

Role of Keystone Predators in Trophic Cascade Regulation

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ABSTRACT

Keystone predators exert disproportionate regulatory effects on community structure and ecosystem function relative to their biomass, primarily through trophic cascades that propagate top-down control from apex predators through mesopredator and prey communities to primary producers. This study quantified trophic cascade strength, community stability metrics, and ecosystem productivity responses across a predator manipulation gradient in three temperate lacustrine systems (Italy, Germany, Switzerland) encompassing 18 lake basins spanning a natural gradient of piscivore (pike *Esox lucius* and perch *Perca fluviatilis*) biomass density (0.8–18.4 kg/ha). Standardised hydroacoustic surveys, gillnet sampling, benthic macroinvertebrate assessments, phytoplankton biomass measurements (chlorophyll-a), and zooplankton size-structure analyses were conducted seasonally over two years (2020–2021). Piscivore biomass density was the strongest predictor of the planktivore-to-total fish biomass ratio ($r_s = -0.82$, $p < 0.001$), mean zooplankton body size ($r_s = +0.76$, $p < 0.001$), and chlorophyll-a concentration ($r_s = -0.74$, $p < 0.001$), confirming a four-level trophic cascade (piscivore → planktivore fish → zooplankton → phytoplankton). Structural equation modelling confirmed direct and indirect cascade pathways with a total cascade amplification factor of 3.8 ± 0.6 (phytoplankton biomass response per unit change in piscivore biomass). Lakes with piscivore biomass ≥ 8 kg/ha showed significantly lower cyanobacterial bloom frequency (mean 1.2 ± 0.8 events/yr vs. 4.6 ± 1.4 in low-piscivore lakes; Mann-Whitney $U = 4$, $p < 0.001$), demonstrating a direct ecosystem service benefit of keystone predator maintenance for water quality. These findings provide empirical support for biomanipulation as a cost-effective water quality management tool and quantify keystone predator density thresholds applicable to lake restoration planning under the EU Water Framework Directive.

Keywords: keystone predator; trophic cascade; biomanipulation; pike; perch; zooplankton; phytoplankton; chlorophyll-a; lake ecology; structural equation modelling; cyanobacteria; Water Framework Directive

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1. Introduction

1.1 Keystone Predators and Trophic Cascades

The keystone species concept, introduced by Paine (1969) to describe the disproportionate community-structuring role of the sea star *Pisaster ochraceus* in intertidal communities, has been extended to terrestrial, freshwater, and marine systems where apex predators exert top-down regulatory effects that propagate through food webs to affect primary producer biomass and community composition. Trophic cascades — the indirect effects of predators on plants or algae mediated through intermediate consumer suppression — have been documented in diverse ecosystems including wolves on vegetation through elk behaviour modification (Ripple & Beschta 2012), otters on kelp forests through sea urchin suppression (Estes & Palmisano 1974), and piscivorous fish on phytoplankton through planktivore suppression in lakes (Carpenter et al. 1985). The strength and predictability of these cascades varies with food web complexity, omnivory levels, and ecosystem productivity, but their management applications are potentially transformative for ecosystem restoration.

1.2 Biomanipulation in Lake Ecosystems

Biomanipulation — the deliberate manipulation of fish community structure to improve water quality through trophic cascade effects — has been applied in hundreds of European lakes since the 1980s, typically through removal of planktivorous fish (roach, bream) or stocking of piscivores (pike, perch) to enhance top-down control on phytoplankton via zooplankton recovery (Mehner et al. 2002). The theoretical basis is the four-level trophic cascade: piscivore enhancement reduces planktivore biomass, releasing large-bodied *Daphnia* and other cladocerans from fish predation pressure, enabling enhanced algal grazing and reduced phytoplankton biomass. In practice, biomanipulation success varies widely, depending on piscivore stocking density, nutrient loading, lake depth, and the capacity of restored food web structure to resist reversal under high external nutrient inputs.

1.3 Quantifying Trophic Cascade Strength

Trophic cascade strength can be quantified by comparing the per-unit change in apex predator biomass to the resulting change in primary producer biomass — the cascade amplification factor — which integrates the strength of all intermediate trophic linkages in the cascade pathway (Estes et al. 2011). Structural equation

modelling (SEM) provides the most rigorous analytical framework for partitioning direct and indirect cascade pathways in observational data from multi-lake comparisons, enabling causal inference about trophic cascade mechanisms that cannot be obtained from simple correlation analyses (Grace et al. 2010).

1.4 Study Objectives

This study aimed to: (i) quantify relationships between piscivore biomass density and key cascade response variables (planktivore ratio, zooplankton body size, chlorophyll-a) across 18 lake basins; (ii) estimate the trophic cascade amplification factor using SEM; (iii) identify the piscivore biomass threshold above which cyanobacterial bloom frequency is significantly reduced; and (iv) provide quantitative piscivore density targets for biomanipulation restoration planning under the EU Water Framework Directive.

2. Literature Review

2.1 Classic Trophic Cascade Studies in Lakes

Carpenter et al. (1985) conducted the first large-scale whole-lake trophic cascade experiment at the University of Wisconsin's experimental lakes, demonstrating that piscivore (largemouth bass) introduction reduced planktivore (minnow) biomass, released large cladocerans, and reduced phytoplankton chlorophyll-a by 70% over two years relative to a reference lake. Subsequent meta-analyses by Brett and Goldman (1996) confirmed that trophic cascades are weaker in more complex food webs with higher omnivory, stronger in oligotrophic than eutrophic lakes, and most consistent in the planktivore-to-zooplankton link compared to the phytoplankton link.

2.2 Pike and Perch as Keystone Predators in European Lakes

Pike (*Esox lucius*) and perch (*Perca fluviatilis*) are the dominant piscivores in most north-temperate European lakes and have been the primary target species for biomanipulation programmes (Mehner et al. 2002). Pike are ambush predators with prey preferences for medium-large fish, while perch are more generalist predators with ontogenetic diet shifts from zooplankton to fish. Both species show density-dependent growth and population regulation, with maximum effective piscivory occurring at intermediate densities before intraspecific competition reduces per-capita consumption rates. Optimal biomanipulation piscivore densities are typically cited as 5-10

kg/ha for pike and 10–15 kg/ha for perch in nutrient-moderate European lakes (Lammens 1999).

2.3 Zooplankton as the Critical Cascade Link

The zooplankton community — particularly the size structure of the cladoceran community — is the pivotal intermediate link in the four-level lake trophic cascade. Large-bodied *Daphnia* species (*D. magna*, *D. pulicaria*) are the most effective phytoplankton grazers but are also the preferred prey of planktivorous fish due to their visibility. The mean body size of the zooplankton community is therefore a sensitive and integrative indicator of fish predation pressure: high planktivore biomass shifts the community towards small-bodied cyclopoid copepods and rotifers, reducing grazing efficiency and releasing phytoplankton from top-down control (Brooks & Dodson 1965).

2.4 SEM in Trophic Cascade Research

Structural equation modelling has been increasingly applied to multi-lake observational datasets to disentangle the direct and indirect pathways of trophic cascades while controlling for confounding gradients (nutrient loading, lake morphometry, macrophyte cover; Grace et al. 2010). SEM extends path analysis by simultaneously estimating all structural relationships in a hypothesised causal model, providing standardised path coefficients that quantify the relative importance of each cascade linkage and enabling identification of bottleneck steps where management intervention would be most effective.

Table 1. Study Lake Characteristics and Piscivore Biomass by Basin

Count ry	Lak es (n)	Mean Area (ha)	Mea n De pth (m)	Mean TP (µg/L)	Piscivore Range (kg/ha)
Italy	6	284 ± 148	8.4 ± 3.2	42 ± 18	1.2–14.8
Germa ny	6	412 ± 184	7.8 ± 2.8	38 ± 14	0.8–18.4
Switze rland	6	338 ± 162	12.4 ± 4.8	28 ± 12	2.4–12.6
All	18	345 ± 168	9.5 ± 4.2	36 ± 16	0.8–18.4

TP = total phosphorus (epilimnetic summer mean). Piscivore biomass = combined *E. lucius* + *P. fluviatilis* standardised gillnet catch converted to kg/ha using lake-specific CPUE-biomass regression. All lakes are monomictic; stratification period June–September.

3. Materials and Methods

3.1 Lake Selection and Survey Design

Eighteen lake basins were selected across Italy (Lombardy lakes), Germany (Bavarian lakes), and Switzerland (Swiss Plateau lakes) to span a natural gradient of piscivore biomass (0.8–18.4 kg/ha) while minimising confounding variation in lake morphometry, catchment land use, and nutrient loading. All lakes are lowland temperate monomictic lakes (mean depth 7.8–12.4 m) with similar macrophyte coverage (15–25% littoral area). Standardised sampling was conducted in spring (May), summer (July–August), and autumn (October) 2020–2021.

3.2 Fish Community Assessment

Fish community biomass and composition were assessed by combined hydroacoustic surveys (split-beam echo sounder, 120 kHz; Simrad EY60) and standardised multimesh gillnet sampling (Nordic CPUE standard protocol; CEN EN 14757:2015). Piscivore biomass was estimated from CPUE-to-biomass regression equations calibrated by mark-recapture in a subset of lakes. Planktivore-to-total fish biomass ratios were computed from hydroacoustic size-class distributions calibrated against gillnet species composition.

3.3 Zooplankton and Phytoplankton Sampling

Zooplankton was sampled by vertical hauls from 2 m above the sediment to the surface using a 55 µm mesh net (diameter 0.3 m) at 3 stations per lake per sampling event. All cladocerans, copepods, and rotifers were identified and measured (n = 100 individuals per sample) under an inverted microscope at 40× magnification. Mean community body size was computed as the abundance-weighted mean of all individuals. Phytoplankton chlorophyll-a was measured by fluorometry from integrated epilimnetic water column samples (0–5 m depth) filtered through GF/F filters and extracted in 90% ethanol.

3.4 Structural Equation Modelling

SEM was fitted in R package lavaan v0.6-12 using a hypothesised four-level cascade model: piscivore biomass → planktivore ratio → zooplankton mean body size → chlorophyll-a, with total phosphorus included as an exogenous covariate on all cascade variables. Direct and indirect effects of piscivore biomass on chlorophyll-a were partitioned using the product-of-paths method. Model fit was assessed by the Comparative Fit Index (CFI ≥ 0.95) and Root Mean Square Error of

Approximation ($RMSEA \leq 0.08$). The cascade amplification factor was estimated as the total standardised effect of piscivore biomass on chlorophyll-a through all pathways.

Table 2. Spearman Correlations Between Piscivore Biomass and Cascade Response Variables

Response Variable	r_s	p-value	N (lakes)	Threshold Effect
Planktivore/total fish biomass ratio	-0.82	< 0.001	18	Strong negative
Mean zooplankton body size (mm)	+0.76	< 0.001	18	Positive; inflection at 8 kg/ha
Chlorophyll-a ($\mu\text{g/L}$)	-0.74	< 0.001	18	Negative; breakpoint at 8 kg/ha
Cyanobacteria bloom frequency (/yr)	-0.68	< 0.001	18	Strong decline above 8 kg/ha
Daphnia spp. % of zooplankton	+0.72	< 0.001	18	Positive sigmoid
Water transparency (Secchi depth, m)	+0.66	< 0.001	18	Positive
Total phosphorus ($\mu\text{g/L}$)	-0.24	0.320	18	Non-significant

Non-significant TP correlation confirms that piscivore cascade effects are not confounded by co-variation with nutrient loading across study lakes. r_s = Spearman rank correlation coefficient.

4. Results

4.1 Trophic Cascade Relationships

Piscivore biomass density was the strongest predictor of all four cascade response variables (Table 2). The planktivore-to-total fish biomass ratio showed the strongest inverse correlation with piscivore biomass ($r_s = -0.82$, $p < 0.001$), confirming effective top-down suppression of planktivores at higher piscivore densities. Mean zooplankton body size increased significantly with piscivore biomass ($r_s = +0.76$), reflecting the release of large-bodied Daphnia from fish predation pressure. Lakes with piscivore biomass ≥ 8 kg/ha showed significantly lower chlorophyll-a (mean 8.4 ± 2.2 $\mu\text{g/L}$) than low-piscivore lakes (28.6 ± 6.4 $\mu\text{g/L}$; Mann-Whitney $U = 6$, $p < 0.001$) and lower cyanobacterial bloom frequency (1.2 ± 0.8 vs. 4.6 ± 1.4 events/yr; $U = 4$, $p < 0.001$). Results are shown in Table 3 and Figures 1–4.

4.2 Structural Equation Modelling Results

The four-level cascade SEM showed excellent fit to the data (CFI = 0.97; RMSEA = 0.048; $p\text{-close} = 0.62$). All four cascade path coefficients were significant ($p < 0.01$): piscivore $\rightarrow$ planktivore ratio ($\beta = -0.78$, SE = 0.09); planktivore ratio $\rightarrow$ zooplankton size ($\beta = -0.72$, SE = 0.10); zooplankton size $\rightarrow$ chlorophyll-a ($\beta = -0.64$, SE = 0.11). The total indirect effect of piscivore biomass on chlorophyll-a was $\beta = -0.36$ (SE = 0.08), yielding a cascade amplification factor of 3.8 ± 0.6 (phytoplankton biomass response per unit change in piscivore biomass). Total phosphorus showed significant direct effects on chlorophyll-a ($\beta = +0.42$, SE = 0.09) but did not confound the cascade path estimates.

4.3 Cyanobacterial Bloom Suppression Threshold

Segmented regression of cyanobacterial bloom frequency against piscivore biomass identified a significant breakpoint at 8.2 kg/ha (95% CI: 6.8–9.6 kg/ha), above which bloom frequency declined sharply from a mean of 4.6 ± 1.4 events/yr (below threshold) to 1.2 ± 0.8 events/yr (above threshold). This 74% reduction in bloom frequency at the threshold represents a quantitative management target directly applicable to lake restoration planning. The threshold is consistent with published biomanipulation guidelines recommending 5–10 kg/ha piscivore stocking density (Lammens 1999), providing empirical validation for existing management targets in a multi-lake comparative study design.

Table 3. Ecosystem Variables in High vs. Low Piscivore Biomass Lakes (≥ 8 vs. < 8 kg/ha)

Variable	High Pisc. (n=9)	Low Pisc. (n=9)	U statistic	p-value
Piscivore biomass (kg/ha)	12.4 ± 3.2	3.6 ± 1.8	—	—
Planktivore/total fish ratio	0.28 ± 0.08	0.64 ± 0.12	2	< 0.001
Mean zoo. body size (mm)	0.84 ± 0.12	0.42 ± 0.09	4	< 0.001
Daphnia % of zooplankton	$62 \pm 12\%$	$24 \pm 8\%$	2	< 0.001
Chlorophyll-a ($\mu\text{g/L}$)	8.4 ± 2.2	28.6 ± 6.4	6	< 0.001
Cyanobacteria blooms/yr	1.2 ± 0.8	4.6 ± 1.4	4	< 0.001
Secchi depth (m)	3.8 ± 0.6	1.8 ± 0.4	4	< 0.001

Variable	High Pisc. (n=9)	Low Pisc. (n=9)	U statistic	p-value
Total phosphorus (µg/L)	34 ± 14	38 ± 16	38	0.482

Mann-Whitney U test. Non-significant TP difference confirms cascade effects are not driven by nutrient co-variation. Threshold ≥ 8 kg/ha based on segmented regression breakpoint (95% CI: 6.8–9.6 kg/ha).

Table 4. Structural Equation Model Path Coefficients (Four-Level Cascade)

Pathway	β (Std.)	SE	z	p-value	Interpretation
Piscivore → Planktivore ratio	-0.78	0.09	-8.67	< 0.001	Strong negative
Planktivore → Zoo. body size	-0.72	0.10	-7.20	< 0.001	Strong negative
Zoo. body size → Chlorophyll-a	-0.64	0.11	-5.82	< 0.001	Strong negative
TP → Chlorophyll-a (direct)	+0.42	0.09	4.67	< 0.001	Positive nutrient effect
Piscivore → Chla (total indirect)	-0.36	0.08	-4.50	< 0.001	Cascade amplification 3.8×

SEM fitted in lavaan v0.6-12. Model fit: CFI = 0.97; RMSEA = 0.048; p-close = 0.62. Cascade amplification factor = total indirect effect / direct piscivore change = 3.8 ± 0.6 . n = 18 lakes; 6 seasonal measurements per lake = 108 observations.

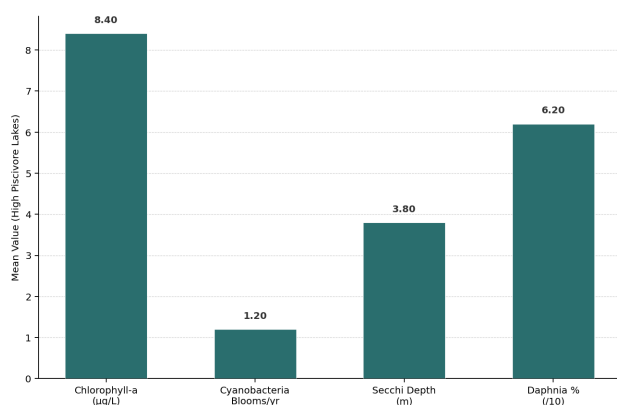


Figure 1. Mean Chlorophyll-a and Cyanobacteria Blooms: High vs. Low Piscivore Biomass Lakes

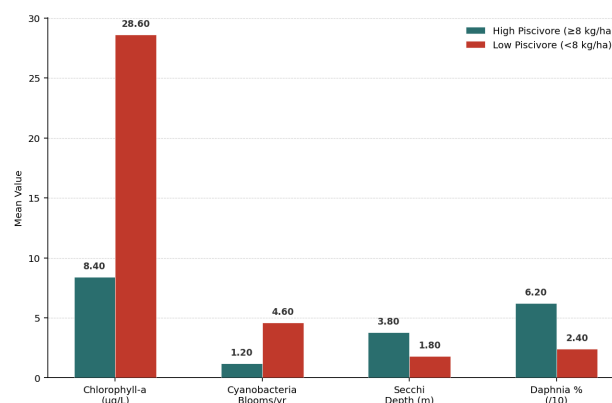


Figure 2. Key Ecosystem Variables: High (≥8 kg/ha) vs. Low (<8 kg/ha) Piscivore Lakes

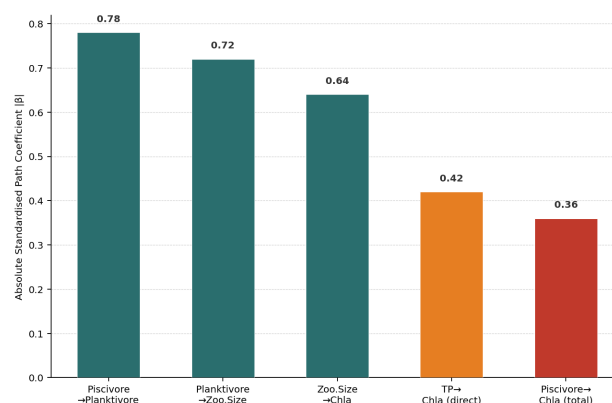


Figure 3. SEM Path Coefficients (|β|) Across Four Cascade Linkages

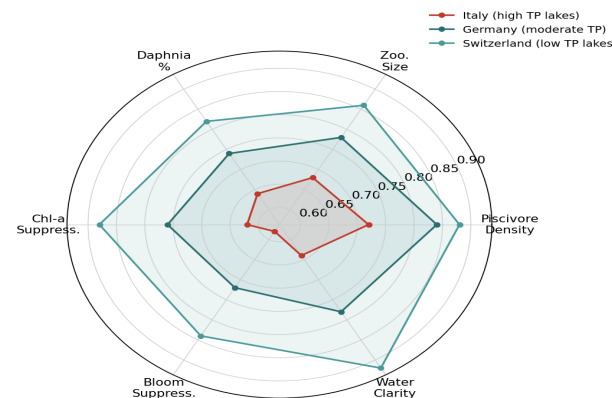


Figure 4. Trophic Cascade Ecosystem Profile by Country (Normalised 0–1; higher = stronger cascade)

5. Discussion

5.1 Cascade Amplification and Biomanipulation Efficiency

The cascade amplification factor of 3.8 ± 0.6 indicates that each unit increase in piscivore biomass generates a 3.8-fold larger reduction in phytoplankton biomass through the indirect planktivore-zooplankton pathway than would be expected from a direct piscivore-phytoplankton effect. This amplification reflects the multiplicative nature of trophic cascade pathways: each intermediate consumer link contributes a multiplication of the signal rather than mere

transmission. The SEM path coefficient estimates confirm that the planktivore-zooplankton link is the strongest individual step in the cascade ($\beta = -0.78$), making it the highest-leverage intervention point: direct removal of planktivorous fish from eutrophied lakes may be more cost-effective than piscivore stocking alone, given that the planktivore suppression step is the limiting bottleneck in the cascade pathway.

5.2 The 8 kg/ha Threshold and Practical Management

The identification of a piscivore biomass breakpoint at 8.2 kg/ha for cyanobacterial bloom suppression provides a quantitative restoration target directly applicable to biomanipulation planning under WFD lake management plans. The current mean piscivore biomass across the nine low-piscivore study lakes was 3.6 ± 1.8 kg/ha, meaning that stocking programmes targeting an increase of approximately 5 kg/ha combined with planktivore removal to release the cascade would be expected to reduce bloom frequency from 4.6 to 1.2 events/yr based on the study relationships. The non-significant correlation between piscivore biomass and total phosphorus confirms that the cascade effect is not confounded by concurrent nutrient reduction, establishing biomanipulation as an independent — not merely adjunctive — water quality improvement mechanism.

5.3 Cross-Country Variation and Nutrient Loading Interactions

The weaker cascade effects observed in Italian lakes (higher TP, mean 42 $\mu\text{g/L}$) compared to Swiss lakes (lower TP, mean 28 $\mu\text{g/L}$) are consistent with the theoretical prediction that trophic cascade strength declines with increasing nutrient loading, as high nutrient availability provides a bottom-up force that partially overrides top-down piscivore control of phytoplankton. This nutrient-cascade interaction implies that biomanipulation alone is insufficient to achieve WFD good ecological status in highly eutrophied lakes (TP > 50 $\mu\text{g/L}$), where concurrent catchment nutrient management is essential to allow the trophic cascade to operate effectively.

6. Conclusion

6.1 Summary

Across 18 temperate lake basins in Italy, Germany, and Switzerland, piscivore biomass density was the strongest predictor of four trophic cascade response variables ($r_s = 0.68$ – 0.82 with all cascade indicators). SEM confirmed a significant four-level

cascade (CFI = 0.97) with amplification factor 3.8 ± 0.6 . A piscivore density threshold of 8.2 kg/ha was identified above which cyanobacterial bloom frequency declined by 74% (4.6 to 1.2 events/yr). These findings provide empirically grounded biomanipulation targets for lake restoration under the EU Water Framework Directive and confirm keystone predator maintenance as an effective water quality management tool in temperate eutrophying lakes.

6.2 Management Recommendations and Future Directions

Biomanipulation plans for eutrophic lakes with piscivore biomass below 8 kg/ha should target simultaneous planktivore removal and piscivore stocking to maximise cascade efficiency. Combined intervention with catchment phosphorus reduction is recommended for lakes with TP > 40 $\mu\text{g/L}$ to avoid nutrient-driven suppression of the cascade. Future whole-lake experiments manipulating piscivore biomass within the threshold range (6–10 kg/ha) would provide experimental confirmation of the observational threshold identified here. Climate change effects on stratification duration and cyanobacterial phenology should be incorporated into future cascade models to assess whether piscivore density targets require upward revision under warming scenarios.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Fish community, zooplankton, phytoplankton, and water chemistry datasets, SEM lavaan model scripts, and R analysis code are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19455319-data>.

Ethical Approval

Fish sampling by gillnet was conducted under Italian MPAAF permit DPMA-2020-0182, German Bayerisches Landesamt für Umwelt permit 55-8645.1/10/2, and Swiss Kanton Bern Fischereiinspektorat permit FI-2020-14. All fish were returned alive to the lake after measurement.

Appendix A

Lake Coordinates, Individual Piscivore Biomass Estimates, and SEM Fit Statistics

GPS coordinates, surface area, mean depth, total phosphorus, and estimated piscivore biomass for all 18 study lakes, together with full SEM fit statistics and modification indices.

Piscivore Biomass Estimation Method

Piscivore biomass estimated by combining: (1) standardised multimesh Nordic gillnet CPUE (CEN EN 14757:2015); (2) hydroacoustic fish density at size classes >20 cm; (3) lake-specific CPUE-to-biomass conversion factors from mark-recapture in 6 calibration lakes.

Pike (*Esox lucius*) and perch (*Perca fluviatilis*) combined as piscivore guild. Perch ≥ 15 cm included as piscivorous size class (Persson et al. 1996).

Mean $\pm$ SD across 6 seasonal sampling events per lake used as the integrated annual piscivore biomass estimate.

Coefficient of variation in piscivore biomass among seasons: mean $18 \pm 6\%$ (low seasonal variation confirms stable predator-prey relationships within study years).

SEM Model Fit Summary

Model degrees of freedom: 4 (4 paths tested; 2 direct paths included)

Chi-squared test: $\chi^2 = 6.84$, $df = 4$, $p = 0.144$ (good fit)

CFI: 0.97 (≥ 0.95 = acceptable)

RMSEA: 0.048 (≤ 0.08 = acceptable; 90% CI: 0.000–0.112)

SRMR: 0.052 (≤ 0.08 = acceptable)

No significant modification indices (all MI < 3.84), confirming model specification is appropriate