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The effects of eutrophication and browning on prey availability and body growth of the three-spined stickleback (*Gasterosteus aculeatus*)

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ABSTRACT

Shallow coastal areas often have high productivity and diversity, in part due to the high availability of light and nutrients. At the same time, they are exposed to multiple environmental pressures, such as browning and eutrophication. Browning is mainly caused by runoff bringing coloured dissolved organic matter (CDOM), reducing light availability in waters, whereas eutrophication is caused by high nutrient loading, leading to eutrophication symptoms such as algal blooms. Existing variation and further change in light and nutrients of coastal areas could have large implications for aquatic food webs, including fish. For instance, reduced light might alter food availability and reduce foraging abilities, whereas increased nutrient supply might, depending on the extent, increase food availability. In this study, we performed a mesocosm experiment, including benthic and pelagic communities, together with young-of-the-year three-spined stickleback (*Gasterosteus aculeatus*) as predators. The three-spined stickleback is not only a common model organism but also an increasingly common and important mesopredator in the Baltic Sea. We examined the extent to which browning and nutrient-enrichment, alone and in combination, influenced the density, biomass, and composition of stickleback prey, and diet choice, body growth and condition of the stickleback. Stickleback body growth was positively affected by nutrient-enrichment, probably because of a positive bottom-up effect with increased primary production, as evident in the much higher chlorophyll-*a* concentrations in the pelagic habitat, and increased food availability. In contrast, there was a marginal negative effect of browning on stickleback body growth and condition, most likely due to negative effects of reduced visibility on feeding rates. We also found that prey availability increased with nutrient-enrichment but not with browning. Interestingly, nutrient-enrichment counteracted the negative effects of browning when combined. Our findings add novel understandings about the potential for both eutrophication and browning to affect coastal food webs and fish body growth in the Baltic Sea.

1. Introduction

Shallow coastal waters are commonly highly productive and diverse ecosystems (Ray, 1991; Raffaelli et al., 2003; Waycott et al., 2009; Cesbron et al., 2019), partly related to the high supply of light and nutrients to benthic habitats, enabling the growth of habitat-forming primary producers (Lefébure et al., 2013; Jäger and Diehl, 2014; Ask et al., 2016; Östman et al., 2016; Cesbron et al., 2019; Kritzberg et al., 2020). Consequently, many fishes thrive in these environments because of shelter and an abundance of both benthic and pelagic invertebrate prey (Raffaelli et al., 2003; Bergström et al., 2015; Kritzer et al., 2016; Östman et al., 2016). However, anthropogenic activities can dramatically alter the availability of light and nutrients, with implications for the structure and function of coastal food webs (Evans et al., 2006; Andersson et al., 2015; Mustaffa et al., 2020).

Light availability in shallow coastal waters is influenced by the inputs of coloured dissolved organic matter (CDOM). Land-use change (e.g. forestry), climate change (e.g. increased precipitation and runoff), and reduced acid deposition has increased concentrations of CDOM in some areas, leading to browning of waters (Evans et al., 2006; de Wit et al., 2016; Kritzberg et al., 2020). Browning can influence both the productivity and composition of aquatic food webs (Solomon et al., 2015; Kritzberg et al., 2020; van Dorst et al., 2020). For instance, browning can reduce benthic primary production, which commonly leads to a lower food web and fish productivity (Ask et al., 2009; Benoît et al., 2016; Leech et al., 2020). Although some studies have found that not all fish are affected (Jönsson et al., 2012; Weidel et al., 2017; Leech et al., 2020), many fish might also be negatively affected by browning

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through impaired visual conditions, reducing foraging rates (Ranåker et al., 2014; Leech et al., 2020; van Dorst et al., 2020). Most studies on the causes and consequences of browning are from freshwater ecosystems (Flöder et al., 2006; Ask et al., 2009; Karlsson et al., 2009; Solomon et al., 2015; Kritzberg et al., 2020). However, increased input of CDOM has also been observed in coastal ecosystems (Wikner and Andersson, 2012; Herrmann et al., 2015; Svedäng et al., 2018) and variation in CDOM concentrations, in turn, contributes to variation in water transparency among coastal areas of the Baltic Sea (Harvey et al., 2019). The lack of knowledge concerning the impacts of browning on coastal ecosystems and fish is problematic, specifically given that climate change and an associated increase in precipitation may lead to increased runoff and further browning.

In contrast to browning, nutrient-enrichment can promote primary productivity (Schindler, 1977; Burkholder and Glibert, 2013), but high concentrations cause eutrophication and shading by triggering excess algal growth (Meyercordt and Meyer-Reil, 1999; Flöder et al., 2006; Smith and Schindler, 2009; Heiskanen et al., 2019). Early stages of eutrophication have in many cases been found to benefit fish due to increased prey availability (e.g. more zooplankton prey due to an increased biomass of phytoplankton; (Burkholder and Glibert, 2013). Severe eutrophication, however, can result in blooms of inedible algae (Smith and Schindler, 2009) and eventually hypoxia, reducing benthic secondary production (Steckbauer et al., 2011) and fish egg survival (Nordheim et al., 2020). Despite extensive research on eutrophication in coastal ecosystems, we know little about the combined effects of eutrophication and browning, especially concerning fish performance.

In the Baltic Sea region, future climate change is predicted to increase precipitation and runoff, bringing more CDOM and nutrients to lakes and coastal areas, resulting in darker and more eutrophic waters or slowing down the rate of the ongoing recovery from eutrophication (Meyercordt and Meyer-Reil, 1999; Faithfull et al., 2011; Wikner and Andersson, 2012; Andersson et al., 2015; Blenckner et al., 2015; Andersen et al., 2017). Such changes in browning and nutrient concentrations might, through bottom-up processes, result in altered fish production (Karlsson et al., 2009; Burkholder and Glibert, 2013; Benoît et al., 2016). As intensified land use and climate warming are threatening coastal ecosystems in general (Harley et al., 2006), and the Baltic Sea's coasts specifically (Andersson et al., 2015), it is key to better understand and disentangle the combined impact of browning and eutrophication on coastal food webs and fish performance.

Here, we ask how browning and nutrient-enrichment in shallow coastal ecosystems affect benthic and pelagic invertebrate communities, and how those changes affect mesopredatory fish which, similar to most small-bodied coastal fish species, commonly feed on both pelagic and benthic prey species (but often more on the latter; Gill and Hart, 1994; Hempson et al., 2017; Jacobson et al., 2019). We specifically hypothesise nutrient-enrichment and browning to have positive and negative effects, respectively, on fish body growth and condition due to shifts in invertebrate prey availability. To test this, we performed a mesocosm experiment, including both benthic and pelagic habitats, with prey organisms from the Baltic Sea archipelago and using the three-spined stickleback (*Gasterosteus aculeatus*, hereafter referred to as stickleback) as a focal species. In doing so, we examined the extent to which browning and nutrient-enrichment influence prey biomass and composition, and the subsequent effects on stickleback diet choice and body growth.

2. Material and methods

2.1. *Study site and species*

This study was conducted in August–September 2020 in Forsmark, Sweden (60°24′12″N 18°10′0″E), next to a coastal area of the Baltic Sea. The brackish semi-enclosed Baltic Sea is threatened not only by climate change, but also by overfishing, runoff, pollution, and eutrophication (Korpinen et al., 2012; Andersson et al., 2015). In many areas of the Baltic Sea, seasonal eutrophication episodes have increased since the 1950s following the increased use of fertilizers, concurrent with expansions in agriculture and meat production (Österblom et al., 2007; Andersen et al., 2017; Heiskanen et al., 2019). At the same time, there have been substantial changes to the Baltic Sea fish community, notable ones being the collapse of the eastern Baltic Sea cod (*Gadus morhua*) population in the early 1990s (Casini et al., 2008; Eero et al., 2015) and a shift from predator to prey fish dominance in some coastal areas, with observations suggesting that sticklebacks have increased substantially (Olsson et al., 2019; Eklöf et al., 2020).

The stickleback is an abundant and generalist mesopredator that occurs across the northern hemisphere and is often used as a model organism in ecological and evolutionary research (Schluter and McPhail, 1992; Gibson, 2005; Moran et al., 2010; Lavin and McPhail, 2011). In the Baltic Sea, they spend most of their adult life in the open sea, but use shallow coastal areas for spawning and as a nursery (Bergström et al., 2015; Olsson et al., 2019). Often being generalist, but sometimes specialist, feeders (Schluter and McPhail, 1992), sticklebacks feed on a range of benthic and pelagic prey items, including zooplankton and zoobenthos as well as fish eggs and larvae (Gill and Hart, 1994; Jakobsen et al., 2003; Nilsson et al., 2019; Olsson et al., 2019).

2.2. *Experimental design*

In order to assess the mechanisms by which eutrophication and light limitation alone and in combination might affect body growth, condition, and diet choice of sticklebacks, we performed an experiment with young-of-the-year (YOY) sticklebacks and their prey organisms using 12 outdoor mesocosms (tanks). Mesocosms were free-standing, 0.68 m diameter x 1.11 m deep cylindrical soft plastic tanks filled with 350 L of seawater from the adjacent waters of Forsmark (Fig. 1b). The experiment consisted of two phases. During the first phase, we induced eutrophication and browning without fish present to allow for the pelagic and benthic communities of algae and invertebrates to establish and respond to treatments without fish present (Fig. 1a). This first phase had a duration of three weeks, allowing for several generations of algal species (Irwin et al., 2015) and for some zooplankton taxa a few generations (Gillooly, 2000) to develop. During the second phase, we added fish to study subsequent effects on fish diet choice and body growth (Fig. 1a). This second phase had a duration of two weeks, allowing for sufficient time to observe a body growth response in sticklebacks, but not too long to avoid fish to deplete all of their food and starve.

We implemented a 2 × 2 full factorial design with four treatments: browning only ($n = 3$), nutrient-enrichment only ($n = 3$), a combination of browning and nutrient-enrichment ($n = 3$), and a control exhibiting no browning or nutrient-enrichment ($n = 3$; Fig. 1). To simulate browning, we added 80 ml of Sera Blackwater Aquatan water conditioner (Sera GmbH, Heinsberg, Germany) to each of the 6 mesocosms on day 1. Sera Blackwater Aquatan has been found to mimic brown waters without considerably increasing concentrations of organic carbon and nutrients, allowing us to mainly see the effect of light limitation (Total Nitrogen: 79 μg N.L^{-1}, Total Phosphorus: 4.75 μg P.L^{-1}, Total Organic Carbon: 2.7 mg C.L^{-1}). To top up what had been removed by sampling water, 8 ml of Sera Blackwater Aquatan was added to each mesocosm on day 12. See below in "*Sampling protocol*" on how we estimated the degree of light limitation by calculating light attenuation coefficients from measurements of photosynthetically active radiation. To induce eutrophication symptoms, similar to what has been observed in the Baltic Sea (HELCOM, 2018), 108 μmol nitrogen L^{-1} (i.e. 1500 μg N L^{-1}, with NH_4NO_3) and 6.8 μmol phosphorus L^{-1} (i.e. 211 μg P L^{-1}, with KH_2PO_4) were added in total to each of the 6 mesocosms (of which 3 were browned). The nutrients were added as a large pulse on day one (60 μmol N L^{-1} and 3.8 μmol P L^{-1}) and then, until fish addition, eight times as small pulses (6 μmol N L^{-1} and 0.38 μmol P L^{-1} each pulse) together with water to replace the sampled water (described below).

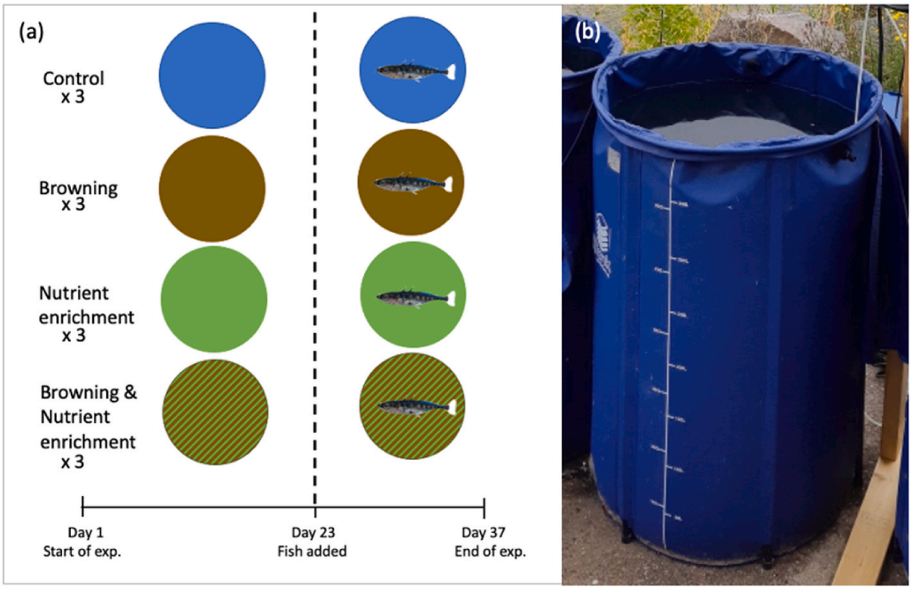

Fig. 1. (a) Mesocosm experimental set-up with three mesocosms for each treatment (total n = 12) and four fish in each (total n = 48). Before fish were added on day 23 there was an initiation phase to allow for the communities of algae and invertebrates to establish and respond to browning and nutrient-enrichment. Sampling was done on day 1, 20, 30, and 37. (b) Photo of one of the mesocosms.

Zooplankton were collected from the adjacent sea using 20-μm and 70-μm mesh nets, and then combined into a single container with seawater. Equal amounts of the seawater containing zooplankton were then distributed to each mesocosm. The mean ± SE density of zooplankton in each mesocosm was 0.020 ± 0.003 mg L^{-1}. To create a natural benthic environment, we filled the mesocosms with a 4 cm layer of sand covered by a 3 cm layer of coastal sediment collected in the nearby area, including naturally occurring microalgae and benthic invertebrates.

We collected YOY sticklebacks from the nearby shoreline using hand nets at ca 0.5 m depth. Once caught, we transferred the fish to the experimental site where they were length-measured and placed into separate containers for several hours to minimize and standardize any impact of handling. Similar to densities which have been found in some coastal areas of the Baltic Sea (Byström et al., 2015) and elsewhere (Rybkina et al., 2017), four individuals of similar size (mean ± SE standard length 1.90 ± 0.05 cm) were then placed into each mesocosm, rendering a total of 48 fish used in the experiment. There was no initial treatment difference in fish length (Generalized linear mixed-effects model: Browning (B) $z = 0.42$, $p = 0.676$, Nutrient-enrichment (N) $z = 0.279$, $p = 0.780$, B:N $z = -0328$, $p = 0.743$). Besides the fish used in the experiment, ten additional YOY sticklebacks (mean ± SE standard length 1.83 ± 0.06 cm) were caught and analysed to enable us to compare the diet composition of the fish in the wild to those used in the experiment.

2.3. Sampling protocol

At the end of the experiment, 43 out of 48 fish were found and caught with a net and then immediately euthanised in a benzocaine solution and stored at −20 °C. The five remaining fish were found, or assumed, dead, of which two were from a brown water mesocosm and three from a mesocosm of each remaining treatment (nutrient-enriched, browned and nutrient-enriched, and control), respectively. We sampled pelagic chlorophyll-*a* (chl-*a*) and zooplankton on day 1, 20 (before fish addition), 30, and 37 (after fish addition). After gently stirring the upper layer of the water, pelagic chl-*a* and zooplankton were collected using a 600 ml Ruttner water sampler at 0.4 m depth (i.e. from the middle of the water column) from three different positions of each mesocosm and then combined as one sample. Each sample was filtered through a 70-μm mesh net and zooplankton were preserved in Lugol's solution. 500 ml of the water was filtered through 47-mm G/F microfiber filters, which were stored frozen until being analysed. The chl-*a* content was extracted with 10 ml of 96% ethanol and the fluorescence was measured in darkness with a spectrofluorometer (LS 30 PerkinElmer, Waltham, MA, USA) at Umeå Marine Sciences Centre.

To compare benthic chl-*a* concentrations between treatments, we sampled small cores of sediment on day 2 and 21 (before fish addition) and 37 (after fish addition). We did this using a 20 ml syringe, with the plain tip removed, attached to a PVC tube enabling us to reach the bottom. The water was removed from the sediment samples before storing them at −20 °C. The sediment was later dry-frozen for 24 h. Thirty millilitres of 96% ethanol was added to 3 g of dry sediment, kept for 12 h in the dark for the chlorophyll extraction, and analysed as above.

To estimate the biomass of benthic macroinvertebrates, we took benthic core samples (6.6 cm diameter) on day 20 (before fish addition) and 37 (after fish addition). We sampled three different positions of each mesocosm, combined the samples, filtered them through a net with 500 μm mesh size, hand-picked all visible organisms, and preserved them in ethanol.

We measured temperature and photosynthetically active radiation (PAR; Figs. S1 and S2) on day 1, 20, 30, and 37. Temperature was measured at the same depth, 0.4 m, as the chl-*a* and zooplankton water samples. PAR was measured at 0.1, 0.4, and 0.65 m depth using a LI-250A light meter with a LI-193SA spherical underwater quantum sensor (LI-COR Biosciences-Biotechnology, Lincoln, NE, USA). The light attenuation coefficient (K_z, m^{-1}) was calculated from PAR measurements as

$$K_z = \ln\left(\frac{PAR_0}{PAR_z}\right) \Big/ z$$

Where PAR_0 is PAR at the surface and PAR_z is PAR at depth z (m). Browning caused a higher light attenuation coefficient (i.e. less light penetration) (Mixed ANOVA: $F_{(1,8)} = 185.01$, $p = <0.0001$), whereas there was only marginally higher light attenuation coefficient with nutrient-enrichment (Mixed ANOVA: $F_{(1,8)} = 5.01$, $p = 0.056$; Fig. S1). There was no interaction effect (Mixed ANOVA: $F_{(1,8)} = 0.06$, $p = 0.811$) or difference over time (Mixed ANOVA: $F_{(1,12)} = 1.88 = p = 0.199$;

Fig. S1). Neither browning (GLMM: $t = 1.55$, $p = 0.121$) nor nutrient-enrichment (GLMM: $t = 1.51$, $p = 0.132$) affected temperature. However, there was a very minor but statistically significant interaction effect (GLMM: $t = -2.145$, $p = 0.032$) and temperature decreased over time in all treatments (GLMM $t = -9.82$, $p < 0.0001$; Fig. S2).

2.4. Laboratory analyses

During the week following the end of the experiment (when fish were euthanised and frozen), the fish were thawed and dabbed dry, then measured and weighed to the nearest mm and 0.01 g in the laboratory. Fulton's condition factor (*K*, also referred to as body condition) was calculated using the formula:

$$K = \frac{100 \times weight\ (g)}{length\ (cm)^3}$$

Next, we removed stomachs to analyse their diet. Zooplankton and zoobenthos found in the water samples, benthic cores, and stomachs, were counted, identified, and measured to the nearest 0.01 mm using a stereomicroscope. We identified cladocerans and rotifers to genus level, whilst copepods were identified as either cyclopoid, calanoid, or nauplii. Benthic invertebrates, of which most were chironomid larvae, were identified to genus level. We measured lengths of up to 15 individuals (all, if fewer were found) of each taxon/group per sample and converted lengths to dry mass using taxa-specific length-weight regressions (Dumont et al., 1975; Bottrell et al., 1976; Méthot et al., 2012).

The experiment was carried out in accordance with national guidelines for animal care and approved by the regional ethical review board in Uppsala, Sweden (5.2.18–4771/17).

2.5. Statistical analyses

All statistical analyses were done using the statistical software *R* version 3.6.1 (R Core Team, 2019). Mesocosms with less than two fish left at the end of the experiment were excluded from the main analyses (one of the browned-only replicates removed). This was done due to the high likelihood for much less competition for food in this mesocosm, making results from this replicate difficult to compare to the other ones. However, the results from the analyses including all mesocosms can be found in the supplements (Tables S3 and S4). Normality was assessed using Q-Q plots and Shapiro-Wilks tests. We analysed treatment effects (browning and nutrient-enrichment) on fish length, weight, and body condition (response variables) with a two-way mixed-design analysis of variance (mixed ANOVA) using the *afex* package (Singmann et al., 2021). Mesocosms were treated as random variables, rending the following statistical model:

response variable ~ browning × nutrient enrichment + mesocosm.

When there was a significant main or interactive effect, we performed follow-up pairwise comparison tests with Tukey adjustments using the *emmeans* package (Lenth et al., 2021). We also analysed treatment effects over time on chl-*a* concentration, and chironomid larvae and zooplankton biomass (total, copepod and rotifer) using a three-way mixed ANOVA:

response variable ~ browning × nutrient-enrichment × day + (day (mesocosm)).

As there were few, if any, cladocerans left after fish addition, we only analysed them on day 20 (as above but removing 'day'). Benthic chl-*a* concentration before (days 2 and 21) and after (day 37) fish addition were analysed separately as sand was found in the benthic cores on the last date, diluting the samples.

To statistically test if there were differences in community and diet composition between treatments for zooplankton, we performed a permutational multivariate analysis of variance (PERMANOVA) using the *adonis* function in the *vegan* package (Oksanen et al., 2020), with 999 permutations and low stress scores (<0.2). Taxa/groups were square-root transformed to reduce the weight of highly abundant species. The PERMANOVA was based on distance matrices of zooplankton taxa/group biomasses and diet taxa/group biomasses and counts using the Bray-Curtis dissimilarity index. Zooplankton community composition was analysed both over time, including day as a third independent variable, and separately on day 20 (before fish addition), and day 30 and 37 (after fish addition). When there was a significant main or interactive effect, we performed follow-up pairwise comparisons using the *pairwise adonis* function.

3. Results

3.1. Fish body growth and condition

There was a marginal significant negative effect of browning on stickleback body condition, but only when no nutrients were added (Fig. 2a; Table 1 and Table S3). Nutrient-enrichment increased stickleback body length (mean ± SE 2.48 ± 0.05 cm) and weight (mean ± SE 0.18 ± 0.01 g), while there was a trend of decreased stickleback body size with browning (mean ± SE standard length: 2.22 ± 0.08 cm, wet weight: 0.11 ± 0.01 g) compared to the control (mean ± SE standard length: 2.31 ± 0.06 cm, wet weight: 0.14 ± 0.01 g; Fig. 2b–c; Table 1 and Table S3). Thus, there was a tendency for nutrient-enrichment and browning to exhibit antagonistic effects on body size and condition, with the negative effect of browning being counteracted by the positive effect of nutrient-enrichment (Combined browning and nutrient-enrichment: mean ± SE standard length: 2.44 ± 0.05 cm, wet weight: 0.16 ± 0.01 g Fig. 2; Table 2).

3.2. Diet

Pelagic zooplankton were the numerically most common prey in the diet of sticklebacks (Fig. 3; but see Fig. S4a for proportions based on biomass). Nutrient-enrichment led to a more diverse taxonomic composition (Fig. 3; PERMANOVA $F_{(1)} = 2.21$, $P = 0.040$). *Keratella* sp. tended to dominate with browning-only (97%), whereas *Chydorus* sp. (38%), adult copepods (21%), nauplii (11%), and chironomid larvae (15%) were all common with nutrient enrichment (Fig. 3). In addition to some amphipods in the diet of wild-caught YOY sticklebacks, the diet composition of the fish in the control was similar to what was found in fish in the wild (Fig. 3 and Fig. S5).

3.3. Invertebrates

The number of chironomid larvae was positively affected by nutrient-enrichment, but decreased in this treatment after fish addition (Fig. 4; Table 2). Before fish addition (day 20) nutrient-enrichment had a positive effect on total zooplankton biomass (Fig. 5a; Table 2) and copepod biomass (Fig. 5b; Table 2). Total zooplankton, copepod, cladoceran, but not rotifer biomass, decreased after fish addition (Fig. 5a–d; Table 2). There was no treatment or time effect on rotifer biomass, albeit a tendency towards lower biomass in the treatment with browning and nutrient-enrichment combined (Fig. 5d; Table 2).

The zooplankton community composition changed over time in all treatments (PERMANOVA: $F_{(2)} = 11.29$, $P = 0.001$), from communities dominated by large copepods and cladocerans, to relatively more small zooplankton, such as rotifers and nauplii (Fig. 6; Fig. S6). Nutrient-enrichment had a significant effect on community composition, likely related to the higher number of zooplankton taxa present with nutrient-enrichment (Fig. 6; PERMANOVA: Day 20, $F_{(1)} = 7.18$, $P = 0.003$; Day 30, $F_{(1)} = 5.05$, $P = 0.017$; Day 37, $F_{(1)} = 4.04$, $P = 0.015$). At the end of the experiment (day 37) the browning only treatment was dominated by small zooplankton, such as *Keratella* sp. and nauplii, whilst the nutrient-enriched treatments, exhibited relatively fewer *Keratella* sp. and instead more adult copepods and nauplii (Fig. 6).

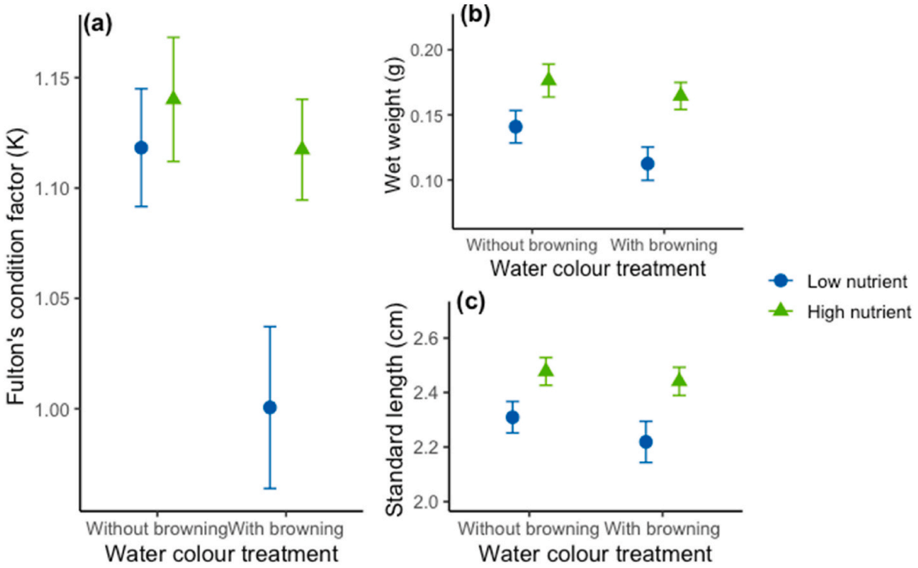

Fig. 2. (a) Fulton's condition factor, (b) wet weight, and (c) standard length of stickleback at the end of the experiment with or without browning and nutrient-enrichment. Points are estimated means (±SE).

Table 1
Mixed ANOVAs for Fulton's body condition, wet weight and standard length. B = Browning, N = Nutrient enrichment. ($p < 0.0001$ "***", $p < 0.001$ "**", $p < 0.05$ "*", $p < 0.1$ "·").

Variable	Parameter	*F*-value	*P*-value
Body condition			
	B	$4.29_{(1,7)}$	0.0770 ·
	N	$3.98_{(1,7)}$	0.0863 ·
	B:N	$1.39_{(1,7)}$	0.2763
Weight			
	B	$4.99_{(1,7)}$	0.0606 ·
	N	$22.25_{(1,7)}$	0.0022 ***
	B:N	$0.55_{(1,7)}$	0.4806
Length			
	B	$4.08_{(1,7)}$	0.0830 ·
	N	$37.02_{(1,7)}$	0.0005 ***
	B:N	$0.61_{(1,7)}$	0.4606

3.4. Chlorophyll-a

Nutrient-enrichment, with and without browning, had a substantial positive effect on pelagic chl-*a* concentrations, while browning alone had a marginally positive effect (Fig. 7a; Table 2). There was no effect of time on pelagic chl-*a* concentration before (day 20) or after (day 37) fish addition in any of the treatments (Fig. 7a; Table 2).

Before fish addition, browning had a negative effect whilst nutrient-enrichment had a positive effect on benthic chl-*a* concentrations (Fig. 7b; Mixed ANOVA Day 21; Browning: $F_{(1,31)} = 0.206$, $P = 0.008$; Nutrient-enrichment $F_{(1,31)} = 0.123$, $P = 0.046$). When browning and nutrient-enrichment were combined, benthic chl-*a* was not affected (Fig. 7b; Mixed ANOVA Day 21: $F_{(1,31)} = 0.003$, $P = 0.760$). After fish addition, treatment differences disappeared (Fig. 7b; Mixed ANOVA; Browning: $F_{(1,8)} = 0.164$ $P = 0.246$; Nutrient-enrichment: $F_{(1,8)} = 0.232$ $P = 0.643$; Combined: $F_{(1,8)} = 0.539$ $P = 0.484$). The samples were not compared between dates as some were unintentionally diluted on the last date.

4. Discussion

Nutrient-enrichment increased stickleback body growth irrespective of water colour. Browning instead tended to reduce body condition and had a slight negative effect on body growth, unless nutrients were added. These differences can largely be explained by prey responses to browning and nutrient-enrichment. Large-bodied zooplankton and chironomid larvae were common both in the mesocosms and in the diet in nutrient-enriched treatments, whereas stickleback stomachs mainly contained rotifers at the end of the experiment in browning-only treatments. These findings support previous studies on how eutrophication (Jamet and Desmolles, 1994; Moran et al., 2010; Hayden et al., 2019) and browning (Hayden et al., 2019; Leech et al., 2020; van Dorst et al.,

Table 2
Mixed ANOVAs for day 20 and 37 for pelagic chlorophyll *a* and chironomid larvae, day 20, 30, and 37 for total zooplankton, copepod, and rotifer biomass, but only day 20 for cladocerans due to zero individuals at later dates. B = browning, N = nutrient-enrichment. ($p < 0.0001$ "***", $p < 0.001$ "**", $p < 0.05$ "*", $p < 0.1$ "·").

Variable	Parameter	*F*-value	*P*-value
Pelagic chlorophyll a			
	B	$6.66_{(1,7)}$	0.0364 *
	N	$146.64_{(1,7)}$	<0.0001 ***
	B:N	$0.34_{(1,7)}$	0.3373
	Day	$0.92_{(1,7)}$	0.9156
Chironomid larvae			
	B	$0.74_{(1,7)}$	0.4182
	N	$5.15_{(1,7)}$	0.0575 ·
	B:N	$0.59_{(1,7)}$	0.4681
	Day	$7.24_{(1,7)}$	0.0311 *
Total Zooplankton			
	B	$0.34_{(1,7)}$	0.5772
	N	$15.98_{(1,7)}$	0.0052 **
	B:N	$4.68_{(1,7)}$	0.0672 ·
	Day	$33.21_{(1,10)}$	<0.0001 ***
Copepod			
	B	$0.01_{(1,7)}$	0.9391
	N	$11.34_{(1,7)}$	0.0119 *
	B:N	$0.93_{(1,7)}$	0.3666
	Day	$14.27_{(1.5,10.8)}$	0.0015 **
Cladocera			
	B	$5.06_{(1,8)}$	0.0547 ·
	N	$0.94_{(1,8)}$	0.3617
	B:N	$0.75_{(1,8)}$	0.4127
Rotifer			
	B	$4.41_{(1,7)}$	0.0739 ·
	N	$4.11_{(1,7)}$	0.0823 ·
	B:N	$0.07_{(1,7)}$	0.8052
	Day	$2.06_{(1.3,8.8)}$	0.1868

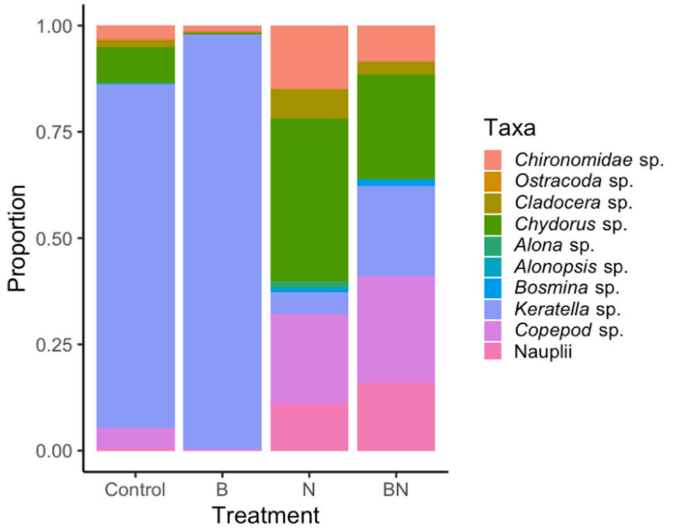

Fig. 3. Stickleback diet composition as relative numbers of different taxa (benthic taxa: Chironomidae sp., Ostracoda sp., cladocera sp., Chydorus sp., Alona sp., and Alonopsis sp.; pelagic taxa: Bosmina sp., Polyphemus sp., Keratella sp., copepod sp., and nauplii). for the control, browning alone ("B"), nutrient-enrichment ("N"), and browning and nutrient-enrichment combination ("BN").

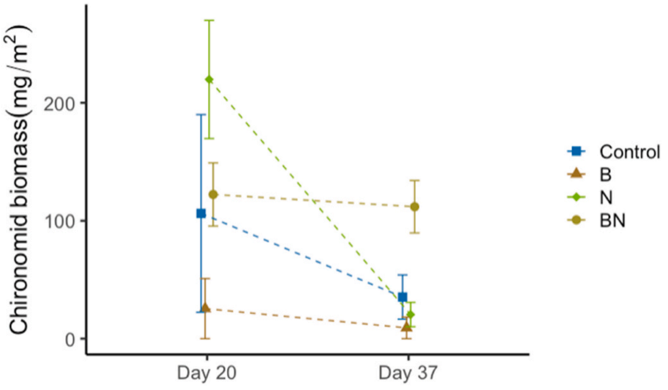

Fig. 4. Biomass of chironomid larvae before (day 20) and after (day 37) fish addition in the treatments without (Control) or with browning ("B"), nutrient enrichment ("N"), or the combination of browning and nutrient-enrichment ("BN"). All values are means (±SE).

2020) in isolation can affect fish body growth and condition via changes in prey composition. Our findings highlight the potential for substantial but antagonistic effects of eutrophication and browning on coastal food webs, including fish.

The positive effect of nutrient-enrichment on fish body growth can be explained by the higher availability of preferred food items (chironomid larvae and large-bodied zooplankton; Welker et al., 1994; Graeb et al., 2004; Sohel et al., 2017) in these treatments by the time that fish were added. The higher benthic chl-*a* concentration together with higher densities of chironomid larvae are in line with findings in natural systems where chironomid larvae generally are more abundant in eutrophic waters, due to the higher availability of organic detritus (Burkholder and Glibert, 2013). The higher abundance of large-bodied zooplankton with nutrient-enrichment is likely explained by higher resource availability, as indicated by the much higher concentrations of pelagic chl-*a* in treatments with added nutrients. This was expected, as an increase in nutrient concentration generally promotes primary productivity (Carpenter et al., 1998; Bonsdorff et al., 2002; Flemming-Lehtinen et al., 2008). In contrast, browning often has a negative impact on primary (at least benthic) productivity (Jansson et al., 2000; Mustaffa et al., 2020), which in our study manifested as lower benthic chl-*a* concentrations. Similar to some previous studies (van Dorst et al., 2020; Huss et al., 2021), but in contrast to others (Leech et al., 2020), browning had a slight positive effect on both pelagic chl-*a* concentrations and large-bodied zooplankton biomass. An explanation could be that the chlorophyll pigment concentration in phytoplankton tends to increase with decreasing light, meaning that the effect on phytoplankton biomass might still have been neutral or negative (Fennel and Boss, 2003; van Dorst et al., 2020). Still, the lack of a decrease in zooplankton biomass with browning suggests that the effect, if any, on phytoplankton biomass was minor. The combination of browning and nutrient-enrichment resulted in a high chl-*a* concentration and zooplankton biomass, suggesting that browning did not change the positive effect of nutrient-enrichment.

The abundance of large-bodied prey (such as copepods and cladocerans) decreased considerably in all treatments after fish addition, suggesting that the sticklebacks depleted most of their preferred prey. Chironomid larvae were in higher abundance in mesocosms with nutrient-enrichment, which likely contributed to increased fish body growth in these treatments. Zooplankton community composition underwent major changes over time and between treatments. Before fish addition, large-bodied zooplankton dominated in all treatments, although the biomass was higher in nutrient-enriched mesocosms. After fish addition, however, large-bodied zooplankton quickly disappeared in the browning-only treatment, which instead was dominated by small zooplankton, such as rotifers and nauplii. In contrast, nutrient-enriched mesocosms still contained some large-bodied zooplankton also at the end of the experiment, although dominated by nauplii. In addition to the early treatment-induced changes in zooplankton biomass, continued change in zooplankton community composition after fish addition may be linked to stickleback feeding and prey selection. Most planktivorous fishes, including stickleback, prefer to prey on large- rather than small-bodied zooplankton, as they have higher nutritional value and are easier to see (Hangelin and Vuorinen, 1988; Ljunggren, 2002; Jakobsen et al., 2003). Thus, given fewer large-bodied zooplankton prey with browning (before fish addition), the sticklebacks most likely depleted them soon after being added and therefore had to go for smaller-bodied and less nutritious/energetically profitable prey such as rotifers, and thus grew somewhat slower in brown waters. The considerable decrease in large-bodied zooplankton biomass after fish addition was not accompanied by any change in chl-*a* concentration. Generally, a decrease in zooplankton biomass should have a positive effect on algal biomass due to decreased grazing pressure (Carpenter and Kitchell, 1988; Shiomoto et al., 1997; Carpenter et al., 1998). Explanations for this lack of a trophic cascade in our experiment could be a too short timeframe or that the phytoplankton community was dominated by grazing resistant algae (Lürling, 2021). Another potential explanation could be that the abundant rotifers maintained a high grazing pressure on phytoplankton throughout the experiment (Abou-Shanab et al., 2016). To better assess the presence and effects of trophic cascades, however, mesocosms for all treatments without fish present for the entire experimental duration would have been favourable.

The greater abundance of preferred stickleback prey (such as copepods and chironomid larvae) with nutrient-enrichment, i.e. in eutrophic waters, suggests that early stages of eutrophication may have a positive effect on juvenile stickleback body growth via bottom-up processes, negating negative effects of browning. The higher abundance of these prey with nutrient-enrichment was mirrored in the sticklebacks' diet. At the end of the experiment, sticklebacks in mesocosms with eutrophic waters fed on a larger variety of prey, including adult copepods, benthic cladocerans (mainly *Chydorus* sp.), nauplii, and chironomid larvae. Interestingly, a large part of their diet consisted of benthic prey, suggesting they were abundant and/or selected for in mesocosms with nutrient-enrichment. Benthic cladocerans, such as *Chydorus* sp. and *Alona* sp., have been found to be more abundant in

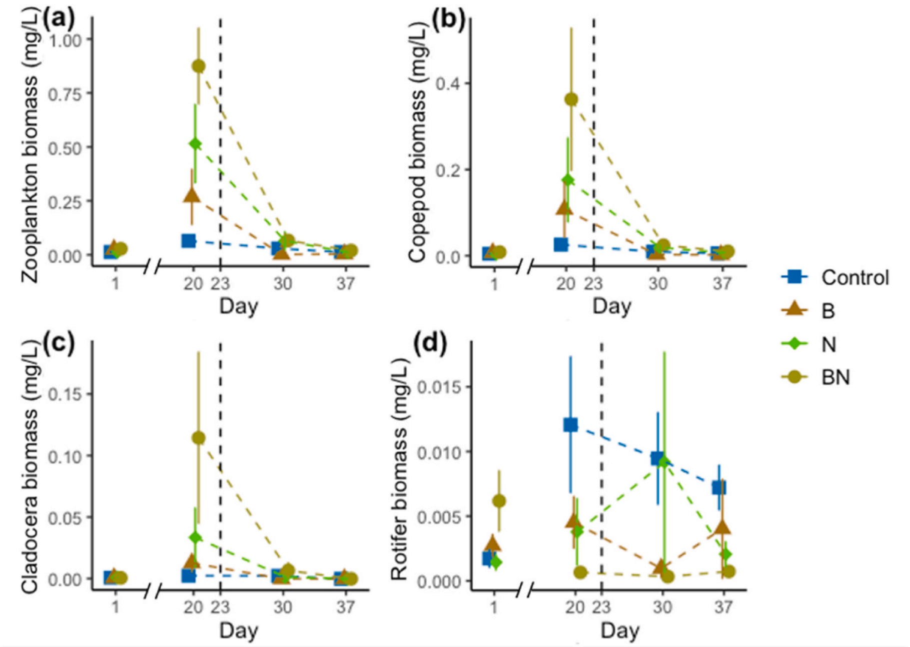

Fig. 5. Zooplankton biomass over time for (a) total zooplankton, (b) copepods, (c) cladocerans, and (d) rotifers in treatments without (Control) or with browning ("B"), nutrient-enrichment ("N"), or the combination of browning and nutrient-enrichment ("BN"). The black vertical dashed line on day 23 indicates when fish were added. Note the different y-axis scales. All values are means (±SE).

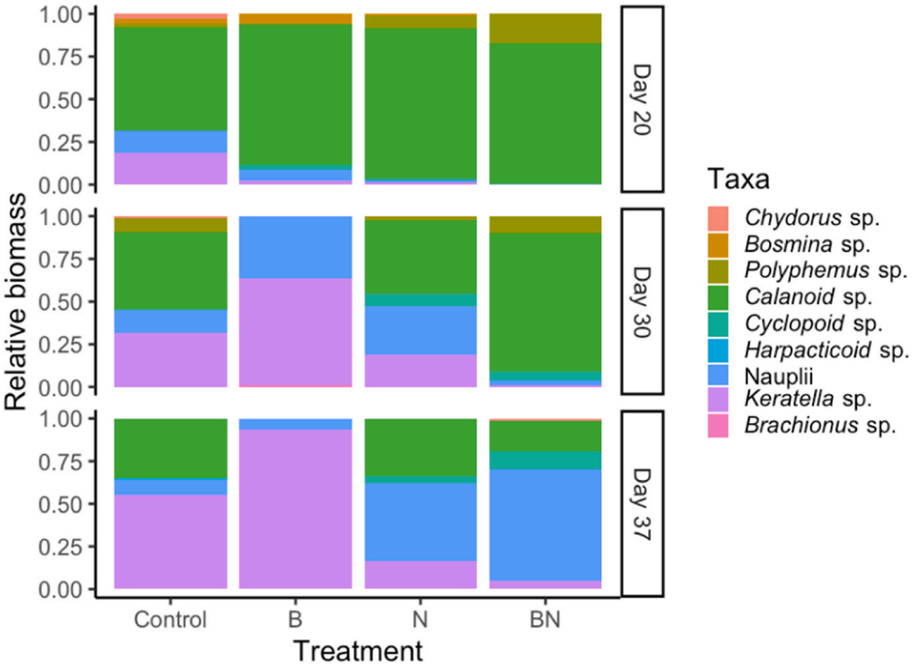

Fig. 6. Zooplankton community composition (relative biomass) on day 20, 30, and 37 for treatments without (Control) or with browning ("B"), nutrient-enrichment ("N"), or the combination of browning and nutrient-enrichment ("BN"). Fish were added on day 23.

eutrophic waters (Whiteside, 1970). However, as we did not sample benthic cladocerans, we cannot know for sure if this was the case in our study. Similar to what has been found in many natural systems (Hall and Gerhardt, 2002; Jakubavičiūtė et al., 2017), we found chironomid larvae to be an important prey item for sticklebacks (especially based on relative biomasses) across all treatments. It should, however, be noted that the diet content at the end of the experiment may not reflect preferences during the whole experiment as some prey items had already been completely or partially depleted in the environment by the time there were caught. For example, the numerically dominating taxa in fish diets at the end of the experiment in treatments without nutrient additions was the rotifer *Keratella* sp., but these small-bodied species are unlikely to be preferred food items and rather reflect that most preferred zooplankton had already been consumed (maximum consumption rate of a 0.14 g stickleback = 0.78 $g*g^{-1} * d^{-1}$ according to (Hovel et al., 2015). Interestingly, even though the browning-only treatment did not decrease overall prey availability, the fish grew slower in brown waters (without nutrient-enrichment). This may be because browning can

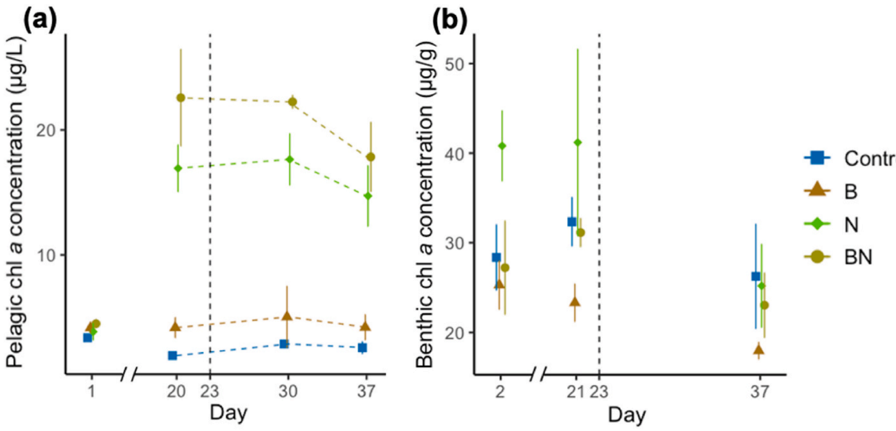

Fig. 7. (a) Pelagic and (b) benthic chlorophyll *a* concentrations over time in treatments without (Control) or with browning ("B"), nutrient-enrichment ("N"), or the combination of browning and nutrient-enrichment ("BN"). The black vertical dashed line on day 23 indicates when fish were added. All values are means (±SE).

negatively affect foraging ability due to reduced visibility (Ranåker et al., 2012; Hedström, 2016; Weidel et al., 2017; van Dorst et al., 2020). Thus, reduced visibility rather than reduced prey availability, or in combination with lack of large prey, might cause negative effects of browning on YOY stickleback body condition and growth. However, not all fishes are negatively affected by a browning-induced reduction in visibility (Jönsson et al., 2012; Weidel et al., 2017; Leech et al., 2020). Therefore, additional studies on how YOY sticklebacks' vision is affected by browning are needed.

There is a general lack of previous studies on how the combination of eutrophication and browning, which we know are affecting water bodies worldwide (Leech et al., 2018; Bergström and Karlsson, 2019), are affecting consumers such as fish via prey responses. Concerning sticklebacks in the Baltic Sea, this is especially problematic as they are exposed to a large natural and human-caused variation and change in trophic status and water colour (Candolin, 2009; Gagnon et al., 2017). They have, in some areas, also undergone a drastic increase in population biomass over the last years (Bergström et al., 2015; Olsson et al., 2019). As changes in these pressures often occur simultaneously and affect other food web components, it is important to also know if and how fish such as sticklebacks respond (Taipale et al., 2018; Hayden et al., 2019). Differences in stickleback body growth and condition between eutrophic, browned waters, and the combination, could have important ramifications for future stickleback population growth and how they interact with other species. For instance, the timing of stickleback diet shifts from zooplankton to zoobenthos and fish prey may change both with bottom-up effects on relative prey abundance and because of faster body growth. In fact, this could potentially worsen the suggested negative interaction between sticklebacks and important coastal piscivores such as perch and pike (Ljunggren et al., 2010; Nilsson et al., 2019; Eklöf et al., 2020). This would especially be the case if increased stickleback body growth in eutrophic areas results in increased predation rates on fish eggs and larvae.

In conclusion, we found that early stages of eutrophication can benefit stickleback body growth by increased prey availability. In contrast, we found that browning can impede stickleback body growth, likely due to reduced visual conditions. However, nutrient-enrichment can negate the negative effects of browning on prey availability and fish body growth and condition. Overall, this study provides new understandings of the combined impact of browning and eutrophication on coastal food webs in general and especially on mesopredatory fish. Furthermore, this study can aid in predictions about how coastal food webs may respond to future changes in water colour and nutrient supply following changes in land use and climate.

Author contributions

All authors contributed to the study design and set up of the experiment. OB and AG carried out the laboratory work. OB performed the statistical analyses and led the writing of the manuscript and AG and MH contributed substantially to revisions of the manuscript. All authors gave final approval for submission and have no conflicts of interest to declare.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Magnus Huss reports financial support was provided by Swedish Research Council Formas.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2022.107762.

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