Light color and nutrient availability alter trophic transfer from algae to zooplankton

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Abstract

Freshwater plankton communities experience both natural variation of light color and nutrient availability and shifts due to eutrophication and brownification. These changes can alter algal community structure, but whether variation of light color impacts trophic transfer from algae to zooplankton is unknown because most research ignores color and focuses on light intensity. We used microcosms inoculated with natural algal communities to test whether differences in light color and nutrients alter trophic transfer to zooplankton. We found that light color is an important driver of differences in *Daphnia* survival and trophic transfer, with the effects of nutrients and trophic pathways differing among light colors. As lakes experience eutrophication and brownification, understanding how shifts in light color impact food webs, and whether these effects are mediated by nutrient availability, is essential to predicting how ecosystem functioning may change in response to these two phenomena.

Introduction

Variation in resource availability can affect multiple trophic levels within a food web, and changes in resources that impact primary producers may also directly or indirectly affect their consumers. In lake ecosystems, algae serve as the foundation of the food web; variation in resources, such as light color and nutrients, can alter algal community diversity and composition (Litchman and Klausmeier 2001; Agawin et al. 2007; Marzetz et al. 2020) which may impact higher trophic levels such as zooplankton. Lakes experience a wide range of natural variation in their light and nutrient environments (Schwaderer et al. 2011; Leech et al. 2018), with light able to vary in both its color and intensity. Variation in light color and phosphorus and nitrogen availability has been shown to impact algal growth and community structure (Guildford and Hecky 2000; Carey et al. 2012; Hintz et al. 2021; Neun et al. 2022; Swanson et al. 2025), but whether variation in these resources also affect higher trophic levels such as zooplankton, and whether any differences in trophic transfer are mediated by shifts in algal communities, is less known.

While prior work has illuminated the effects of differences in nutrient availability on trophic transfer in freshwater food webs (Elser et al. 2001; Yuan and Pollard, 2018; Keva et al. 2021), the role of light color is not as well understood. Light color describes a fundamental characteristic of light which is a key resource in aquatic ecosystems; therefore determining whether light color affects trophic transfer from algal producers to zooplankton grazers is essential to broadening our understanding of how resource variation can directly and indirectly affect multiple trophic levels and potentially impact ecosystem functioning. Additionally, the effects of light color on trophic transfer may be context dependent. As changes in light color and nutrients can occur concomitantly, it is essential to determine whether differences in light color

and nutrient availability interact with one another to alter trophic transfer in freshwater food webs.

In addition to natural variation in light color and nutrients, lakes are undergoing shifts in their light and nutrient environments due to eutrophication and brownification. Eutrophication is causing nutrient loads, particularly nitrogen and phosphorus, to increase (Schindler et al. 2016). Eutrophication can increase primary productivity, which leads to more dense algal communities (de Senerpont Domis et al. 2013), and can also cause shifts in community composition, primarily towards communities dominated by cyanobacteria (Carey et al. 2012; O'Neil et al. 2012; Filstrup et al. 2014). Concurrently, brownification is causing lakes to become browner in color via an increase in terrestrial colored dissolved organic matter (CDOM) (Blanchet et al. 2022) which alters the color of light that is available to algae for photosynthesis. CDOM absorbs light in the ultraviolet and blue wavelengths of the visible light spectrum (Blanchet et al. 2022) which causes relatively less blue light, but relatively more green and red light to be available in the environment. As primary producers algae use absorptive pigments to harness light energy which subsequently drives photosynthesis. Algal pigment compositions, however, vary across taxa which means different taxa are best adapted to different light colors (Stomp et al. 2004; Luimstra et al. 2020; Neun et al. 2022). This interspecific pigment variation allows for niche partitioning by light color (Stomp et al. 2004, Stomp et al. 2008). Brownification induced changes in the color of light available to algae for photosynthesis may lead to shifts in the community towards taxa that can better exploit green or red wavelengths of light. Taken together, natural variation in light color and nutrients, along with directional shifts driven by brownification and eutrophication, may be creating novel environmental contexts in which trophic transfer is occurring in lake ecosystems.

Variation in light color and nutrient availability may also affect zooplankton via shifts in algal community composition. Zooplankton are a diverse group of heterotrophic plankton that feed upon algae and greatly contribute to trophic transfer by occupying an intermediate level in aquatic food webs, thereby serving as a link from primary producers to higher trophic levels (Vanni 2002; Ger et al. 2014; Hébert et al. 2016; Hébert et al. 2017). Zooplankton also contribute to ecosystem functioning in lakes through the biochemical cycling of nutrients like nitrogen, phosphorus, and carbon (Vanni 2002; Hambright et al. 2007). One mechanism through which differences in light color and nutrients may impact zooplankton is by shifting the composition of the algal community to taxa of reduced nutritional quality or digestibility for zooplankton. Cyanobacteria, in particular, can be poor quality food for zooplankton because they can be filamentous (DeMott et al. 2001), produce harmful toxins (Leflaive and Ten-Hage 2007), alter energy transfer between trophic levels (Major et al. 2017) and are nutritionally suboptimal (Brett et al. 2000). If certain light color and nutrient conditions lead to algal communities with more filamentous cyanobacteria, we might expect those communities to negatively impact zooplankton fitness.

We took an experimental microcosm approach to investigate how differences in light color and nitrogen and phosphorus availability alter algal community composition and trophic transfer from algae to zooplankton. *Daphnia* are a keystone species in lakes (Persson et al. 2007) and play a focal role in food webs by facilitating energy transfer from producers to higher trophic levels by consuming algae and then themselves being consumed by planktivorous fish and macroinvertebrates (Carpenter and Kitchell 1993; Lampert and Sommer 2007). The algal community results are available from Swanson et al. 2025. Here, we briefly review relevant results about the algal communities from Swanson et al. 2025 but mainly focus on the results

from the trophic transfer portion of the experiment and integrate the algal community results to inform potential underlying mechanisms for how differences in light color and nutrient availability alter trophic transfer from algae to *Daphnia*.

Methods

Microcosm design

Field sampling, microcosm experimental design, and algal community enumeration were described in detail in Swanson et al. 2025. In brief, microcosms were inoculated with algae from natural communities sampled from an oligotrophic lake, Lake Jocassee (34° 57′ 36″ N, 82° 55′ 10″ W) and a eutrophic lake, Lake Murray (34° 3′ 56.86″ N, 81° 19′ 44.29″ W), in South Carolina. 1 L of water was taken at four separate depths (surface, half Secchi depth, Secchi depth, and 1.5 times Secchi depth). Before inoculating the microcosms, we created a natural species pool of algae by combining all the samples from both lakes together which yielded 8 L of lake water.

Microcosm experimental treatments consisted of four light color treatments, blue, green, red, and broad, crossed with two nutrient treatments, high nutrient or low nutrient, for a total of eight possible treatments with each treatment replicated in triplicate. Microcosms were 400 mL in volume, with 200 mL consisting of lake water drawn from the regional species pool and 200 mL consisted of a lab-made modified Waris-Harris medium with either 1 mg/L (high nutrient) or 1 μg/L (low nutrient) of ammonium phosphate depending on the nutrient treatment. Microcosms were placed in a temperature-controlled growth chamber kept at 20° C with 12h/12h day-night cycle. Microcosms were illuminated with a constant 30 μmol/photons/m^2s^{-1} from above by LED lights. Microcosms were allowed to run for 54 days and were sampled at the start and end of the

experiment. 10 mL were sampled from each microcosm and preserved in 5% Lugol's iodine solution for future enumeration of the algal communities. See Swanson et al. 2025 for full details on experimental design.

Daphnia juvenile specific growth rate

To determine whether differences in light color and nutrient availability affect trophic transfer from algae to zooplankton we calculated juvenile specific growth rate (JSGR) as a proxy for trophic transfer in *Daphnia*. JSGR is a strong proxy for trophic transfer because it is a growth rate that is calculated before reproductive maturity; therefore, all of an individuals' energy is being put towards growth (Lampert and Trubetskova 1996). We established a population of a *Daphnia pulex-pulicaria* hybrid in the lab and used neonates from this population as our experimental individuals. We started with 58 female *Daphnia* that were kept individually in 250 mL Pyrex beakers filled with 150 mL of filtered lake water. Individuals were fed daily a high food diet consisting of 20,000 cells/mL of the green alga *Ankistrodesmus falcatus* and were transferred every other day into new beakers with fresh lake water. *Daphnia* were kept in growth chambers at 20° C on a 12-hour/12-hour day-night cycle. We maintained our *Daphnia* population under these conditions for the first three clutches of their life and then used neonates from the fourth clutch as our experimental individuals. 24 hours before adding the neonates to the microcosms we moved the mothers of our experimental individuals into new beakers and did not feed them. This ensured all the neonates added to the microcosms only consumed algae from our experimental algal communities. We collected a total of 196 *Daphnia* neonates from our 58 mothers. 18 of these individuals were immediately sacrificed, mounted on microscope slides, and placed in a drying oven for 24 hours at 37° C. After 24 hours these 18 individuals were weighed

on a Mettler-Toledo UMX2 balance (Mettler-Toledo, Columbus, Ohio, USA). We used these individuals to determine the average birth mass for our experimental *Daphnia* neonates. With the remaining collected neonates, we placed seven individuals into each microcosm on day 54 of the experiment and allowed them to feed on the algal communities within for four days. The microcosms were kept in the same light conditions during the feeding phase as the algae community establishment phase. After four days we removed the neonates, recorded the number of surviving individuals per microcosm, placed the survivors on microscope slides. and dried and weighed these individuals using the same methods as above. During the weighing process, 12 individuals were unable to be weighed due to human error (three from blue light high nutrient microcosm replicate 1, all seven from blue light high nutrient microcosm replicate 2, and two from blue light low nutrient microcosm replicate 3). JSGR was calculated following Lampert and Trubetskova 1996 where growth rate (g) is calculated from individual dry mass (W_1 and W_2) at two time points (t_1 and t_2) (Equation 1). Individuals that did not survive the four-day feeding period were included in the analysis with a growth rate of -1, which converts to a mass of roughly 0.1 ug at t_2. We decided to use a negative growth rate that represents a small ending mass because it is likely that the neonates that died lost mass over time as opposed to their mass remaining static over the four-day feeding period. In contrast, we could have treated those growth rates as zeroes or dropped them from our analysis. Using zero for the growth rate of dead individuals would implausibly assume that these animals were in physiological stasis until their death, while dropping dead individuals from our analysis would obfuscate the true effects of the treatments on trophic transfer. Additionally, we saw one individual survive with a negative growth rate, which indicates that negative a JSGR is biologically realistic. We were able to confirm death of neonates by finding their corpses in the microcosms.

$$g = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$ (Equation 1)

Statistical analysis

All analyses were done in R version 4.3.2 (R Core Team 2023). We tested for differences in survivorship among treatments with a chi-square test using the function *chisq_test* in the *rstatix* package (Kassambara 2023b). We ran a type III ANOVA using the *anova* function in the *stats* package to determine whether light color, nutrient level, and their interaction were significant drivers of differences in JSGR. We also tested which treatments were driving differences in JSGR due to light color and nutrient level with a linear model. We originally used a linear mixed effect model with JSGR as the response variable with light color, nutrient level, and the interaction between the two as fixed effects and microcosm as a random effect using the *lmer* function in the *lme4* package (Bates et al. 2015). We generated an ANOVA-like table for random effects using the *rand* function from the *lmerTest* package (Kuznetsova et al. 2017), which compares model fit with random effects to a model without and indicated that a linear model without microcosm as a random effect was a better fit to the data than model with the random effect (Table S1). Therefore, we report results from the linear model without a random effect. Model residuals were visually inspected using the check_model function in the *performance* package (Lüdecke et al. 2021). We made boxplots for the proportions of filamentous cyanobacteria, green algae, and non-filamentous cyanobacteria in each treatment, proportion of survivors by treatment, and JSGR by treatment using the *ggplot2* (Wickham 2016) and *ggpubr* (Kassambra 2023a) packages. We only visualized proportions of filamentous cyanobacteria, green algae, and non-filamentous cyanobacteria as they were the three most dominant groups in our microcosms.

We investigated the direct and indirect effects of differences in light color and nutrients on JSGR through a piecewise structural equation model (SEM) with a multigroup analysis using the *piecewiseSEM* package (Lefcheck 2016). Our SEM consisted of four linear models with JSGR, the abundance of filamentous cyanobacteria, non-filamentous cyanobacteria, and green algae as response variables. For JSGR, the predictor variables were nutrient level, and the abundance of filamentous cyanobacteria, non-filamentous cyanobacteria, and green algae. Each algal group was then modeled as a response variable with a single predictor, nutrient level, apart from the green algae model, which had the abundance of non-filamentous cyanobacteria included as a predictor after a significant test of directed separation result following a prior SEM run. We then used a multigroup analysis, with light color as our grouping variable to investigate the interaction between light color and our predictor variables. Multigroup analysis applies an interaction across all coefficients in a SEM; therefore, we were able to identify if the effects of our predictor variables on all response variables across all four linear models differed with light color. Within our models we coded nutrient level as an ordinal variable with 1 indicating low nutrients and 2 indication high nutrients. We made this choice, as opposed to keeping nutrient level as a categorical variable due to the difficulty of achieving a good fit model with a categorical variable included in the piecewise linear models and as the grouping variable in our multigroup analysis. Overall, the multigroup analysis yielded information as to which coefficients are constrained to the global SEM model (no interaction with light color) and which change with light color. This produced four separate SEMs, one for each light color in our experiment. We show the general SEM structure in Figure 4 with different color paths for significantly different coefficients in each light color. We assessed goodness of fit for the global model fit with a Fisher's C test and a chi-squared test with $p > 0.05$ indicating a good fit.

Results

Differences in algal group across treatments

Differences in light color and nutrients created significantly different algal communities in the microcosms (Swanson et al. 2025). Blue light conditions had less cyanobacteria, both filamentous and nonfilamentous, than other light colors across nutrient levels (Figure 1). Broad and red light had relatively high proportions of cyanobacteria across nutrient levels, and green light had relatively low cyanobacteria proportions in low nutrient conditions but relatively high proportions in high nutrient conditions (Figure 1). Broad light high nutrient showed high variability in the proportion of filamentous cyanobacteria and green algae, while green light treatments showed high variability in the proportion of nonfilamentous cyanobacteria and green algae across nutrient levels (Figure 1). Red light had relatively high proportions of filamentous and nonfilamentous cyanobacteria across nutrient levels (Figure 1). Blue and green light both had relatively high amounts of green algae across nutrient levels, while broad and red light conditions had lower proportions of green algae at low nutrient levels compared to high nutrient levels (Figure 1). More detailed algal community results can be found in Swanson et al. 2025.

Daphnia survivorship

Our chi-square test showed significant differences in neonate survival across treatments (N=168; χ^2=92.24065; df=7; p=4.29 x 10^{-17}) (Figure 2a). Interestingly, we saw all 21 neonates in the broad light high nutrient replicates die during their four-day feeding period in the microcosms. In contrast, we saw all neonates survive in the blue low and green low treatments, and high survivorship in broad low (18/21 neonates), red low (20/21 neonates), and blue high (20/21 neonates). Red high (11/21 neonates) and green high (12/21 neonates) had intermediate levels of

survival. Across all light colors, the low nutrient treatment had a greater number of surviving neonates when compared to the high nutrient treatment.

Daphnia juvenile specific growth rate

Our ANOVA showed that light color, nutrient level, and their interaction all had a significant effect on JSGR (Table 2). The linear model (df=7; 148; F=21.66; adj. r^2=0.4827; p=<0.001) showed that broad light, green light, and red light all significantly decreased JSGR relative to blue light. Low nutrient level alone did not have a significant effect on JSGR relative to high nutrients (Table S2). The interaction between low nutrients and broad, green, and red light were all significant drivers of differences in JSGR relative to the blue light high nutrient treatment, with the direction and magnitude of the effect dependent on the specific interaction (Table S2).

Green light high nutrient and blue light high nutrient had the highest median JSGR (0.457 μg/μg day^{-1} and 0.368 μg/μg day^{-1}, respectively). Blue light low nutrient (0.287 μg/μg day^{-1}), red light low nutrient (0.279 μg/μg day^{-1}), green light low nutrient (0.275 μg/μg day^{-1}), and broad light low nutrient (0.235 μg/μg day^{-1}) all had intermediate median JSGR, while red light high nutrient (0.104 μg/μg day^{-1}) had the lowest median JSGR (Figure 2). We were unable to calculate JSGR for our broad light high nutrient treatments due to total neonate death during the feeding phase.

Structural equation model and multigroup analysis

Our goodness-of-fit test yielded a Fisher's C of 4.656 with a p of 0.296 with two degrees of freedom and a χ^2 of 2.433 with a p of 0.324, implying a good model fit to our data. Multigroup analysis revealed that all potential model-wide interactions were significant, therefore no

coefficients were constrained to the global model and differ across light colors (Table S3). Paths across light colors also differ in their statistical significance (Figure 3; Tables S4:S7), indicating that model structure differs across light color as well. Therefore, whether the effects of nutrients on JSGR were mediated by algae were dependent on light color (Figure 3). In blue light, there were no significant effects on JSGR by nutrient or algal groups (Figure 3). In broad light, nutrient level had a significant negative effect on JSGR, indicating that as nutrient level shifted from low to high JSGR decreased, but was not directly mediated by any algal groups (Figure 3). In green light the density of each algal group had a significant effect on JSGR, with green algae having a large positive effect, nonfilamentous cyanobacteria having a moderate positive effect, and filamentous cyanobacteria having a large negative effect (Figure 3; Tables S6). In green light, therefore, increases in green algae and nonfilamentous cyanobacteria increased JSGR and increases in filamentous cyanobacteria decreased JSGR In red light, nutrient level and nonfilamentous cyanobacteria density both had a moderate negative effect on JSGR (Figure 3; Tables S7). Overall, the trophic path from nutrients to algal producers to zooplankton consumers differed depending on light color.

Discussion

Differences in neonate survival

To our surprise, we saw significant differences in *Daphnia* survivorship among treatments (Table 1). Across all light colors we saw greater survivorship in low nutrient than high nutrient treatments (Figure 2a). The most unexpected result was the death of all the neonates in the broad light high nutrient microcosms. Broad light high nutrient was the treatment with the densest algal community and three of its four most abundant taxa were filamentous cyanobacteria, specifically

the genera *Jaaginema, Pseudanabeana*, and *Anabaena* (Swanson et al. 2025). *Pseudanabaena* and *Anabaena* are genera that contain species that can produce toxins (Carmichael et al. 1975; Hu et al. 2005) that are known to have harmful effects on zooplankton (DeMott et al. 1991; Rohrlack et al.1999). Therefore, a algal community with an abundance of filamentous cyanobacteria may explain why all the *Daphnia* neonates did not survive in the broad light high nutrient microcosms. In contrast, we saw the highest survival in blue light across both nutrient levels (Figure 2). These were the two treatments with the lowest algal densities, were the only treatments to not have cyanobacteria as the most abundant taxa, and those communities were shifted towards green algae and cryptophytes relative to other treatments (Swanson et al. 2025). The absence of high densities of cyanobacteria, particularly filamentous cyanobacteria, may explain why survivorship was high in our blue light treatments, regardless of nutrient level.

Effects of light color, nutrients, and algal communities on trophic transfer

We found that light color, nutrient level, and their interaction all had a significant effect on trophic transfer from algae to our *Daphnia* neonates (Table 1). Differences in light color also yielded different trophic paths, showing that the trophic path from nutrients to producers to consumers is dependent on light color (Figure 3). We saw that only two light colors, red and green, had trophic paths where the effects of nutrient level on JSGR were mediated by changes in algal groups (Figure 3). The underlying mechanism through which differences in light color and nutrients may have affected trophic transfer is that those differences altered algal communities which then provided algae of different nutritional quality and quantity to the *Daphnia* neonates.

Daphnia growth rate is highly dependent on the quantity and quality of the food in their environment (Sterner 1997; Sterner and Schultz 1998; Ravet and Brett 2006; DeMott et al. 2010). Our treatments with high growth rates, such as the blue light treatments, had high proportions of green algae and low proportions of cyanobacteria (Figure 1) and more cryptophytes than other treatments (Swanson et al. 2025). Green algae and cryptophytes can be high quality food sources for zooplankton, particularly in high nutrient environments (Lundstedt and Brett 1991; Sterner and Schulz 1998), which may explain the high growth rates in blue light. The broad light low nutrient treatment, in contrast, had high proportions of cyanobacteria and low proportions of green algae (Figure 1), with the nonfilamentous cyanobacterium *Aphanocapsa* and the filamentous cyanobacteria *Jaaginema*, *Aphanizomenon*, and *Pseudanabaena* as some of its most abundant taxa (Swanson et al. 2025). Cyanobacteria, particularly filamentous cyanobacteria, are generally poor food for zooplankton because of their lack of nutritional quality (Gulati and DeMott 1997; Müller-Navarra et al. 2000), the ability of some taxa to produce toxins (Leflaive and Ten-Hage 2007; Ger et al. 2010) and because zooplankton cannot process filamentous cyanobacteria as quickly as they can other algae (Gliwicz and Lampert 1990; DeMott et al. 2001). Out of our treatments that led to relatively poor growth rates four had low levels of nutrient availability. This may have led to nutrient limited algae in those treatments, which are poor quality food for *Daphnia* (Kilham et al. 1997; Brett et al. 2000).

Another factor that may have contributed to low growth rates is differences in algal digestibility. Algae differ in their resistance to digestion by zooplankton with more digestion resistant taxa considered to be poorer quality food (Kerfoot et al. 1988; Brett et al. 2000; DeMott and Tessier 2002). Unprotected flagellates, such as cryptophytes and green algae are good

364 quality food for *Daphnia* (Infante and Litt 1985; Kerfoot et al. 1988: Lundstedt and Brett 1991)
365 whereas taxa with natural defenses such as thicker cell walls, gelatinous membranes, spines, or
366 toxins are poor quality food for zooplankton (Kerfoot et al. 1988; Mayeli et al. 2004; Tillmanns
367 et al. 2008; DeMott et al. 2010). Digestion in *Daphnia* also differs across life stages (DeMott et
368 al. 2010). Algal resistance to digestion strongly impacts juvenile growth as they are inferior to
369 adults at consuming algae with defenses against digestion (DeMott et al. 2010). Since we used
370 juvenile growth rate as a proxy for trophic transfer, we would expect there to be an effect of algal
371 digestibility on growth.

372 The different trophic paths that were mediated by changes to algae reflect shifts towards
373 algal groups that are of lower food quality and decreased digestibility. In green light, going from
374 low to high nutrients increased filamentous cyanobacteria density, which itself had a negative
375 effect on JSGR (Figure 3). Increases in green algae and nonfilamentous cyanobacteria density
376 also had a positive effect on JSGR in green light but were not affected by differences in nutrients
377 (Figure 3). The negative effect of an increase in filamentous cyanobacteria on JSGR is consistent
378 with those taxa being of poorer nutritional quality and lower digestibility relative to other algae.
379 Increases in green algae and nonfilamentous cyanobacteria density leading to higher JSGR also
380 fits within the nutritional quality and digestibility framework, with green algae being more easily
381 digested and of higher food quality, and nonfilamentous cyanobacteria lacking some of the
382 defenses of filamentous cyanobacteria. In red light, going from low to high nutrients decreased
383 nonfilamentous cyanobacteria density, which had a negative effect on JSGR (Figure 3).
384 Decreases in the proportion of nonfilamentous cyanobacteria occurred concomitantly with
385 decreases in the proportion of filamentous cyanobacteria and increases in the proportion of green
386 algae (Figure 1). Red light high nutrient was the treatment with the lowest median JSGR, but

within the community nutritional quality and digestibility framework we would expect decreases in cyanobacteria and increases in green algae to lead to higher growth rates. The results from the red light high nutrient treatment, therefore, do not support the idea of community nutritional quality and digestibility affecting JSGR. Overall, differences in algal digestibility, along with differences in food quality and quantity, may partially explain the differences in JSGR among treatments. Differences in light color and nutrients created environments that led to differences in survivorship and JSGR for our *Daphnia* neonates. One key detail to note is that light intensity was kept constant throughout the experiment, therefore the only differences in light as a resource were in the wavelengths of light available and not in its intensity. There is, however, the possibility that the different colors of light directly influenced the feeding behavior of our *Daphnia*. There appears, however, to be no prior work done on this in the *Daphnia* ecology literature. Establishing the effects of different light colors, if any, on feeding behavior in *Daphnia* is an interesting avenue for future research as it may represent a direct effect of brownification induced shifts in light color on *Daphnia* behavior and trophic transfer in lake ecosystems.

Implications for lake ecosystems

Whether lakes experience eutrophication, brownification, or both, freshwater plankton communities will undoubtedly be affected by changes in their light and nutrient environment. Our results show that differences in light color have significant effects on trophic transfer from algae to *Daphnia*, with those effects differing by nutrient level and being mediated by algal community composition. Red and broad light conditions led to relatively poor growth rates compared to green and blue light (Figure 2b) with the effect of nutrients on JSGR being

mediated by algae in red and green light (Figure 3). As brownification makes lakes darker in color, the underwater light spectrum is predicted to shift away from blue and towards green and red light (Creed et al. 2018; Blanchet et al. 2022). Our results indicate that red light is particularly detrimental to *Daphnia* juvenile growth; if brownification continues, or is exacerbated, we might expect lakes that shift to become red light dominant to experience decreased trophic transfer from algae to zooplankton. Decreased trophic transfer has a variety of implications for lake ecosystems because zooplankton serve as both predators of algae and prey to higher trophic levels like fish and invertebrates (Hébert et al. 2016; Hébert et al. 2017). Decreased zooplankton growth, therefore, could potentially alter the growth and feeding behavior of higher trophic levels that feed on zooplankton, such as fish and invertebrate predators. While we did not examine the effect of differences in light color and nutrient level on multiple zooplankton taxa, these environmental changes could possibly shift zooplankton communities in a way that alters ecosystem functioning. For example, if the zooplankton community sees a shift towards larger taxa, smaller predators such as phantom midge larvae may become gape limited and therefore experience a reduction in fitness. Understanding how differences in light color and nutrient availability affect trophic transfer through freshwater food webs is essential to predicting how limnetic ecosystem functioning will be expected to change in the face of continued eutrophication and brownification.

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635

Table 1: ANOVA summary statistics for the effects of light color, nutrient level, and their interaction on juvenile specific growth rate. Significant *p*-values are in bold.

	Df	Sum of squares	Mean square error	*F*	*p*
Light color	3	11.506	3.835	20.783	**<0.001**
Nutrient level	1	11.803	11.803	63.956	**<0.001**
Light x nutrient	3	4.678	1.559	8.45	**<0.001**
Residuals	148	27.313	0.185		

Figure 1: Proportions of filamentous cyanobacteria, green algae, and nonfilamentous cyanobacteria for each treatment at the end of the experiment. Point and box color corresponds to each light color treatment, with black representing the broad light treatment.

Figure 2: a) Proportion of survivors by treatment of *Daphnia* neonates at the end of the four-day feeding phase used to calculate juvenile specific growth rate and b) juvenile specific growth rate of *Daphnia* neonates by treatment. In both panels line and point color correspond to light color treatment, with black representing the broad light treatment.

Figure 3: Structure of SEMs for each light color treatment. Only significant path coefficients are shown. Line color corresponds to light color treatment with black representing the broad light treatment. Solid lines represent positive relationships between variables and dashed lines represent negative relationships. Values associated with lines are standardized path coefficients and line width is indicative of the absolute magnitude of the path coefficient.

Figure 1:

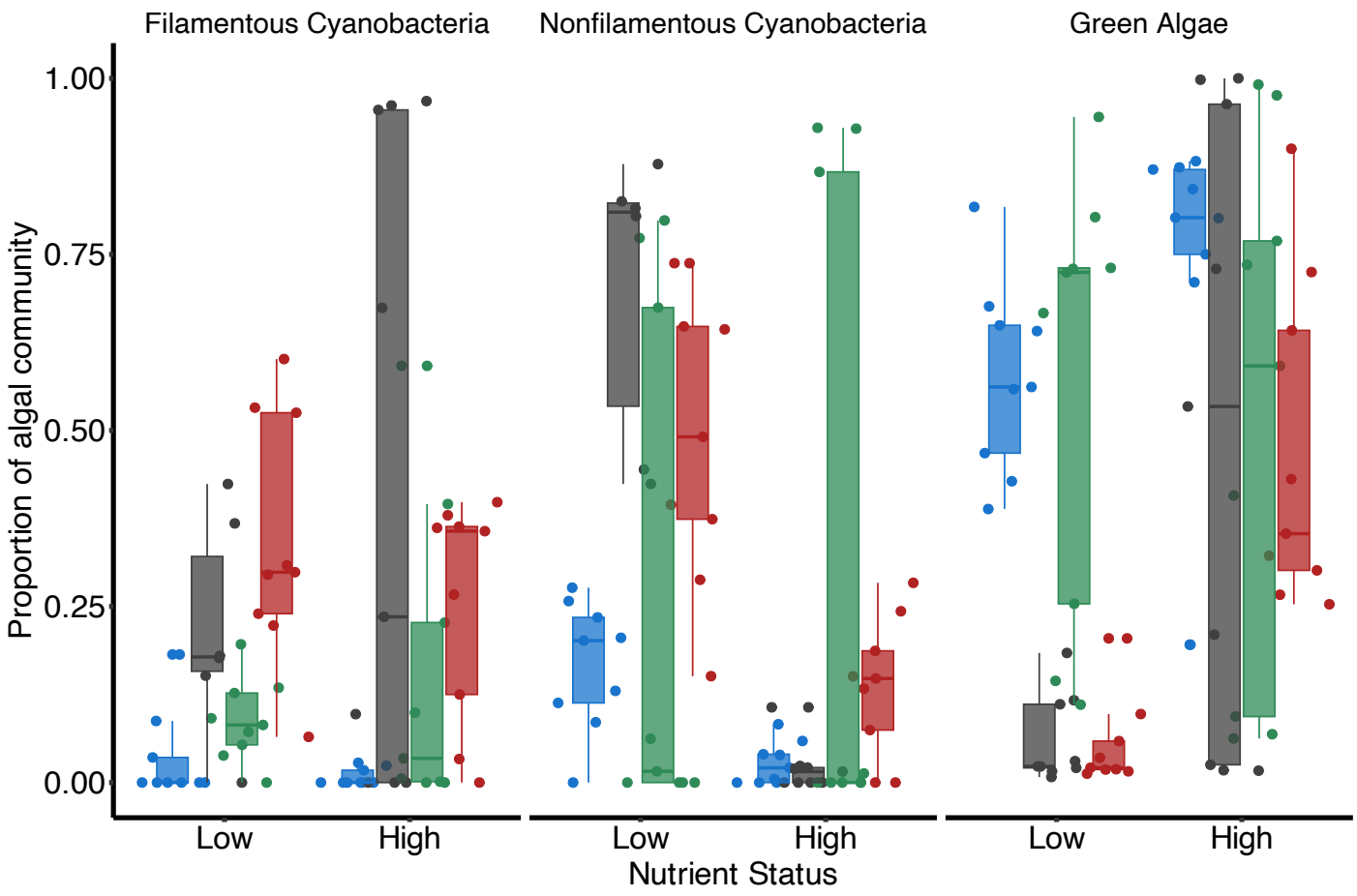
Filamentous Cyanobacteria
Nonfilamentous Cyanobacteria
Green Algae
Proportion of algal community
1.00
0.75
0.50
0.25
0.00
Low
High
Low
High
Low
High
Nutrient Status

Figure 2:

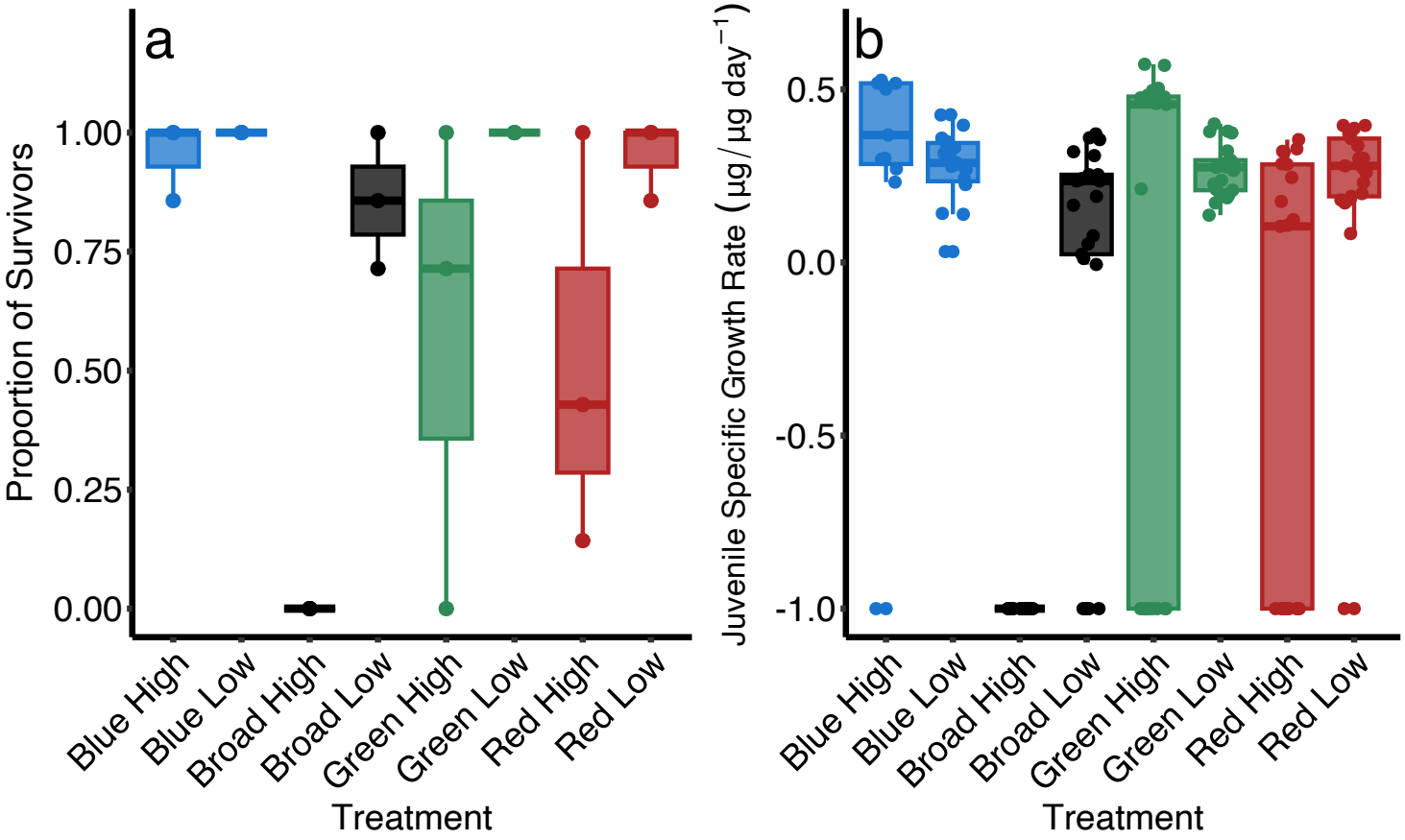
a
Proportion of Survivors
1.00
0.75
0.50
0.25
0.00
Blue High
Blue Low
Broad High
Broad Low
Green High
Green Low
Red High
Red Low
Treatment
b
Juvenile Specific Growth Rate (µg/µg day^{-1})
0.5
0.0
-0.5
-1.0
Blue High
Blue Low
Broad High
Broad Low
Green High
Green Low
Red High
Red Low
Treatment

Figure 3:

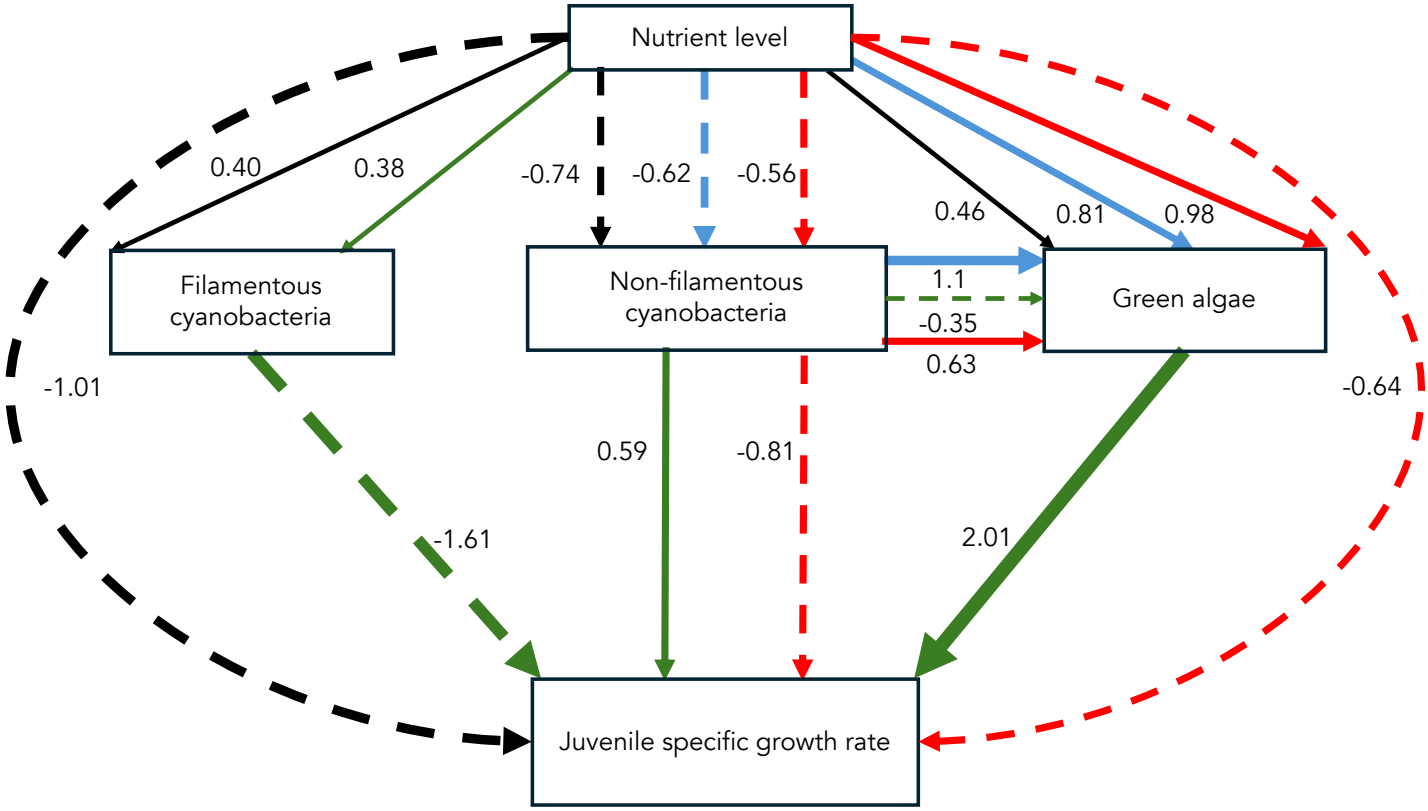
Nutrient level
Filamentous cyanobacteria
Non-filamentous cyanobacteria
Green algae
Juvenile specific growth rate
0.40
0.38
-0.74
-0.62
-0.56
0.46
0.81
0.98
1.1
-0.35
0.63
-1.01
-0.64
0.59
-0.81
-1.61
2.01

Table S1: ANOVA-like table for the random effect of microcosm in our linear mixed effects model

Model	Number of parameters	log likelihood	AIC	Likelihood ratio	Df	*p*
No random effects	10	-68.299	156.6			
Random effect: Microcosm	9	-96.76	211.52	56.923	1	**4.53E-14**

Table S2: Output of the light color x nutrient level linear model

Term	Estimate	SE	*t*	*p*
Intercept	0.277	0.13	2.141	**0.034**
Broad Light	-1.277	0.16	-7.989	**<0.001**
Green Light	-0.436	0.16	-2.729	**0.007**
Red Light	-0.628	0.16	-3.925	**<0.001**
Low Nutrients	0.006	0.163	0.034	0.97
Broad x Low Nutrient	1.027	0.21	4.893	**<0.001**
Green x Low Nutrient	0.42	0.21	1.999	**0.047**
Red x Low Nutrient	0.562	0.21	2.678	**0.008**

Table S3: Model wide interaction coefficients for the piecewise SEM.

Response	Predictor	Test.Stat	DF	*p*
JSGR	Nutrient level x Light color	3.20E+00	1	**0.0001**
JSGR	Light color x Nonfilamentous cyano	3.20E+00	1	**0**
JSGR	Light color x Filamentous cyano	3.20E+00	1	**0.0018**
JSGR	Light color x Green algae	3.20E+00	1	**0.0001**
Nonfilamentous cyano	Nutrient level x Light color	4.43E+11	1	**0**
Filamentous cyano	Nutrient level x Light color	1.22E+12	1	**0.0002**
Green algae	Nutrient level x Light color	1.52E+11	1	**0**
Green algae	Light color x Nonfilamentous cyano	1.52E+11	1	**0**

Table S4: Model coefficients and statistics from the structural equation model and multigroup analysis with blue light as the grouping factor. Significant *p*-values are in bold.

Blue Light	Response	Predictor	Estimate	Std.Error	DF	Crit.Value	*p*	Std.Estimate
	JSGR	Nutrient level	0.0175	0.2328	25	0.0753	0.9405	0.0318
	JSGR	Nonfilamentous cyano	0	0	25	0.0139	0.989	0.0078
	JSGR	Filamentous cyano	0	0	25	0.478	0.6368	0.1181
	JSGR	Green algae	0	0	25	0.0264	0.9792	0.012
	Nonfilamentous cyano	Nutrient level	-29123.035	7008.8407	28	-4.1552	**0.0003**	-0.6176
	Filamentous cyano	Nutrient level	-1725.2221	935.4111	28	-1.8443	0.0757	-0.3291
	Green algae	Nutrient level	50181.7877	7747.4932	27	6.4772	**0**	0.8091
	Green algae	Nonfilamentous cyano	1.4178	0.1643	27	8.6295	**0**	1.078

Table S5: Model coefficients and statistics from the structural equation model and multigroup analysis with broad light as the grouping factor. Significant *p*-values are in bold.

Broad Light	Response	Predictor	Estimate	Std.Error	DF	Crit.Value	*p*	Std.Estimate
	JSGR	Nutrient level	-1.2187	0.1763	37	-6.9121	**0**	-1.0131
	JSGR	Nonfilamentous cyano	0	0	37	-1.5838	0.1217	-0.194
	JSGR	Filamentous cyano	0	0	37	0.1972	0.8447	0.0191
	JSGR	Green algae	0	0	37	0.0645	0.9489	0.0066
	Nonfilamentous cyano	Nutrient level	-357793.65	51375.1261	40	-6.9643	**0**	-0.7403
	Filamentous cyano	Nutrient level	677079.365	244262.625	40	2.7719	**0.0084**	0.4014
	Green algae	Nutrient level	86320.7238	38579.8663	39	2.2375	**0.031**	0.4608
	Green algae	Nonfilamentous cyano	-0.0212	0.0798	39	-0.265	0.7924	-0.0546

Table S6: Model coefficients and statistics from the structural equation model and multigroup analysis with green light as the grouping factor. Significant *p*-values are in bold.

Green Light	Response	Predictor	Estimate	Std.Error	DF	Crit.Value	*p*	Std.Estimate
	JSGR	Nutrient level	-0.0289	0.202	37	-0.1431	0.887	-0.0257
	JSGR	Nonfilamentous cyano	0	0	37	6.1338	**0**	0.588
	JSGR	Filamentous cyano	0	0	37	-3.4831	**0.0013**	-1.6097
	JSGR	Green algae	0	0	37	4.7773	**0**	2.0082
	Nonfilamentous cyano	Nutrient level	120523.81	77890.3439	40	1.5474	0.1297	0.2376
	Filamentous cyano	Nutrient level	47833.3333	18578.6357	40	2.5746	**0.0138**	0.377
	Green algae	Nutrient level	17183.9684	18934.2422	39	0.9076	0.3697	0.1404
	Green algae	Nonfilamentous cyano	-0.0848	0.0373	39	-2.2712	**0.0287**	-0.3513

Table S7: Model coefficients and statistics from the structural equation model and multigroup analysis with red light as the grouping factor. Significant *p*-values are in bold.

Red Light	Response	Predictor	Estimate	Std.Error	DF	Crit.Value	***p***	Std.Estimate
	JSGR	Nutrient level	-0.7188	0.2989	37	-2.405	**0.0213**	-0.6399
	JSGR	Nonfilamentous cyano	0	0	37	-2.4075	**0.0212**	-0.8148
	JSGR	Filamentous cyano	0	0	37	1.9844	0.0547	0.5028
	JSGR	Green algae	0	0	37	-1.6998	0.0976	-0.3377
	Nonfilamentous cyano	Nutrient level	-136523.81	31957.5363	40	-4.272	**0.0001**	-0.5597
	Filamentous cyano	Nutrient level	-70809.524	50284.7042	40	-1.4082	0.1668	-0.2173
	Green algae	Nutrient level	166286.193	18726.1501	39	8.8799	**0**	0.9836
	Green algae	Nonfilamentous cyano	0.4397	0.0768	39	5.7265	**0**	0.6343