by different grey levels of respective time series (see legend). The average temperature at 0.5 m was 17.8 ± 1.3°C (mean ± SD) while the average temperature at 2.5 m depth was 16.6 ± 0.4°C. This indicates that the average temperature during the experiment did not differ between 0.5 and 2.5 m depth. Temperature was even more similar between the two depths during the first six days (27 May to 1 June 2022) of the experiment (17.1 ± 0.8°C at 0.5 m vs. 16.7 ± 0.5°C at 2.5 m) while it only deviated for the last three days of the experiment (19.3 ± 0.7°C at 0.5 m compared to 16.8 ± 0.2°C at 2.5 m). Such a small difference in temperature should not be of high relevance as it only occurred during the last three days of the phytoplankton incubation. (B) Monitored light intensity (in lux) measured every minute at the same depths as for temperature in (A). Vertical grey bars indicate night-time.

Figure S3. Seston food characteristics after incubation under different levels of nutrient supply, water depth and light spectrum. (A) Particulate organic carbon (POC, mg L^{-1}), (B) molar nitrogen-to-carbon ratio (N:C), (C) molar phosphorus-to-carbon ratio (P:C), (D) total fatty acids (total FA, g per gC), (E) saturated fatty acids (SFA, g per gC), (F) monounsaturated fatty acids (MUFA, g per gC), (G) omega-3 polyunsaturated fatty acids (ω3 PUFA, g per gC) and (H) omega-6 PUFA (g per gC). For each parameter, nutrient treatments (ambient (−NP), replete (+NP)) are separated in columns and incubation depths (0.5 and 2.5 m) are separated in rows. Light spectra are full (Full), blue (B), green (G), and red (R) light spectrum and shown on the *x* axis. Squares show always the mean of replicates (dots; $n = 3$ for fatty acids and $n = 4$ otherwise) with the respective standard error (error bars).

Figure S4. (A) Relationship between phytoplankton chlorophyll *a* (chl *a*) and seston carbon (C). Nutrient treatments of incubated phytoplankton communities are indicated by the size of data points, depths of incubation are marked with different symbols and the light spectra (full (Full), blue (B), green (G), and red (R)) are shown by different colours (see legend). (B) Ratios of chl *a* to C as mean with standard error for the two depths of incubation. Nutrient treatments are indicated by different symbols and light spectra by different colours as in (A) (see legend).

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Figure S5. Growth rates of *Daphnia pulex* in relation to data scores of principal components from PCA including seston elemental ratios and fatty acids (A1–A9), and from PCA including phytoplankton pigments (B1–B9). Nutrient treatments of incubated lake seston are indicated by the size of data points, depths of incubation are marked with different symbols and the light spectra (full (Full), blue (B), green (G), and red (R)) are shown by different colours (see legend). Solid black lines represent linear regression models with their respective R^2 metric denoted on top. Grey shadings represent the 5%–95% quantiles. The number of replicates was $n = 4$ for scores from the pigment PCA, and $n = 3$ for the other.

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