Water quality in a shallow eutrophic lake is unaffected by extensive thinning of planktivorous and benthivorous fish species

Polauke, Emma; Stage Sø, Jonas; Carl, Henrik; Møller, Peter Rask; Reitzel, Kasper; Sand-Jensen, Kaj; Kragh, Theis

Published in:
Journal of Environmental Management

DOI:
10.1016/j.jenvman.2024.120570

Publication date:
2024

Document version
Publisher's PDF, also known as Version of record

Document license:
CC BY

Citation for published version (APA):
Research article

Water quality in a shallow eutrophic lake is unaffected by extensive thinning of planktivorous and benthivorous fish species

Emma Polauke a,*, Jonas Stage So a, Henrik Carl c, Peter Rask Møller c, Kasper Reitze a, Kaj Sand-Jensen b, Theis Kragh b

a University of Southern Denmark, Campusvej 55, 5230, Odense M, Denmark
b University of Copenhagen, Universitetsparken 4, 3 Floor, 2100, Copenhagen, Denmark
b Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, 1 Floor, 2100, Copenhagen, Denmark

ARTICLE INFO
Handling editor: Lixiao Zhang

Keywords:
Fish biomanipulation
Cyprinids
Fish biomass per unit effort
Secchi depth
Successive fish thinning
Bioturbation

ABSTRACT

Ambitious to fulfill the European Water Framework Directive obligations, the European governments support projects to rehabilitate lakes with poor water quality. However, most lake restorations having relied on biomanipulation by fish thinning have failed to improve or even maintain water quality. Previous attempts removed all target fish species simultaneously, thus making it impossible to assess the specific impact of each feeding group on water chemistry. Lake Bromme was selected for extensive, time-selective fish biomanipulation to improve water clarity and promote submerged macrophytes and piscivorous fish stocks over a three-year monitoring period. Thinning of adult benthivorous bream (Abramis brama) and tench (Tinca tinca) was conducted throughout year one while thinning in years two and three targeted planktivorous roach (Rutilus rutilus), juvenile bream, and small perch (Perca fluviatilis). Yearly fish surveys assessed changes in fish population structure and biomass. Water quality parameters were monitored continually, and the cover of submerged macrophytes was surveyed annually via sonar. We found no improvement in water clarity or reductions of nutrients, organic particles, chlorophyll concentrations, or watercolor, despite a 6-fold thinning of total estimated fish biomass, from 112 to 19 kg ha⁻¹. Over the period, the macrophyte cover increased from 0.8 to 13.5 %. but no recruitment of large piscivorous fish (perch and pike (Esox lucius) > 10 cm) was detected. We found higher correlations of particle concentration and water clarity to water temperature than to wind speed, which indicates sediment particle resuspension by the remaining fish community (mostly carp (Cyprinus carpio) that forage on benthos in shallow lakes. Further system-ecological research in Lake Bromme should evaluate whether thinning the stock of carp and increasing plant cover may improve water quality and test which optical properties sustain high water turbidity and prevent shallow, eutrophic lakes like Lake Bromme from responding to intense fish thinning.

1. Introduction

Re-establishing good water quality in eutrophic freshwater lakes is often hindered by internal phosphorus (P) cycling deriving from the historical nutrient accumulation in the sediments (Jeppesen et al., 2000; Sand-Jensen et al., 2017). Thus, many lakes continue to suffer from dense summer phytoplankton blooms and turbid water, which constrain submerged macrophytes and maintain unbalanced food webs (Jeppesen et al., 2000). The European Water Framework Directive aims to establish habitability for aquatic biodiversity, ensure access to safe freshwater resources, and facilitate recreational interest by obtaining good water quality, thus, much effort is dedicated to lake restoration. High external P loading is often identified as a primary reason for sustained poor water quality, but wastewater management and restricted P application on nearby farmland have reduced external P loading. However, the problem of internal P loading in European lakes remains, despite broad lake restoration efforts (Van De Bund and Van Donk, 2002).

Some have proposed that an imbalance in a lake’s food webs might contribute to an unfavorable eutrophic state (Jeppesen et al., 2000; Sondergaard et al., 2008). Meanwhile, it has also been suggested that biomanipulation of the functional structure of biological communities might promote a more balanced trophic structure (Gulati et al., 2008).
Many European lakes have been subjected to a variety of biomanipulation attempts having involved planting submerged macrophytes to inhibit sediment resuspension and nutrient retention, stockking mussels to enhance grazing pressure on phytoplankton, or altering the fish composition (Van De Bund and Van Donk, 2002; Gulati et al., 2008). The latter has frequently been part of attempts to reduce sediment bioturbation and increase herbivorous zooplankton to enhance their grazing pressure on phytoplankton (Drenner and Hambright, 1999; Olin et al., 2006; Søndergaard et al., 2008).

A balanced, well-functioning fish community is achieved when planktivorous and benthic-feeding fish coexist with a sustainable stock of piscivores that can regulate the recruitment of fish fry and maintain the stock of mature fish at an eco-appropriate level (Hambright et al., 1991; Gulati et al., 2008). However, facilitating such a balance is fraught with difficulties. High densities of small cyprinids like roach (Rutilus rutilus L.) often harm water quality as they consume large quantities of herbivorous zooplankton and increase water turbidity while scavenging the littoral sediments for plants, residue, and invertebrates (Brabrand et al., 2002). In Northern European lakes, the main piscivores are European perch (Perca fluviatilis L.) and pike (Esox lucius L.). Even young perch control cyprinid yearlings effectively (Beeck et al., 2002), and, while young pike may also predate on fish fry, and adult pike can engulf larger prey fish than perch; pike is generally unable to effectively constrain the density of 0+ cyprinid stocks (Skov et al., 2003).

Ideally, fish thinning should serve as a ‘shock therapy’ that induces a regime shift from an algae-dominated lake ecosystem favoring cyprinids to a stable, top-down food web regulated by piscivorous fish (Hansson et al., 1998). Such an environment can be stimulated by removing >75% (Perrow et al., 1997) of fish biomass quickly, within one to three years (Hansson et al., 1998), either alone or combined with the stocking of predatory fish (Juraïda et al., 2016). Manipulation of fish populations may be directed towards thinning adult and juvenile fish, as well as removing fish larvae and egg strips manually (Juraïda et al., 2016). While thinning planktivorous fish should facilitate the survival of more herbivorous zooplankton to graze on the phytoplankton, the thinning of benthivorous fish should reduce sediment resuspension, decrease predation pressure on benthic macroinvertebrates, and in combination, improve the underwater light climate and facilitate the presence of submerged macrophytes (Meijer et al., 1990; Zambrano et al., 2001; Huser et al., 2022). The ambient light intensity is also a fundamental factor controlling physiological processes in fish (e.g., growth rate, feeding, and spawning activities) according to the species’ adaptations in morphology and behavior (Ruchin, 2021). Thus, less turbid water may also contribute to restructuring the functionality of the lakes’ fish communities. As good recruitment of large, adult piscivorous fish is highly dependent on sufficient refuge and food availability for juveniles (Beeck et al., 2002), thus, thinning large juvenile cohorts may be necessary to prevent intra- as well as interspecific competition and promote fast growth of large adult stages (Juraïda et al., 2016).

We hypothesized that: 1) reducing the stocks of large benthic feeding cyprinids (bream and tench) would reduce sediment resuspension; 2) thinning planktivorous fish (roach, small bream, and small perch) would suppress the phytoplankton biomass; and 3) the two effects in combination would improve water quality and underwater light conditions for submerged macrophytes. Simultaneously, we examined the influence of temporal variation of precipitation, wind speed, and water temperature (as a proxy for fish feeding activity) on water chemistry.

2. Materials and methods

2.1. Study site

Lake Bromme is a small (12.5 ha), shallow (mean depth 1.48 m, maximum depth 2.4 m), alkaline, eutrophic lake located near the city of Munke Bjergby, in Soro Municipality, Denmark (55°28′52″N, 11°30′54″E (Fig. 1). The catchment (1.1 m² (Müller and Rostgaard, 2018)) is mainly forested and includes a nearby coniferous plantation and a few houses. The lake is classified as a calcareous, non-brown water lake. The lake was once used to store raw timber that fell during a storm in 1967. Today, only a few timbers remain in the lake, which despite having a distinct cloudy yellowish-brown color (Høj and Dahl, 1993),
does not contain high levels of colored dissolved organic materials, thus degradation of the logs is not affecting the water coloration. The state of Lake Bromme’s water chemistry and biota have for decades been monitored within the Danish lake monitoring program. Mean summer Secchi transparency is between 0.72 m and 1.30 m (May–September averages, 2001–2017). The lake has no surface inflow; incoming water derives from precipitation and diffusive seepage, and the estimated water retention time is 1.5 years (Müller and Rostgaard, 2018). At high water levels in winter and after heavy rainfall, water flows from the lake through a shallow ditch to a downstream lake (Fig. 1), though with a negligible possibility of fish migration. Lake Bromme is eutrophic (28 \( \mu \text{g L}^{-1} \) total phosphorus and 1.066–1559 \( \mu \text{g L}^{-1} \) total nitrogen). The external P loading, equivalent to 21 \( \mu \text{g L}^{-1} \), was modeled based on external P inputs from complementary Danish catchment compositions (Kragh, 2022), with no major input from ducks, swans, geese, or piscivorous birds (e.g., cormorants), and the mean summer level of chlorophyll \( a \) was relatively modest (19–32 \( \mu \text{g L}^{-1} \), 1998–2009). During the latest national standardized fish survey in 2013, the lake’s fish biomass was estimated at six tons (437 kg ha\(^{-1} \)), heavily dominated by bream and roach, with a negligible presence of piscivorous perch and pike (\( >10 \text{ cm} \); Müller and Rostgaard, 2018). Following the Danish lake restoration recommendations (Søndergaard et al., 2020), 80 %, equivalent to 4800 kg, of the non-predatory fish biomass was to be removed.

Fig. 1. Map of Denmark with the location of Lake Bromme shown with a red dot (55°28’52”N, 11°30’54”E). Map A illustrates water depth (0.5 m intervals) produced from sonar mapping. A sediment density map (B) was produced from sonar analysis showing areas with soft-density sediments (brown and orange colors) and hard-density sediments (turquoise and light blue colors). The outer blue contour illustrates areas covered in reeds or too shallow (0.5 m) to be mapped by the transducer. The inter-annual progression in the cover of submerged macrophytes between the summer of 2019 (light green) and 2021 (dark green) mapped from sonar analysis are shown in map C. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Historical data of the submerged macrophyte community indicate a downward trend in the relative plant-covered area from 5.18 % in 2005 to 3.3 % in 2013, presumably caused by the high water turbidity (Müller and Rostgaard, 2018).

National routine monitoring of the fish diversity, conducted as part of the NOVANA program, found nine fish species, including the piscivorous perch and pike, the omnivorous roach, sunbleak (Leuciscus delineatus), rudd (Scardinius erythrophthalmus L.) primarily feeding in the pelagic, and the opportunistic, benthic feeding bream, ruffe (Gymnocephalus cernua L.), carp, and crucian carp (Carassius carassius L.) searching for food in the upper sediments (The-Danish-Environmental-Protection-Agency, 2023). Like many other Danish lakes (Carl and Rask Møller, 2012), Lake Bromme contains a small stock of old, adult carp kept for private recreational fishing. According to the fishing rights owner, no recreational fishing for carp took place during the biomanipulation, thus no use of pre-bait, adding nutrients to the lake, and no recent stocking of new carp was performed. The presence of opportunistic and piscivorous European eel (Anguilla anguilla L.) and benthivorous tench (Tinca tinca L.) was known from recent recordings during recreational fishing submitted to the Danish fish database ‘Fishatlas’ (DK: Fiskeatlas).

During the latest national standardized fish survey in 2013, the lake’s fish biomass was estimated at six tons (437 kg ha\(^{-1} \)), heavily dominated by bream and roach, with a negligible presence of piscivorous perch and pike (\( >10 \text{ cm} \); Müller and Rostgaard, 2018). Following the Danish lake restoration recommendations (Søndergaard et al., 2020), 80 %, equivalent to 4800 kg, of the non-predatory fish biomass was to be removed.

### 2.2. Fieldwork

The field study was conducted between March 2019 and September 2021. Standardized fish surveys were conducted yearly to assess selected species’ density and population structure. The water’s physicochemical parameters were measured throughout the study. Data on weather conditions (precipitation, air temperature, and wind speed and direction) were retrieved from the Danish Meteorological Institute. Lake bathymetry, sediment density (hardness), and submerged macrophyte cover were measured by sonar and side-scan analyses following Kragh et al. (2017) and Bastrup-Spohr et al. (2016). Data on sediment chemical properties was retrieved from the Danish national lake survey database (The-Danish-Environmental-Protection-Agency, 2023). The relationships between wind speed and direction on water clarity and suspended particulate organic matter in the lake water were examined with a linear model to evaluate the effect of the seasonal weather conditions on water turbidity.

**Fish removal** – Fish thinning was conducted at weekly intervals, initially targeting large bream and, later, planktivorous roach, young bream, and small perch (\( <10 \text{ cm} \)). With the intention of sparing piscivorous fish (perch \( >10 \text{ cm} \) and all pike) while culling large bream, we used a combination of three-dimensional fish traps, cod, eel, and...
shrimp fykes, and umbrella fish traps baited with a mix of ground-bait, corn, and maggots. The opening apparatus of the umbrella fish traps was modified to allow for more convenient and fast handling of the entrapped fish. The traps and fykes were deployed from a boat and checked every 1–3 days; entrapped live piscivore specimens were released. Up to 52 umbrella fish traps were operated at a time. Cast nets were thrown a few times from a boat to thin schools of small cyprinids. Umbrella fish traps and fykes were replaced by gillnets in mid-June 2019. To selectively target roach, small bream, and small perch, fine-meshed gillnets (10–60 mm) were deployed from April 2020 to September 2021. All removed fish were sorted into species and weighed. An intermediate plastic bulk container (1000 L) equipped with a pound net was installed in late March 2020 to entrapping large cyprinids missed in year one.

Fish surveys – Fish surveys were conducted twice annually to assess the population structure and biomass of species in response to the thinning. Three of the fish surveys were conducted within the standard official period between August 15 and September 15 (herein the “standardized fish surveys”) as described in the following. Each year, we also conducted a similar fish survey earlier in the summer, between late June and mid-July, to allow for examination of the adult fish growth and survival rate over the summer. Six pelagic gillnets (multi-mesh, with EU-standardized dimensions, 30 × 1.5 m with 2.5 m sections of different mesh sizes (CEI)) were equipped with floaters and anchors and placed from a boat overnight. The gillnets were repeatedly deployed at the same sites, located with GPS, and retrieved the following morning after fewer fish would decrease food competition, the condition of all roach per-unit data was calculated for two size groups: longer and shorter than 20 cm via the data of the tench and perch caught during the fish surveys was examined by calculating s condition factor K, K = 100 × W/L^2, with L being the total length of the fish (cm), W being the fresh mass of the fish (g) (Schreck and Moyle, 1990). The progressions of roach and perch fitness in response to whether the thinning improved food availability were tested by a paired, two-tailed t-test on fish caught during the first and final standardized fish surveys.

Fish biomass estimation – In order to acquire the most reliable estimate of the total fish community, we applied several estimation methods to assess the densities of the respective fish species. For the species caught during the fish surveys (roach, roach, ruffe, sunbleak, and rudd), we utilized the species’ BPUEs obtained during the fish surveys conducted in the first two years together with the continually removed quantity of fish biomass to generate linear regression models that described the decline in the species’ biomasses over time and identify upper and lower confidence intervals. The R packages ‘Tidyverse’ and ‘FSA’ (Fish Stock Assessment) (Ogle, 2016) were used.

Large bream and tench cannot be estimated from potential catches in the gillnets used in standardized fish surveys, as they are rarely entangled in relatively small mesh sizes. Thus, we estimated the reduction of tench (>30 cm) and large bream (>20 cm) via the data of the tench and bream that were caught in baited fish traps during the spring of 2019, where the catch rates of both species were high.

No new carp were added during the biomanipulation period, nor was the recruitment of carp fry produced by the present stock presumed, as though carp may produce offspring in Danish lakes, successful recruitment of fry has only been confirmed within a few shallow ponds due to insufficiently high water temperatures during the spawning period and predation by other fish species (Carl and Rask Møller, 2012). As the carp stock mainly contained mirror carp (which have unique scales in mosaic patterns and thus are recognizable in photos), reporting on carp recaptures done by skilled carp fishers who have been fishing in Lake Bromme for years was also taken into consideration for the carp estimate. This estimate was weighted alongside minimum estimates obtained by visual assessments of sun-basking carp in the sun-exposed regions with shallow water observed during several fishing trips in year one. We thereby estimated the presence of a minimum of 60 fish of 6.5 kg (personal comment H. Carl). Removal of carp was avoided in 2019 and 2020, to preserve the lakes’ recreational sport-fishing value, but some were removed in April 2021 by angling.

After we discovered European eels during our fishing in the spring of 2019, we conducted a capture-recapture study to estimate the population size and biomass, thereby gaining a better understanding of the total fish community structure. The eels were marked using Northwest Marine Technology, Inc. Visible Implant Elastomer system (NMT, Inc. (Northwest Marine Technology, 2017)) between September 5, 2019, and June 16, 2020. In this period (226 days), we captured 24 eels in fykes, baited fish traps, and the intermediate bulk container, which were all marked and weighted. During the period, we recaptured four marked eels (Supplementary Table 1). By relying on visual recognition of injected subdermal colored elastomer tags, the eel population was estimated according to Schnabel’s mark-recapture model (Schnabel, 1938).

Catches of crucian carp only constituted two fish, therefore, no estimates of the population’s density could be calculated.

Water chemistry – Water chemistry was measured almost weekly. Chlorophyll a (μg L\(^{-1}\)) was measured as a proxy for the pelagic phytoplankton biomass and was measured immediately on duplicate water samples filtered through GF/F filters (Whatman, UK) and subsequently extracted in ethanol and measured spectrophotometrically according to Jespersen et al. (1987). Alkalinity and initial pH were measured on unfiltred water by acido-sometric Gran titration (Gran, 1952). Samples for later nutrient analyses were stored at −18 °C. Duplicate water samples for total nitrogen (TN, μg N L\(^{-1}\)) and total P (TP, μg P L\(^{-1}\)) were acid-boiled in an autoclave and measured on a SKALAR autosampler. Soluble Reactive Phosphate (SRP, μg P L\(^{-1}\)) was measured on GF/F filtered water samples using the molybdenum-blue method and spectrophotometric measurements (Grasshoff et al., 1999).

Suspended particulate organic carbon (POC, mg C L\(^{-1}\)) was measured using the procedure introduced by Kragh and Sandegård (2004), with small modifications. Duplicate water samples were filtered onto combusted GF/F filters. The filters were dried using compressed air and stored in separate wells in a closed plastic container at −18 °C until analysis. For analysis, the organic particles on the filters were combusted at 650 °C, and the developed CO\(_2\) was measured on an IRGA (ADC225-MK3, ADC-gas). Dissolved chloride added to filters served as standards for reference.

We calculated the relative organic phytoplankton carbon biomass, assuming a carbon/chlorophyll a ratio of 50 % (Riemann et al., 1989) and a maximum value of 100 % to assess the contribution (percentage) of algae biomass to the POC (mg C L\(^{-1}\)) level. Water clarity was measured as Secchi depth, and the water light attenuation coefficients, Kd, were estimated as Kd = 2.303/Secchi depth (m\(^{-1}\)), following Kirk (1994). Light absorbance of colored dissolved organic matter (CDOM) was measured in a scanning spectrophotometer (Thermo Scientific Gen10S UV–Vis P) across the 400–700 nm spectrum and converted to the mean light absorption coefficient (m\(^{-1}\)) (Madsen-Ostbye et al., 2018). Continuous data loggers, installed on a pole in the northern part of the lake, measured water temperature (HOBO UA-002-64) and
photosynthetic active radiation light (PAR; Odyssey Submersible Photoselastic Active Radiation Logger, New Zealand) once and four times per hour, respectively. Light sensors were cleaned every hour with automatic hydro-wipers (Zebra-Tech Dataflow Odyssey PAR Sensor Hydro-wiper, New Zealand). The loggers were removed during the cold period between 2020 and 2021 to avoid the risk of damaging them from ice potentially covering the water’s surface. As Secchi depths were measured for a longer part of the year than the loggers remained in the lake, we calculated the light attenuation as formerly described according to Kirk (1994), while using the PAR data to validate the Secchi measurements. Previous levels of water physicochemical variables estimated before the initiation of this biomanipulation project (2019–2021), and data on the upper sediments (0–10 cm) content of total P, and iron (Fe) were retrieved from the National Danish database (The-Danish-Environmental-Protection-Agency, 2023).

In-vitro lake water clearance rate assessment – To assess Lake Bromme’s water clearance rate/progression during controlled conditions without the influence of wind-induced particle resuspension, the addition of allochthonous materials led from the catchment to the lake during precipitation and particle resuspension maintained by benthic feeding fish, we sampled lake water and surface sediment (approximately the upper 0–10 cm) from the northern littoral zone on a day during summer with a Secchi depth of 47.5 cm. In the lab, the raw sediment (including present benthos) and the lake water were added to an aquarium with approximately 6 cm of sediment depth. The aquarium was placed in a temperature and circadian rhythm light-controlled room at 20 °C and was monitored daily during the following weeks.

Sonar analysis – Sonar analysis was conducted each year during summer by boat using Lowrance HDS-12 Gen3 and HDS-16 Live equipped with a Lowrance Hybrid Dual Imaging (HDI) Skimmer, Lowrance Active Imaging 3-in-1, and an AIRMAR TM150M Transducer as described in Kragh et al. (2017). The analyses provided data on lake bathymetry, sediment properties, and macrophyte coverage (Bastrup-Spohr et al., 2016). Historical data records of the macrophyte cover were retrieved from the National Danish database (The-Danish-Environmental-Protection-Agency, 2023).

Water quality drivers – In order to examine the relative importance of local climatic conditions upon water turbidity (POC mg C L−1), precipitation (mm) and wind direction and speed (m s−1) were retrieved from the Danish Meteorological Institute. The effect of wave disturbance on sediment resuspension was assessed with a MIKE 21 hydrodynamic model (Danish Hydraulic Institute, Denmark, Warren and Bach, 1992). The model uses water depth, wind speed, and direction to calculate the sediment shear stress, expressed as the wave disturbance (Newton, N m−2) per square meter of sediment surface (m−2). The lake was split into an ungritted mesh of 1151 triangles ranging in size from 0.9 to 100 m2, with each triangle assigned the average depth within that triangle. Water depths accorded with the bathymetry map (Fig. 1). Daily average wind speed and direction used in the model were collected from a nearby weather station in Flakkebjerg, Denmark, located 20 km away from Lake Bromme (Institute, 2023). The effect of the sediment shear stress on water POC concentrations was tested in two linear models, using sediment shear stress on the day of the POC measurement, and the day before, as independent variables, respectively. A conceptual animation sequence visualizing the spatiotemporal patterns of the sediment shear stress across the whole lakebeded throughout the study period (864 days) was produced using MIKE 21.

We analyzed the relationship between water temperature and POC concentrations and interpreted the data in accordance with the contemporary composition of the fish community to assess the potential regulatory effect of fish-mediated sediment suspension as a water temperature-driven causal factor on turbidity.

3. Results

3.1. Biomanipulation of fish

Fish biomass estimates and removal – In all, fish biomass of 93.4 kg ha−1 was removed from April 1, 2019, through September 14, 2021 (Table 1, Fig. 2, Supplementary Table 2).

Among benthivores, we estimated the stock of large bream before the thinning to be 165 individuals (between 147 and 182 95 % CI) and 200 kg biomass in total, 16.0 kg ha−1 (between 185 and 215 kg in total 95 % CI) (Supplementary Table 3). We removed 18 kg ha−1 (225 kg in total) and 160 large bream. The start estimate of tench was 38.9 kg in total, 3.1 kg ha−1 (between 38.5 and 44.9 kg in total 95 % CI), and 32 individuals (between 31 and 40 95 % CI). We removed 38 tench with a compiled biomass of 48 kg. We removed 14.8 kg ha−1 large bream and 3.1 kg ha−1 kg tench in April and May 2019, but the catches drastically decreased after mid-June. In the first half of 2020, the umbrella fish traps and fykes entrapped an additional 2.3 kg ha−1 bream and 0.8 kg ha−1 tench. A minor quantity of small bream and a few young tench were removed by gillnets when these replaced umbrella fish traps in mid-June 2020, and during 2021, 0.8 kg ha−1 small bream was caught, but no tench. Carp avoided traps and gillnets, but seven (3.8 kg ha−1) were removed by angling in March 2021. Thus, compared to the initial stock estimate (60 carp of 6.5 kg) being 31 kg ha−1 in 2019, this declined to 27 kg ha−1 due to angling. Only two crucian carp (0.2 kg ha−1) were caught during all three years, thus no population estimates exist.

The BPUEs of the species caught during the six fish surveys are presented in Fig. 3, and the species’ NPUEs and BPUEs with 95 % CI are shown in supplementary Table 4. We estimated the initial total roach biomass to be 636 kg, 50 kg ha−1, which dominated the relative catch composition in the first years (Fig. 3). We removed 9.2 kg ha−1 roach in April 2019, but by the end of the month, the catch efficiency markedly decreased. In 2020, gillnets caught large quantities (40.4 kg ha−1). The roach stock was further reduced in 2021 by 4.8 kg ha−1. In total, we removed 681 kg of roach (54.4 kg ha−1). Our estimates indicated an initial total stock of perch of 96 kg, 7.7 kg perch ha−1 (average 9.5 cm) was removed in 2019. Additional 0.5 kg ha−1 and 0.8 kg ha−1 were later removed in 2020 and 2021. The perch population was reduced by 108 kg in total, 8.6 kg ha−1, thus exceeding the initial estimate. While being relatively sparse in the fish surveys the first two years, perch biomass dominated the catch composition by the end of the biomanipulation. We did not observe any increased recruitment of large perch >10 cm over the period. Rudd, ruffe, and sunbleak were generally scarce in both the fish surveys and regular fishing all years and constituted a compiled removed biomass of 41 kg (‘Others’ in Fig. 3).

A few pike (1.2 kg ha−1) were caught during the regular fishing each year but were absent in most fish surveys, thus no population estimate was calculated.

Eel was highly abundant in the three-dimensional traps in spring 2019 and frequently detected in 2020 and 2021, displaying their characteristic ‘knotting’ of the gillnet mesh and biting of entangled fish. Between September 5, 2019, and June 16, 2020, we marked a total of 24 eels. Four of these eels were recaptured (Supplementary Table 1), providing a stock estimate of 72 eel (between 36 and 291 95 % CI). The average weight was 0.420 kg (between 0.960 and 0.140 kg). The estimated eel biomass was small, 30 kg in total (between 15 and 121 kg 95 % CI), 2.4 kg ha−1, according to capture, tagging, and recaptures.

All years, we observed higher BPUEs in the early summer compared to later in the summer (Fig. 3). We found BPUEs of 2.8 kg in August 2019, decreasing to 0.22 kg by September 2021. In summary, the estimated total fish biomass before the thinning was initiated was 1.404 kg (between 1163 and 1645 kg) (112 kg ha−1). By removal of 1.169 kg (93.3 kg ha−1), the fish density was reduced from an estimated 112 kg ha−1 to 19 kg ha−1 by the end of the biomanipulation, equivalent to a 6-fold decrease.

Fish fitness – No significant changes in the fitness of perch (t-test, p =
0.31) and roach (p = 0.18) were observed between the first and last of the fish surveys (see bar plots in supplementary Figure 1).

3.2. Environmental conditions

Summer Secchi depths remained low (mean 0.68–0.80 m) and were about the same in the study years (Fig. 4A) and earlier years (0.72–0.80 m, Table 2). Secchi depths were closely correlated with vertical attenuation of PAR light ($R^2 = 0.94$). Correlations of Secchi depths with POC and chlorophyll $a$ concentrations were similar for the entire monitoring period (POC: $R^2 = 0.25$, Chl: $R^2 = 0.31$), generally fitting best with the periodic summer and winter chlorophyll $a$ levels (Chl: May–Sep, $R^2 = 0.35$, Oct–Apr, $R^2 = 0.75$; POC: May–Sep, $R^2 = 0.01$, Oct–Apr, $R^2 = 0.31$) (Supplementary Table 4). Meanwhile, the levels of CDOM had only a vague influence on the Secchi depths (Entire period: $R^2 = 0.025$; May–Sep: $R^2 = 0.006$; Oct–Apr 0.0002) (Supplementary Table 4).

Lake water clearance rate assessment - During the first days of inspecting the water turbidity in the aquarium, the water was highly unclear and clouded. The following week, the water in the aquarium got gradually clearer, and on day 14, it was clear, resembling the in-lake conditions during the cold period where the Secchi depths were >2 m (Fig. 4, left) and light attenuation ($K_d$) was low at 0.96–1.04 m$^{-1}$ (Fig. 4, right).

Water chemistry - The TP concentrations remained stable during the three years of fish thinning, ranging between 45 and 47 μg P L$^{-1}$, which resembled concentrations recorded in previous monitoring years (Fig. 5A, Table 2) (The-Danish-Environmental-Protection-Agency, 2023). SRP concentrations were low during all three years (4–9 μg P L$^{-1}$) (Fig. 5B–Table 2), with frequent peaks during the summer of 2021. Mean summer TN concentrations ranged from 1038 to 1328 μg N L$^{-1}$, with a

### Table 1

<table>
<thead>
<tr>
<th>Year</th>
<th>Roach</th>
<th>Bream</th>
<th>Perch</th>
<th>Carp</th>
<th>Tench</th>
<th>Pike</th>
<th>Rudd</th>
<th>Ruffe</th>
<th>Crucian carp</th>
<th>Sunbleak</th>
<th>Eel</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td>2019</td>
<td>9.2</td>
<td>14.8</td>
<td>0.8</td>
<td>0</td>
<td>3.1</td>
<td>0.8</td>
<td>0.6</td>
<td>0.03</td>
<td>0.1</td>
<td>0</td>
<td>29.5</td>
<td>29.5</td>
</tr>
<tr>
<td>2020</td>
<td>40.4</td>
<td>2.3</td>
<td>7.4</td>
<td>0</td>
<td>0.8</td>
<td>0.1</td>
<td>1.1</td>
<td>0.9</td>
<td>0.1</td>
<td>0.02</td>
<td>53.2</td>
<td>53.2</td>
</tr>
<tr>
<td>2021</td>
<td>4.8</td>
<td>0.6</td>
<td>0.5</td>
<td>3.8</td>
<td>0</td>
<td>0.3</td>
<td>0.04</td>
<td>0.5</td>
<td>0</td>
<td>0.01</td>
<td>10.7</td>
<td>10.7</td>
</tr>
<tr>
<td>Sum</td>
<td>54.4</td>
<td>18.7</td>
<td>8.7</td>
<td>3.8</td>
<td>3.8</td>
<td>1.2</td>
<td>1.8</td>
<td>1.5</td>
<td>0.2</td>
<td>0.1</td>
<td>93.4</td>
<td>93.4</td>
</tr>
</tbody>
</table>
0.002, October–April (Fig. 5 A). Secchi depth (m) and vertical light attenuation coefficients, Kd, throughout the biomanipulation period (B). PLEASE USE COLOR FOR PRINT. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Annual means of water chemical variables during summer (May 1 – September 30) and winter (October 1 – April 30). Pre-treatment data from 2005 to 2013 were retrieved from the National Danish database. ‘-‘ indicates no available data (The-Danish-Environmental-Protection-Agency, 2023).

<table>
<thead>
<tr>
<th>Year</th>
<th>Period</th>
<th>Secchi (m)</th>
<th>TN (µg L⁻¹)</th>
<th>TP (µg L⁻¹)</th>
<th>SRF (µg L⁻¹)</th>
<th>Chlorophyll a (µg L⁻¹)</th>
<th>POC (mg C L⁻¹)</th>
<th>CDOM (m⁻¹)</th>
<th>pH</th>
<th>Alkalinity Meq⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>May 1 – Sep 30</td>
<td>0.72</td>
<td>1559</td>
<td>57</td>
<td>–</td>
<td>32</td>
<td>–</td>
<td>–</td>
<td>8.4</td>
<td>3.0</td>
</tr>
<tr>
<td>2013</td>
<td>May 1 – Sep 30</td>
<td>0.80</td>
<td>1066</td>
<td>28</td>
<td>–</td>
<td>13</td>
<td>25</td>
<td>–</td>
<td>8.2</td>
<td>3.2</td>
</tr>
<tr>
<td>2019</td>
<td>May 1 – Sep 30</td>
<td>0.68</td>
<td>1328</td>
<td>45</td>
<td>5</td>
<td>18</td>
<td>16</td>
<td>8.7</td>
<td>8.0</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td>Oct 1 – April 30</td>
<td>1.17</td>
<td>1734</td>
<td>47</td>
<td>5</td>
<td></td>
<td>8.7</td>
<td>8.0</td>
<td>2.5</td>
<td></td>
</tr>
<tr>
<td>2020</td>
<td>May 1 – Sep 30</td>
<td>0.80</td>
<td>1306</td>
<td>47</td>
<td>4</td>
<td>19</td>
<td>26</td>
<td>11.7</td>
<td>7.9</td>
<td>2.9</td>
</tr>
<tr>
<td></td>
<td>Oct 1 – April 30</td>
<td>1.76</td>
<td>1660</td>
<td>45</td>
<td>9</td>
<td>10</td>
<td>21</td>
<td>6.2</td>
<td>7.8</td>
<td>2.2</td>
</tr>
<tr>
<td>2021</td>
<td>May 1 – Sep 30</td>
<td>0.71</td>
<td>1038</td>
<td>45</td>
<td>5</td>
<td>20</td>
<td>22</td>
<td>7.7</td>
<td>8.0</td>
<td>2.2</td>
</tr>
</tbody>
</table>

The sediment density was mapped in 2019 (Fig. 1, middle). The sonar maps showed high sediment density areas being located in the littoral and western regions, and soft sediment density sites being located in the central and northern regions. Examination of the upper sediment showed a mean total P of 1.5 mg g DW⁻¹ and Fe content of 11 mg g DW⁻¹, equivalent to a Fe:P of 7.6 (2016 (The-Danish-Environmental-Protection-Agency, 2023)).

Sediment properties – The sediment density was mapped in 2019 (Fig. 1, middle). The sonar maps showed high sediment density areas being located in the littoral and western regions, and soft sediment density sites being located in the central and northern regions. Examination of the upper sediment showed a mean total P of 1.5 mg g DW⁻¹ and Fe content of 11 mg g DW⁻¹, equivalent to a Fe:P of 7.6 (2016 (The-Danish-Environmental-Protection-Agency, 2023)).

Macrophyte cover – The macrophyte cover over the sediment was examined in July between 2019 and 2021 via sonar side scan. The inter-annual spatial development cover of submerged macrophytes is visualized in Fig. 1 (right). The cover of fully submerged plants increased over the three years from 0.8 % in 2019, 3.9 % in 2020, and 13.5 % in 2021. In 2019, the plants were mostly found in the northern region. Over the years, higher plant densities were observed in areas where plants had been present in the former years, and by 2021, the cover had also expanded noticeably in the southern region. The larger species, shining pondweed Potamogeton lucens, and sago pondweed Stuckenia pectinata, expanded most prominently. The cover of submerged and floating parts of yellow waterlily Nuphar lutea remained constant at 8 %.

3.3. Drivers of water quality

We assessed the effects of the thinning on the progression of the water quality by analyzing the three years’ monthly mean summer (May–Sep) values of water turbidity and nutrients in relation to the monthly estimated standing fish biomass (kg ha⁻¹) for months where fishing removal and sampling of water was conducted contemporarily (Fig. 6). The Secchi depths declined as the standing fish biomass was reduced (Fig. 6 A). Chlorophyll a and TP levels increased with decreasing fish biomass (Fig. 6 B and C), while TN and PO levels slightly decreased (Fig. 6 D and E).

To assess the influence of weather conditions on water turbidity, we analyzed precipitation, wind speed, and water temperature in relation to POC. Precipitation may transfer particles from the catchment to the lake, wind speed is a model proxy for wind-induced shear stress and particle resuspension from surface sediment, and water temperature may serve as a proxy for the feeding intensity of benthivore fish. Precipitation did not correlate with water turbidity (POC or CDOM) or nutrient levels (TN or TP) over the three years (Supplementary Table 7).

Two models were developed to assess the influence of wind-driven shear stress on suspended POC concentration, by incorporating average wind speed data retrieved for the day of POC sampling as its independent variable. Scatter plots of the two models can be found in Supplementary Figure 4. Model 1 showed a non-significant negative correlation of POC (mg C L⁻¹) with mean weighted shear stress (p = 0.49, t-value = −0.7, estimate = −243, R² = −0.008). Model 2, which uses wind speeds for the day before sampling, indicated a significant negative relationship between increasing POC levels and weighted mean...
shear stress (p = 0.01, t-value = -2.7, estimate = -708, R^2 = -0.09).
Thus, we regard the result as an output of other effects. The whole-lake
spatiotemporal analysis of wind-induced lakebed shear stress showed
that the effect of shear stress was highest during periods of high wind
speeds and had the highest impact on sediment resuspension in the
shallow, coastal areas, whereas the open central region was seemingly
unaffected. An animation showing the bed shear stress in Lake Bromme
can be found in supplementary materials for Fig. 5.

Summer water temperatures were high (>20 °C) and winter tem-
peratures low (2.1 °C Dec–Feb average, Fig. 7). The lake was ice-covered
during the early months of 2021. Average daily water temperatures
correlated positively with POC levels, mainly during the cold period
(May–Sep: R^2 = 0.014, Oct–Apr: 0.43, Entire period: 0.30) (Supple-
mentary Figure 6).

4. Discussion

Lake Bromme was continually biomanipulated over three years
through successive thinning of various fish species and feeding groups to
promote good water quality, more piscivorous fish, and increased cover
of macrophytes. Water chemical parameters, fish quality, and macro-
phytes were systematically monitored throughout the biomanipulation
to assess the effects of thinning the respective feeding groups on the lake
ecosystem. However, the water quality in the shallow eutrophic lake was
unaffected by extensive thinning of planktivorous and benthivorous fish
species. Common suggestions for effectless fish-manipulation projects
most often relate to complex and synergistic issues of insufficient
reduction of planktivorous fish, lack of piscivorous fish, and sustained P
pollution issues promoting dense algae blooms while macrophytes and
densities of herbivorous zooplankton groups remain sparse (Gulati et al.,
2008; George, 2021). Ambitious to explore the underlying
system-ecological causalities for the unresponsive Lake Bromme, the
post-biomanipulation state of the lake is discussed.

Attempting to calculate reliable estimates of fish population den-
sities, especially in fish communities consisting of numerous species, is
highly challenging due to the respective species’ characteristics in
morphology, behavior, and home range, as well as the lake ecosystems’
size, bathymetry, and structural features (e.g., macrophytes). To miti-
gate these challenges to evaluate the thinning efforts, we applied several
methods for estimating the respective species’ initial biomasses and
repeatedly monitored the populations’ densities in the course of the fish
thinning.

For perch and roach, we moved approximately 113 % and 107 % of
the biomasses that were initially estimated. This decline was reflected in
the very low BPUEs of both species, which were caught at the final fish
survey. Only a few sunbleak, rudd, and ruffe, were observed and
removed during the biomanipulation. We did not estimate the density of
small bream, as this size group, in contrast to the indented outcome of
the thinning, exhibited a stock recruitment rather than a decline during
the fish surveys, likely as a result of the decimation of fish within the

![Fig. 5. Water chemical variables: Total P (A), SRP (B), Total N and monthly removed and estimated standing fish biomass (kg ha⁻¹) (C), pH and alkalinity (D), chlorophyll a (E), POC and CDOM (F) assessed throughout the biomanipulation period. PLEASE USE COLOR FOR PRINT. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)](image-url)
same feeding niche. Therefore, it was not possible to calculate an estimate based on the thinning efforts of this group. We calculated estimates of large bream and tench from the catch rates in the baited traps during year 1. Compared to our total catch of bream and tench, the removed quantities nicely matched what we initially estimated for both species (Supplementary Table 3). Though we shifted from using baited traps to gillnets, entrapment of bream and tench in the intermediate bulk container was continuously rare, thus indicating, that these stocks were efficiently reduced in year 1. Pike and crucian carp were not estimated due to low catch efficiencies. Given that crucian carp was present in large densities, based on former experiences (unpublish data), we would assume to have caught more in the baited fish traps and the intermediate bulk container. As pike was not a target species for removal, assessment of the pike population was not prioritized in this study, but population assessment should be attempted through an individual recognition study (Kristensen et al., 2020). Similarly, estimation of the carp stock should ideally be performed through a mark-recapture study to obtain reliable stock estimates. Still, as the carp were initially preserved to ensure Lake Bromme’s recreational value, we did not remove carp until year three, to assess whether the removal of a few carp would promote any improvement in the water quality.

In summary, we estimated an initial fish biomass of 1.404 kg (between 1163 and 1645 kg) and removed 1.169 kg equivalent to a reduction of 83 % (between 71 and 100 %). Considering the challenges of estimating true fish stock densities, the quantities removed during the biomanipulation closely reflected what was initially estimated, thereby implying a drastic reduction in the total fish density. While upper confidence intervals for perch and roach implied, that we could have removed an additional 15 kg perch ha$^{-1}$ and 5.5 kg roach ha$^{-1}$ compared to the removed biomass, we removed above or very close to what was estimated for the remaining targeted species. This was supported by the very low catch rates of large cyprinids early in the thinning, and by the BPUEs of the smaller fish species observed in the final fish survey. We, therefore, advocate, that to acquire reliable estimates for different fish species for biomanipulation purposes, efforts should be put into both applying the ideal approach for encountering the species (baited traps, angling, etc.) and in detail noting the species’ removed quantities over time, to continually assess the decline in the estimated biomass.

We hypothesized that reducing the abundance of benthivores fish
would reduce the suspended particle concentration due to less sediment disturbance from fish. However, POC levels and water clarity did not decrease following the removal of bream and tench. We also hypothesized that thinning zooplanktivorous fish (roach, small bream, and small perch) would reduce predation on herbivorous zooplankton and thereby lower phytoplankton chlorophyll. However, the summer-average chlorophyll a concentration was slightly higher in 2021 than in previous years. Also, POC levels remained the same throughout the period, as did the vertical light attenuation and Secchi depth. Extensive fish thinning did not improve the lake’s water quality.

TN declined over the period, perhaps as a combined result of fewer fish contributing to the nutrient turnover by defeating and enhanced N uptake from the increase in macrophytes (Meijer et al. 1996, 1994). While the TP levels fluctuated more in the first years, the summer averages remained unchanged. SRP levels were generally very low and stable in 2019–2020 but fluctuated and had higher peaks in 2021. In addition to P limitation, the relatively low chlorophyll a concentrations may have been due to light limitation by high particle levels, which thereby limited the phytoplankton production (Krågh et al., 2017).

No recreational carp fishing or stocking was performed in Lake Bromme during the biomanipulation, which otherwise, due to the addition of pre-baiting rich in nutrients like P may add to eutrophication, thus complicating the restoration efforts (Arlinghaus and Meiner, 2003; Skeate et al., 2022). Thus, no significant nutrient loadings from ground baits reached the lake during the study period. The bait added to the catchment. The chlorophyll levels correlated better with the Secchi depth and POC concentrations. There was a substantial decrease in Secchi depth when POC concentrations were higher, presumably in the summer and winter periods, we do not assume any profound internal P loading could likely be expected during prolonged periods with low oxygen saturation in the bottom water (Jensen et al., 1992; Reitzel et al., 2005). However, as we detected similar mean water P levels during the summer and winter winters, we do not assume any profound internal P loading during 2019–2021. Moreover, as the water P levels were stable during all seasons, including the warm periods where the feeding activity of the benthic-feeding fish should be highest, thus their increased disturbing of the sediments should transfer more settled particles into the water body, the large cyprinids did assimilate not significantly regulate the water P dynamics within the lake.

Fish biomanipulation guidelines state that 75–80 % of the fish biomass must be removed before improved water quality will be noticeable (Perrow et al., 1997; Hansson et al., 1998). Presuming we meet this criterion, by reducing the estimated biomass between 71 and 100 %, the water quality did still not improve. Thus, in an attempt to identify reasons, we assessed possible alternative drivers of water quality.

We analyzed the relationships of POC, chlorophyll a and nutrient concentrations, and Secchi depth with precipitation, wind-induced shear stress, and water temperature (the latter as a proxy for benthivore fish activity). No correlations were found between precipitation and POC, Secchi depth, and nutrients, indicating that negligible loads of particles and particle-bound nutrients reached the lake via run-off from the catchment. The chlorophyll levels correlated better with the Secchi depths than the POC levels. However, regardless of season, the algae carbon only constituted a minor fraction of the POC, thus implying, that the algae biomass had little influence on the water’s particle pressure and that the remaining carbon fractions should derive from other C-rich compounds.

In shallow water bodies, wind-induced shear stress might reduce water quality by triggering wind-wave erosion of the surface sediment and sustaining the suspension of particulate matter in the water (Martinsen et al., 2022). Fish may enhance wind-induced sediment resuspension as they feed in surface sediment: their constant transfer of settled particles to the water body could make the lakebed more sensitive to wind-wave erosion (Scheffer et al., 2003). Despite Lake Bromme’s shallow water, which exposes its surface sediment to wind-generated shear stress (Martinsen et al., 2022), we found no relationship between POC and shear stress. With prevailing wind from the southwest, the fetch of the wind across the surface is likely too short to induce sufficient turbulence in the bottom water and cause sediment erosion (Supplementary Figure 5).

So why does Lake Bromme fall into the category of lakes that are unresponsive to fish biomanipulation? In a comprehensive systematic review regarding the effects of reducing planktivorous and benthivorous fish on the water quality in eutrophic lakes, Bernes et al. (2015) argue that most unresponsive lakes exhibit high intervention strength from a combination of lake physicochemical properties and the intensity of the applied fishing effort. Common characteristics of these lakes are large surface areas, high water retention, low TP values before fish reduction, and low fishing intensity. Bernes also argues that small lakes with initial high chlorophyll a and TP levels are the most responsive to biomanipulation. Meanwhile, a prerequisite for successful restoration programs has been suggested at a summer water TP of <80–150 μg L⁻¹ (Jeppesen et al., 1990), which Lake Bromme is far below. Lake Bromme is small and eutrophic, has experienced intense fishing pressure through a 6-fold thinning of total estimated fish biomass to just 19 kg ha⁻¹, and with mean summer water P values <50 μg L⁻¹, thus was expected to fall into – or close to – the category of expectedly responsive lakes. Nevertheless, Lake Bromme remained unresponsive.

Alternative causes for Lake Bromme’s unresponsiveness could involve factors and mechanisms that are unaffected by the species of fish we manipulated, and the fish species populations which remained relatively untouched. We identified extensive temporal variation in both Secchi depth and POC concentrations. There was a substantial decrease in Secchi depth when POC concentrations were higher, presumably independent of chlorophyll a concentration, which only constituted a very small fraction of the suspended particulate organic carbon (Supplementary Table 5). As the highest peaks in chlorophyll a were observed in the late summer, the algae biomass was likely dominated by cyanobacteria, which are often inedible to the herbivorous zooplankton. However, no examinations of the relative densities or species compositions of the phytoplankton or zooplankton were conducted in this study.

Secchi depths in late winter were 3–4 times higher than during summer, where the shallower Secchi depths coincided with higher summer water temperatures, while wind impact was not significant. We propose that these temporal changes in water clarity are driven primarily by an increase in the biological activity of fish feeding on bottom invertebrates, leading to the resuspension of sediment particles (Meijer et al., 1990). It is known that large, bottom-feeding cyprinids can cause intensive sediment resuspension (Breukelaar et al., 1994; Huser et al., 2022). The stocks of large bream and tench were presumably drastically thinned, but the carp were not, thus the carp stock would likely continue to transport large loads of settled particles into the water column, thus keeping the water quality low.

Prolonged periods during summer with low winds and high water temperatures did not yield clear water. Conversely, the highest Secchi depths >2 m occurred during the windy and cold periods. Our in-vitro water clearance assessment without fish present showed that the water cleared after two weeks. While finding no correlations between POC levels and precipitation, and the wind models implied that wind did

E. Polauke et al.
not influence POC, we found some seasonal correlations to water temperature. Given that the thermal requirements for carp to initiate and stimulate their foraging activities are water temperatures above 12 °C (Elliott, 1981), this reflects our findings by around this temperature measured lower Secchi depths during the summer period, when the carp are hyperactive and feeding. Likewise, we measured higher Secchi depths during late winter, when the overwintering carp were likely to be dormant, thus supporting our assumption that the turbidity in Lake Bromme is primarily driven by the biological activities of carp causing sediment resuspension when searching for benthos (Su et al., 2023). We estimated that carp density declined only from 31 to 27 kg ha⁻¹. Though we thinned bream and tench efficiently, the remaining carp feeding near the lakebed in the warm period might continue to resuspend sediment particles, thus maintaining the turbid water. The ecological impacts of benthivore fish are highly dependent on a lake basin’s morphology and its sediment’s biogeochemical properties, such as substrate types, prey abundance, and plant cover (Meijer et al., 1996; Lougheed et al., 1996).

Assuming our initial estimate of 60 carp was realistic, the removal of the seven carp left the stock 88% intact (27 kg ha⁻¹ or 4.2 medium-sized carp ha⁻¹). Given that the stocks of other large benthivorous fish were removed, this would imply that even a very low density of carp inhabiting food-depleted lakes with loose surface sediments is enough to prevent improving water quality. However, as many lakes are valued for their recreational and socio-economical aspects related to sports fishing for carp, maintaining carp conflicts with the ambitions of establishing good water quality, which therefore should be considered when selecting the lakes for fish manipulation (Artinghaus and Mehner, 2003; Skeate et al., 2022). While stocking planktonic filter-feeding carp sp. into eutrophic Chinese freshwater lakes has shown potential as a nontraditional biomanipulation tool for combating algal blooms, releasing such non-native cyprinids to enhance bottom-up biocontrol is prohibited in Danish lake management (Chen et al., 2023).

Identifying and assessing the effects of benthivorous carp and other sediment feeders in regard to water turbidity and nutrient turnover dynamics in eutrophic lakes would be a valuable future study (Su et al., 2023). Uncovering a possible impact of carp, as well as other large benthivorous cyprinids, on turbidity requires continued monitoring of physicochemical variables after removing the carp stock.

We hypothesized that increased macrophyte cover should follow the fish reduction as a result of improved underwater light conditions due to decreased sediment resuspension from fewer fish disturbing the sediment and uprooting the macrophytes (Meijer et al., 1990). Sonar side-scans revealed that the plant cover had increased from 0.8 % in 2019 to 13.5 % in 2021. Larger submerged species reaching from the lakebed to the water surface exhibited the highest increase in cover, as the poor light conditions would not be a critically limiting factor near the surface water. Many environmental features regulate the macrophyte communities in lakes, including water depth, slope, and sediment characteristics and textures, which restrict the areas being colonizable, and the degree of physical disturbance and herbivores grazing (Lauridsen et al., 2003). The increase in plant cover was highest in areas with high sediment densities, where plants were already present (Fig. 1), thus indicating new shoots were more likely derived from existing plants than from seeds. Lake Bromme is generally shallow, with the deepest site <2.5 m, meaning, that in a clear-water state with good light conditions, the total lakebed could likely be densely colonized.

As water clarity did not improve, and could therefore not be assumed to be the key promoter of the macrophyte’s growth, we propose that less feeding and disturbance induced by the reduced stocks of bream and tench on the submerged macrophytes may be responsible for the increased plant cover (Lammens et al., 2002). Though rudd is known for consuming macrophytes, the abundance of rudd was probably too low to have an influence. Meanwhile, due to insufficient animal prey, roach might have been grazing on the plants (Horppila, 1994). We thus submit that roach reduction in 2020 and 2021, in combination with the continued vacancy of large bream and tench during 2019–2020, may have stimulated the increase in plant cover from a decreased grazing pressure.

Both the planktivorous and benthivorous fish stocks were drastically reduced. However, no increase in the abundance of piscivorous fish species was detected post-biomanipulation. Thus, a natural bottleneck limiting recruitment of cyprinid fry was likely not established, therefore, the prospects of reaching better water quality or maintaining the positive development in the macrophytes by ensuring high predation pressure on future cohorts of cyprinids, are likely limited. Continued measurements in Lake Bromme will enable us to assess how the macrophytes and the fish community respond to the ongoing fish manipulations and whether further expansion of the plant cover may eventually significantly enhance particle settling and turn the turbid lake into a clear-water lake. This should be assisted by detailed characterization of the optical properties (e.g., complexes of resuspended biological components, mineral and humic colloids, and dissolved organic material) that collectively influence the lake water’s light attenuation and Secchi depth.

Funding

We thank Aage V. Jensen’s Nature Foundation and Poul Due Jensen’s Foundation for grants supporting the Ph.D. research program of EP and facilitating the research and monitoring activities during the biomanipulation at Lake Bromme. The fish thinning program and parts of the lake survey program at Lake Bromme were financed by the Danish Environmental Protection Agency under the River Basin Management Plans 2015-2021.

CRediT authorship contribution statement

Emma Polauke: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Jonas Stage So: Writing – review & editing, Writing – original draft, Software, Methodology, Investigation, Formal analysis. Henrik Carl: Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. Peter Rask Møller: Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Methodology. Kasper Reitzel: Funding acquisition. Kaj Sand-Jensen: Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Investigation, Formal analysis. Theis Krågh: Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgment

We would like to thank Marcus Krag and Lasse Borg Pedersen for their dedicated participation in the field and laboratory work, which was essential to the project. We also thank David Stulgross for his inputs and linguistic revisions of this manuscript and are grateful for the thoughtful and insightful comments and suggestions of the reviewers.


