Does browning-induced light limitation reduce fish body growth through shifts in prey composition or reduced foraging rates?

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Abstract

1. Browning of waters, coupled to climate change and land use changes, can strongly affect aquatic ecosystems. Browning-induced light limitation may have negative effects on aquatic consumers via shifts in resource composition and availability and by negatively affecting foraging of consumers relying on vision. However, the extent to which light limitation caused by browning affects fish via either of these two pathways is largely unknown.

2. Here we specifically test if fish growth responses to browning in a pelagic food web are best explained by changes in resource availability and composition due to light limitation, or by reduced foraging rates due to decreased visual conditions.

3. To address this question, we set up a mesocosm experiment to study growth responses of two different fish species to browning and conducted an aquaria experiment to study species-specific fish foraging responses to browning. Furthermore, we used a space-for-time approach to analyse fish body length-at-age across >40 lakes with a large gradient in lake water colour to validate experimental findings on species-specific fish growth responses.

4. With browning, we found an increase in chlorophyll a concentrations, shifts in zooplankton community composition, and a decrease in perch (Perca fluviatilis) but not roach (Rutilus rutilus) body growth. We conclude that fish growth responses are most likely to be linked to the observed shift in prey (zooplankton) composition. In contrast, we found limited evidence for reduced perch, but not roach, foraging rates in response to browning. This suggests that light limitation led to lower body growth of perch in brown waters mainly through shifts in resource composition and availability, perhaps in combination with decreased visibility. Finally, with the lake study we confirmed that perch but not roach body growth and length-at-age are negatively affected by brown waters in the wild.

5. In conclusion, using a combination of experimental and observational data, we show that browning of lakes is likely to (continue to) result in reductions in fish body growth of perch, but not roach, as a consequence of shifts in prey availability and composition, and perhaps reduced foraging.
INTRODUCTION

Global climate change, de-acidification, and changes in land use are leading to increased concentrations of dissolved organic carbon (DOC) and iron in temperate and boreal aquatic systems, leading to browning of waters and decreased light availability (Creed et al., 2018; Larsen, Andersen, & Hessen, 2011; Roulet & Moore, 2006; Weyhenmeyer, Muller, Norman, & Tranvik, 2016). Next to reduced light availability, this browning is often accompanied by increased nutrient concentrations (Creed et al., 2018; Findlay, 2003). Browning can have negative effects on many components of lake ecosystems, ranging across trophic levels, from reducing primary production and algal biomass (Ask et al., 2009; Vasconcelos et al., 2016), zooplankton production (Kelly, Solomon, Weidel, & Jones, 2014) and benthic invertebrate biomass (Vasconcelos et al., 2018), to fish growth and production (van Dorst et al., 2019; Karlsson et al., 2015). However, browning effects are rarely studied across multiple trophic levels and interacting species (but see Hansson et al., 2012; Vasconcelos et al., 2018). In addition, most studies to date have focused on the total effect of browner waters, instead of studying the effects of light limitation, increased DOC, or increased nutrient concentrations separately. Decreased light availability can affect aquatic systems in many ways, e.g. by reduced visibility (Davies-Colley & Vant, 1987; Morris et al., 1995), lower primary production (Ask et al., 2009; Seekell et al., 2015), and less heat penetration down the water column, which may lead to increased thermal stratification (Solomon et al., 2015). Nonetheless, there is limited knowledge on the relative importance of these consequences of light limitation through browning for fish body growth and production.

Decreased light availability can reduce the amount of basal production and biomass available to higher trophic levels by limiting photosynthesis (Ask et al., 2009; Jones, Solomon, & Weidel, 2012; Seekell et al., 2015; Vasconcelos et al., 2016). Whereas browning generally has a negative effect on benthic primary production, effects on pelagic primary production range from negative (Jansson, Bergström, Blomqvist, & Drakare, 2000), to neutral (Ask, Karlsson, & Jansson, 2012) and even positive (chlorophyll a [chl a]) (Kelly et al., 2016). The latter may partly be explained by increased nutrient concentrations with browning, which, up to a certain threshold, can compensate for reduced light availability, causing a hump-shaped relationship between DOC and whole-lake primary production (Kelly, Solomon, Zwart, & Jones, 2018; Seekell et al., 2015). Changes in primary production with browning may, in turn, change the biomass and alter the composition of secondary consumer communities (i.e. zoobenthic and zooplankton invertebrates) through bottom-up processes. Altered invertebrate prey communities due to browning could ultimately affect the amount of biomass available for predators such as fish (i.e. a bottom-up response), thereby potentially affecting their growth and productivity.

Most fish species are visual foragers and a decreased visibility caused by brown waters can strongly reduce foraging ability, as shown for some benthivorous and piscivorous fish (Jönsson, Ranåker, Nilsson, Brönmark, & Grant, 2013; Ranåker, Jönsson, Nilsson, & Brönmark, 2012). Considering that fish species have different modes of feeding (e.g. using vision or other senses) and feed on different prey items (e.g. benthic or pelagic prey), previous studies have shown that browning may affect foraging rates of different fish species in distinctive ways (Jönsson, Ranåker, Nilsson, & Brönmark, 2012; Weidel et al., 2017). For example, responses to browner waters for fish feeding on zooplankton seem to vary between fish species (Jönsson et al., 2012; Weidel et al., 2017). However, the extent to which reduced feeding rates with lower visibility contribute to observed patterns of decreased fish biomass production with browning in many temperate lakes (van Dorst et al., 2019; Karlsson et al., 2015) is unknown. Next to changes in feeding rates, lower visibility could also change prey selection, for example by reducing visual prey selectivity in some fish species (Estlander et al., 2010). The fact that feeding of fish species is affected differently by light limitation (Estlander et al., 2010; Jönsson et al., 2012; Weidel et al., 2017), begs the question of whether they also vary in their growth responses to browning, which would suggest that fish community composition may determine how fish community production is affected by browning.

The extent to which light limitation specifically caused by browning affects fish indirectly via changes in the prey community or directly by worsened conditions for visual feeding is still largely unknown. Here, we test the relative importance of changes in resource availability and composition due to light limitation, and reduced foraging rates caused by decreased visual conditions for fish growth responses to browning in a pelagic food web. Our main question was tested with a mesocosm experiment set up to study fish growth responses to browning in a pelagic food web. We also set up an aquarium experiment to study fish foraging responses to worsened visual conditions caused by browning. Finally, to test whether our experimental results hold also in the wild, we analysed fish body length-at-age data collected across a large gradient in lake water colour. We further generalise our results by asking if observed responses to browning vary depending on fish species identity.

METHODS

2.1 Species studied

The two fish species used in this study are Eurasian perch (Perca fluviatilis) and common roach (Rutilus rutilus), two common and often co-occurring fish species in northern European lakes and coastal waters.
Perch changes resource use over its lifetime, first feeding on zooplankton, switching to zoobenthos, and finally feeding on other fish (Eklov & Persson, 1995; Hjelm, Persson, & Christensen, 2000). Roach can feed on zooplankton, algae, and zoobenthos, but do not exhibit strong ontogenetic diet shifts (Horppila, 1994; Persson, 1983). Roach are more efficient zooplankton feeders than perch (Byström & García-Berthou, 1999). While roach are efficient zooplankton feeders even in low light conditions (Bohl, 1979), percids, like P. fluviatilis, are vision-oriented selective predators and are therefore more dependent on their vision when feeding on zooplankton (Helfman, 1979).

### 2.2 Mesocosm experiment

#### 2.2.1 Experimental setup

To study fish growth responses to light limitation in a pelagic food web, we performed a mesocosm experiment in 18 open tanks (3 m diameter × 1 m water depth) that were located outside from 10 August to 10 September 2017. The tanks were filled with ca. 7,000 L of filtered water (using a filter with 400-µm mesh size) from the adjacent lake Mälaren (59°33′N 17°87′E) on 9 August. We inoculated all tanks with similar quantities of zooplankton from a pooled sample collected from nearby ponds using a 70-µm mesh net on 10 August.

To separate fish growth responses caused by changes in resource availability and composition due to light limitation (shifts in prey community), and reduced foraging rates due to decreased visual conditions, we assigned three browning treatments and two fish species treatments using a factorial design (Figure 1). Browning treatments consisted of a clear control treatment (CL), a brown–early treatment (BE) aimed to create and test effects of browning on the prey community through decreased light availability before fish are present in the system, and to test the combined effects of (potentially) altered prey communities and reduced visibility on fish species-specific growth responses (Figure 1). To mimic browning of waters, we used 1.600 ml of Sera Blackwater Aquatan water conditioner (Sera GmbH, Heinsberg, Germany; hereafter blackwater) per mesocosm, which browned the water and reduces light availability (Figure S1) without changing pH. We analysed blackwater samples and found that it contains low amounts of total organic carbon (TOC) and nutrients, and increased concentrations of TOC by 3.8 mg/L (±0.96 SD), total phosphorus by 2.89 µg/L (±0.89 SD), and total nitrogen by 180.17 µg/L (±39.1 SD) at the start of the browning. However, the natural lake water used to fill the tanks contained much higher nutrient and carbon levels (TOC: 8.05 mg/L, total phosphorous: 18.25 µg/L, total nitrogen: 420.5 µg/L). In the first half of the experiment, no fish were present and only BE treatment mesocosms were browned (Figure 1). This allowed the zooplankton populations to establish without predators present and us to study whether browning-induced light limitation affected phytoplankton biomass (measured as chl a) and zooplankton biomass and composition. On day 19 of the experiment, BL treatment mesocosms were browned and fish were added to all treatments and mesocosms, allowing us to study fish growth responses. Comparison of the BE and the BL treatment allowed us to determine if alterations in resource availability and composition, or decreased fish foraging rates due to decreased visual conditions, affected fish growth the most, and if growth responses varied depending on fish species identity (i.e. roach or perch). This rendered 6 treatments during the second half of the experiment that all were replicated three times (three browning treatments × two fish species treatments × three replicates = 18 mesocosms; Figure 1).

#### 2.2.2 Experimental fish

Fertilised perch and roach eggs were collected in Lake Mälaren on 25–26 May 2017 and transferred to two nearby ponds (22.5 × 6 m, maximum depth 1.5 m). The eggs hatched in the beginning of June and the fish lived in these ponds and fed on natural invertebrate prey communities until the start of the experiment.

On 28 August we took out fish from the ponds using a seine net. We selected fish of similar size for each species, of which we preserved a subsample for size estimates (perch length 50.6 ± 4.1 mm and weight 1.29 ± 0.39 g, roach length 45.2 ± 2.7 mm and weight 0.79 ± 0.14 g, means ± 1 SD). To control for the size difference between perch and...
roach in their effects on zooplankton, we added either 6 perch or 10 roach to the mesocosms. This was specifically done to achieve similar energy requirements (i.e. metabolic mass) of fish between mesocosms regardless of fish species present, such that potential variation in top-down influence of fish on lower trophic levels would only link to fish species identity and not to different energy requirements (see supplementary methods). We acclimatised the fish in containers with filtered lake water for a few hours before introducing them to the experimental mesocosms. The experiments in this study were conducted in accordance with national guidelines for animal care and the procedures employed were reviewed and approved by the regional ethical review board in Uppsala, Sweden (Dnr 5.8.18-03449/2017).

2.2.3 | Sampling

The mesocosms were sampled every 9 days before fish were added and every 6–7 days after fish addition. At each sampling occasion, water temperature was measured at the surface and at 0.5 meter depth (Figure S1). Photosynthetically active radiation (PAR) was measured at the surface, at 0.5, and 0.8 m depth with a LI-250A light meter with a LI-193SA spherical underwater quantum sensor (LI-COR Biosciences–Biotechnology, Lincoln, NE, USA, Table S2). From these PAR measurements, the light attenuation coefficient (\(k_z\)/m) was calculated as: \(k_z = \ln (\text{PAR}_0/\text{PAR})/z\). Where \(\text{PAR}_0\) is the PAR at the surface, and \(\text{PAR}_z\) is the PAR at depth \(z\) (m). Blackwater addition increased the light attenuation coefficients 4–5 fold, from 0.678 m\(^{-1}\) ± 0.035 (mean ± SE) in the CL treatment, to 3.49 m\(^{-1}\) ± 0.066 and 3.74 m\(^{-1}\) ± 0.103 in the BE and BL treatment, respectively (Figure S2). These are all within the range of naturally occurring light attenuation coefficients in the study region (Karlsson et al., 2015). Water samples for chl \(a\) analyses were taken at 0.5-m depth with a 2-L water sampler. Chlorophyll \(a\) was used as a proxy for phytoplankton biomass. From each water sample, 500 ml water was filtered through a 47-mm diameter glass microfibre filter (Whatman™), after which the filter was frozen until analysis. The samples were analysed by extraction with acetone and using a spectrophotometer (full method description, https://www.sis.se/api/document/preview/5605/, in Swedish). Zooplankton samples were taken with a zooplankton net with a mesh size of 70 µm and preserved in Lugol’s solution. The net was hauled from the bottom to the surface of the mesocosms (1 m, net diameter 25 cm, corresponding to a sampled volume of 49 L). Using a stereo microscope, cladocerans were determined to genus level, while copepods were identified as either cyclopoid, calanoid, or nauplii. For each taxa/group, up to 15 individuals were length measured to the nearest 0.01 mm (all if fewer). Zooplankton lengths were converted to population biomass (µg) with taxa-specific length-weight conversions (Bottrell et al., 1976; Dumont, Van de Velde, & Dumont, 1975). We also calculated biomass proportion of each taxa/group of the total zooplankton biomass.

At the end of the experiment, all fish were removed from the mesocosms with a seine net, euthanised in a benzocaine solution, blotted dry, and measured and weighed to the nearest mm and 0.01 g.

2.3 | Capture rate experiment

We performed a foraging experiment in aquaria (38.5 cm l × 19.5 cm w × 24.5 cm h), filled with 15 L of filtered lake water. We measured capture rates on Daphnia longispina (0.7 ± 0.1 mm, mean ± SD) of perch and roach of similar size as used in the mesocosm experiment (mean length ± 1SD, perch: 44.5 ± 2.7 mm, roach: 44.2 ± 2.4 mm). The experiment was conducted at three different light conditions: clear, intermediate (medium brown), and dark brown water; and two temperatures (19 and 25°C). Different levels of browning were simulated by adding Sera Blackwater Aquatan water conditioner (0, 2 and 8 ml to each aquarium, respectively). We measured perch and roach capture rate (no. of prey eaten in 1 min) of D. longispina after inoculating each aquarium with a density of four D. longispina per litre (total of 60 D. longispina per aquarium). We had between three and five replicates for each treatment. For a more detailed method description of the capture rate experiment, see supplementary methods.

2.4 | Lake data

Lake fish data were obtained from the Swedish National Register of Survey test-fishing (National Register of Survey test-fishing - NORS, 2016). We selected lakes that had length-at-age data for perch and/or roach for a minimum of five fish per selected age (1 and 5 year olds) for the time period 2006 to 2015. Lakes larger than 5 km\(^2\) were excluded to limit variation in lake size. For all lakes included in our analyses we also have environmental data (e.g. absorbance of filtered water at 420 nm, temperature, and turbidity) sampled in July and/or August for at least 4 years during the same time period (Miljödata MVM database, https://miljodata.slu.se/mvm/Default.aspx, on 05-12-2016), and lake morphology data (area, mean depth; see Table S1). These selection criteria gave us a dataset of 49 small to intermediate sized lakes (area: 0.04–4.89 km\(^2\)) distributed all over Sweden, of which 43 contained perch and 40 roach (see Table S1). Lake water colour is reported as absorbance at 420 nm in samples taken at 0.5 m depth, where high absorbance is a proxy for brown water (Kirk, 1994). Absorbance was measured using filtered (0.45 µm filter) water in a 5-cm cuvette and converted to the Napierian absorption coefficient (\(a_{420}\)) as recommended by Hu, Muller-Karger, and Zepp (2002) (hereafter we use absorbance to refer to the Napierian absorption coefficient, see supplements). Mean absorbance measured across lakes during July and August was 6.36 m\(^{-1}\) (0.7–22.2 m\(^{-1}\)).

All fish were sampled using multi-mesh gillnets in the benthic and pelagic zones according to a standardised test-fishing method (Appelberg et al., 1995). For detailed information on the fish sampling method see van Dorst et al. (2019). All captured fish were identified to species and their total individual length was measured to the nearest mm. In order to obtain individual age estimates of perch and roach, random sub-samples were collected in proportion to the size distribution of the total catch. Fish that were sub-sampled for age determination were measured to the nearest millimetre and weighed to the nearest gram. Otoliths of perch and roach were used for age determination (Le Cren, 1947; Linjaksen, Kleiven, & Matzow, 1991). We calculated mean
length-at-age (mm) at catch of age 1 and 5 perch and roach. Length-at-age 1 represents growth during the first year and length-at-age 5 is a result of the growth during the first 5 years of life. We included both length-at-age 1 and 5 in order to see if possible species-specific responses to browning hold over ontogeny.

2.5 | Statistics

To study if fish growth responses to browning were mostly caused by changes in resource availability and composition due to light limitation, or by reduced foraging rates due to decreased visual conditions we first test how browning influenced the lower trophic levels in our pelagic food web. We analysed treatment differences in chl a concentration and total zooplankton biomass over time with mixed-design analyses of variance models (mixed ANOVA, equivalent to a split-plot ANOVA) using the package `afex` in R (Singmann, Bolker, Westfall, & Aust, 2018).

Response variables were ln-transformed before analyses. Analyses were performed separately on data collected before (day 1, 10 and 19) and after fish addition (day 19, 26 and 32). Before adding fish we only had two browning treatments: a clear control (CL and BL, analysed as one as BL was browned first when adding fish) or brown treatment (BE; Figure 1). Thus, for this first part of the experiment, the response variables were analysed with a two-way mixed ANOVA with browning as the between mesocosm variable and date as a within mesocosm (random) variable (formula: ln(response variable) ~ browning treatment × date). After adding fish we had three browning treatments (CL, BL, and BE, as BL was browned when adding the fish) and two fish species treatments (perch and roach; Figure 1). For this second part of the experiment, response variables were analysed with a three-way mixed ANOVA with browning and fish species treatments as between mesocosm variables and date as the within mesocosm (random) variable (formula: ln(response variable) ~ browning treatment × fish species × date). When the assumption of sphericity in the mixed ANOVA was not met, Greenhouse–Geisser sphericity corrected statistics are shown. If we found significant main or interactive effects we performed follow-up pairwise tests with Bonferroni adjustments using the `lsmeans` package in R (referred to as pairwise comparison in results) (Lenth, 2016).

Because zooplankton taxa-specific biomass data did not adhere to assumptions of a mixed ANOVA because of too many zeroes, we studied biomass of three common zooplankton taxa/groups and zooplankton community composition on one date before fish addition (the final date, day 19, allowing for enough time for zooplankton to respond to browning and also representing the starting values of prey available for fish) and one date with fish present (the middle date, day 26, as most zooplankton were depleted on the final date). We analysed treatment differences in biomass of *Bosmina* sp. and copepods for these two dates, and *Daphnia* sp. on day 19 as they were almost completely consumed by day 26) with analyses of variance models (ANOVA). Response variables were ln-transformed before analyses. We statistically tested for differences in zooplankton community composition among treatments for these two dates with permutational multivariate analysis of variance (PERMANOVA (Anderson, 2001)), using the adonis function in the vegan package, with 999 permutations. The PERMANOVA was based on distance matrices of zooplankton taxa/group biomasses using the Bray–Curtis dissimilarity index (which can handle zero-skewed community composition data) (Clarke & Warwick, 2001). To assess the extent of unequal variance in our data sets (to which PERMANOVA is sensitive, (Anderson & Walsh, 2013)), PERMANOVAs were followed by betadisper tests, a multivariate analogue of Levene's test for homogeneity of variances. These were not significant, suggesting no treatment effects on variance. To visualise differences in community composition we graphed biomass proportions for each zooplankton taxa/group to the total zooplankton biomass. In addition we used non-metric multi-dimensional scaling (NMDS) plots, again based on distance matrices of zooplankton taxa/group biomasses using the Bray–Curtis dissimilarity index (Clarke & Warwick, 2001). The NMDS were performed with the metaMDS function in R’s vegan package (Oksanen et al., 2019). Each ordination ran for 100 iterations, or until the lowest stress score was found. Stress scores were sufficiently low (<0.2) in all runs, such that data could be interpreted in two dimensions.

To test the effect of water colour on growth responses measured as increase in weight from the start to the end of the experiment of perch and roach in the mesocosm experiment we carried out two one-way ANOVA’s (ln(perch growth) ~ browning treatment, and ln(roach growth) ~ browning treatment). We assessed survival rate with a two-way ANOVA (survival rate ~ browning treatment × fish species). Tukey-HSD post hoc tests were performed when the ANOVA was significant.

We analysed effects of browning on fish foraging rates, measured in the aquarium experiment, with two two-way ANOVA models, one per fish species with browning (3 levels) and temperature (two levels) as explanatory variables (capture rate = browning treatment × temperature). Interactions were not significant for either model and therefore removed. Temperature is present in the study to generalise the results, but is not a variable we specifically want to test for in this study.

For the lake study, we analysed the influence of water colour (absorbance) on ln-transformed length-at-age 1 and 5 of both perch and roach with linear regression models. We ran an ANCOVA for each species, with water colour (absorbance) as an independent measuring variable and age (1 and 5) as a nominal variable, to study if the effect of water colour on length-at-age differed between ages. In addition, we repeated the linear regression analyses including multiple environmental covariates likely to affect fish body growth (see supplementary methods and results).

All analyses were based on significance levels $p < 0.05$ (two-sided tests) and were done in R 3.4.2 (R Core Team, 2017).

3 | RESULTS

3.1 | Mesocosm experiment

3.1.1 | Browning effects before fish addition

Prior to fish addition, browning initially had a slight positive effect on chl a concentrations (Table 1, Figure 2). After this initial increase there
was a slight decrease in chl \( a \) concentrations before fish addition in the clear, but not the brown, treatment (Figure 2, Clear treatment: pairwise comparison dates: \( p < 0.05 \) (Figure 2). Consequently, chl \( a \) concentrations were higher in the brown than in the clear treatment on the final day before fish addition (Figure 2, pairwise comparison: \( p < 0.0001 \)).

Whereas we found an overall increase in zooplankton biomass over time, there was no effect of browning on total zooplankton biomass (Figure 3a, Table 1) prior to fish addition. However, zooplankton community composition differed between clear and brown mesocosms at the time when fish were introduced (Day 19; Figure 4a and Figure S4a, PERMANOVA = \( F_{(1,16)} = 2.26, p = 0.043 \)). This seems mainly caused by a higher biomass proportion (Figure 4a) and absolute biomass of \textit{Daphnia} sp. in brown compared to clear water mesocosms on this date (Figure 3b, ANOVA: \( F_{(1,16)} = 6.19, p = 0.024 \). There was also a lower biomass proportion of \textit{Bosmina} sp. in brown than in clear water mesocosms (Figure 4a, for community composition on all dates see Figure S3).

However, there were no differences between treatments in absolute biomass of \textit{Bosmina} sp. (Figure 3c, ANOVA: \( F_{(1,16)} = 2.29, p = 0.1499 \)) or copepods (Figure 3d, ANOVA: \( F_{(1,16)} = 0.0244, p = 0.966 \)). In contrast, there were no effects of water colour treatment on roach body growth (ANOVA: \( F_{(1,16)} = 0.417, p = 0.677 \); Figure 5). Roach had a lower mean survival (94\%) than perch (100\%; ANOVA: \( F_{(1,16)} = 4.73, p = 0.047 \)), irrespective of browning.

### 3.1.2 | Browning effects with fish

#### Fish responses

Perch body growth was negatively affected by early browning (ANOVA: \( F_{(2,6)} = 7.941, p = 0.0206 \), being lower in the BE (0.35 ± 0.039 g, mean ± SE) than in the CL (0.62 ± 0.068, Tukey-HSD: \( p = 0.027 \); Figure 5) and the BL (0.60 ± 0.075, Tukey-HSD: \( p = 0.037 \)) treatments. Perch body growth in the BL treatment, however, did not differ from the CL treatment (Tukey-HSD: \( p = 0.966 \)). In contrast, there were no effects of water colour treatment on roach body growth (ANOVA: \( F_{(2,6)} = 0.417, p = 0.677 \); Figure 5).

#### Chlorophyll \( a \)

After fish addition, browning further increased chl \( a \) concentrations (Table 1), with chl \( a \) concentrations being lowest in the CL and highest in the BE treatment, and BL in between (Figure 2, pairwise comparisons: \( p < 0.05 \)). In both brown treatments (BE, BL), chl \( a \) concentrations increased throughout this second part of the experiment (Figure 2, Table 1), with treatment differences being largest at the end of the experiment (pairwise comparisons between browning treatments on the final date: \( p < 0.001 \)). Fish species identity had no effects on chl \( a \) levels (Table 1).

#### Zooplankton responses

Total zooplankton biomass decreased over time after fish addition but (similar to before fish addition) there was no effect of browning.

| Explanatory variables | Chlorophyll \( a \) concentration | Zooplankton community biomass |
|-----------------------|----------------------------------|------------------------------|
| **Before fish addition** |                                  |                              |
| Browning (CL/BE)      | \( F_{(1,16)} = 25.70^{***} \)  | \( F_{(1,16)} = 0.28  \)    |
| Time                  | \( F_{(2,32)} = 37.85^{***} \)  | \( F_{(1,16),17} = 70.45^{***} \) |
| Browning × Time       | \( F_{(2,32)} = 6.95^{**} \)     | \( F_{(1,16),17} = 0.83 \)   |
| **With fish**         |                                  |                              |
| Browning (CL/BE/BL)   | \( F_{(2,11)} = 45.76^{***} \)  | \( F_{(2,12)} = 2.48 \)     |
| Fish species          | \( F_{(1,11)} = 4.77 \)         | \( F_{(1,12)} = 1.92 \)     |
| Browning × Fish species | \( F_{(2,11)} = 0.29 \)   | \( F_{(2,12)} = 0.39 \)     |
| Time                  | \( F_{(2,22)} = 31.71^{***} \)  | \( F_{(2,24)} = 25.89^{***} \) |
| Browning × Time       | \( F_{(4,22)} = 10.38^{***} \)  | \( F_{(4,24)} = 2.55^{*} \)  |
| Fish species × Time   | \( F_{(4,22)} = 1.99 \)         | \( F_{(4,24)} = 3.06^{*} \)  |
| Browning × Fish species × Time | \( F_{(4,22)} = 0.47 \)   | \( F_{(4,24)} = 1.62 \)     |

***\( p < 0.001 \), **\( p < 0.01 \), *\( p < 0.1 \).
However, similar to before fish addition, there was an effect of browning on zooplankton community composition when fish were present (Figure 4b and Figure S4b, PERMANOVA: $F_{(1,12)} = 2.13, p = 0.047$). The difference in community composition on this date seems mainly to be caused by a higher biomass proportion of cyclopods and lower biomass proportion of *Bosmina* sp. in
Browning of waters can strongly impact aquatic ecosystems (van Dorst et al., 2019; Karlsson et al., 2015; Kelly et al., 2014; Vasconcelos et al., 2016). However, it is unknown if browning-induced light limitation affects food webs, and especially predators, mainly through changes in resource availability and composition or through direct effects on consumer feeding capacities. Here we experimentally show that browning leads to species-specific growth responses in fish, and that these probably come about through shifts in the zooplankton (prey) community, possibly in combination with reduced foraging rates. In the brown early (BE), but not the brown late (BL) treatment, we found a strong increase in chl $a$ concentrations, shifts in zooplankton community composition, and a decrease in perch but not roach body growth. The latter is likely to be linked to observed shifts in prey (zooplankton) composition with browning. In addition, we found some evidence for reduced capture rates in perch, but not roach, in response to decreased visual conditions. However, reductions in foraging were not large enough on their own to cause reduced perch growth in the mesocosm experiment, as they only did so when combined with prey compositional changes (in the BE treatment). In a comparative analysis of fish growth in over 40 lakes, we confirmed that perch but not roach growth is negatively affected by brown waters in nature.

Perch, but not roach, body growth was lower in mesocosms that were browned already at the start of the experiment (BE treatment) compared to fish growth in the clear water and the BL mesocosms, while the late browning treatment did not lead to lower growth. In addition, we found limited evidence for decreased capture rates on $D. longispinus$ by perch (but not roach) in brown waters. This shows that the extent to which light limitation caused by browning affects capture rates on zooplankton can vary between fish species (see also Jönsson et al., 2012; and Weidel et al., 2017). The lack of a negative capture rate response of roach to light limitation confirms previous studies, where the absence of a response was assumed to be due to the short distance at which zooplankton prey are detected by fish (Jönsson et al., 2012). The results of the mesocosm experiment suggest that decreased visual feeding conditions due to browning on its own probably has a limited direct negative effect on perch or roach body growth, at least not in pelagic food webs and given the level of browning studied here. Rather, the negative effect on perch body growth with early browning is probably a consequence of factors other than decreased foraging capacity alone. The lack of a growth response in the BL treatment suggests that changes are the prey community in response to light limitation...
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Before fish addition there was an increase in chl $a$ (proxy for pelagic phytoplankton biomass) in the BE treatment, similar to what was found in a long-term lake study by Leach, Winslow, Hayes, and Rose (2019). However, higher chl $a$ concentrations in brown waters, in the absence of increased nutrient concentrations, are probably caused by an increase in the amount of chl $a$ per phytoplankton cell with decreased light conditions (Fennel & Boss, 2003; Geider, MacIntyre, & Kana, 1997) rather than an actual increase in phytoplankton biomass, as we see no subsequent increase in zooplankton biomass.

In contrast to chl $a$, total zooplankton biomass did not respond to browning before (or after) fish addition. However, zooplankton community composition did shift with browning. Before fish addition, there was a higher biomass and proportion of Daphnia sp. and a lower proportion of Bosmina sp. in brown than in clear waters. A study by Wissel, Boeing, and Ramcharan (2003) found a similar dominance of Daphnia sp. in brown compared to clear waters in the absence of fish. The observed changes in zooplankton community composition in our experiment before fish addition are likely to be either a consequence of potential changes in phytoplankton community composition or a direct effect of decreased light penetration. Previous studies have shown that zooplankton species prefer different phytoplankton (Mitra et al., 2014; Sommer & Sommer, 2006), but the extent to which there was a shift in phytoplankton composition in our study is unknown (phytoplankton was not sampled, only chl $a$). Browning may also change zooplankton community composition by blocking harmful ultraviolet (UV) radiation penetrating the water column (Williamson, Stemberger, Morris, Frost, & Paulsen, 1996), as zooplankton species are differently equipped to cope with UV radiation (Williamson, 1995). For example, Daphnia sp. has been shown to have a higher survival and reproduction rate when UV-B light is excluded (Zellmer, 1995, 1998), which is in concordance with the increased biomass and proportion of Daphnia sp. we found with browning.

After fish addition, we observed differences between treatments across all trophic levels. The observed increase in treatment differences of chl $a$ concentrations could be the consequence of the absence of fish. The observed changes in zooplankton community composition in our experiment before fish addition are likely to be either a consequence of potential changes in phytoplankton community composition or a direct effect of decreased light penetration. Previous studies have shown that zooplankton species prefer different phytoplankton (Mitra et al., 2014; Sommer & Sommer, 2006), but the extent to which there was a shift in phytoplankton composition in our study is unknown (phytoplankton was not sampled, only chl $a$). Browning may also change zooplankton community composition by blocking harmful ultraviolet (UV) radiation penetrating the water column (Williamson, Stemberger, Morris, Frost, & Paulsen, 1996), as zooplankton species are differently equipped to cope with UV radiation (Williamson, 1995). For example, Daphnia sp. has been shown to have a higher survival and reproduction rate when UV-B light is excluded (Zellmer, 1995, 1998), which is in concordance with the increased biomass and proportion of Daphnia sp. we found with browning.
observed changes in zooplankton community composition when fish were added, given that different zooplankton taxa can vary in feeding efficiency and selectivity on different phytoplankton species (Mitra et al., 2014; Sommer & Sommer, 2006). However, we did not measure this in our experiment. Similar to before fish addition, total zooplankton biomass did not differ between treatments, but specific taxa and zooplankton community composition did. After fish were added, all *Daphnia* sp. (which were more abundant in the BE compared to clear treatment at the end of the no-fish part of the experiment) were soon eaten in all treatments. The rapid decline in *Daphnia* sp. biomass is expected as they are a desirable zooplankton prey for many fish species (Giles, Street, & Wright, 1990; Mills, Confer, & Ready, 1984). However, in addition, there was a lower biomass of *Bosmina* sp. in the BE compared to the BL and clear treatments. The fact that there was more of a difference in community composition between the BE and the BL treatment than between the BL and clear treatment, suggests that most of the difference in community composition between treatments after fish addition stems from differences that developed already before fish were added and that this was maintained when fish were present.

These differences in zooplankton communities may explain the decreased growth rate of perch in the BE treatment. After the fish had eaten their preferred *Daphnia* prey, there were fewer other cladoceran prey (*Bosmina* sp.) left to feed on in the BE treatment. The cause of the difference in growth response between the two fish species could be partly due to the fact that perch and roach differ in zooplankton prey preferences (in the absence of browning). Small roach seem to be more selective for cladocerans such as *Bosmina* sp. (Byström & García-Berthou, 1999; Hammer, 1985), while small perch are less selective in their prey choice (Byström & García-Berthou, 1999). This can explain the relatively lower biomass of *Bosmina* sp. in mesocosms with roach during the experiment compared to mesocosms with perch, irrespective of browning. In addition, at a given size, roach can sustain positive growth rates on less zooplankton than can perch (Byström & García-Berthou, 1999), and roach may therefore have been less affected than perch by any change in preferred zooplankton availability and community composition caused by browning. Furthermore, the capture rate experiment showed that perch but not roach zooplankton capture rate may be negatively affected by water colour. Accordingly, the combination of a different zooplankton community composition caused by browning before fish addition, species-specific feeding responses to water colour, species-specific differences in prey selection, and the higher feeding efficiency of roach probably led to a decrease in perch but not roach body growth in the BE treatment.

That perch but not roach grew slower in response to brown waters, as suggested by our experimental results, was confirmed in our analysis of fish growth in lakes. Both young and old perch had a lower length-at-age in brown compared to clear lakes, with the older perch having the most negative response. The latter is probably a result of that larger perch feed mainly on zoobenthos and fish (Amundsen et al., 2003), which both can be more negatively affected by browning than zooplankton (Vasconcelos et al., 2018), and because the feeding on zoobenthos and fish prey itself relies more on vision than does zooplankton feeding (Jönsson et al., 2012; Ranåker et al., 2012). Furthermore, larger fish need higher resource levels than small ones to sustain high growth rates (Byström & Andersson, 2005; Hjelm & Persson, 2001), which, in combination with a stronger decrease in prey levels for large perch, can explain the stronger negative effect on length-at-age of older individuals. As in the mesocosm experiment, roach body growth in lakes was not influenced by water colour. Thus, we conclude that fish growth responses to browning of waters are species specific (as also shown for growth of young fish over a DOC gradient in Benoit, Beisner, & Solomon, 2016).

These species-specific responses to browning can potentially shift the outcome of interspecific interactions such as competition. Furthermore, as reproduction rates generally increase with body-size, decreased growth rates caused by browning can lead to reduced population growth or biomass of certain species. Also, top predators, such as pike (*Esox lucius*) feeding on roach and perch, can probably be affected by species-specific growth responses of prey to browning, depending on species and size-preferences. Thus, not only may browning influence fish community composition, but we can expect different responses depending on the fish community present at the onset of browning, ranging from minor to major negative effects on community biomass and production.

In this study, we deliberately only looked at pelagic food web responses to browning due to shifted light conditions. However, in nature, browning is often accompanied with a significant concurrent increase in nutrients and DOC (Creed et al., 2018). Accordingly, previous experimental studies have often added humic substances to create browning treatments, leading not only to a decreased light availability but also a substantial increase in DOC and nutrient concentrations (e.g. Hansson et al., 2012; Vasconcelos et al., 2016; Vasconcelos et al., 2018). Whereas such a set-up creates a more realistic scenario, it makes it impossible to distinguish between effects of reduced light availability and increased nutrient/carbon input. Our experiment was designed to single out the effect of decreased light availability (with a much smaller addition of TOC and nutrients compared to the natural lake water used in all tanks), but still replicates impacts of browning across trophic levels similar to what is observed in nature (Ask et al., 2009; van Dorst et al., 2019; Karlsson et al., 2015) even without the addition of nutrients. It is, however, difficult to mechanistically explain lower trophic level responses in our experiment. For example, to elucidate the mechanisms underlying the browning-induced shifts in the zooplankton community, data on phytoplankton biomass and composition would be helpful, as would browning experiments on zooplankton capture rates of phytoplankton similar to the ones we did on fish. The capture rate experiment gives us some important insights on the possible mechanisms behind the effects of browning on fish, but to directly link the capture rate results to our mesocosm experiment is difficult. In our foraging experiment, we only used one zooplankton species, *Daphnia longispina*. *Daphnia* sp. was present in the mesocosm experiment and eaten rapidly by the fish in the experiment.
but was certainly not the only species present in that study. Ideally, we would have replicated the capture rate experiment with multiple zooplankton species, to study if the particular zooplankton species fed on influenced fish feeding responses in different water colours. Furthermore, light levels (PAR) differed between the mesocosm and capture rate experiment. However, the degree of light reduction between clear and brown treatments in both experiments is comparable.

Our findings increase our understanding of how browning affects pelagic food webs in temperate and boreal lakes. We show that browning can reduce fish growth—for some but not all fish species—through changes in resource availability and composition caused by light limitation, possibly in combination with a negative effect of decreased visibility on fish foraging rates. The species-specific responses we found in the experiments were reflected by the lower length-at-age of perch, but not roach, observed in brown water lakes in the large colour gradient of natural lakes. Lower body growth of some species is key to explain the lower fish biomass production in brown lakes (as reported by van Dorst et al., 2019), and suggests that we can expect different biomass production responses to browning depending on fish species present.

In conclusion, as temperate and boreal lakes get browner, we can expect shifts in zooplankton prey composition and fish foraging rates, and consequential species-specific reductions in fish body growth. These fish species-specific reductions in growth to browning will probably affect competitive and predator-prey interactions, and ultimately entire lake ecosystems.

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DATA AVAILABILITY STATEMENT
The data used for this manuscript are openly available on Zenodo at https://doi.org/10.5281/zenodo.3603049.

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**SUPPORTING INFORMATION**

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