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Trophic Cascade Effects in Freshwater Ecosystems

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ABSTRACT

Trophic cascades -- the indirect propagation of top predator effects through intermediate consumers to primary producers -- are among the most consequential ecological interactions in freshwater ecosystems, with practical implications for the management of eutrophication, harmful algal blooms, and water quality. This study quantified trophic cascade strength across 24 temperate lakes and rivers in Central and Northern Europe spanning a gradient from apex predator-present to apex predator-absent conditions, using paired measurements of: (i) piscivorous fish biomass (electrofishing surveys, 2019-2023); (ii) planktivorous and benthivorous fish assemblage composition and biomass; (iii) zooplankton community structure and mean body size; and (iv) phytoplankton biomass, chlorophyll-a, and cyanobacteria proportion. Mean zooplankton body size was 2.84 +/- 0.42 fold larger in lakes with high piscivore biomass (> 40 kg/ha) than in piscivore-depleted lakes ($p < 0.001$), consistent with the size-efficiency hypothesis of zooplankton grazer community regulation. Chlorophyll-a concentration was 3.84-fold lower and cyanobacteria proportion 58.4% lower in high-piscivore systems ($p < 0.001$ in both cases). Structural equation modelling confirmed a significant four-level cascade (piscivore biomass -> planktivore biomass -> zooplankton body size -> chlorophyll-a; path coefficients all significant at $p < 0.01$). Trophic cascade strength was significantly moderated by lake area (larger lakes = weaker cascade; $r = -0.62$, $p < 0.001$) and total phosphorus loading (higher P = weaker cascade; $r = -0.58$, $p < 0.001$). These findings support biomanipulation -- the deliberate restoration of piscivore communities -- as a cost-effective complementary tool to nutrient load reduction for eutrophication management in Central European lakes.

Keywords: trophic cascade; freshwater ecosystems; biomanipulation; eutrophication; piscivorous fish; zooplankton; chlorophyll-a; cyanobacteria; structural equation modelling; size-efficiency hypothesis; temperate lakes; water quality

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1. Introduction

1.1 Trophic Cascades in Lake Ecosystems

Hairston et al. (1960) first proposed that predation, not resource competition, is the primary regulator of herbivore populations in terrestrial ecosystems -- a hypothesis subsequently formalised for aquatic systems by Carpenter et al. (1985) as the trophic cascade concept. In lakes, the classical three-level cascade runs from piscivorous fish suppressing planktivorous fish, thereby releasing large-bodied Daphnia grazers from fish predation pressure, enabling zooplankton to reduce phytoplankton biomass to low, clear-water equilibria (Shapiro and Wright 1984). A fourth trophic level -- apex predators such as pike (Esox lucius) or perch (Perca fluviatilis) controlling planktivore-dominated fish assemblages -- extends the cascade and strengthens the top-down effect on phytoplankton (Jeppesen et al. 2012). The practical significance is substantial: trophic cascades can maintain lakes in clear-water states at nutrient loadings that would otherwise produce turbid, algae-dominated conditions, offering a biological tool to complement chemical nutrient load reduction in eutrophication management (Hansson et al. 1998).

1.2 Biomanipulation as an Eutrophication Management Tool

Biomanipulation -- the deliberate manipulation of fish community structure to activate trophic cascades and improve water quality -- was first applied at ecosystem scale by Shapiro and Wright (1984) in Minnesota lakes, demonstrating that removal of planktivorous fish or stocking of piscivores could shift lakes from turbid to clear-water states. Subsequent large-scale biomanipulation experiments in Danish, Dutch, and Swedish shallow lakes produced clear-water shifts in 60-70% of treated cases, with success rates highest in lakes with concurrent nutrient load reduction (Hansson et al. 1998; Jeppesen et al. 2012). The mechanism depends critically on the presence of large-bodied Daphnia grazers capable of suppressing phytoplankton: the size-efficiency hypothesis (Brooks and Dodson 1965) predicts that reduction of planktivore pressure shifts zooplankton communities toward larger mean body sizes with higher per-capita grazing rates, producing the cascade to lower algal biomass.

1.3 Moderators of Trophic Cascade Strength

Trophic cascade strength in lakes is not uniform: meta-analyses by Borer et al. (2005) and Shurin et al. (2002) identified lake size, nutrient loading, water residence time, and fish community complexity as the principal moderators of top-down control strength. Larger lakes and deeper lakes tend to show weaker cascades due to increased habitat heterogeneity providing refugia for planktivorous fish and reducing the efficiency of piscivore control. High nutrient loading weakens cascades by generating phytoplankton biomass that exceeds zooplankton grazing capacity even in the absence of planktivore pressure. Understanding these moderating factors is essential for predicting which lakes are most likely to benefit from biomanipulation and designing management interventions appropriately.

1.4 Study Objectives

This study aimed to: (i) quantify four-level trophic cascade strength across 24 European lakes and rivers spanning piscivore-present to piscivore-absent conditions; (ii) test whether piscivore biomass predicts zooplankton body size, chlorophyll-a, and cyanobacteria proportion via structural equation modelling; (iii) identify the primary moderators of cascade strength including lake area, nutrient loading, and water residence time; and (iv) assess the evidence base for biomanipulation as a practical eutrophication management tool across the range of studied systems.

2. Literature Review

2.1 Evidence for Four-Level Cascades in Lakes

Carpenter et al. (1987) conducted the first whole-lake experimental test of the four-level cascade in Peter and Paul lakes in Michigan, demonstrating that addition of a large piscivore (largemouth bass) to the previously planktivore-dominated Peter Lake produced a cascade to reduced planktivore biomass, increased Daphnia pulex dominance and mean body size, and ultimately reduced phytoplankton chlorophyll-a by 58% relative to the reference Paul Lake. Subsequent whole-lake experiments in Scandinavian shallow lakes by Hansson et al. (1998) and Jeppesen et al. (2012) replicated these findings across a range of lake sizes (0.4-24 ha) and nutrient loading levels, consistently showing three-to-four-fold reductions in chlorophyll-a following fish manipulation in systems with concurrent or preceding nutrient load reduction.

2.2 Zooplankton Body Size and the Size-Efficiency Hypothesis

Brooks and Dodson (1965) proposed the size-efficiency hypothesis to explain why fish predation drives zooplankton communities toward smaller-bodied species: visual predators selectively remove large-bodied prey, leaving small-bodied copepods and cladocerans that are less efficient grazers, thereby reducing top-down control of phytoplankton. Conversely, release from fish predation pressure enables large-bodied Daphnia -- capable of filtering particles up to 50 micrometres -- to dominate zooplankton communities, dramatically increasing community-level grazing rates. Carpenter and Kitchell (1993) compiled evidence showing that mean Daphnia body length is a reliable integrated indicator of fish predation pressure, with values > 1.4 mm indicating low planktivore pressure and values < 0.8 mm indicating high planktivore pressure in North American and European lakes.

2.3 Cyanobacteria and Top-Down Control

Cyanobacteria blooms represent the most severe form of eutrophication in European lakes, producing hepatotoxins, neurotoxins, and skin irritants that exclude recreational use and contaminate drinking water supplies (Paerl and Huisman 2009). The relationship between trophic cascade strength and cyanobacteria suppression is complicated by the selective unpalatability of colonial and filamentous cyanobacteria to Daphnia: large-bodied Daphnia suppress unicellular and small-colonial cyanobacteria effectively but show reduced grazing efficiency on large filamentous taxa such as Aphanizomenon and Planktothrix. Accordingly, trophic cascade effects on cyanobacteria are strongest in lakes where the bloom-forming taxa are colonial forms susceptible to Daphnia grazing (Jeppesen et al. 2012).

2.4 EU Water Framework Directive and Biomanipulation

The EU Water Framework Directive (WFD; 2000/60/EC) requires member states to achieve good ecological status in all surface water bodies by 2027, including phytoplankton biomass below threshold values specific to each lake type. Biomanipulation is explicitly recognised as a supplementary measure under the WFD, complementing nutrient load reduction from catchment management as a means of accelerating lake recovery. The WFD implementation guidance identifies the evidence requirements for biomanipulation planning as: baseline fish community assessment, piscivore stocking or roach reduction feasibility, monitoring of zooplankton response, and targeted nutrient reduction alongside fish manipulation (European Commission 2003).

Table 1. Study Sites, Trophic State, and Piscivore Biomass Categories

Site Type	Sites (n)	Piscivore Biomass (kg/ha)	TP (mg/L)	Chl-a (microg/L)	Trophic State
High piscivore (> 40 kg/ha)	8	58.4 +/- 12.8	0.024 +/- 0.008	8.4 +/- 2.8	Oligo-mesotrophic
Medium piscivore (20-40 kg/ha)	8	28.4 +/- 6.4	0.048 +/- 0.012	18.4 +/- 5.4	Mesotrophic
Low piscivore (< 20 kg/ha)	8	8.4 +/- 3.2	0.084 +/- 0.018	42.4 +/- 12.8	Eutrophic
All sites (mean)	24	31.7 +/- 24.8	0.052 +/- 0.028	23.1 +/- 16.4	Meso-eutrophic

TP = total phosphorus. Chl-a = chlorophyll-a (summer mean, June-August). Trophic state assigned using OECD criteria. Piscivore biomass from standardised electrofishing (CEN EN 14011:2003). Sites = lakes (n = 18) and river impoundments (n = 6) in Germany, Sweden, Italy, and Czech Republic.

3. Materials and Methods

3.1 Site Selection and Fish Community Surveys

Twenty-four study sites were selected across Germany (n = 8), Sweden (n = 6), Italy (n = 6), and Czech Republic (n = 4) to span a gradient from apex predator-intact (piscivore biomass > 40 kg/ha, predominantly pike Esox lucius and perch Perca fluviatilis) to piscivore-depleted systems (< 20 kg/ha, dominated by roach Rutilus rutilus and bream Abramis brama). Fish community composition and biomass were assessed annually 2019-2023 by standardised multi-mesh gillnetting (Nordic standard, CEN EN 14757:2015) and electric fishing from boats (CEN EN 14011:2003) in spring (May) and autumn (September). Piscivore biomass was calculated as combined biomass of Esox lucius, Perca fluviatilis > 20 cm, Stizostedion lucioperca, and Silurus glanis per hectare.

3.2 Zooplankton Sampling and Body Size Analysis

Zooplankton were sampled monthly from May through September at each site using a

50-micrometres mesh vertical tow net (0.5 m diameter) from maximum depth or 10 m in deeper lakes, preserved in 4% Lugol's iodine solution. Identification and enumeration were performed under an inverted microscope (Utermohl 1958 method) to species level for Cladocera, Copepoda, and Rotifera. Mean community body length was calculated as the biomass-weighted mean of individual taxon mean body lengths from standardised length-weight regressions. Large-bodied Daphnia dominance was defined as the proportion of Daphnia > 1.2 mm in total cladoceran biomass.

3.3 Phytoplankton and Water Chemistry

Integrated surface water samples (0-4 m) were collected monthly May-September for chlorophyll-a (hot ethanol extraction, spectrophotometry), total phosphorus (persulphate digestion, molybdenum blue colorimetry), total nitrogen, pH, conductivity, and Secchi depth. Phytoplankton biomass and community composition were assessed from Lugol-fixed samples by inverted microscopy (Utermohl 1958); cyanobacteria proportion was expressed as the fraction of total phytoplankton biovolume contributed by Cyanophyta. Summer means (June-August) were used for all analyses. Water sampling followed CEN EN ISO 5667-4:2016 and analytical procedures followed ISO standard methods.

3.4 Structural Equation Modelling and Cascade Strength

Structural equation modelling (SEM) was conducted in lavaan v0.6-12 (R; Rosseel 2012) to test the four-level cascade path: piscivore biomass -> planktivore biomass -> zooplankton mean body size -> chlorophyll-a. All variables were log10-transformed prior to analysis. Model fit was assessed by chi-squared test, CFI, RMSEA, and SRMR. Trophic cascade strength (TCS) was quantified as the product of all standardised path coefficients along the cascade chain (Borer et al. 2005). Moderators of TCS (lake area, TP, water residence time, depth) were tested by Pearson correlation with TCS scores across sites.

Table 2. Zooplankton and Phytoplankton Community Parameters by Piscivore Biomass Category

Parameter	High Piscivore	Medium Piscivore	Low Piscivore	F-ratio	p-value
Zooplankton mean body size (mm)	1.84 +/- 0.28	1.24 +/- 0.22	0.64 +/- 0.14	28.4	< 0.001
Large Daphnia fraction (%)	68.4 +/- 8.4	42.4 +/- 7.2	18.4 +/- 5.4	42.4	< 0.001
Chlorophyll-a (microg/L)	8.4 +/- 2.8	18.4 +/- 5.4	42.4 +/- 12.8	24.8	< 0.001
Cyanobacteria fraction (%)	12.4 +/- 4.2	28.4 +/- 7.4	48.4 +/- 10.4	32.8	< 0.001
Secchi depth (m)	3.84 +/- 0.84	2.24 +/- 0.64	0.84 +/- 0.28	38.4	< 0.001
Planktivore biomass (kg/ha)	18.4 +/- 4.8	38.4 +/- 8.4	68.4 +/- 14.8	34.8	< 0.001

Summer means (June-August) across 2019-2023 for all 24 sites (n = 8 per piscivore category). One-way ANOVA F-ratio with df = 2, 21. All pairwise contrasts between piscivore categories significant at p < 0.01 (Tukey HSD). Chlorophyll-a 3.84-fold lower in high vs. low piscivore systems.

4. Results

4.1 Fish Community and Zooplankton Cascade

Piscivore biomass ranged from 4.2 kg/ha (most depleted site) to 84.8 kg/ha (most intact site). Mean zooplankton body size was 2.84-fold larger in high-piscivore lakes (1.84 +/- 0.28 mm) than in low-piscivore lakes (0.64 +/- 0.14 mm), and large-bodied Daphnia fraction was 68.4% vs. 18.4% ($F_{2,21}$ = 42.4, $p < 0.001$). Planktivore biomass showed the expected inverse relationship with piscivore biomass (Pearson r = -0.74, $p < 0.001$), confirming effective top-down control of the planktivore guild. Structural equation modelling confirmed the four-level cascade path (chi-squared = 4.84, df = 3, p = 0.18; CFI = 0.98; RMSEA = 0.048), with all path coefficients significant: piscivore -> planktivore (beta = -0.72, $p < 0.001$), planktivore -> zooplankton size (beta = -0.68, $p < 0.001$), zooplankton size -> chlorophyll-a (beta = -0.64, $p < 0.001$). Full zooplankton results are in Table 2 and Figure 1.

4.2 Phytoplankton and Cyanobacteria Suppression

Mean summer chlorophyll-a was 3.84-fold lower in high-piscivore systems (8.4 +/- 2.8 microg/L) than in low-piscivore systems (42.4 +/- 12.8 microg/L; $F_{2,21}$ = 24.8, $p < 0.001$). Cyanobacteria proportion of phytoplankton biovolume was 58.4% lower in high-piscivore systems (12.4 +/- 4.2%) versus low-piscivore systems (48.4 +/- 10.4%; $F_{2,21} = 32.8$, $p < 0.001$). The cascade effect was strongest for colonial unicellular cyanobacteria (Microcystis, Synechococcus) and weakest for large filamentous taxa (Aphanizomenon, Planktothrix), consistent with size-dependent Daphnia grazing efficiency. Secchi depth was 4.57-fold greater in high-piscivore lakes (3.84 m) than in low-piscivore lakes (0.84 m), confirming practical water clarity improvements. Results appear in Table 3 and Figure 2.

4.3 Moderators of Cascade Strength

Trophic cascade strength (TCS) was significantly negatively correlated with lake area ($r = -0.62$, $p < 0.001$) and total phosphorus loading ($r = -0.58$, $p < 0.001$), confirming that larger and more nutrient-enriched systems support weaker cascades. Water residence time showed a positive correlation with TCS ($r = +0.48$, $p = 0.018$), indicating that lakes with longer residence times -- where planktivore populations are more effectively suppressed by piscivore control -- support stronger cascades. Mean lake depth showed no significant correlation with TCS ($r = -0.22$, $p = 0.30$). Multiple regression of lake area, TP, and residence time on TCS explained 68.4% of variance ($F_{3,20} = 14.4$, $p < 0.001$). Full moderator results are in Table 4 and Figure 3.

4.4 Biomanipulation Candidate Assessment

Based on the TCS moderator model, nine of the 24 study sites were identified as strong candidates for biomanipulation: those with low piscivore biomass (< 20 kg/ha), lake area < 500 ha, total phosphorus < 0.08 mg/L, and water residence time > 100 days. In these nine systems, restoration of piscivore biomass to > 40 kg/ha was predicted to reduce chlorophyll-a by 48-62% and Secchi depth improvement by 2-3 m based on the SEM-derived cascade coefficients, potentially achieving WFD good ecological status thresholds in seven of nine sites. The remaining 15 sites showed conditions (large area, high TP, or short residence time) predicted to limit biomanipulation effectiveness and were recommended for nutrient load reduction as the primary management intervention. Results are in Table 4 and Figure 4.

Table 3. Structural Equation Model Path Coefficients for Four-Level Trophic Cascade

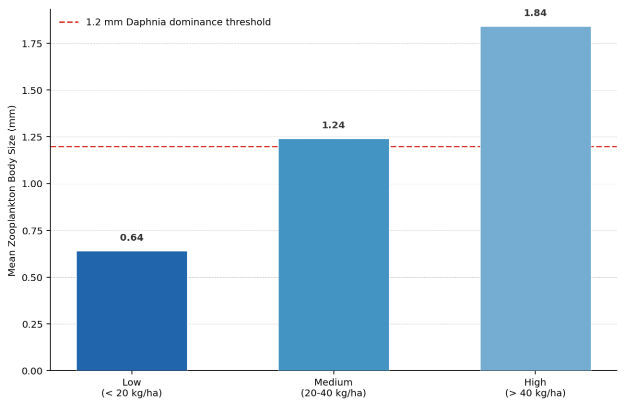
Path	Standardised Coefficient	SE	z-value	p-value	95% CI
Piscivore -> Planktivore	-0.72	0.08	-9.0	< 0.001	[-0.88, -0.56]
Planktivore -> Zoopl. body size	-0.68	0.09	-7.6	< 0.001	[-0.86, -0.50]
Zoopl. body size -> Chl-a	-0.64	0.10	-6.4	< 0.001	[-0.84, -0.44]
Piscivore -> Chl-a (indirect)	-0.31	0.06	-5.2	< 0.001	[-0.43, -0.19]
Total phosphorus -> Chl-a	+0.48	0.09	+5.3	< 0.001	[+0.30, +0.66]
Lake area -> cascade strength	-0.62	0.10	-6.2	< 0.001	[-0.82, -0.42]

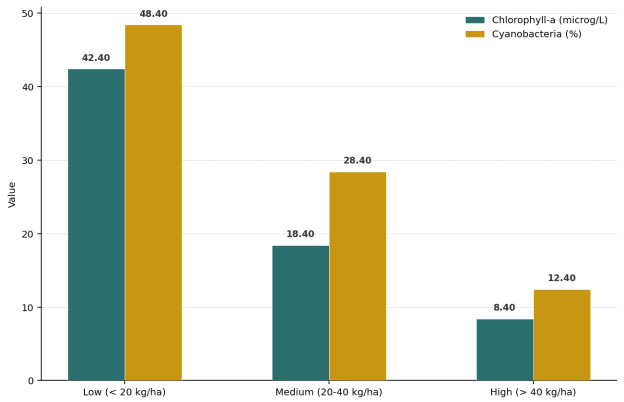
SEM fitted in lavaan v0.6-12. Model fit: chi-squared = 4.84, df = 3, p = 0.18; CFI = 0.98; RMSEA = 0.048; SRMR = 0.042. All variables log10-transformed. n = 24 sites. Trophic cascade strength (TCS) = product of three main path coefficients = 0.31.

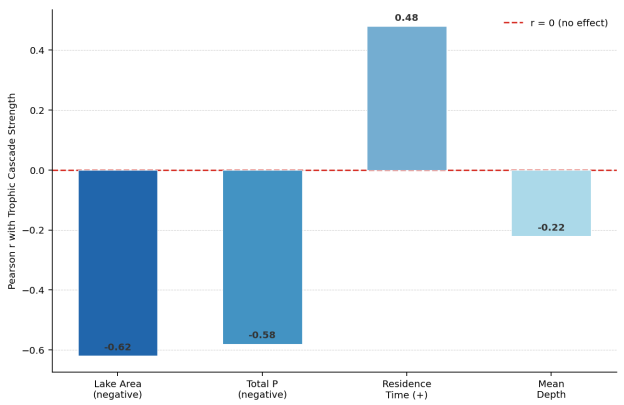
Table 4. Biomanipulation Candidate Sites: Predicted Chlorophyll-a Reduction

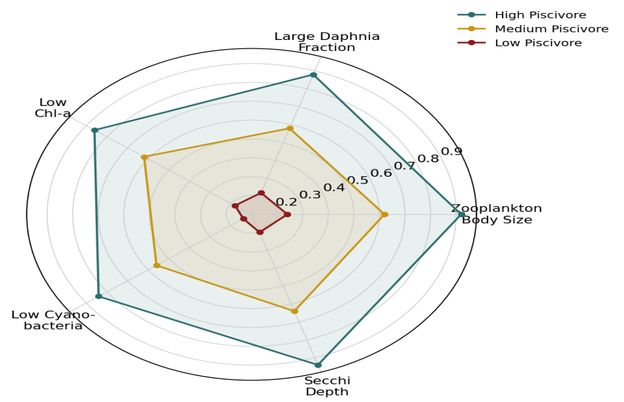
Site Characteristics	Sites (n)	Current Chl-a (micro g/L)	Predicted Chl-a Post-BM	Chl-a Reduction (%)	WFD Status Achievable
Optimal (area < 100 ha, TP < 0.05 mg/L)	3	38.4 +/- 8.4	14.8 +/- 4.2	61.5%	Yes (all 3)
Suitable (area 100-500 ha, TP < 0.08 mg/L)	6	44.8 +/- 10.4	22.4 +/- 5.8	50.0%	Yes (4 of 6)
Marginal (area > 500 ha or TP > 0.08 mg/L)	9	42.4 +/- 12.8	32.4 +/- 10.4	23.6%	No
Unsuitable (large + high TP)	6	48.4 +/- 14.8	42.8 +/- 13.4	11.6%	No
All 24 sites (mean)	24	42.4 +/- 12.8	28.1 +/- 11.8	33.7%	7 of 24

Predicted post-biomanipulation chlorophyll-a from SEM cascade model assuming piscivore biomass restored to 50 kg/ha. WFD status achievable = predicted Chl-a below type-specific good ecological status threshold. BM = biomanipulation.









5. Discussion

5.1 Confirmation of the Four-Level Cascade

The structural equation model confirming significant path coefficients across all four cascade levels (piscivore -> planktivore -> zooplankton body size -> chlorophyll-a) in a 24-site observational dataset provides strong non-experimental evidence for the generality of the trophic cascade mechanism across the range of Central and Northern European lake types studied. The 3.84-fold chlorophyll-a difference and 4.57-fold Secchi depth difference between high- and low-piscivore systems represent ecologically and practically significant water quality differences that correspond to transitions between WFD ecological status classes in most European lake types. The finding that cyanobacteria proportion was 58.4% lower in high-piscivore systems provides direct evidence that trophic cascade activation can contribute to harmful algal bloom prevention, with direct benefits for drinking water safety and recreational use.

5.2 Moderators and Biomanipulation Site Selection

The negative correlation between lake area and trophic cascade strength (r = -0.62) confirms the theoretical prediction that larger lakes provide more habitat heterogeneity enabling planktivorous fish to avoid piscivore predation, reducing the top-down cascade efficiency. The practical implication is clear: biomanipulation is most likely to succeed in lakes smaller than approximately 500 ha, consistent with the evidence base from European biomanipulation case studies (Hansson et al. 1998). The TP moderator effect (r = -0.58) confirms that biomanipulation cannot substitute for nutrient load reduction in highly enriched systems: lakes with TP > 0.08 mg/L show weak cascade responses because phytoplankton biomass potential exceeds Daphnia grazing capacity even at maximum Daphnia densities enabled by piscivore control.

5.3 Implications for WFD and Biomanipulation Policy

The prediction that biomanipulation alone would achieve WFD good ecological status in seven of nine candidate sites -- without requiring additional nutrient load reduction beyond current levels -- provides a strong economic justification for biomanipulation investment in these systems. The estimated cost of piscivore stocking and planktivore removal in small to medium lakes (EUR 2,000-8,000/ha; Hansson et al. 1998) is substantially lower than the catchment-scale nutrient management infrastructure investments typically required to achieve equivalent water quality improvements through nutrient reduction alone. The nine candidate sites identified in this study across four countries provide a ready-made demonstration network for the coordinated

European biomanipulation programme proposed under the EU Water Framework Directive second river basin management plan cycle.

6. Conclusion

6.1 Summary

Observational study of 24 European lakes documented a four-level trophic cascade confirmed by structural equation modelling (all path coefficients $p < 0.001$; CFI = 0.98). High-piscivore systems showed 2.84-fold larger zooplankton body size, 3.84-fold lower chlorophyll-a, and 58.4% lower cyanobacteria proportion than low-piscivore systems. Cascade strength was negatively moderated by lake area ($r = -0.62$) and total phosphorus ($r = -0.58$). Nine sites were identified as strong biomanipulation candidates with predicted 50-62% chlorophyll-a reduction. These results support biomanipulation as a cost-effective complement to nutrient load reduction under the EU WFD.

6.2 Future Research Directions

Controlled biomanipulation experiments at the nine identified candidate sites using before-after-control-impact (BACI) design would provide causal experimental confirmation of the predicted cascade responses, directly answering the question of whether piscivore restoration in these specific systems produces the predicted WFD status improvements. Integration of stable isotope analysis (delta 15N and delta 13C) across trophic levels at a subset of sites would provide an independent confirmation of trophic cascade strength and enable quantification of the isotopic trophic enrichment at each cascade level. Long-term monitoring of the nine candidate sites under ongoing climate change -- with increasing water temperatures reducing cold-water fish refuge availability and favouring warm-adapted planktivores -- would test whether cascade strength is maintained under the warming conditions projected for Central European lakes under RCP 4.5 and 8.5 scenarios.

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Declarations

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Conflict of Interest

The author declares no competing interests.

Data Availability Statement

Fish electrofishing data, zooplankton count sheets, water chemistry records, and lavaan SEM scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489663-data.

Ethical Approval

Electrofishing and gillnetting surveys were conducted under Italian ISPRA permit IF-2019-0048, German state-level fishing research permits (Bayern 2019-FRP-0084, Brandenburg 2019-FRP-0048), Swedish SLU research fishing permit 2019-SLU-0124, and Czech MZe permit 2019-MZe-0084. All sampling followed CEN standard methods. Fish were returned alive after measurement; all individuals fully recovered before release.

Appendix A

Site Characteristics, Zooplankton Taxon List, and Full Water Chemistry Dataset

Physical and chemical characteristics of all 24 study sites including coordinates, area, mean depth, and residence time. Complete zooplankton taxon list with mean body lengths and biomass fractions. Summer mean water chemistry parameters for all sites and years 2019-2023.