Received: 26 November 2019 | Revised: 3 March 2020 | Accepted: 31 March 2020
DOI: 10.1111/fwb.13517

ORIGINAL ARTICLE

Freshwater Biology WILEY

Cypriniform fish in running waters reduce hyporheic oxygen depletion in a eutrophic river

Dirk Hübner[1] | Madlen Gerke[2] | Roman Fricke[1,3] | Jörg Schneider[4] |
Carola Winkelmann[2]

[1]Bürogemeinschaft für fisch- und gewässerökologische Studien, Marburg, Germany
[2]Institute for Integrated Natural Sciences, University of Koblenz-Landau, Koblenz, Germany
[3]Department of Ecology, Animal Ecology, University of Marburg, Marburg, Germany
[4]Bürogemeinschaft für fisch- und gewässerökologische Studien, Frankfurt, Germany

Correspondence
Madlen Gerke, Institute for Integrated Natural Sciences, University of Koblenz-Landau, Koblenz, Germany.
Email: madlen.gerke@me.com

Funding information
Federal Office for Agriculture and Food of Germany, Grant/Award Number: 2813BM011

Abstract

1. The hyporheic zone is an important habitat for benthic invertebrates and early-developmental stages of gravel spawning fish. However, the eutrophication of running waters and, in turn, the excessive periphyton biomass leads to its biological clogging. The result of these processes is oxygen depletion and a reduction in the habitat quality of the hyporheic zone.
2. This study assessed whether top-down effects of two important European river fish species, the large herbivorous cypriniform common nase (*Chondrostoma nasus*, L.) and the large omnivorous cypriniform European chub (*Squalius cephalus*, L.), can reduce eutrophication effects in the hyporheic zone. A 4-week mesocosm-based field experiment in a eutrophic river was conducted using cage enclosures stocked or not with either nase or chub.
3. The top-down control of periphyton was expected to reduce biological clogging and thereby increase oxygen availability in the hyporheic zone. Accordingly, we hypothesised that in enclosures stocked with either fish the concentrations of dissolved oxygen in the hyporheic zone would be higher and the periphyton biomass would be lower than in enclosures without fish stocking.
4. Hyporheic oxygen concentrations were significantly higher in enclosures stocked with either nase or chub than in enclosures without fish stocking. However, periphyton ash-free dry mass was significantly reduced only in enclosures stocked with nase, not in those stocked with chub. Thus, the positive effects of nase and chub on hyporheic oxygen availability were caused by different mechanisms.
5. Our results demonstrate that nase and chub can reduce eutrophication effects in the hyporheic zone of running waters. Hence, protecting and enhancing stocks of herbivorous and omnivorous fish will contribute to restoring the hyporheic zone in efforts to preserve biodiversity in eutrophic rivers.

KEYWORDS
benthic grazing, biological clogging, biomanipulation, *Chondrostoma nasus*, *Squalius cephalus*

Dirk Hübner and Madlen Gerke should be considered joint first author.

1 | INTRODUCTION

The hyporheic zone is the connecting ecotone between river and groundwater ecosystems (Brunke, 1999). An intact hyporheic zone provides key ecological functions: it acts as a filter that mediates the exchange of water, nutrients, organic matter, and contaminants; it plays a crucial role in biogeochemical cycling and buffers against physical and chemical influences (Brunke & Gonser, 1997; Findlay, 1995; Stanford & Ward, 1988). It also serves as an important habitat and refuge for benthic invertebrates and the early developmental stages of gravel-spawning fish (Baxter & Hauer, 2000; Brunke & Gonser, 1997; Findlay, 1995; Williams & Hynes, 1974). Due to the importance of the hyporheic zone for ecosystem functioning and biodiversity, efforts aimed at stream restoration must also include restoration of the hyporheic zone (Boulton, 2007; Hester & Gooseff, 2010).

The ecological functionality of the hyporheic zone strongly depends on its permeability, with negative effects induced by the clogging of riverbed sediments (Brunke & Gonser, 1997). Regulated rivers within agricultural catchments, common in Central Europe, are especially prone to a reduced permeability of their hyporheic zones by two different clogging processes, physical and biological (Brunke, 1999; Brunke & Gonser, 1997; Hartwig & Borchardt, 2015; Ibisch, Seydell, & Borchardt, 2009). Physical clogging by anorganic fine sediments (e.g. as a result of erosion from agricultural fields) reduces the pore space and therefore the seepage rate, which in turn impairs the hydrological connectivity of surface water and groundwater (Brunke & Gonser, 1997; Hartwig & Borchardt, 2015). Biological clogging of the hyporheic zone is due to the excessive periphyton growth in nutrient-enriched streams and shallow rivers that is induced by eutrophication (Hartwig & Borchardt, 2015; Ibisch et al., 2009). The resulting oxygen depletion (Hartwig & Borchardt, 2015; Ibisch et al., 2009) strongly reduces habitat quality for gravel-spawning fish and sensitive invertebrates, such as juvenile freshwater mussels (Geist & Auerswald, 2007; Hübner, Borchardt, & Fischer, 2009; Keckeis, Bauer-Nemeschkal, & Kamler, 1996; Malcolm, Youngson, & Soulsby, 2003). Extensive clogging also impairs invertebrate communities (Jones, Growns, Arnold, McCall, & Bowes, 2015) and decreases biodiversity (Descloux, Datry, & Marmonier, 2013).

Biological clogging is subject to temporal variation but its overall extent is related to the nutrient-driven accrual of periphyton biomass (Ibisch et al., 2009). The accumulation of periphyton mats on substrates that leads to biological clogging is counteracted by the removal of periphyton by floods or grazing. Grazing by fish and invertebrates controls periphyton biomass (Feminella & Hawkins, 1995; Hillebrand, 2009; Holomuzki, Feminella, & Power, 2010), decreases periphyton biomass accumulation in nutrient-enriched rivers (Gerke et al., 2018; Peterson et al., 1993; Sturt, Jansen, & Harrison, 2011), and may alter periphyton community structure (e.g. Abe, Uchida, Nagumo, & Tanaka, 2007; Gelwick & Matthews, 1992; Lamberti & Resh, 1983; Pringle & Hamazaki, 1997). Clogging is also influenced by algal morphology, as the filamentous branches of green algae (e.g. the abundant *Cladophora* sp.) tend to trap sediments from the water (Berger, Henriksson, Kautsky, & Malm, 2003; Dodds, 1991), which may increase external clogging of the hyporheic zone.

In standing waters, the enhancement of zooplankton grazing by biomanipulation is a well-established technique to control eutrophication effects (Benndorf, 1990; Hansson et al., 1998; Shapiro & Wright, 1984). However, whether the active enhancement of grazing might be similarly used to control the effects of eutrophication in running waters is unknown. Given the potentially strong impact of the top-down control of periphyton by grazing in rivers, we expected that enhancing stocks of herbivorous and omnivorous fish would lead to increased indirect control of the eutrophication effects in rivers, especially those in which a drastic reduction in nutrient input and the restoration of flood dynamics are not feasible.

In North and South American streams, strong direct effects of herbivorous fish on periphyton have been observed both in small-scale experiments (Flecker et al., 2002; Martin, Gido, Bello, Dodds, & Veach, 2016; Schneck, Schwarzbold, & Melo, 2013; Veach, Troia, Jumpponen, & Dodds, 2018; Wootton & Oemke, 1992) and on a mesohabitat scale (Gelwick & Matthews, 1992; Power, Dudley, & Cooper, 1989; Power, Matthews, & Stewart, 1985; Stewart, 1987). Grazing fish were also shown to reduce the filament lengths of filamentous green algae (e.g. Bertrand & Gido, 2007; Martin et al., 2016; Murdock, Dodds, Gido, & Whiles, 2011). In Central European rivers, the large cypriniform common nase *Chondrostoma nasus* (Linnaeus, 1758) (Leuciscidae: Leuciscinae) is the only obligate herbivorous fish species (Vater, 1997) and it is specialised for feeding on periphyton (Corse et al., 2010; Freyhof, 1995). Nase typically swim in shoals and scrape periphyton from coarse substrates. Despite large-scale population declines, the common nase remains one of the most abundant fish species in many European rivers (Reckendorfer, Keckeis, Tiitu, Winkler, & Zornig, 2001) and its potential for reducing eutrophication effects in rivers may be accordingly significant.

Indirect top-down effects cascading through three trophic levels, from zoobenthivorous fish to invertebrate grazers and then to periphyton, have been demonstrated in several small-scale experiments (e.g. Dahl, 1998; Gerke et al., 2018; Pagnucco, Remmal, & Ricciardi, 2016) and under near-natural conditions in stream ecosystems (Winkelmann et al., 2014). In two mesocosm experiments conducted in a Northern California river, predatory and omnivorous fish were shown to induce a four-level trophic cascade down to periphyton, by releasing grazing invertebrates from predation pressure (Power, 1990; Wootton & Power, 1993). In Central European rivers, one of the most widespread, common and at least partially piscivorous fish species is the large omnivorous cypriniform European chub *Squalius cephalus* (Linnaeus, 1758) (Leuciscidae: Leuciscinae). While it partially feeds on periphyton, especially on filamentous algae (Balestrieri, Prigioni, Remonti, Sgrosso, & Priore, 2006; Hellawell, 1971), and benthic invertebrates, with progressing age and size it increasingly preys on small zoobenthivorous fish such as minnows, *Phoxinus phoxinus* (Linnaeus, 1758) and bullheads, *Cottus gobio* (Linnaeus, 1758) (Hellawell, 1971; Mann, 1976). Thus, we predicted that, in addition to its potential direct top-down effects on periphyton by feeding on filamentous algae, large chub would indirectly reduce periphyton biomass, and therefore eutrophication effects as well, via a four-level trophic cascade. Specifically, in response to a reduction in the local density of zoobenthivorous fish through either chub predation or displacement, benthic invertebrates would be released from predation pressure, thus increasing invertebrate grazing and reducing periphyton biomass.

To assess whether the top-down effects of herbivorous nase and omnivorous chub lead to a reduction in eutrophication effects in the hyporheic zone, we conducted a mesocosm-based field experiment using cage enclosures in a eutrophic river. The top-down control of periphyton by nase and chub was expected to reduce biological clogging, ultimately resulting in an increased oxygen supply in the hyporheic zone. Accordingly, we hypothesised that enclosures stocked with either nase or chub would show (1) higher oxygen concentrations within the hyporheic zone and (2) a lower periphyton biomass than in enclosures without fish stocking. Along with a reduction of periphyton biomass, we expected grazing-induced changes in the structure of the periphyton community, especially regarding the proportion of green algae within the periphyton. The feeding activity of nase was expected to directly reduce periphyton biomass and that of omnivorous chub to directly and/or indirectly reduce periphyton biomass via the above-described four-level trophic cascade.

2 | MATERIAL AND METHODS

2.1 | Experimental site

The experiment was conducted in the hyporhithral zone of the river Nister (Rhineland-Palatinate, Germany, 50°43′24 N, 7°44′24 E), a small gravel-bed river with a catchment area of 246 km^2. The average mean discharge is 6.3 m^3/s in winter and 2.4 m^3/s in summer (measured at Heimborn, ID 2724030100; data supplied by the State Office for Environment of Rhineland-Palatinate). The land use type in the catchment area is dominated by forestry, pasture and agriculture. At the experimental site, the Nister flows from east to west and the land use type is forest on its right bank (north) and pasture on its left bank (south). Therefore, the river is only partly shaded, on the right bank side. The river's width here averages 15 m. The river bed is relatively homogenous and mainly consists of cobbles (6.3–20 cm). Due to phosphate emissions in the catchment area from several minor municipal wastewater treatment plants and diffuse emissions from local agriculture, the river is highly eutrophic, with the effects including oxygen oversaturation and an extremely high pH during the daytime, especially during the spring algal bloom (Gerke et al., 2018). The hyporheic zone in the river is impaired by clogging especially during summer, as indicated by high proportions of fine sediments in the substrate and low hyporheic oxygen concentrations (unpublished data, see Appendix S1 for details). Moreover, high differences of electrical conductivity and pH-values between surface water and hyporheic water suggest reduced subsurface–surface exchange (Geist & Auerswald, 2007).

The benthic algal and cyanobacterial community in the river is dominated by adnate and loosely attached diatoms, but filamentous cyanobacteria (e.g. *Homoeothrix* sp.) and filamentous green algae (*Ulothrix* sp., *Cladophora* sp.) can become dominant during late spring and summer. The experiment described herein was conducted in early summer, after both the spring peak of the algal bloom and the breakdown of periphyton biomass. The invertebrate community is dominated by chironomid larvae and scraping grazers, such as the mayfly *Ephemerella ignita* (Poda, 1761) and the snail *Ancylus fluviatilis* (Müller, 1774).

The obligate herbivorous common nase dominates the community of large fish, followed by the omnivorous European chub (estimated local biomass densities of fish >15 cm assessed in a 550 m river stretch directly upstream of the experimental site: common nase: 75 g/m^2, European chub: 18 g/m^2). On a mesohabitat scale, much higher natural fish densities can be expected in run sections, as they are the preferred feeding habitats of nase (Huber & Kirchhofer, 1998). In contrast, due to high predation risk in the river from cormorants, *Phalacrocorax carbo sinensis* (Linnaeus, 1758), shallow riffles are usually avoided by large fish. Among the small zoobenthivorous fish, bullhead, common minnow, and stone loach, *Barbatula barbatula* (Linnaeus, 1758), occur in high densities (Gerke et al., 2018).

2.2 | Experimental setup

The enclosure experiment was conducted using in situ fish cages (8 m^2) and three treatment groups: (1) enclosures stocked with common nase; (2) enclosures stocked with European chub; and (3) control enclosures without fish stocking. The fish biomass density (mean ± standard deviation) was 308.6 ± 0.3 g/m^2 for enclosures stocked with nase and 312.5 ± 1.7 g/m^2 for enclosures stocked with chub, achieved by stocking each enclosure with six to nine nase individuals (total length of 28.0–34.5 cm, mean total length 30.8 cm) or four chub individuals (total length of 28.5–43.0 cm, mean total length 37.3 cm). The fish used for the experiment were caught in the vicinity of the cage locations by electrofishing (using EFGI 650, Bretschneider Spezialelektronik). Electrofishing was approved by the fisheries department of the local environmental agency, the SGD Nord (Rhineland-Palatinate, Germany).

Overall, 12 enclosures were arranged in four experimental blocks over a river section of *c.* 150 m, with one enclosure representing each treatment within each block. All enclosures were positioned in a run section with moderate water depth and current velocity (see Appendix S2 for details), representing a typical feeding habitat of adult nase and chub. Current velocity and water depth were similar among the three treatments (see Appendix S2). The three different treatment enclosures within a block were staggered, with the central enclosure shifted, so as to reduce mutual hydrological interference (Figure 1). Thus, control enclosures in the three blocks were positioned upstream of the fish enclosures and/or in a shifted position in the middle of the river, while the fish enclosures stocked with nase

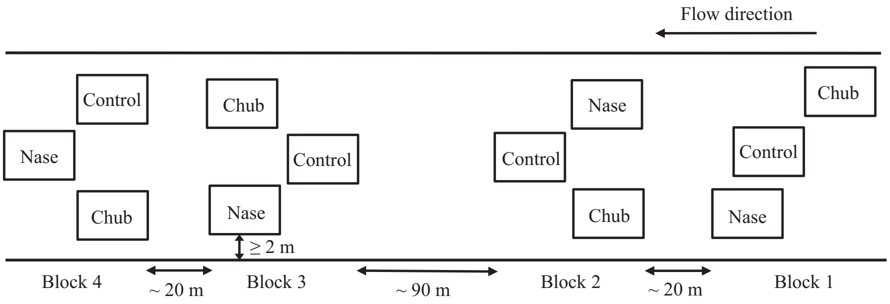

FIGURE 1 Experimental setup showing the arrangement of the experimental blocks and of the treatments (enclosures stocked with nase or with chub and control enclosures without fish stocking) within each block.

or chub were positioned in an alternating sequence (see Figure 1). This arrangement was chosen to ensure that water flow through the control enclosures was optimal and never impaired by the enclosures stocked with fish. This excluded the possibility that any positive effects of the fish treatments were due to a higher water flow in the respective enclosure. The distance between experimental blocks was at least 20 m; the second and third experimental blocks were separated by *c.* 90 m because the water depth in the intermediate section was insufficient for large fish.

Each cage enclosure (length × width × height: 4 × 2 × 0.5 m) was constructed using 18 robust vertical PVC pipes (46 mm in diameter) as a core frame. Flexible horizontal PVC pipes (19 mm in diameter) were attached on all sides with a spacing of 20 mm. This spacing distance minimised the flow resistance of the enclosures and allowed small fish to pass through the cage interstices. The enclosure walls were regularly cleaned to remove deposited litter. The top openings of the enclosures were covered with removable fishing net (mesh size 25 mm) to prevent both the fish from jumping over the enclosure walls and the entry of bird predators while the side walls of the enclosures were not additionally equipped with net. The bottom of the enclosures remained open and allowed the fish to access the natural river bed. The transition zone between the enclosure walls and the river bed was secured against digging fish with a strip of fishing net (mesh size 25 mm) that was attached to the lowest part of the enclosure walls and buried in the substratum along their edge. The enclosures were fixed within the river bed using iron bars. Overall, the enclosures proved sufficiently stable also at high water levels. Two weeks prior to the installation of the enclosures, a multilevel probe (manufactured by the central workshop of the University Kassel, Kassel, Germany) for the extraction of hyporheic water, following Lenk et al. (1999), was buried at the planned location of each enclosure. The enclosures were installed on 31 May 2017 and the experiment was started by stocking the enclosures with fish one week later, on 7 June 2017. The fish remained within the enclosures for 4 weeks, until 5 July 2017.

2.3 | Sampling

The concentration of hyporheic dissolved oxygen was sampled weekly beginning 1 week prior to the start of the experiment (directly before the installation of the enclosures on 31 May 2017) and continuing until the end of the experiment (5 July 2017). The multilevel probes (Lenk et al., 1999) allowed the collection of hyporheic water samples from three different depths (8, 13, and 23 cm) within the riverbed. Water samples from each depth horizon were obtained using a polypropylene syringe (B. Braun Melsungen AG, Melsungen, Germany) and their dissolved oxygen content was immediately measured (WTW, Multi 3430 with FDO 925 probe, Wissenschaftlich Technische Werkstätten, Weilheim; Germany).

Periphyton was sampled according to the same weekly schedule (except on 7 June 2017) as the water samples. For periphyton sampling, six stones were randomly chosen from the area of each enclosure and their periphyton pooled to yield one sample per enclosure. Periphyton was removed by carefully brushing the stone surface with a coarse brush and river water. The resulting periphyton suspensions were transported in the dark to the laboratory.

Benthic invertebrates were sampled one week prior to the start of the experiment (directly before installation of the enclosures on 31 May 2017) and at the end of the experiment (5 July 2017). Sampling was performed using a Surber sampler (0.08 m^2, mesh size 500 µm) positioned at the upstream end of each enclosure. The invertebrate samples were rinsed over a 500 µm-sieve and stored in 70% ethanol.

2.4 | Laboratory analyses

Periphyton biomass was characterised based on the total periphyton biomass (estimated as ash-free dry mass, in mg AFDM/cm^2), as a measure of total organic matter, and the autotrophic periphyton biomass (estimated as the chlorophyll *a* concentration in µg Chl *a*/cm^2), as a measure of the mass of photosynthetically active algae. Both were quantified based on the total volume of the obtained periphyton suspension and the sampled area of the stones. The surface area of the stones was estimated by carefully wrapping each stone in aluminium foil; overlapping areas were cut off, and the foil was then weighed. After their total volumes were determined, the periphyton suspensions were homogenised using a magnetic stirrer to ensure comparable aliquots.

Ash-free dry mass was quantified by transferring 10-ml aliquots to pre-weighed ceramic crucibles and then drying the samples at 105°C for 24 hr. The dried samples were weighed, ashed in a muffle furnace at 510°C for 5 hr and then reweighed. Chlorophyll *a* concentrations were measured by centrifuging triplicate 2-mL aliquots at 16,060 *g* for 3 min (Micro 200R; Hettich Zentrifugen).

The supernatants were discarded, and the pellets stored at − 80°C. Chlorophyll *a* was extracted and then analysed spectrophotometrically according to Mewes, Spielvogel, and Winkelmann (2017). In short, four 3-mm glass beads and 1.8 ml of 96% ethanol buffered with 1 g $MgCO_3$/L was added to each pellet and the mixtures were then homogenised using a mixing mill (MM 400, Retsch Technology GmbH). Chl *a* was extracted for at least 3 hr at room temperature in the dark. Subsequently, the samples were centrifuged for 3 min at 3,421 *g* (Micro 200R), and Chl *a* in the supernatant was measured spectrophotometrically (Specord 205; Analytic Jena, Jena, Germany) at 665 nm, correcting for turbidity at 750 nm. If the sample absorbance exceeded 1, the sample was appropriately diluted with buffered ethanol to obtain a reading <1. The Chl *a* concentration was calculated per area as described in Mewes et al. (2017).

For later analyses of benthic algal and cyanobacterial community composition, additional 2-mL aliquots were taken from the homogenised periphyton suspensions and stored at −80°C. The mean percentage of each taxonomic group (diatoms, green algae and cyanobacteria) in the suspension was estimated microscopically (400× magnification) and expressed relative to the total area covered by algae and cyanobacteria on the slide (set to 100% in each microscopic field of view). The mean percentage of each group was estimated from 50 fields of view per slide, and three slides were analysed per sample.

All individuals from each benthic macroinvertebrate sample were sorted under a dissecting microscope, identified to the lowest practicable taxonomic level and counted. For each taxon in each sample, at least 50 undamaged individuals were measured to the nearest 0.1 mm. If <50 individuals occurred for one taxon per sample, all individuals of the sample were measured. Invertebrate biomass was estimated by calculating the individual body mass (dry mass) using length–weight regressions (Baumgärtner & Rothhaupt, 2003; Benke, Huryn, Smock, & Wallace, 1999; Burgherr & Meyer, 1997; Gerke et al., 2018; Mährlein, Pätzig, Brauns, & Dolman, 2016; Meyer, 1989; Smock, 1980). To calculate the total biomass of invertebrate grazers in each sample, the biomass of each herbivorous and omnivorous species was weighted according to the average proportion of plant food in the diet of that species (Schmedje & Colling, 1996).

2.5 | Data analyses

To assess the effects of stocking the enclosures with nase or chub on the extent of biological clogging, we tested the effects of the fish treatments on hyporheic oxygen concentrations. The effect on periphyton biomass of stocking the enclosures with nase or chub was examined by measuring the effects of the fish treatments on AFDM and the Chl *a* concentration. Whether the fish treatments changed the proportion of green algae within periphyton was also determined. Potential effects of the fish treatments on invertebrate grazing were investigated by measuring the effects of the fish treatments on overall invertebrate biomass and specifically on invertebrate grazer biomass. In all cases, with the exception of the effect of chub on benthic invertebrates, the effects of the fish treatments were tested against the control treatment without fish stocking. The effect of chub on invertebrate biomass (and specifically on grazer biomass) was tested against the other two treatments combined by applying orthogonal contrasts (contrast I: chub versus nase and control; contrast II: nase versus control). In general, all univariate statistical analyses were calculated by applying a generalised linear mixed model (GLMM) in which the treatment was a fixed factor and the experimental block a random factor, in order to account for differences in the localities of the enclosures. In the analyses of the hyporheic oxygen concentration, the depth horizon was included as a fixed factor and the interaction treatment × depth was entered into the model. Parameters were estimated using the maximum likelihood method. Differences in invertebrate community composition were assessed using permutational multivariate analysis of variance (PERMANOVA) based on the Bray–Curtis dissimilarities calculated from the invertebrate biomass (fourth-root transformed). A PERMANOVA was performed with 999 permutations stratified within the experimental blocks. For a detailed assessment of the potential effect of chub treatment on invertebrate community composition, in addition to the full model, the orthogonal contrasts chub versus nase and control (contrast I) and nase versus control (contrast II) were analysed as well.

Prior to the tests of the hypotheses, we examined whether the habitat quality at the different enclosure sites differed so as to cause a bias in the results, by testing for potential differences between the enclosures in the initial values (before installation of the enclosures and fish stocking) of the dependent variables used for hypothesis testing according to the future fish stocking treatment. The same statistical methods as described above were applied, except that, rather than the control treatment, the overall model was used as the testing framework. There were no significant effects of future treatment on the dependent variables prior to the experiment (Table B1 in Appendix S2). Consequently, the measurements obtained after termination of the experiment were used for hypothesis testing without a correction for the initial values.

Both the statistical analyses and graph plotting were performed using R version 3.6.1 (R Development Core Team, 2019). Generalised linear mixed models were applied using the *lme* function included in the R-package *nmle* (Pinheiro et al., 2018). PERMANOVA was performed using the *adonis* function from the R-package *vegan* (Oksanen et al., 2018).

3 | RESULTS

In accordance with our first hypothesis, in which higher oxygen concentrations were predicted for fish-stocked enclosures within the hyporheic zone, at the end of the experiment the hyporheic oxygen concentration was significantly higher in enclosures stocked with either nase (p = 0.001) or chub (p = 0.02) than in control enclosures without fish stocking (GLMM, n = 4; Figure 2). Prior to the experiment,

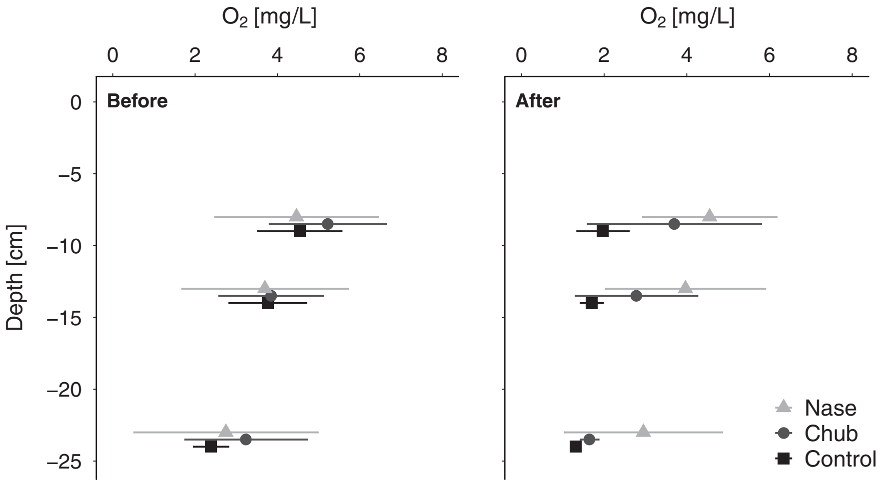

FIGURE 2 Mean oxygen concentration in the hyporheic zone (8, 13, and 23 cm depth) in enclosures stocked with nase or with chub and in control enclosures without fish stocking ($n = 4$). Left: before the installation of the enclosures (1 week prior to the start of the experiment), Right: at the end of the experiment. Error bars represent the standard deviations.

the hyporheic oxygen concentrations did not differ among the future treatments ($p = 0.59$, see Table B1 in Appendix S2 for details; Figure 2). While the oxygen concentration decreased with increasing hyporheic depth ($p = 0.007$), the effects of the fish treatments were independent of the depth horizon (overall treatment × depth: $p = 0.73$). Water samples from enclosures stocked with fish had a 1.6 mg/L higher average oxygen concentration than samples taken from control enclosures. However, despite the positive effect of fish stocking, hyporheic oxygen concentrations generally decreased during the course of the experiment across all treatments (Table 1, Figure 2) and water temperature did not increase in a way that would explain this decrease (see Appendix S3 for details). Therefore, the process of biological clogging was not averted by the presence of large fish but only attenuated or decelerated, especially within the upper two depth horizons.

The second hypothesis, that top-down control of fish would reduce periphyton biomass, was only partly supported. Total periphyton biomass at the end of the experiment was significantly lower in enclosures stocked with nase than in control enclosures ($p = 0.048$), with 30.5% less AFDM on average in the former (GLMM, $n = 4$; Figure 3a). By contrast, total periphyton biomass did not significantly differ between enclosures stocked with chub and control enclosures ($p = 0.98$, GLMM, $n = 4$; Figure 3a). Autotrophic periphyton biomass, measured as Chl *a*, was not reduced compared to the control enclosures in either the nase- or the chub-stocked enclosures ($p = 0.26$ and $p = 0.49$ respectively; GLMM, $n = 4$; Figure 3b). Despite the significant difference in total periphyton biomass at the end of the experiment, the top-down pressure of nase varied over time (see Appendix S3 for details).

TABLE 1 Average difference in the oxygen concentration in the hyporheic zone at the end of the experiment compared to the initial values

Depth [cm]	Enclosures without fish stocking [mg/L O$_2$]	Enclosures stocked with fish [mg/L O$_2$]
8	−2.57	−0.72
13	−2.07	−0.40
23	−1.08	−0.84

The nase and chub treatments also differed in their effect on the general composition of the algal community (Table 2). The estimated proportion of green algae was significantly lower in enclosures stocked with nase than in control enclosures ($p = 0.02$) while there was no significant effect of chub ($p = 0.27$; GLMM, $n = 4$). At the end of the experiment, green algae were largely dominated by *Cladophora* sp.

As predicted, indirect top-down effects of European chub on benthic macroinvertebrates were observed, including an overall effect of the treatments on invertebrate biomass ($p = 0.048$, $n = 4$, ANOVA of GLMM). At the end of the experiment, total invertebrate biomass in the enclosures stocked with chub differed significantly from that in the other two treatments (contrast I: $p = 0.02$, GLMM, Figure 4), whereas there was no difference in the total invertebrate biomass between the enclosures stocked with nase and the control enclosures (contrast II: $p = 0.33$, GLMM, Figure 4). The invertebrate biomass in the chub-stocked enclosures exceeded, on average, that in the other treatments, by 65.1%. However, there was no overall treatment effect on grazer biomass ($p = 0.44$, $n = 4$, ANOVA of GLMM) and grazer biomass did not differ between the enclosures stocked with chub and the other two treatments (contrast I: $p = 0.30$; contrast II: $p = 0.49$; GLMM; Figure 4). This would also explain the lack of effects of the chub treatment on periphyton biomass.

Generally, benthic invertebrate community composition was affected by the fish treatments (PERMANOVA full model: $p = 0.04$, $R^2 = 0.17$), although this effect was weaker than the effect of the experimental blocks, which accounted for the majority of the differences in the community composition ($p = 0.004$, $R^2 = 0.51$). A comparison of the benthic invertebrate community composition in the enclosures stocked with chub versus the other treatments revealed statistically significant but weak effects of chub on the community composition (PERMANOVA contrast I: $p = 0.02$, $R^2 = 0.11$). There were no significant effects of the enclosures stocked with nase compared to the control enclosures (PERMANOVA contrast II: $p = 0.41$, $R^2 = 0.06$).

FIGURE 3 (a) Mean ash-free dry mass (AFDM) and (b) mean chlorophyll *a* (Chla) concentration in enclosures stocked with nase or with chub and in control enclosures without fish stocking (*n* = 4) at the end of the experiment. Error bars represent the standard deviations.

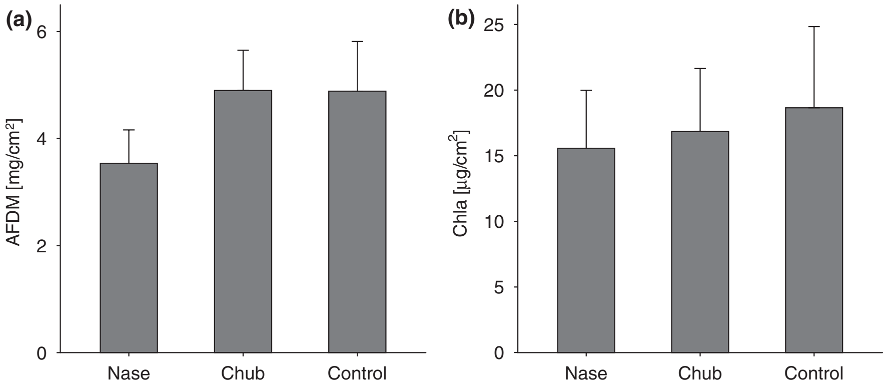

TABLE 2 Estimated proportion (mean ± standard deviation) of higher periphyton taxa contributing to the algal and cyanobacterial communities in the three treatments (*n* = 4) at the end of the experiment

	Diatoms [%]	Green algae [%]	Cyanobacteria [%]
Nase	64 ± 9	17 ± 6	20 ± 10
Chub	63 ± 8	30 ± 7	7 ± 7
Control	57 ± 5	34 ± 9	9 ± 11

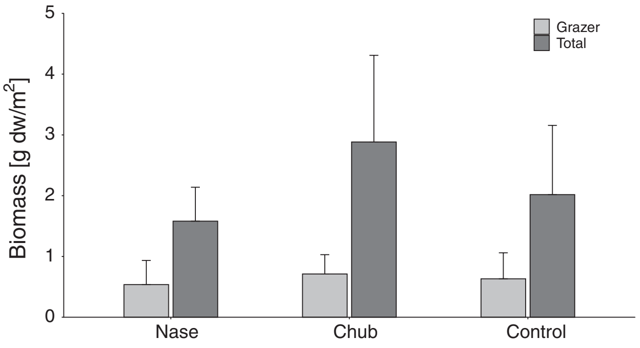

FIGURE 4 Mean total invertebrate biomass and mean biomass of invertebrate grazers in enclosures stocked with nase or with chub and in control enclosures without fish stocking (*n* = 4) at the end of the experiment. Error bars represent the standard deviations.

4 | DISCUSSION

Biological clogging of the hyporheic zone is a severe consequence of eutrophication in running waters, as it causes oxygen depletion (Hartwig & Borchardt, 2015; Ibisch et al., 2009), which in turn strongly reduces habitat quality in this important ecotone (Geist & Auerswald, 2007; Hübner et al., 2009; Malcolm et al., 2003). Our mesocosm experiment showed positive effects of both herbivorous and omnivorous fish on oxygen availability in the hyporheic zone of a eutrophic river, suggesting a reduction of biological clogging. To our knowledge, this is the first study demonstrating that top-down effects by fish can reduce the impact of eutrophication in the hyporheic zone of running waters.

During the experiment, hyporheic oxygen concentrations decreased across all treatments. A similar decrease regularly occurred in the late spring and early summer in nearby stretches of the river (own unpublished data 2015–2019). Clogging might have been more pronounced during the experiment due to the decelerated water flow caused by the enclosure cages and the subsequent increase in local sedimentation. Nevertheless, oxygen concentrations were less significantly decreased in enclosures stocked with fish than in control enclosures without fish stocking. This indicates either a reduced or a considerably slowed clogging in the presence of these fish species.

The positive effects of herbivorous nase and omnivorous chub on hyporheic oxygen availability were caused by different mechanisms. Initially, we expected that nase, as a specialised periphyton feeder (Corse et al., 2010; Freyhof, 1995), would directly reduce periphyton biomass accrual, thereby reducing biological clogging. Our results support this expectation, as judged by the significantly lower total periphyton biomass (AFDM) measured at the end of the experiment in enclosures stocked with nase. Several other studies have similarly shown that herbivorous fish can reduce periphyton, both on a small scale (e.g. Flecker et al., 2002; Martin et al., 2016; Schneck et al., 2013; Veach et al., 2018; Wootton & Oemke, 1992) and on a mesohabitat scale (Gelwick & Matthews, 1992; Power et al., 1985,1989; Stewart, 1987). However, compared to the mean hyporheic oxygen concentration, which was more than twice as high in enclosures stocked with nase than in those without fish stocking, the reduction in the mean AFDM was rather small. Thus, even a small reduction of periphyton biomass is sufficient to cause a large increase in hyporheic oxygen availability. Because hyporheic oxygen availability is mainly controlled by water transport and heterotrophic respiration rates (Brunke & Gonser, 1997), it might be affected by two different processes associated with biological clogging: (1) the reduced permeability of the hyporheic zone as a consequence of both external clogging by benthic algae (Battin & Sengschmitt, 1999; Ibisch et al., 2009) and internal clogging by infiltrated algal cells (Kloep & Röske, 2004); and (2) an increase in biological oxygen demand in the hyporheic zone due to the enhanced decomposition of decaying algae (Rode, Hartwig, Wagenschein, Kebede, & Borchardt, 2015). In this respect, the relatively large effect of herbivorous nase on hyporheic oxygen availability may have reflected the reduced input of organic matter into the hyporheic zone by fish grazing, resulting in a decreased biological oxygen demand but only a slight reduction in the extent of external clogging.

In contrast to total periphyton biomass, autotrophic periphyton biomass (measured as Chl *a*) was not lower in the enclosures stocked with nase. One explanation for this result is the masking of grazing effects on Chl *a* by compensatory growth due to high rates of algal productivity. The autotrophic growth rate at the experimental site was presumably high, due to high nutrient and light availability (Lamberti, Gregory, Ashkenas, Steinman, & McIntire, 1989; Sturt et al., 2011). Moreover, fish grazing might even have stimulated algal growth. Benthic grazing reduces competition for nutrients and light by removing the upper layers of algae, thereby offering optimal growth conditions for new algae (Lamberti & Resh, 1983; McCormick & Stevenson, 1989,1991).

In this respect, as an indicator of periphyton biomass accumulation over time, AFDM may be more appropriate than Chl *a* because it includes live, dead, and senescent algae (Lamberti et al., 1989). Support for a stimulation of algal growth by fish grazing comes from our finding of a significantly lower proportion of green algae, especially filamentous *Cladophora*, in the nase-stocked enclosures, which indicated grazing-induced changes in periphyton community structure. The lower proportion of filamentous green algae in the nase-stocked enclosures may have additionally contributed to reducing the extent of clogging, given the potential of the enhanced trapping of sediments in the filamentous branches of *Cladophora* (Berger et al., 2003; Dodds, 1991) to increase external clogging of the hyporheic zone.

Among the possible mechanisms underlying the increased oxygen availability in the chub-stocked enclosures was the ability of these fish to reduce biological clogging by exerting indirect top-down effects on periphyton. We expected that chub negatively affect the densities of small zoobenthivorous fish either by predation (Hellawell, 1971; Mann, 1976) or by displacement (Magurran, 1989). The subsequent release of benthic invertebrates was expected to promote invertebrate biomass and, in turn, grazer biomass, eventually leading to increased grazing. The results showed that the presence of chub positively affected total benthic invertebrate biomass, thus indicating a negative effect of the fish on zoobenthivorous fish densities in the enclosures. However, the biomass of invertebrate grazers was not promoted by the presence of chub, which would explain why periphyton biomass in enclosures stocked with chub was not reduced. Hence, the positive effects of chub on benthic invertebrate biomass did not cascade down to periphyton. This result was surprising, because the results of a small-scale experiment conducted close to the experimental site indicated the strong impact of the cascading effects of zoobenthivorous fish on periphyton biomass in the Nister (Gerke et al., 2018). Moreover, four-level trophic cascades induced by predatory and omnivorous fish were found in two mesocosm experiments in a Northern California river (Power, 1990; Wootton & Power, 1993). The absence of a similar cascade down to periphyton in our experiment can be explained by the fact that chub is an opportunistic feeder (Balestrieri et al., 2006) that also feeds on large invertebrate grazers such as mayfly larvae. These are generally highly susceptible to predation while grazing on the stone surface (Kohler & McPeek, 1989).

The observed positive effect of chub on the oxygen availability in the hyporheic zone can be best explained by the enhancement of bioturbation. Benthic foraging by chub might have disturbed the river bed, thereby increasing permeability in the upper layer of the hyporheic zone. This scenario seems likely because chub and other benthic-feeding fish can act as *zoogeomorphic agents*, by increasing the mobility of sediments and thereby causing substrate coarsening (Pledger, Rice, & Millett, 2016,2017; Statzner, Sagnes, Champagne, & Viboud, 2003).

On larger spatial scales, the top-down effects of herbivorous nase that lead to an increased oxygen availability in the hyporheic zone might be more important than those of chub, due to the shoaling behaviour of nase. Specifically, adult nase typically form large single-species shoals of a dozen up to several hundred individuals that move actively within defined home ranges (Huber & Kirchhofer, 1998; Lusk, 1967). Within the feeding habitats of their home range, the densities and consequently the top-down effects of nase are presumably similar to those observed in our mesocosm experiment. The effects of chub might be less intense at larger scales because biomass in the enclosures exceeded those found in the river. Nonetheless, natural assemblages of river fish accommodate several species and rheophilic cypriniform fish such as nase and chub are important species in the hyporhithral and epipotamal zones of European rivers (Aarts & Nienhuis, 2003). As in our experiment both nase and chub positively affected hyporheic oxygen availability, under natural conditions the sympatric occurrence of the two species is likely to have synergistic effects. Hence, protecting and enhancing the stocks of both herbivorous and omnivorous fish may contribute to a reduction of eutrophication effects and a restoration of the hyporheic zone in running waters.

Although the effects of nase and chub on hyporheic oxygen concentration were not strong enough to impede or even reverse clogging, these fish may play an important role in the river's local biodiversity. In Central European rivers, the period during which fish eggs and larvae of several fish species develop within the hyporheic zone (intragravel period) coincides with the spring algal peak. Among these species are the salmonid grayling, *Thymallus thymallus* (Linnaeus, 1758) and the cypriniforms common barbel, *Barbus barbus* (Linnaeus, 1758), and nase (Britton & Pegg, 2011; Hübner et al., 2009; Kamler, Keckeis, & Bauer-Nemeschkal, 1998). A low oxygen supply due to the reduced permeability of spawning gravels has been identified as a critical factor compromising the survival of salmonid eggs and larvae (e.g. Malcolm et al., 2003; Soulsby, Youngson, Moir, & Malcolm, 2001; Suttle, Power, Levine, & McNeely, 2004), and the survival of grayling eggs and larvae is negatively affected by eutrophication (Hübner et al., 2009). Lithophilic cypriniforms such as nase also require a permeable and well-oxygenated hyporheic zone for successful development (Duerregger et al., 2018; Keckeis et al., 1996; Nagel, Pander, Mueller, & Geist, 2019). High densities of large herbivorous and omnivorous fish are therefore likely to substantially improve habitat quality in the short intra-gravel period of spring spawning fish such as grayling, barbel, and nase.

ACKNOWLEDGEMENTS

We especially wish to thank Christian Sodemann and Manfred Fetthauer for their technical advice and valuable support during field work. We also thank Michael Götten, Theresa Graf, Tobias Ebelhäuser, Mark Huffsmith, and all the colleagues and students who helped with field sampling and laboratory analyses. We are also grateful to Wendy Ran for linguistic support. This work was financially supported by the Federal Office for Agriculture and Food of Germany (grant number 2813BM011).

CONFLICTS OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data supporting the findings of this study are available in the owncloud repository (Hübner, Gerke, Fricke, Schneider, & Winkelmann, 2020; https://cloud.uni-koblenz-landau.de/s/yjPsJAp57mmQTZL).

ORCID

Madlen Gerke https://orcid.org/0000-0003-2404-6225

REFERENCES

Aarts, B. G. W., & Nienhuis, P. H. (2003). Fish zonations and guilds as the basis for assessment of ecological integrity of large rivers. *Hydrobiologia*, *500*, 157–178. https://doi.org/10.1023/A:1024638726162

Abe, S.-I., Uchida, K., Nagumo, T., & Tanaka, J. (2007). Alterations in the biomass-specific productivity of periphyton assemblages mediated by fish grazing. *Freshwater Biology*, *52*, 1486–1493. https://doi.org/10.1111/j.1365-2427.2007.01780.x

Balestrieri, A., Prigioni, C., Remonti, L., Sgrosso, S., & Priore, G. (2006). Feeding ecology of *Leuciscus cephalus* and *Rutilus rubilio* in southern Italy. *Italian Journal of Zoology*, *73*, 129–135. https://doi.org/10.1080/11250000600679561

Battin, T. J., & Sengschmitt, D. (1999). Linking sediment biofilms, hydrodynamics, and river bed clogging: Evidence from a large river. *Microbial Ecology*, *37*, 185–196. https://doi.org/10.1007/s002489900142

Baumgärtner, D., & Rothhaupt, K.-O. (2003). Predictive length–dry mass regressions for freshwater invertebrates in a pre-alpine lake littoral. *International Review of Hydrobiology*, *88*, 453–463. https://doi.org/10.1002/iroh.200310632

Baxter, C. V., & Hauer, F. R. (2000). Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). *Canadian Journal of Fisheries and Aquatic Sciences*, *57*, 1470–1481. https://doi.org/10.1139/f00-056

Benke, A. C., Huryn, A. D., Smock, L. A., & Wallace, J. B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the Southeastern United States. *Journal of the North American Benthological Society*, *18*, 308–343. https://doi.org/10.2307/1468447

Benndorf, J. (1990). Conditions for effective biomanipulation; conclusions derived from whole-lake experiments in Europe. *Hydrobiologia*, *200/201*, 187–203.

Berger, R., Henriksson, E., Kautsky, L., &Malm, T. (2003). Effects of filamentous algae and deposited matter on the survival of *Fucus vesiculosus* L. germlings in the Baltic Sea. *Aquatic Ecology*, *37*, 1–11.

Bertrand, K. N., & Gido, K. B. (2007). Effects of the herbivorous minnow, southern redbelly dace (*Phoxinus erythrogaster*), on stream productivity and ecosystem structure. *Oecologia*, *151*, 69–81. https://doi.org/10.1007/s00442-006-0569-y

Boulton, A. J. (2007). Hyporheic rehabilitation in rivers: Restoring vertical connectivity. *Freshwater Biology*, *52*, 632–650. https://doi.org/10.1111/j.1365-2427.2006.01710.x

Britton, J. R., & Pegg, J. (2011). Ecology of European barbel *Barbus barbus*: Implications for river, fishery, and conservation management. *Reviews in Fisheries Science*, *19*, 321–330. https://doi.org/10.1080/10641262.2011.599886

Brunke, M. (1999). Colmation and depth filtration within streambeds: Retention of particles in hyporheic interstices. *International Review of Hydrobiology*, *84*(2), 99–117.

Brunke, M., & Gonser, T. (1997). The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology*, *37*, 1–33. https://doi.org/10.1046/j.1365-2427.1997.00143.x

Burgherr, P., & Meyer, E. I. (1997). Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. *Archiv Für Hydrobiologie*, *139*(1), 101–112.

Corse, E., Costedoat, C., Chappaz, R., Pech, N., Martin, J.-F., & Gilles, A. (2010). A PCR-based method for diet analysis in freshwater organisms using 18S rDNA barcoding on faeces. *Molecular Ecology Resources*, *10*, 96–108. https://doi.org/10.1111/j.1755-0998.2009.02795.x

Dahl, J. (1998). Effects of a benthivorous and a drift-feeding fish on a benthic stream assemblage. *Oecologia*, *116*, 426–432. https://doi.org/10.1007/s004420050606

Descloux, S., Datry, T., & Marmonier, P. (2013). Benthic and hyporheic invertebrate assemblages along a gradient of increasing streambed colmation by fine sediment. *Aquatic Sciences*, *75*, 493–507. https://doi.org/10.1007/s00027-013-0295-6

Dodds, W. K. (1991). Community interactions between the filamentous alga *Cladophora glomerata* (L.) Kuetzing, its epiphytes, and epiphyte grazers. *Oecologia*, *85*, 572–580. https://doi.org/10.1007/BF00323770

Duerregger, A., Pander, J., Palt, M., Mueller, M., Nagel, C., & Geist, J. (2018). The importance of stream interstitial conditions for the early-life-stage development of the European nase (*Chondrostoma nasus* L.). *Ecology of Freshwater Fish*, *27*, 920–932. https://doi.org/10.1111/eff.12403

Feminella, J. W., & Hawkins, C. P. (1995). Interactions between stream herbivores and periphyton: A quantitative analysis of past experiments. *Journal of the North American Benthological Society*, *14*, 465–509. https://doi.org/10.2307/1467536

Findlay, S. (1995). Importance of surface–subsurface exchange in stream ecosystems: The hyporheic zone. *Limnology and Oceanography*, 159–164.https://doi.org/10.4319/lo.1995.40.1.0159

Flecker, A. S., Taylor, B. W., Bernhardt, E. S., Hood, J. M., Cornwell, W. K., Cassatt, S. R. … Altman, N. S. (2002). Interactions between herbivorous fishes and limiting nutrients in a tropical stream ecosystem. *Ecology*, *83*, 1831–1844. https://doi.org/10.1890/0012-9658(2002)083[1831:IBHFAL]2.0.CO;2

Freyhof, J. (1995). Feeding traces as an indicator of habitat choice in Nase, *Chondrostoma nasus*. *Folia Zoologica*, *44*, 57–61.

Geist, J., & Auerswald, K. (2007). Physicochemical stream bed characteristics and recruitment of the freshwater pearl mussel (*Margaritifera margaritifera*). *Freshwater Biology*, *52*, 2299–2316. https://doi.org/10.1111/j.1365-2427.2007.01812.x

Gelwick, F. P., & Matthews, W. J. (1992). Effects of an algivorous minnow on temperate stream ecosystem properties. *Ecology*, *73*, 1630–1645. https://doi.org/10.2307/1940016

Gerke, M., Cob Chaves, D., Richter, M., Mewes, D., Schneider, J., Hübner, D., & Winkelmann, C. (2018). Benthic grazing in a eutrophic river: Cascading effects of zoobenthivorous fish mask direct effects of herbivorous fish. *PeerJ*, *6*, e4381. https://doi.org/10.7717/peerj.4381

Hansson, L.-A., Annadotter, H., Bergman, E., Hamrin, S. F., Jeppesen, E., Kairesalo, T. … Strand, J. (1998). Biomanipulation as an application of food-chain theory: Constraints, synthesis, and recommendations for temperate lakes. *Ecosystems*, *1*, 558–574.

Hartwig, M., & Borchardt, D. (2015). Alteration of key hyporheic functions through biological and physical clogging along a nutrient and fine-sediment gradient. *Ecohydrology*, *8*, 961–975. https://doi.org/10.1002/eco.1571

Hellawell, J. M. (1971). The autecology of the chub, *Squalius cephalus* (L.), of the River Lugg and the Afon Llynfi.: III. Diet and Feeding Habits. *Freshwater Biology*, *1*, 369–387. https://doi.org/10.1111/j.1365-2427.1971.tb01569.x

Hester, E. T., & Gooseff, M. N. (2010). Moving beyond the banks: Hyporheic restoration is fundamental to restoring ecological services and functions of streams. *Environmental Science & Technology*, *44*, 1521–1525. https://doi.org/10.1021/es902988n

Hillebrand, H. (2009). Meta-analysis of grazer control of periphyton biomass across aquatic ecosystems. *Journal of Phycology*, *45*, 798–806. https://doi.org/10.1111/j.1529-8817.2009.00702.x

Holomuzki, J. R., Feminella, J. W., & Power, M. E. (2010). Biotic interactions in freshwater benthic habitats. *Journal of the North American Benthological Society*, *29*, 220–244. https://doi.org/10.1899/08-044.1

Huber, M., & Kirchhofer, A. (1998). Radio telemetry as a tool to study habitat use of nase (*Chondrostoma nasus* L.) in medium-sized rivers. *Hydrobiologia*, *371–372*, 309–319. https://doi.org/10.1023/A:1017005523302

Hübner, D., Borchardt, D., & Fischer, J. (2009). Cascading effects of eutrophication on intragravel life stages of European Grayling (*Thymallus thymallus* L.). *Fundamental and Applied Limnology, Advances in Applied Limnology*, *61*, 205–224.

Hübner, D., Gerke, M., Fricke, R., Schneider, J., & Winkelmann, C. (2020) Cypriniform fish in running waters reduce hyporheic oxygen depletion in a eutrophic river. *Owncloud Repository*. https://cloud.uni-koblenz-landau.de/s/yjPsJAp57mmQTZL.

Ibisch, R. B., Seydell, I., & Borchardt, D. (2009). Influence of periphyton biomass dynamics on biological colmation processes in the hyporheic zone of a gravel bed river (River Lahn, Germany). *Fundamental and Applied Limnology, Advances in Applied Limnology*, *61*, 87–104.

Jones, I., Growns, I., Arnold, A., McCall, S., & Bowes, M. (2015). The effects of increased flow and fine sediment on hyporheic invertebrates and nutrients in stream mesocosms. *Freshwater Biology*, *60*, 813–826. https://doi.org/10.1111/fwb.12536

Kamler, E., Keckeis, H., & Bauer-Nemeschkal, E. (1998). Temperature-induced changes of survival, development and yolk partitioning in *Chondrostoma nasus*. *Journal of Fish Biology*, *53*, 658–682. https://doi.org/10.1111/j.1095-8649.1998.tb01009.x

Keckeis, H., Bauer-Nemeschkal, E., & Kamler, E. (1996). Effects of reduced oxygen level on the mortality and hatching rate of *Chondrostoma nasus* embryos. *Journal of Fish Biology*, *49*, 430–440. https://doi.org/10.1111/j.1095-8649.1996.tb00039.x

Kloep, F., & Röske, I. (2004). Transport of algal cells in hyporheic sediments of the river Elbe (Germany). *International Review of Hydrobiology*, *89*, 88–101. https://doi.org/10.1002/iroh.200310662

Kohler, S. L., & McPeek, M. A. (1989). Predation risk and the foraging behavior of competing stream insects. *Ecology*, *70*, 1811–1825. https://doi.org/10.2307/1938114

Lamberti, G. A., Gregory, S. V., Ashkenas, L. R., Steinman, A. D.,& McIntire, C. D. (1989). Productive capacity of periphyton as a determinant of plant-herbivore interactions in streams. *Ecology*, *70*, 1840–1856. https://doi.org/10.2307/1938117

Lamberti, G. A., & Resh, V. H. (1983). Stream periphyton and insect herbivores: An experimental study of grazing by a caddisfly population. *Ecology*, *64*, 1124–1135. https://doi.org/10.2307/1937823

Lenk, M., Saenger, N., Träbing, K., Killich, F., Fischer, J., & Borchardt, D. (1999). Die Multi-Level-Interstitialsonde: Methoden zur tiefenorientierten Untersuchung von Gewässersedimenten. In U. Kern, I. Westrich&S. Bonn (Eds.), *DVWK schriften 128* (pp. 150–157). Bonn, Germany: Wirtschafts- und Verlagsgesellschaft Gas und Wasser.

Lusk, S. (1967). Population dynamics of *Chondrostoma Nasus* (Linnaeus, 1758) in the Rokytná river. *Acta Scientiarum Naturalium*,*1*, 473–522.

Magurran, A. E. (1989). Acquired recognition of predator odour in the European minnow (*Phoxinus phoxinus*). *Ethology*, *82*, 216–223. https://doi.org/10.1111/j.1439-0310.1989.tb00501.x

Mährlein, M., Pätzig, M., Brauns, M., & Dolman, A. M. (2016). Length–mass relationships for lake macroinvertebrates corrected for back-transformation and preservation effects. *Hydrobiologia*, *768*, 37–50. https://doi.org/10.1007/s10750-015-2526-4

Malcolm, I. A., Youngson, A. F., & Soulsby, C. (2003). Survival of salmonid eggs in a degraded gravel-bed stream: Effects of groundwater-surface water interactions. *River Research and Applications*, *19*, 303–316. https://doi.org/10.1002/rra.706

Mann, R. H. K. (1976). Observations on the age, growth, reproduction and food of the chub *Squalius cephalus* (L.) in the river Stour. *Dorset. Journal of Fish Biology*, *8*, 265–288. https://doi.org/10.1111/j.1095-8649.1976.tb03950.x

Martin, E. C., Gido, K. B., Bello, N., Dodds, W. K., & Veach, A. (2016). Increasing fish taxonomic and functional richness affects ecosystem properties of small headwater prairie streams. *Freshwater Biology*, *61*, 887–898. https://doi.org/10.1111/fwb.12752

McCormick, P. V., & Stevenson, R. J. (1989). Effects of snail grazing on benthic algal community structure in different nutrient environments. *Journal of the North American Benthological Society*, *8*,162–172. https://doi.org/10.2307/1467634

McCormick, P. V., & Stevenson, R. J. (1991). Grazer control of nutrient availability in the periphyton. *Oecologia*, *86*, 287–291. https://doi.org/10.1007/BF00317542

Mewes, D., Spielvogel, S., & Winkelmann, C. (2017). RNA/DNA ratio as a growth indicator of stream periphyton. *Freshwater Biology*, *62*, 807–818. https://doi.org/10.1111/fwb.12903

Meyer, E. (1989). The relationship between body length parameters and dry mass in running water invertebrates. *Archiv Für Hydrobiologie*, *117*, 191–203.

Murdock, J. N., Dodds, W. K., Gido, K. B., & Whiles, M. R. (2011). Dynamic influences of nutrients and grazing fish on periphyton during recovery from flood. *Journal of the North American Benthological Society*, *30*, 331–345. https://doi.org/10.1899/10-039.1

Nagel, C., Pander, J., Mueller, M., & Geist, J. (2019). Substrate composition determines emergence success and development of European nase larvae (*Chondrostoma nasus* L.). *Ecology of Freshwater Fish*, *29*(1), 121–131. https://doi.org/10.1111/eff.12500.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., … Wagner, H. (2018). vegan: community ecology package. R package version 2.4-6. Retrieved from https://CRAN.R-project.org/package=vegan.

Pagnucco, K. S., Remmal, Y., & Ricciardi, A. (2016). An invasive benthic fish magnifies trophic cascades and alters pelagic communities in an experimental freshwater system. *Freshwater Science*, *35*, 654–665. https://doi.org/10.1086/685285

Peterson, B. J., Deegan, L., Helfrich, J., Hobbie, J. E., Hullar, M., Moller, B., …Volk, G. (1993). Biological responses of a tundra river to fertilization. *Ecology*, *74*, 653–672. https://doi.org/10.2307/1940794

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D.&R Core Team (2018). nlme: Linear and nonlinear mixed effects models. R package version 3.1-131. Retrieved from https://CRAN.R-project.org/package=nlme.

Pledger, A. G., Rice, S. P., &Millett, J. (2016). Bed disturbance via foraging fish increases bedload transport during subsequent high flows and is controlled by fish size and species. *Geomorphology*, *253*, 83–93. https://doi.org/10.1016/j.geomorph.2015.09.021

Pledger, A. G., Rice, S. P., &Millett, J. (2017). Foraging fish as zoogeomorphic agents: An assessment of fish impacts at patch, barform, and reach scales. *Journal of Geophysical Research: Earth Surface*, *122*, 2105–2123. https://doi.org/10.1002/2017JF004362

Power, M. E. (1990). Effects of fish in river food webs. *Science (New York, N.Y.)*, *250*, 811–814. https://doi.org/10.1126/science.250.4982.811

Power, M. E., Dudley, T. L., &Cooper, S. D. (1989). Grazing catfish, fishing birds, and attached algae in a Panamanian stream. *Environmental Biology of Fishes*, *26*, 285–294. https://doi.org/10.1007/BF00002465

Power, M. E., Matthews, W. J., & Stewart, A. J. (1985). Grazing minnows, piscivorous bass, and stream algae: Dynamics of a strong interaction. *Ecology*, *66*, 1448–1456. https://doi.org/10.2307/1938007

Pringle, C. M., & Hamazaki, T. (1997). Effects of fishes on algal response to storms in a tropical stream. *Ecology*, *78*, 2432–2442. https://doi.org/10.2307/2265904

R Development Core Team (2019). *A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical computing. Retrieved from https://www.r-project.org/.

Reckendorfer, W., Keckeis, H., Tiitu, V., Winkler, G., & Zornig, H. (2001). Diet shifts in 0+ nase, *Chondrostoma nasus*: Size-specific differences and the effect of food availability. *Archiv Für Hydrobiologie*, *135*(*Suppl. Large Rivers 12*), 425–440.

Rode, M., Hartwig, M., Wagenschein, D., Kebede, T., & Borchardt, D. (2015). The importance of hyporheic zone processes on ecological functioning and solute transport of streams and rivers. In L. Chicharo, F. Müller, & N. Fohrer (Eds.), *Ecosystem services and river basin ecohydrology* (pp. 57–82). Dordrecht, The Netherlands: Springer.

Schmedje, U., & Colling, M. (1996). Ökologische Typisierung der aquatischen Makrofauna. In: *Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft* (543 pp). München, Germany: Bayerisches Landesamt für Wasserwirtschaft.

Schneck, F., Schwarzbold, A., & Melo, A. S. (2013). Substrate roughness, fish grazers, and mesohabitat type interact to determine algal biomass and sediment accrual in a high-altitude subtropical stream. *Hydrobiologia*, *711*, 165–173. https://doi.org/10.1007/s10750-013-1477-x

Shapiro, J., & Wright, D. I. (1984). Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. *Freshwater Biology*, *14*, 371–383. https://doi.org/10.1111/j.1365-2427.1984.tb00161.x

Smock, L. A. (1980). Relationships between body size and biomass of aquatic insects. *Freshwater Biology*, *10*, 375–383. https://doi.org/10.1111/j.1365-2427.1980.tb01211.x

Soulsby, C., Youngson, A. F., Moir, H. J., & Malcolm, I. A. (2001). Fine sediment influence on salmonid spawning habitat in a lowland agricultural stream: A preliminary assessment. *Science of the Total Environment*, *265*, 295–307. https://doi.org/10.1016/S0048-9697(00)00672-0

Stanford, J. A., & Ward, J. V. (1988). The hyporheic habitat of river ecosystems. *Nature*, *335*, 64–66. https://doi.org/10.1038/335064a0

Statzner, B., Sagnes, P., Champagne, J.-Y., & Viboud, S. (2003). Contribution of benthic fish to the patch dynamics of gravel and sand transport in streams. *Water Resources Research*, *39*, https://doi.org/10.1029/2003WR002270

Stewart, A. J. (1987). Responses of stream algae to grazing minnows and nutrients: A field test for interactions. *Oecologia*, *72*, 1–7.https://doi.org/10.1007/BF00385036

Sturt, M. M., Jansen, M. A. K., & Harrison, S. S. C. (2011). Invertebrate grazing and riparian shade as controllers of nuisance algae in a eutrophic river. *Freshwater Biology*, *56*, 2580–2593. https://doi.org/10.1111/j.1365-2427.2011.02684.x

Suttle, K. B., Power, M. E., Levine, J. M., & McNeely, C. (2004). How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. *Ecological Applications*, *14*, 969–974. https://doi.org/10.1890/03-5190

Vater, M. (1997). Age growth of the undermouth *Chondrostoma nasus* in the Slovak stretch of the Danube river. *Biologia*, *Bratislava*, *52*, 653–661.

Veach, A. M., Troia, M. J., Jumpponen, A., & Dodds, W. K. (2018). Top–down effects of a grazing, omnivorous minnow (*Campostoma anomalum*) on stream microbial communities. *Freshwater Science*, *37*, 121–133. https://doi.org/10.1086/696292

Williams, D., & Hynes, H. B. N. (1974). The occurrence of benthos deep in the substratum of a stream. *Freshwater Biology*, *4*, 233–256. https://doi.org/10.1111/j.1365-2427.1974.tb00094.x

Winkelmann, C., Schneider, J., Mewes, D., Schmidt, S. I., Worischka, S., Hellmann, C., & Benndorf, J. (2014). Top-down and bottom-up control of periphyton by benthivorous fish and light supply in two streams. *Freshwater Biology*, *59*, 803–818. https://doi.org/10.1111/fwb.12305

Wootton, J. T., & Oemke, M. P. (1992). Latitudinal differences in fish community trophic structure, and the role of fish herbivory in a Costa Rican stream. *Environmental Biology of Fishes*, *35*, 311–319. https://doi.org/10.1007/BF00001899

Wootton, J. T., & Power, M. E. (1993). Productivity, consumers and the structure of a river food chain. *Proceedings of the National Academy of Sciences of the United States of America*, *90*, 1384–1387. https://doi.org/10.1073/pnas.90.4.1384

SUPPORTING INFORMATION

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

How to cite this article: Hübner D, Gerke M, Fricke R, Schneider J, Winkelmann C. Cypriniform fish in running waters reduce hyporheic oxygen depletion in a eutrophic river. *Freshwater Biology*. 2020;00:1–11. https://doi.org/10.1111/fwb.13517