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Zooplanktivore fish body growth responses to browning-induced light limitation vary over ontogeny, but not with fish density

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Abstract

Ongoing climate change is leading to browning of many lakes and coastal areas, which can impair fish body growth and biomass production. However, whether and how effects of light limitation caused by browning on fish body growth vary over early ontogeny is unknown. In this study, we set up a mesocosm experiment to test whether roach (*Rutilus rutilus*) body growth responses to browning depend on body size, and if findings are robust over roach densities. We also studied a potential mechanism for size-specific responses by conducting an aquaria experiment to test if size-specific prey selectivity in roach changes with browning. We found that roach body growth responses to browning-induced light limitation vary over ontogeny (independent of roach density), negatively affecting body growth of young-of-the-year (YOY) but not of 1-year-old individuals. We also show that this difference in growth response is likely a consequence of browning-induced alterations in zooplankton community composition and variation in prey selectivity between YOY and 1-year-old fish. This suggests that we should account for the diverse effects of browning over fish ontogeny, mediated via altered prey composition and ontogenetic changes in prey preference, when assessing overall impacts of browning on aquatic ecosystems.

KEYWORDS
body size, browning, climate change, density, prey selectivity, roach

1 | INTRODUCTION

Climate change, changes in land use and recovery from acidification are leading to "browning" of many temperate lakes and coastal areas, due to increased concentrations of dissolved organic carbon (DOC) and iron (Creed et al., 2018; Larsen et al., 2011; Roulet & Moore, 2006; Weyhenmeyer et al., 2016). This browning reduces light availability in the water, negatively affecting feeding rates (Jönsson et al., 2013; Ranåker et al., 2012), body growth (van Dorst et al., 2019, 2020) and biomass production (van Dorst et al., 2019) of fish. However, these responses may not be the same for all fish individuals and species. Observational studies over large water colour gradients suggest that growth responses to browning can vary over ontogeny (van Dorst et al., 2020). Knowing how fish respond to environmental drivers over ontogeny is important because of the different ecological roles fish can have over their lifetime, which influence interactions with competitors, prey and predators (Svanbäck et al., 2015; Werner & Gilliam, 1984). However, experimental studies on potential variation in responses to browning over ontogeny in fish are lacking.

Browning-induced light limitation could affect fish directly, as browning can deteriorate visual conditions (Davies-Colley & Vant, 1987; Morris et al., 1995). Impaired visual conditions can limit foraging by predatory fish relying on vision (Jönsson et al., 2013; Ranåker et al., 2012), especially individuals feeding on larger prey like benthos or other fish as such feeding is more reliant on spotting prey from longer distances (De Robertis et al., 2003; Jönsson et al., 2012), although feeding on zooplankton can also be negatively affected by browning (Weidel et al., 2017). The extent to which feeding on zooplankton prey is affected by browning likely varies with fish species identity (van Dorst et al., 2020; Jönsson et al., 2012; Weidel et al., 2017). This is probably a consequence of species-specific visual sensitivity, making some species better at coping with reduced visibility than others (Henderson & Northcote, 1985; Job & Bellwood, 2000). How much foraging rates are reduced due to browning may thus depend both on variation in preferred diet among individuals within a species and on fish species identity. Browning-induced light limitation can also affect prey selectivity of fish; for example, fish may select for a certain zooplankton prey in clear but not in brown waters (Estlander et al., 2010) or switch from positively selecting one species in clear waters to another in brown or shaded waters (Chaguaceda, 2020).

Browning-induced light limitation can also indirectly affect fish through effects on overall resource availability (Ask et al., 2009; Seekell et al., 2015). By limiting photosynthesis, browning can decrease primary production, reducing the biomass available for higher trophic levels (Ask et al., 2009; Jones et al., 2012; Seekell et al., 2015; Vasconcelos et al., 2016). This negative impact on resource availability is especially strong for benthic systems (Karlsson et al., 2009; Vasconcelos et al., 2018), but can be positive, negative or neutral with respect to pelagic resource production (phytoplankton and zooplankton; Ask et al., 2012; van Dorst et al., 2020; Kelly et al., 2016; Leech et al., 2020; Olson et al., 2020; Vasconcelos et al., 2018). Not only may browning-induced light limitation alter resource production and biomass, but also zooplankton prey community composition (van Dorst et al., 2020; Robidoux et al., 2015; Williamson et al., 2015). Shifts in prey composition and biomass can both limit resource intake for fish, especially in combination with reduced foraging rates due to reduced visibility, and thus negatively affect fish body growth (van Dorst et al., 2020) and productivity (Craig et al., 2017; van Dorst et al., 2019; Karlsson et al., 2015).

A fish's diet preferences (Werner & Gilliam, 1984), feeding rates (Rall et al., 2012) and demands for resources to meet metabolic needs (Byström & Andersson, 2005; Hjelm & Persson, 2001) change over ontogeny, mainly due to increased body size. Both preferred prey identity and size usually change with fish body size, due to increased energy requirements (Werner & Gilliam, 1984) and altered fish behaviour, morphology and foraging capacity (Anneville et al., 2010). As browning also may affect prey community composition (van Dorst et al., 2020; Robidoux et al., 2015), feeding rates (Jönsson et al., 2012; Weidel et al., 2017) and resource abundance (Vasconcelos et al., 2018), browning may therefore have varying effects depending on fish body size. Given ontogenetic differences in prey preferences, changes in prey species and/or size composition in response to browning may affect fish differently over ontogeny. As smaller fish in many cases have poorer eyesight than larger ones (Fernald, 1990; Miller et al., 1993; Otten, 1980) likely due to their smaller eyes and pupils (Caves et al., 2017), their feeding rates and prey selectivity might be more affected by reduced light availability compared to larger fish. On the other hand, a decrease in prey abundance could lead to more negative body growth responses in large than in small fish, because of their greater need for high resource densities to sustain positive growth rates (Byström & Andersson, 2005; Hjelm & Persson, 2001). There are thus several mechanisms by which body growth responses in fish to browning-induced light limitation may differ depending on body size, but whether they do is still unknown. Moreover, the only observations suggesting that browning responses may vary with body size were made in a species with distinct ontogenetic shifts in diet (European perch, *Perca fluviatilis*; van Dorst et al. (2019); van Dorst et al. (2020)). In these studies, small fish feeding on pelagic resources were less negatively affected by browning than larger fish feeding on benthic invertebrates and fish. Whether light limitation (controlling for other factors) causes size-specific responses in fish is unknown, as is the role of size-specific prey selectivity for such responses. It is also currently not known whether the effects of browning, including size-specific effects, vary with competitive intensity (e.g. conspecific density). If browning affects fish through decreasing zooplankton resources, the potential negative effect of browning may be reinforced at high competitive intensity (i.e. high consumption rates).

Here, we test whether fish body growth responses to browning-induced light limitation differ over early ontogeny (and therefore body size), using a species that lacks distinct ontogenetic diet shifts (common roach, *Rutilus rutilus*, hereafter “roach”), and study shifts in prey selectivity as a potential mechanism. Roach is among the most common planktivorous fish species in European lakes and coastal waters, occurring naturally across a wide range of environmental conditions, including both clear and relatively brown waters (van Dorst et al., 2020). Roach can feed on zooplankton, algae and zoobenthos, but do not exhibit distinct ontogenetic diet shifts (Horppila, 1994; Persson, 1983). They are very efficient zooplankton feeders throughout their lifetime (Byström & García-Berthou, 1999), even in low light conditions (Bohl, 1979; Nurminen et al., 2010). To test whether responses to browning-induced light limitation vary over early ontogeny (and therefore body size), we conducted (1) a pelagic mesocosm experiment to study growth responses of young-of-the-year (YOY) and 1-year-old roach to browning under different roach densities and (2) an aquaria experiment to test whether there are size-specific differences in prey selectivity of roach in clear and brown waters.

2 | METHODS

2.1 | Mesocosm experiment

2.1.1 | Experimental set -up

To study size-dependent growth responses of roach to browning-induced light limitation and to see whether these responses are robust to variation in roach density, we performed a mesocosm experiment in 20 outdoor tanks (3 m diameter ×1 m water depth) from 6 August to 5 September 2018. The tanks were filled with circa 7000 L of filtered water (using a filter with 400 µm mesh size) from the adjacent lake Mälaren (59°33'N 17°87'E) on 5 August. We inoculated all tanks with similar amounts of zooplankton from a pooled sample collected from nearby ponds using a 70 µm mesh net on 6 August (day 1 of the experiment).

To test for the effects of browning, body size and fish density on roach growth responses, we had two water colour treatments (clear and brown) and two density treatments (low and high roach density) in which we had two size/age classes of roach (young-of-the-year (YOY) and 1-year-olds) together in each mesocosm. We used a fully factorial design that gave us four different combinations of light and density, with four replicates of each treatment. We also had two clear and two brown control (i.e. without fish) mesocosms. The water colour treatments started on the first day of the experiment when half of the tanks were browned with 1600 ml Sera Blackwater Aquatan water conditioner (Sera GmbH) per mesocosm. The conditioner browns the water and reduces light availability (Figure S1), without changing the pH or substantially increasing nutrient levels (see van Dorst et al., 2020). The density treatment started when fish were added to the experiment (Day 10 of the experiment). The low-density treatment consisted of four 1-year-old and ten YOY roach and the high-density treatment of ten 1-year-old and 25 YOY roach in each mesocosm (for origin and size of fish see below), leading to a ratio of 2.5 (YOY to 1-year-old fish) in both density treatments. We used different numbers of YOY and 1-year-old roach to achieve more similar energy requirements between groups of YOY and 1-year-olds, such that variation in top–down influence of the roach on lower trophic levels between the size groups was minimised.

2.1.2 | Experimental fish

Fertilised roach eggs were collected in Lake Mälaren on 25–26 May 2017 and on 14 May 2018, 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. Thus, in 2017 (1-year-old) fish lived in the pond for 14.5 months and the fish born in 2018 (YOY) for 3 months. On 15 August 2018 (day 10 of the experiment), we collected roach from the ponds using a seine net. We selected fish of similar size for each cohort, of which we preserved a subsample for size estimates (1-year-olds: total length 58.6 ± 5.9 mm and weight 1.95 ± 0.63 g, YOY: total length 31.3 ± 4.0 mm and weight 0.28 ± 0.11 g, means ± 1 SD). We acclimatised the fish in containers with filtered lake water for a few hours before introducing them to the mesocosms (Day 10 of the experiment). 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).

2.1.3 | Sampling

The mesocosms were sampled on day 1, 9, 16, 24 and 30 of the experiment. At each sampling occasion, we measured water temperature at the surface and at 0.5-m depth (Figure S2), and photosynthetically active radiation (PAR) at the surface and at 0.5 m depth with a LI-250A light meter with a LI-193SA spherical underwater quantum sensor (LI–COR Biosciences–Biotechnology). From these PAR measurements, we calculated the light attenuation coefficient ($k_{z,}$ m^{-1}) as $k_z = \ln\left(\frac{PAR_0}{PAR_z}\right)/z$. Here, PAR_0 is the PAR at the surface, and PAR_z is the PAR at depth z (0.5 m). Browning increased the light attenuation coefficients 5.5 fold, from 0.65 m^{-1} ± 0.02 (mean ± SE) in the clear treatment, to 3.63 m^{-1} ± 0.06 in the brown treatment (means over the experimental period, Figure S1). These values are within the range of naturally occurring light attenuation coefficients in Swedish lakes (Karlsson et al., 2015). We took water samples for chlorophyll *a* (chl *a*) analyses (as a proxy for phytoplankton biomass) at 0.5-metre depth with a 2 L water sampler. From each water sample, we filtered 500 ml water through a 47 mm diameter glass microfiber 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. We hauled the net from the bottom to the surface of the mesocosms twice at opposite sides of the mesocosm (1 m, net diameter 25 cm, corresponding to a total sampled volume of 98 L). We used a stereo microscope to determine cladocerans to genus level, while we identified copepods as either cyclopoid, calanoid or nauplii. For each genus/group, we length measured up to 15 individuals (all if fewer) to the nearest 0.01 mm. Zooplankton lengths were converted to biomass (µg) with genus/group-specific length–weight conversions (Bottrell et al., 1976; Dumont et al., 1975), and we calculated genus/group and total zooplankton community biomass. We also calculated biomass proportion of each genus/group.

At the end of the experiment (Day 30), we removed all fish from the mesocosms with a seine net, euthanised them in a benzocaine solution, blotted them dry, and measured and weighed them to the nearest mm and 0.01 gram. We calculated weight-specific growth rates of each individual using

$$G_{W,\mathrm{start}} = \frac{W_{\mathrm{end}} - W_{\mathrm{start}}}{W_{\mathrm{start}}} * 100$$

where $G_{W,\mathrm{start}}$ is the weight-specific growth rate (%) during the experiment based on the mean weight (W) of fish (per size class) when put into the mesocosms (Day 10). Mean weight-specific growth rates were calculated per size class for each mesocosm, and treatment means were calculated from these.

2.2 | Prey selectivity experiment

The aim of the aquarium experiment was to test whether there were size-specific differences in prey selectivity of roach in clear versus brown waters. The roach in the aquarium experiment had the same origin and size as the roach used in the mesocosm experiment. We collected fish from the ponds with a seine net the day prior to the start of the experiment (same day as mesocosm experiment). Before the start of the selectivity experiment, YOY fish were acclimatised for 24 h, and 1-year-old fish for 45 h. Both YOY and 1-year-old fish were starved for 24 h before the start of the selectivity experiment.

The selectivity experiment was carried out over two days in 6 large aquaria (67 cm length*42.5 cm width*72 cm height), filled with 156 L (55 cm water depth) of filtered water from lake Mälaren. We covered the bottom, back and sides of the aquaria with dark blue plastic. A 20 W halogen light bulb was hung 20 cm above each aquarium, and a white fabric was placed in between the aquarium and the light bulb in order to create closer to natural light conditions. No other lights were present in the room. The experiment was conducted at two different water colour conditions: clear and brown water. Browning was simulated by adding 70 ml Sera Blackwater Aquatan water conditioner (Sera GmbH) per aquarium. The clear treatment contained regular filtered lake water. The light attenuation coefficient (calculated the same way as for the mesocosm experiment) was 0.77 m^{-1} ± 0.04 (mean ±SE) in the clear treatment and 3.04 m^{-1} ± 0.11 in the brown treatment (calculated from PAR measured at the surface and bottom of each aquarium). We studied two different sizes/cohorts of fish and added either two 1-year-olds, or ten YOY fish in one experimental trial (for mean body sizes see experimental fish, above). We used different numbers of YOY and 1-year-old roach to achieve more similar energy requirements between groups of YOY and 1-year-olds, such that there would be similar top–down effects of roach on their prey between treatments. We had three replicates of each factorial combination. After letting the fish acclimatise for half an hour in the aquarium, we added 500 ml of a known mix of zooplankton (two subsamples were taken for analyses) from a pooled sample collected from nearby ponds using a 70 µm mesh to each aquarium and gently stirred the water to distribute zooplankton evenly in the aquarium. Then, we let the fish eat for three hours, after which we sampled each aquarium with a vertical haul from the bottom to the surface with a 25 cm diameter zooplankton net with mesh size 70 µm. At the end of the experiment, the fish were removed from the aquarium and euthanised in a benzocaine solution.

We used a stereo microscope to determine cladocerans to genus level, while we identified copepods as either cyclopoid, calanoid or nauplii. We did this both for the zooplankton community that was introduced into the aquaria, as for the samples collected after fish had been feeding for three hours, and calculated the proportion of each prey group in each sample.

2.3 | Statistics

2.3.1 | Mesocosm experiment

To test whether roach mean body growth responses to browning depend on body size, and whether those responses are robust over roach densities, we used a linear mixed model with water colour, body size, density and their interactions as fixed factors, and included mesocosm as a random variable to account for both body size treatments being present in each mesocosm (ln(body growth) ~ Water Colour × Body size × Fish density + (1|Mesocosm)), using the R package *lme4* (Bates et al., 2015). We tested the significance of all fixed effects and their interactions based on likelihood ratios (with the R function "anova") by first examining interactions and then comparing models with or without main effects. We respected the marginality rules and compared models without one main effect or interaction with the full model without the higher level interactions containing this main effect or interaction. The final model selected included the significant main factors and interactions. We analysed normality of the residuals by visual inspection of Q-Q and residual density plots. We conducted post hoc comparisons, with Tukey adjustments, between combinations of our explanatory variables (from significant two-way interactions from the best linear mixed model) using estimated marginal means, in the R package *emmeans* (Lenth, 2020). Survival rates were high for all treatments (94–100% per treatment) and not analysed further. We analysed treatment differences in chl *a* concentration and 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 et al., 2018). Response variables were ln-transformed before analyses and analysed with a three-way mixed ANOVA with browning and fish density as between-mesocosm variables and date as a within-mesocosm (random) variable (ln(response variable)~Water colour × Fish density × Time). When the assumption of sphericity in the mixed ANOVA was not met, we show Greenhouse–Geisser sphericity corrected statistics. Normality of the residuals was assessed by visually examining Q-Q plots, and the assumption of homogeneity of variance was tested with Levene's tests. If we found significant main or interactive effects, we performed follow-up pairwise tests with Bonferroni adjustments using the *emmeans* package in R (referred to as pairwise comparisons in results). Pairwise tests for day 1 and 9 of the experiment were only done for colour and not for density treatments, as no fish were present on these days. Significance was based on $p < 0.05$ (two-sided tests).

To test whether zooplankton community composition differed among treatments for day 9 (one day before fish addition) and day 16 (6 days after fish were added, meaning that the effects of fish feeding should be visible in the prey community, but the communities were not depleted) of the experiment, we used permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001), using the *adonis* function in the *vegan* package (Oksanen et al., 2019), with 999 permutations. The PERMANOVA was based on distance matrices of zooplankton genus/group biomasses using the Bray–Curtis dissimilarity index, which can handle zero-skewed community composition data (Clarke & Warwick, 2001). As the fish density treatment was not present yet on day 9, we decided to perform separate analyses for day 9 and 16. To visualise differences in community composition on day 9 and 16, we graphed biomass proportions for each zooplankton genus/group across treatments (for graphs of day 1, 24 and 30 see Supporting Information). We also used non-metric multidimensional scaling (NMDS) plots for visualisation, again based on distance matrices of zooplankton genus/group biomasses using the Bray–Curtis dissimilarity index (Clarke & Warwick, 2001). We performed the NMDS 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.

2.3.2 | Prey selectivity experiment

To determine whether there were size-specific differences in prey selectivity of roach in clear versus brown waters, we tested whether zooplankton prey communities after fish feeding differed among treatment combinations with a PERMANOVA (as for the mesocosm experiment). To visualise differences between water colour and fish size treatments on zooplankton community composition before and after fish feeding, we graphed biomass proportions for each zooplankton genus/group across treatments (see Supporting Information). We also used NMDS plots for visualisation of the zooplankton communities after fish feeding (as for the mesocosm experiment). To determine whether there was selection for or against a certain prey group, we compared the proportion of each prey group from each treatment (fish size and water colour) to the proportion that was introduced to the experiment with a Welch two-sample t test (because of unequal variance). If the proportion after feeding was higher than the proportion before fish addition, we regarded this as selection against this prey group, and if the proportion after feeding was lower than the proportion before fish addition, we regarded this as selection for this prey group. Finally, if the proportion after and the proportion before did not differ from each other this was regarded as neutral selection for this prey group. We also determined whether water colour and body size affected the proportion of each prey item left after feeding with ANOVA's.

Significance was based on $p < 0.05$ (two-sided tests). All statistical tests were done in R 3.6.3 (R Core Team, 2017).

3 | RESULTS

3.1 | Mesocosm experiment

3.1.1 | Fish growth response

Roach body growth responses to browning varied with body size ($\chi^2(1) = 5.6825$, $p = 0.0171$, Table 1, Figure 1). Body growth rates of YOY roach were lower in the brown than the clear treatment (Tukey: $p = 0.0059$, Figure 1a,b), while growth rates of 1-year-olds were not affected by water colour (Tukey: $p = 0.765$, Figure 1c,d). Roach growth responses to browning did not depend on fish density ($\chi^2(1) = 1.3226$, $p = 0.2501$, Table 1, Figure 1). We did, however, find a significant interaction between body size and roach density on body growth ($\chi^2(2) = 16.614$, $p < 0.001$, Table 1, Figure 1). Body growth of both YOY and 1-year-olds was lower in high than low-density treatments (Tukey tests: $p < 0.05$, Figure 1). However, growth rates did not differ between YOY and 1-year-old roach at high densities (Tukey tests: $p = 0.51$, Figure 1b,d), while YOY roach had much higher growth rates than 1-year-olds at low densities (Tukey tests: $p < 0.001$, Figure 1a,c).

TABLE 1 Likelihood ratio tests (LRT) of the effect of water colour (Clear/Brown), fish size (YOY/1-year-olds) and roach density (Low/High) (and their interactions) on roach body growth (Df for each factor was 1) with χ^2 and p values

Explanatory variables	LRT-χ^2	p	Best model—Value	Best model—SE
Intercept			94.6	6.37
Water colour	7.838	0.005**	−27.2	7.35
Body Size	16.987	<0.001***	−58.7	7.37
Fish density	23.903	<0.001***	−60.9	7.35
Water colour × Body size	5.6825	0.0171*	20.0	8.51
Water colour × Fish density	1.323	0.250		
Fish Density × Body size	16.614	<0.001***	40.2	8.51
Water colour × Body size × Fish density	1.764	0.184		

Mean values and standard errors (SE) of the selected linear mixed model. The best model based on significant likelihood ratios was: Size-specific growth ~Water colour + Body size + Density + Water colour × Body size + Density × Body size (conditional $R^2 = 0.86$, marginal $R^2 = 0.80$). The intercept corresponds to YOY, low density and clear water colour. (***p < 0.001, **p < 0.01, *p < 0.05)

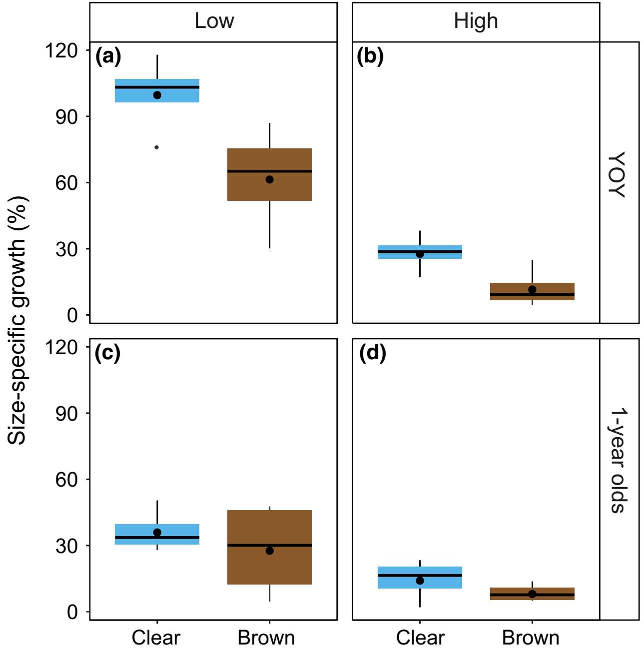

FIGURE 1 Size-specific growth rates (% wet weight) of young-of-the-year (YOY, top) and 1-year-old (bottom) roach individuals in clear (blue) and brown (brown) waters for low (left column) and high (right column) roach density. Large black dots are mean values and the box represents the median, and 25th and 75th quantiles, and whiskers represent the smallest observation greater than or equal to lower hinge −1.5 * IQR (interquartile range) and the largest observation less than or equal to upper hinge +1.5 * IQR. The small black dot is an outlier

3.1.2 | Zooplankton prey responses

Total zooplankton biomass was the same in all (water colour and density) treatments before fish were added (Table 2, Figure 2, pairwise comparisons $p > 0.05$ on day 1 and 9), but differed thereafter. After fish were added (day 16, 24 and 30), there was no overall difference in zooplankton biomass between water colour treatments on any day (Table 2, pairwise comparisons $p > 0.05$). On day 16 and 30, zooplankton biomass was lower in high than low roach density treatments (pairwise comparisons $p < 0.01$), meaning there was less prey available for roach in high-density treatments. This was true regardless of water colour treatment (pairwise comparisons $p > 0.05$). On day 24, the effect of water colour on zooplankton biomass differed depending on roach density. At low roach density, there was a higher zooplankton biomass in clear than brown waters (pairwise comparison $p = 0.0017$). In contrast, at high roach density there was a slightly higher zooplankton biomass in brown than clear waters (pairwise comparison $p = 0.0070$). In brown waters, roach density had no effect on total zooplankton biomass (pairwise comparison $p = 0.195$).

TABLE 2 Mixed ANOVA model of the effects of water colour (Clear/Brown), fish density (Low/High) and time (day 1, 9, 16, 24 and 30) on total zooplankton community biomass

Explanatory variables	F	p
Water colour	$F_{(1, 12)} = 0.36$	0.558
Fish density	$F_{(1, 12)} = 112.98$	$<0.001^{***}$
Water colour × Fish density	$F_{(1, 12)} = 6.44$	0.026^{*}
Time	$F_{(4, 48)} = 112.40$	$<0.001^{***}$
Water colour × Time	$F_{(4, 48)} = 0.21$	0.933
Fish density × Time	$F_{(4, 48)} = 24.08$	$<0.001^{***}$
Water colour × Fish density × Time	$F_{(4, 48)} = 6.44$	$<0.001^{***}$

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

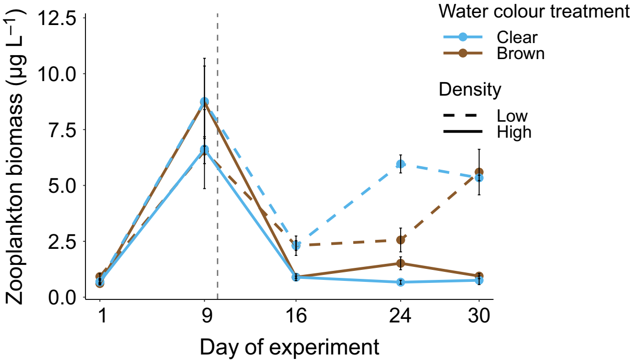

FIGURE 2 Zooplankton biomass. Total zooplankton community biomass during the experiment in the different water colour (Clear = blue, Brown = brown) and density (Low = dashed, High = solid) treatments (means ± SE over replicate mesocosms). Roach were added to the experiment on day 10 (vertical grey dashed line). For a figure including controls, see Figure S3 and for genus/group-specific biomasses, see Figure S4

In contrast to total zooplankton biomass, zooplankton community composition differed between the clear and brown treatment on day 9 of the experiment (day before fish were introduced, Figure 3a,b, PERMANOVA: $F_{(1,14)} = 11.39$, $p = 0.001$). Most notably, there was a higher proportion of *Polyphemus* sp. and a lower proportion of *Bosmina* sp. in the clear compared to the brown treatment. This difference in community composition between the clear and brown treatments disappeared within a week after fish addition (day 16, PERMANOVA: $F_{(1,12)} = 1.77$, $p = 0.149$), but there was a difference between the roach density treatments (Figure 3c,d, PERMANOVA: $F_{(1,12)} = 13.22$, $p = 0.001$). In the high-density treatment, there were mostly copepods left, while there were also *Polyphemus* sp. (in clear treatments) and *Bosmina* sp. left in the low-density treatment (Figure 3c,d). On day 24, there were mostly only copepods left regardless of treatment (Figure S5).

Chl *a* concentrations were higher in the brown than in the clear treatment on day 9, 16 and 30 of the experiment, but did not differ between colour treatments on day 1 and 24 (Table S2 and Figure S6). Chl *a* concentrations were not affected by fish density.

3.2 | Prey preference experiment

Overall zooplankton community composition after fish feeding differed between water colours (PERMANOVA: $F_{(1,8)} = 2.953$, $p = 0.048$)

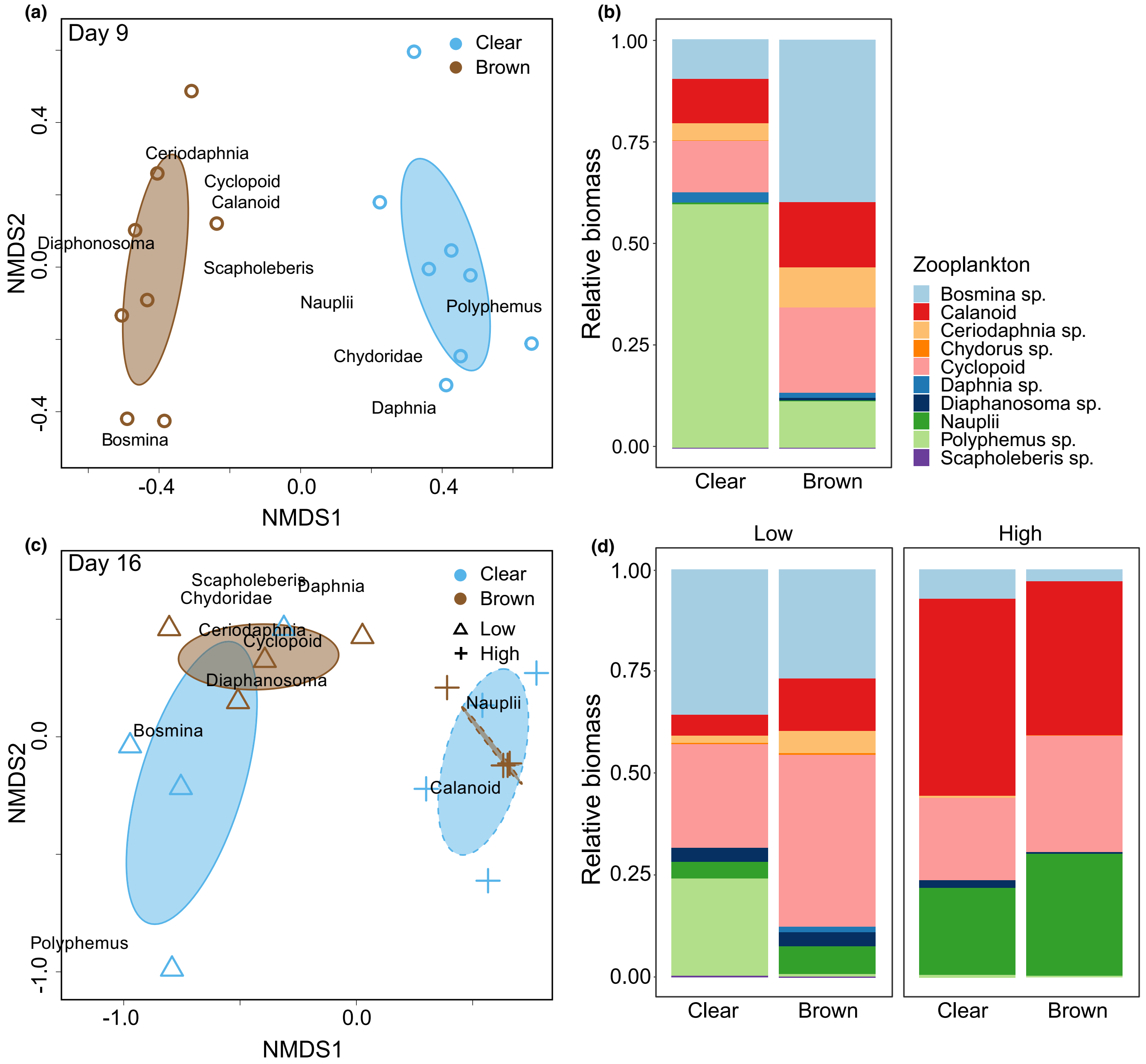

FIGURE 3 Zooplankton community composition. Zooplankton community composition in the different water colour and roach density treatments shown as nonmetric multidimensional scaling (NMDS) plots (in a and c) and relative biomasses (in b and d), before fish was added (day 9; in a and b) and six days after fish introduction (day 16; in c and d). In a) and c), coloured areas are ellipse areas of standard deviation per treatment (stress values 0.11 for both NMDS), solid lines represent the low-density treatment, and dashed lines the high-density treatment. For NMDS plots and community composition on day 1, 24 and 30, see Figure S5

and between sizes (PERMANOVA: $F_{(1,8)} = 7.715$, $p = 0.001$), which indicates differences in selectivity depending on water colour and between YOY and 1-year-old roach (but no interaction, Figure S7). There were some differences in selectivity between YOY and 1-year-olds for specific prey groups (Figure 4, Table S2). In the clear-water treatment, YOY fish had a positive selection for *Polyphemus* sp. and selected against nauplii (Figure 4, Table S2). In brown water, they had a positive selection for *Daphnia* sp. and *Ceriodaphnia* sp. and still selected against nauplii (Figure 4, Table S2). 1-year-old fish seemed less selective and only positively selected for *Ceriodaphnia* sp. in the brown treatment (Figure 4, Table S2). After feeding for three hours, the proportion of cyclopoids left in the clear treatment depended on roach body size (Figure 4, Table S3). There were marginally significant differences between YOY and 1-year-olds (but not between water colour treatments) in the proportion of *Bosmina* sp., *Polyphemus* sp., nauplii and *Ceriodaphnia* sp. after feeding (Figure 4, Table S3).

4 | DISCUSSION

Recent studies have shown that fish body growth and biomass production can be much lower in brown than in clear-water lakes (van

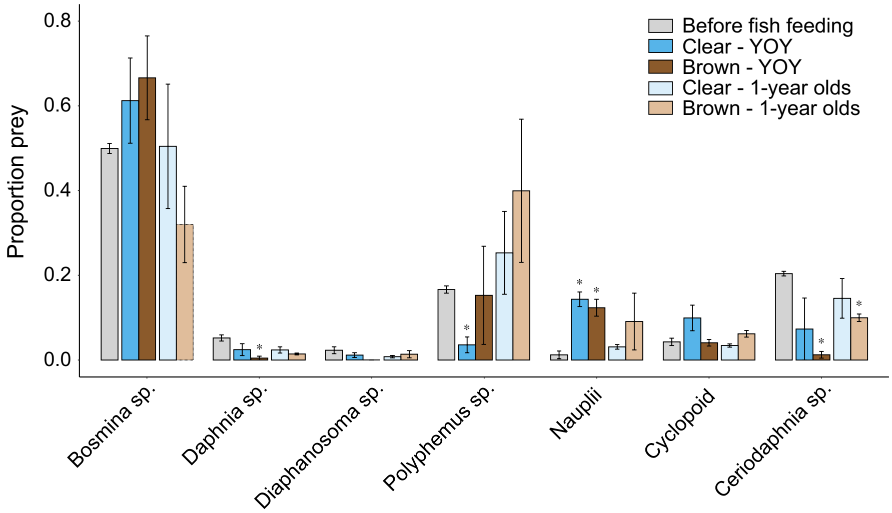

FIGURE 4 Proportions of prey from the prey selectivity experiment. Proportions of each zooplankton genus/group (mean ± SE) in the aquaria are shown for before fish feeding, and after feeding by young-of-the-year (YOY) and 1-year-old roach, in both clear and brown waters. Significant differences ($p < 0.05$) in proportion of a prey group after compared to before fish feeding are marked with *. If the mean proportion after feeding was higher than before fish feeding, we regarded this as selection against this prey group, if the mean proportion after feeding was lower than before fish addition, we regarded this as selection for this prey group, and if the mean proportion after and before feeding did not differ from each other, we regarded this as neutral selection for this prey group

Dorst et al., 2019; Karlsson et al., 2015). Observations across spatial gradients of water colour also suggest that fish growth responses to browning may vary over ontogeny (van Dorst et al., 2019), but this has not been tested experimentally, and potential mechanisms have therefore been unknown. Here, we experimentally show that body growth responses of roach to browning-induced light limitation differ over early ontogeny. Browning decreased body growth of YOY, but not of larger 1-year-old roach. We also show that this divergent effect of browning is likely a result of browning-induced changes in zooplankton prey community composition combined with differences in zooplankton prey selectivity over ontogeny.

Our finding of ontogenetic (size-specific) differences in body growth responses to browning of roach differs from previous studies, which report no effect of browning on roach body growth (van Dorst et al., 2020; Estlander et al., 2010). However, neither of the earlier studies included roach smaller than 40 mm. This suggests that only small YOY roach are affected by browning. Interestingly, the opposite pattern was found in another fish species (perch) in comparative lake studies, with a larger negative effect of brown water on body growth of large than of small fish (van Dorst et al., 2019, 2020). These different responses could result from the greater shift in diet over ontogeny in perch than in roach, as perch shift from feeding on zooplankton to benthic invertebrates to fish (Eklöv & Persson, 1995; Hjelm et al., 2000), whereas roach do not have such distinct shifts (Horppila, 1994; Persson, 1983). Benthic invertebrates and fish biomass (Karlsson et al., 2009; Vasconcelos et al., 2018) and also feeding on these prey (Jönsson et al., 2013; Ranåker et al., 2012) may be more negatively affected by browning than zooplankton biomass (van Dorst et al., 2020; Kelly et al., 2016) and feeding on zooplankton (Jönsson et al., 2012; Weidel et al., 2017). This shows that the extent and direction of size-dependent body growth responses to browning can vary depending on species identity and potentially shifts in diet use over ontogeny.

The difference in body growth responses to browning between YOY and 1-year-olds may be a consequence of the altered zooplankton community composition following browning, in combination with a difference in prey selectivity between YOY and 1-year-olds. In the mesocosm experiment, the most notable difference in zooplankton composition before fish addition was the much lower proportion of *Polyphemus* sp. in the brown treatment. *Polyphemus* sp. is a visual predator attracted by light and has lower feeding rates in dark conditions (Haney & Mattson, 1980; Packard, 2001). The brown, light-limited treatment likely impaired the feeding of *Polyphemus* sp., which could explain its lower abundance in this treatment. Whereas YOY roach had a positive selection for *Polyphemus* sp. in clear waters in the prey selectivity experiment, 1-year-old roach did not select for *Polyphemus* sp. in either clear or brown waters (although the difference between treatments with YOY and 1-year-olds in the proportion of *Polyphemus* sp. after feeding was only marginally significant). YOY roach are therefore more likely than 1-year-olds to be affected by the browning-induced reduction in availability of *Polyphemus* sp. Thus, the potential difference in preference for *Polyphemus* sp. combined with the lower proportion of *Polyphemus* sp. in brown waters could be a reason why YOY but not 1-year-old roach body growth was negatively affected by browning in our experiment. Although it is unknown (to the best of our knowledge) whether similar changes in community composition happen with browning in natural lakes, a similar negative response of *Polyphemus* sp. to browning was found in a previous mesocosm experiment (van Dorst et al., 2020). In addition to shifts in prey composition, the fact that body growth responses to browning vary with body size might be a consequence of a size-specific decrease in feeding rates (irrespective of prey availability) in brown waters. As eyesight in fish improves with body size (Miller et al., 1993), likely due to larger eyes and pupils (Caves et al., 2017), it could be speculated that the larger fish can better maintain high feeding rates in low light conditions. However, whereas this may be the case for some fish species, previous experimental studies showed that feeding rates of neither smaller (Jönsson et al., 2012) nor intermediately sized (van Dorst et al., 2020) roach were affected by browning. Thus, we argue that a combination of browning-induced changes in community composition and ontogenetic differences in prey selectivity, rather than size-specific feeding rate responses, is the likely cause of the size-specific growth response of roach to browning in our experiment.

Browning did not reduce total zooplankton biomass, but high roach densities did. Accordingly, body growth of both YOY and 1-year-olds was lower at high roach densities. As larger fish have greater demands for resources to sustain high growth rates (e.g. Hjelm & Persson, 2001), we hypothesised that larger roach would be more negatively affected by browning at high roach densities and low resource levels. Still, the difference in body growth responses to browning between YOY and 1-year-old roach did not change with roach density. Rather, we found an additive negative effect of browning and density, suggesting that body growth of YOY roach will be very low in brown lakes with intense resource competition. The finding that the decreased growth of YOY (but not 1-year-olds) in brown waters was not further affected by roach density, strengthens our hypothesis that prey community composition, and not only overall prey biomass, shape roach body growth responses to browning.

Next to potential differences in prey selectivity between YOY and 1-year-old (regardless of water colour), we found an overall difference in zooplankton community composition between clear and brown waters after fish feeding (regardless of body size) in the prey selectivity experiment. This indicates an effect of water colour on roach prey selectivity, which can potentially alter zooplankton communities in lakes. Differences in selectivity for certain zooplankton prey items between clear and brown (high DOC) waters were also found in studies with perch (Chaguaceda, 2020; Estlander et al., 2010), where they speculated that these were a consequence of differences in pigmentation between zooplankton groups, which could affect their visibility to fish differently in clear and brown waters. Accordingly, Jönsson et al. (2011) showed that highly pigmented copepods were selected for in clear waters, while transparent copepods were selected for in brown waters. This differential feeding in brown waters may affect zooplankton communities in lakes where planktivorous fish such as roach have strong structuring effects through selective feeding (Brooks & Dodson, 1965; Lazzaro, 1987), which can also have consequences for competing fish species.

Although we show that small YOY roach can be negatively affected by browning, this negative effect does not seem to carry over and reduce size at older age in natural populations (van Dorst et al., 2020). There may be a couple of reasons for this. First, strong year classes of YOY roach usually suppress zooplankton biomass and alter zooplankton size and species composition (Cryer et al., 1986; Mehner & Thiel, 1999), which decreases resource availability for older fish in the population as well as for other species (Persson & De Roos, 2012). Browning and the potential for associated changes in YOY roach prey selectivity could weaken control of certain zooplankton prey by YOY roach. If those zooplankton prey species constitute important prey for larger/older roach, this could be a potential contributing factor for the lack of negative effects of browning found on size at older age in natural systems. Moreover, reduced juvenile growth rates increase the time period during which fish are vulnerable to predators (Post & Prankevicius, 1987), which could reduce population biomass and competition among adults, thereby mitigating the negative effects of browning on YOY and preventing reduced size at age of older roach in natural populations. However, feeding by these predators is likely negatively affected by browning as well (Jönsson et al., 2012; Ranåker et al., 2012), possibly also influencing the effect of browning on roach in natural waters. Another reason for why the decreased growth rates of YOY roach in our experiment are not visible at older age of roach sampled along natural water colour gradients (as in the study by van Dorst et al., 2020) could be that roach populations can develop local adaptations to cope with natural variation in water colour. Another cause for different findings on fish in natural systems could be our experimental set-up. Although we inoculated our mesocosms with natural zooplankton assemblages, natural lake food webs are more complex and responses of zooplankton communities in lakes to browning may thus differ from what we show experimentally, which could alter fish responses to browning. Our experimental results highlight the need to further study the potential for variable responses to browning over ontogeny in fish, including responses of the very smallest fish individuals, at a larger spatial scale and over a longer time.

In summary, our findings illuminate how browning affects zooplanktivorous fish and the interactions with their zooplankton prey. We experimentally show that the effect of browning-induced light limitation on roach body growth differs over early ontogeny, and that this is likely due to a combination of browning-induced shifts in zooplankton prey community composition and size-specific differences in prey selectivity. We therefore argue that it is important to monitor fish growth responses over ontogeny as well as changes in prey composition when assessing browning impacts on lake ecosystems. Quantifying how browning effects vary with ontogeny is especially important as such responses may influence competitive and predator–prey interactions, population size structure and thus entire lake ecosystems.

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CONFLICT OF INTEREST

There is no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data used for this manuscript are openly available on Zenodo at: 10.5281/zenodo.4603020.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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