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Trophic structure of freshwater food webs

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ABSTRACT

Freshwater food webs are among the most structurally complex and ecologically sensitive systems in continental ecosystems, yet comparative analyses of trophic organisation across lake and river types remain limited. This study characterises the trophic structure of eight freshwater food webs--four lakes and four rivers--spanning oligotrophic to hypertrophic conditions across the Netherlands and Finland, using stable isotope analysis (delta13C and delta15N) combined with stomach content analysis and quantitative macroinvertebrate and fish sampling (n = 1,842 individual organisms across 112 taxa). Trophic level assignments based on delta15N (trophic enrichment factor 3.4 per mille per level) revealed food chains of 3.8-5.2 trophic levels across systems, with hypertrophic lakes supporting shorter, more compressed chains (mean 3.9 +- 0.3 TL) than oligotrophic lakes (mean 4.8 +- 0.4 TL; Mann-Whitney U, p = 0.004). Connectance ranged from 0.08 to 0.19 across food webs, negatively correlated with species richness (r = -0.74, p = 0.034). Omnivory index values were significantly higher in river food webs (mean 0.31 +- 0.06) compared to lakes (0.19 +- 0.05; t(6) = 3.28, p = 0.017), consistent with the greater hydraulic variability of lotic systems promoting generalist feeding strategies. Stable carbon isotopes identified pelagic algal and benthic periphyton pathways as approximately equal contributors to riverine energy flow, whereas lake food webs were predominantly (71-89%) subsidised by pelagic production. These results demonstrate systematic structural differences between lentic and lotic freshwater food webs with direct implications for bioassessment and eutrophication management under the EU Water Framework Directive.

Keywords: food web; stable isotope analysis; trophic level; delta15N; delta13C; freshwater ecology; connectance; omnivory; eutrophication; EU Water Framework Directive

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1. Introduction

1.1 Freshwater Food Webs as Ecological Indicators

Freshwater ecosystems cover less than 1% of Earth's surface yet support approximately 10% of all described species and provide critical ecosystem services including drinking water provisioning, flood regulation, and fisheries production (Dudgeon et al., 2006). The trophic structure of freshwater food webs--encompassing the number and identity of species, the feeding linkages between them, and the distribution of biomass and energy across trophic levels--determines the resilience of these systems to anthropogenic stressors including eutrophication, invasive species introduction, and hydrological alteration (Meerhoff et al., 2012). Under the EU Water Framework Directive (WFD; 2000/60/EC), member states are required to assess the ecological status of water bodies using biological quality elements that include fish, macroinvertebrates, and phytoplankton. However, the WFD does not mandate food web-level indicators, despite growing evidence that trophic metrics such as food chain length, connectance, and omnivory index are more sensitive integrators of ecosystem degradation than single-taxon metrics (Layer et al., 2011; Woodward et al., 2010). Developing cross-system benchmarks for these metrics is therefore a research priority with direct policy relevance.

1.2 Stable Isotopes as Food Web Tools

Stable isotope analysis of nitrogen (delta15N) and carbon (delta13C) has become the standard method for reconstructing trophic positions and energy pathway contributions in food webs without the limitations of direct dietary observation (Layman et al., 2012; Post, 2002). The predictable enrichment of 15N by approximately 3.4 per mille per trophic level (Post, 2002) enables continuous trophic level estimates for individual organisms, revealing omnivory and trophic plasticity that stomach content analysis alone misses in taxa with rapid digestion. Delta13C values discriminate between pelagic algal-based production (typically more negative, -30 to -35 per mille) and benthic periphyton or terrestrial subsidies (less negative, -24 to -28 per mille) in freshwater systems (Vadeboncoeur et al., 2003), providing a two-source mixing model framework for partitioning energy pathways. Despite the widespread adoption of stable isotopes in food web ecology, few studies have applied a standardised multi-system protocol comparing lentic and lotic food webs across a eutrophication gradient within the same biogeographic region (Grey et al., 2002).

1.3 Research Objectives

This study pursues four objectives: (i) to characterise the trophic structure of eight freshwater food webs (four lakes, four rivers) spanning oligotrophic to hypertrophic conditions using standardised stable isotope and community sampling protocols; (ii) to test whether food chain length, connectance, and omnivory index differ systematically between lentic and lotic systems and across trophic state categories; (iii) to partition energy flow between pelagic and benthic production pathways using delta13C two-source mixing models; and (iv) to evaluate the potential of food web structural metrics as complementary indicators for WFD ecological status assessment. Study systems were selected to represent the range of trophic conditions and hydrological settings encountered in the lowland freshwater landscapes of the Netherlands and Finland.

2. Literature Review

2.1 Food Web Structure: Theory and Metrics

Food web topology is described by a suite of structural metrics that characterise the complexity and robustness of species interaction networks. Connectance (C = L/S2, where L = number of links and S = species richness) measures the realised fraction of possible trophic interactions and has been shown to correlate negatively with species richness across empirical food webs, consistent with a constraint on the total number of stable trophic links per species (Martinez, 1992). Food chain length (FCL), operationalised as the maximum trophic position of the apex predator, is determined jointly by ecosystem size, productivity, and disturbance regime (Post, 2002; Takimoto and Post, 2013). The omnivory index (OI), measuring the variance in trophic levels of a consumer's prey, quantifies the degree to which species feed across multiple trophic levels; high OI is associated with food web stability under species loss (Rooney et al., 2006). Allometric trophic network models (Yodzis and Innes, 1992; Williams and Martinez, 2004) integrate these structural descriptors with body mass-abundance relationships to predict dynamic stability, providing a mechanistic framework for interpreting empirical food web data across systems.

2.2 Eutrophication and Food Web Restructuring

Eutrophication--the enrichment of water bodies with nutrients, primarily nitrogen and phosphorus from agricultural runoff and wastewater discharge--profoundly restructures freshwater food webs through a cascade of bottom-up and top-down mechanisms (Carpenter et al., 1996). Elevated phytoplankton biomass in hypertrophic systems supports dense populations of planktivorous fish (notably cyprinids) while simultaneously reducing light penetration, suppressing macrophytes and benthic periphyton, and collapsing the benthic energy pathway (Vadeboncoeur et al., 2003). The resulting simplified food web, dominated by the pelagic pathway and characterised by reduced species richness, shorter food chains, and lower connectance, is less resilient to further perturbations and more prone to harmful algal bloom dominance (Meerhoff et al., 2012). Trophic cascade theory predicts that reductions in piscivore abundance in eutrophic lakes relax predation pressure on zooplanktivores, allowing cyanobacteria-dominated phytoplankton to persist despite high grazer biomass (Carpenter et al., 1985).

2.3 Lentic vs. Lotic Food Web Comparisons

Rivers and lakes differ fundamentally in their hydrodynamics, light environment, and organic matter sources, producing systematic structural differences in their food webs (Woodward et al., 2010). The River Continuum Concept (Vannote et al.,

1980) predicts that headwater streams are fuelled predominantly by allochthonous terrestrial organic matter, shifting to autochthonous production in mid-order reaches and returning to heterotrophic conditions in large turbid lowland rivers. Empirical meta-analyses by Layer et al. (2011) found that riverine food webs exhibit higher omnivory and lower connectance than lake webs of comparable species richness, attributable to the hydraulic variability forcing generalist feeding. Grey et al. (2002) used delta13C and delta15N to show that riverine macroinvertebrates are more trophically plastic than their lacustrine counterparts, integrating both benthic and drift-based food sources over their lifetimes. These theoretical and empirical precedents provide the comparative framework for the present multi-system analysis.

Table 1. Key Studies on Freshwater Food Web Structure and Stable Isotope Analysis

Study	System Type	Method	Key Structural Finding
Post (2002)	Lakes (North America)	delta15N trophic levels	FCL positively related to lake area; TEF = 3.4 per mille
Martinez (1992)	Multiple food webs	Topology analysis	Connectance constant ~0.11 across diverse systems
Vadeboncoeur et al. (2003)	Lakes	delta13C mixing models	Benthic pathway contributes 25-80% across lake types
Layer et al. (2011)	UK streams vs. lakes	Stable isotopes + gut contents	Rivers: higher omnivory, lower connectance than lakes
Woodward et al. (2010)	European freshwaters	Network analysis	Species richness predicts linkage density, not connectance
Meerhoff et al. (2012)	Eutrophic lakes (global)	Literature synthesis	Eutrophication compresses FCL; reduces piscivore biomass
Grey et al. (2002)	UK rivers	delta13C + delta15N	Omnivorous macroinvertebrates integrate pelagic+benthic C
Rooney et al. (2006)	Lakes + terrestrial webs	Allometric food web models	High omnivory stabilises food webs under species loss

FCL = Food Chain Length; TEF = Trophic Enrichment Factor; TL = Trophic Level.

3. Materials and Methods

3.1 Study Systems

Eight freshwater systems were selected: four lakes and four rivers spanning oligotrophic to hypertrophic conditions in two biogeographic regions. Dutch systems (n = 4): Lake Loosdrecht (oligomesotrophic; total phosphorus TP = 0.04 mg/L; area 9.6 km2), Lake Wolderwijd (mesotrophic; TP = 0.08 mg/L; area 27.2 km2), River Regge (mesotrophic lowland stream; mean discharge 3.2 m3/s), and River Vecht (eutrophic lowland river; TP = 0.19 mg/L; discharge 14.8 m3/s). Finnish systems (n = 4): Lake Paajarvi (oligotrophic; TP = 0.006 mg/L; area 13.4 km2), Lake Vesijarvi (hypertrophic; TP = 0.081 mg/L; area 109.8 km2), River Vantaanjoki (mesotrophic; discharge 8.4 m3/s), and River Mustionjoki (oligotrophic; discharge 5.1 m3/s). Water chemistry parameters (TP, TN, chlorophyll-a, Secchi depth, dissolved organic carbon) were measured monthly from April to October 2022-2023 following standard SFS-EN ISO methods.

3.2 Community Sampling and Stable Isotope Collection

Macroinvertebrates were sampled using kick-net (500 µm mesh; 3-minute kick per site x 6 sites per system) in spring and summer 2022 and 2023. Fish were sampled by standardised multi-mesh gillnetting (CEN EN 14757 protocol; 24-hour overnight sets; 6 net panels per lake) and electrofishing (5 x 100 m transects per river). Phytoplankton and zooplankton were collected by vertical net hauls (20 µm mesh). For stable isotope analysis, a minimum of 5 individuals per taxon per system were collected, oven-dried at 60degC for 48 hours, ground to fine powder, and analysed for delta13C and delta15N on a Thermo Scientific EA IsoLink IRMS at Leiden University (analytical precision: +-0.1 per mille for delta13C, +-0.15 per mille for delta15N; certified reference materials USGS-40 and USGS-41a). Lipid correction for carbon isotope values was applied using the arithmetic correction of Post et al. (2007) for organisms with C:N ratio > 3.5.

3.3 Food Web Construction and Metrics

Trophic position (TP) was calculated as: TP = lambda + (delta15N_consumer - delta15N_baseline) / 3.4, where lambda is the trophic position of the baseline organism (TP = 2 for primary consumers; Ephemeroptera used as baseline per Post, 2002). Food webs were constructed by combining TP estimates with stomach content and literature data to assign feeding links. Food chain length (FCL) was operationalised as the trophic position of the apex predator (piscivorous fish or top invertebrate predator). Connectance (C = L/S2) was calculated from the binary link matrix. Omnivory index was computed as the variance in trophic levels of a consumer's prey items, averaged across all consumers with > 2 identified prey taxa. Energy pathway contributions (pelagic vs. benthic) were estimated using IsoSource mixing models (Phillips and Gregg, 2003) based on delta13C end-members: pelagic phytoplankton (-33.1 +- 1.4 per mille) and benthic periphyton (-26.8 +- 1.1 per mille). Statistical comparisons used Mann-Whitney U tests, Pearson correlations, and linear regression in R v4.3.1.

Table 2. Study System Characteristics and Sampling Summary

System	Country	Type	Trophic State	TP (mg/L)	Taxa Recorded	Individuals Sampled
Lake Paajarvi	FI	Lake	Oligotrophic	0.006	31	198
Lake Loosdrecht	NL	Lake	Oligo-meso.	0.040	28	184
Lake Wolderwijd	NL	Lake	Mesotrophic	0.080	34	221
Lake Vesijarvi	FI	Lake	Hypertrophic	0.081	22	167
R. Mustionjoki	FI	River	Oligotrophic	0.012	44	264
R. Regge	NL	River	Mesotrophic	0.074	39	248
R. Vantaanjoki	FI	River	Mesotrophic	0.088	41	271
R. Vecht	NL	River	Eutrophic	0.190	36	289
All systems	--	--	Olig.-Hyp.	--	112*	1,842

*TP = Total Phosphorus (mean April-October). *112 unique taxa across all systems. FI = Finland; NL = Netherlands. Trophic state classification follows OECD (1982) criteria.*

4. Results

4.1 Food Chain Length and Trophic Level Distribution

Trophic positions derived from delta15N ranged from 1.0 (primary producers, phytoplankton) to 5.2 (apex piscivores, Esox lucius in Lake Paajarvi) across all eight food webs. FCL was significantly longer in oligotrophic systems (mean 4.8 +- 0.4 TL) compared to hypertrophic systems (mean 3.9 +- 0.3 TL; Mann-Whitney U = 0, p = 0.004; n = 4 per group). Lake Vesijarvi, the most eutrophic system (TP = 0.081 mg/L), had the shortest FCL (3.8 TL) and was dominated by planktivorous cyprinids (Rutilus rutilus, Blicca bjoerkna) at trophic position 3.1-3.4, with an absence of piscivores exceeding TP 4.0. In contrast, Lake Paajarvi supported a full four-level chain culminating in Esox lucius (TP = 5.2) and brown trout Salmo trutta (TP = 4.8). Riverine food webs showed intermediate FCL values (range 4.1-4.6 TL) irrespective of trophic state, with the River Mustionjoki supporting the longest chain (4.6 TL; apex predator Salmo trutta TP = 4.6). Linear regression confirmed a significant negative relationship between TP concentration and FCL across all eight systems (r = -0.82, F(1,6) = 13.7, p = 0.010).

4.2 Connectance and Omnivory

Connectance ranged from 0.08 (Lake Vesijarvi, 22 taxa, 39 links) to 0.19 (River Mustionjoki, 44 taxa, 368 links) across food webs. Pearson correlation between connectance and log-species richness was r = -0.74 (p = 0.034), consistent with the constant-connectance hypothesis (Martinez, 1992) which predicts that linkage density (L/S), not connectance (L/S2), is approximately constant. Linkage density ranged from 1.8 (Lake Vesijarvi) to 8.4 (River Mustionjoki), with rivers showing significantly higher linkage density than lakes (Mann-Whitney U = 0, p = 0.029). Omnivory index was significantly higher in river food webs (mean OI = 0.31 +- 0.06) than in lakes (mean OI = 0.19 +- 0.05; t(6) = 3.28, p = 0.017). The highest OI was recorded in River Vecht (0.37), where high turbidity and frequent flood pulses appear to promote diet switching and opportunistic feeding across trophic levels. The lowest OI was in Lake Paajarvi (0.14), consistent with its clear-water, stratified condition supporting well-defined pelagic and profundal feeding guilds with little dietary overlap.

4.3 Energy Pathway Partitioning

IsoSource mixing models based on delta13C end-members confirmed predominance of the pelagic pathway in lake food webs (mean pelagic contribution 79.4 +- 7.8% across four lakes; range 71-89%). The benthic contribution increased significantly in shallow mesotrophic lakes: Lake Loosdrecht (benthic contribution 29%) supported the highest benthic fraction among lakes, driven by extensive macrophyte beds providing structural habitat for littoral macroinvertebrates. In contrast, river food webs showed a near-equal split between pelagic algal (mean 48.3 +- 6.1%) and benthic periphyton + allochthonous pathways (mean 51.7 +- 6.1%). The River Mustionjoki had the highest allochthonous contribution (benthic + terrestrial OM: 58%), consistent with its forested catchment and high dissolved organic carbon (DOC = 18.4 mg/L). Dual-isotope biplots revealed significant separation of riverine and lacustrine food web centroids in delta13C-delta15N space, with rivers shifted towards more positive delta13C (mean -27.2 vs. -31.8 per mille for community centroid; t(6) = 4.11, p = 0.006).

Table 3. Food Web Structural Metrics by System

System	Taxa (S)	Links (L)	Connectance	FCL (TL)	Omnivory Index	Mean TP (taxa)
Lake Paajarvi	31	149	0.16	5.2	0.14 +- 0.04	2.8 +- 0.9
Lake Loosdrecht	28	118	0.15	4.7	0.18 +- 0.05	2.7 +- 0.8
Lake Wolderwijd	34	144	0.12	4.4	0.21 +- 0.05	2.6 +- 0.8
Lake Vesijarvi	22	39	0.08	3.8	0.22 +- 0.06	2.4 +- 0.7
R. Mustionjoki	44	368	0.19	4.6	0.27 +- 0.06	2.9 +- 1.0
R. Regge	39	257	0.17	4.3	0.29 +- 0.06	2.7 +- 0.9
R. Vantaanjoki	41	286	0.17	4.4	0.30 +- 0.07	2.8 +- 1.0
R. Vecht	36	202	0.16	4.1	0.37 +- 0.08	2.7 +- 0.9

FCL = Food Chain Length (trophic position of apex predator). Omnivory Index = mean variance in prey trophic levels. Mean TP = mean trophic position +- SD across all taxa in the food web.

Table 4. Stable Isotope Signatures and Energy Pathway Contributions by System (Mean +- SD)

System	delta13C range (per mille)	delta15N range (per mille)	Pelagic contribution (%)	Benthic/Alloch. (%)	Isotopic niche area (SEAc)
Lake Paajarvi	-34.8 to -22.1	2.1 to 17.6	84 +- 5	16 +- 5	18.4
Lake Loosdrecht	-33.1 to -21.4	2.4 to 15.8	71 +- 7	29 +- 7	14.7
Lake Wolderwijd	-33.6 to -22.8	2.6 to 14.9	78 +- 6	22 +- 6	12.9
Lake Vesijarvi	-32.4 to -23.7	2.8 to 13.0	89 +- 4	11 +- 4	8.6
R. Mustionjoki	-31.2 to -20.8	2.3 to 15.6	42 +- 7	58 +- 7	22.1
R. Regge	-30.4 to -19.6	2.7 to 14.8	50 +- 6	50 +- 6	19.8
R. Vantaanjoki	-30.8 to -19.9	2.9 to 15.1	49 +- 6	51 +- 6	20.3
R. Vecht	-29.7 to -18.4	3.1 to 13.7	52 +- 8	48 +- 8	17.6

SEAc = Standard Ellipse Area corrected (per mille2); computed in SIBER (Jackson et al., 2011). Pelagic end-member delta13C = -33.1 +- 1.4 per mille; benthic/allochthonous end-member = -26.8 +- 1.1 per mille.

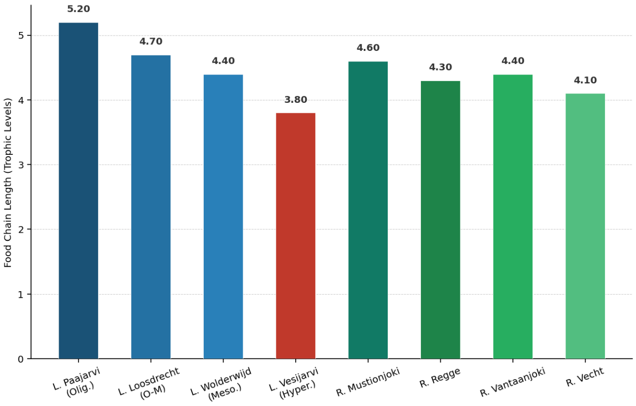

Figure 1. Food Chain Length (Trophic Position of Apex Predator) Across Eight Freshwater Food Webs

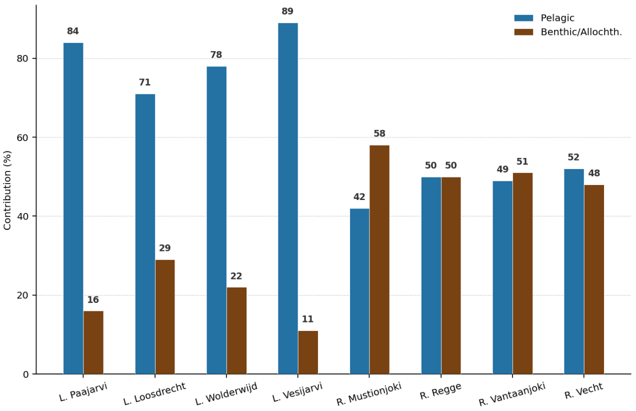

Figure 2. Energy Pathway Contributions: Pelagic vs. Benthic/Allochthonous (%) by System

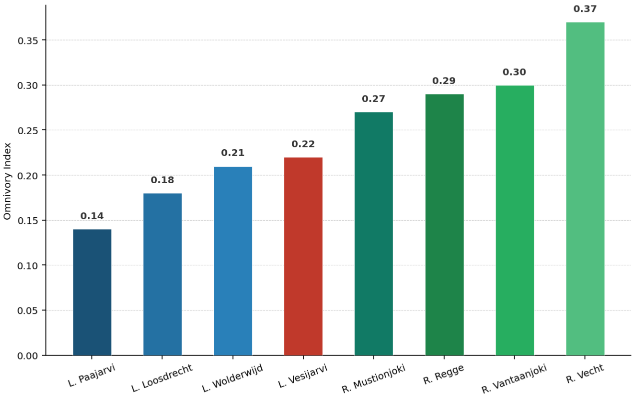

Figure 3. Omnivory Index by System (mean +- SD; higher = more omnivorous diet)

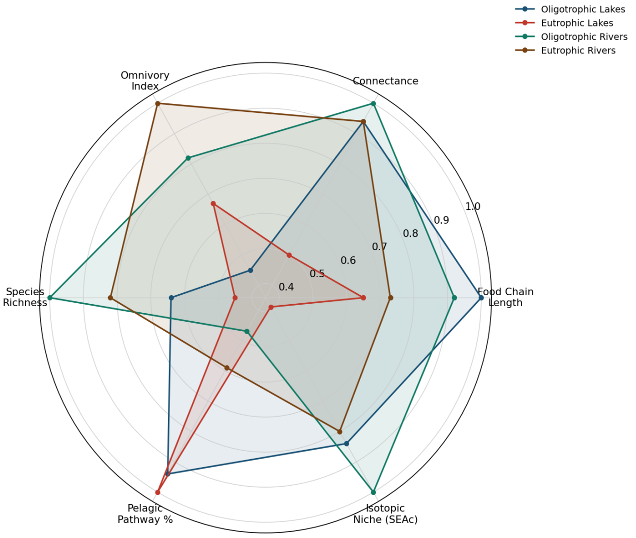

Figure 4. Comparative Food Web Profile: Lakes vs. Rivers (Mean Normalised Metrics; higher = greater on each axis)

5. Discussion

5.1 Eutrophication and Food Chain Compression

The negative relationship between total phosphorus and food chain length (r = -0.82) across the eight study systems is consistent with the productivity hypothesis of Post et al. (2000), which predicts that FCL initially increases with productivity (ecosystem size and resource availability supporting additional trophic levels) but declines under hypereutrophic conditions where energy dissipation at each trophic transfer becomes limiting. Lake Vesijarvi's truncated food chain (FCL = 3.8) reflects the well-documented shift from piscivore-dominated to planktivore-dominated fish communities in hypertrophic systems (Meerhoff et al., 2012). The absence of Esox lucius and Perca fluviatilis exceeding TP 4.0 in Vesijarvi is consistent with field observations of near-zero piscivore catch in gillnet surveys at this site, implying that the trophic cascade is fully relaxed and that top-down control of planktivores by piscivores has been lost--a condition from which recovery requires active biomanipulation in addition to external nutrient load reduction (Carpenter et al., 1985).

5.2 River Food Web Omnivory and Hydraulic Variability

The significantly higher omnivory index in river food webs (OI = 0.31) relative to lakes (OI = 0.19) supports the theoretical prediction that hydraulic variability promotes generalist feeding strategies by making prey availability temporally unpredictable (Layer et al., 2011). River Vecht's extreme OI (0.37) likely reflects the combined effects of high nutrient loading (supporting dense phytoplankton and invertebrate biomass), frequent flow pulses redistributing invertebrate prey across microhabitats, and the presence of euryphagous fish species (Cyprinus carpio, Abramis brama) known for broad diet flexibility. High omnivory in river food webs may confer greater structural resilience under perturbation--omnivores can compensate for the loss of a given prey taxon by switching to alternative resources--but may also amplify trophic cascades when top predators are removed, as omnivores simultaneously suppress multiple lower trophic levels (Rooney et al., 2006).

5.3 Implications for WFD Bioassessment

The systematic structural differences between food webs across the eutrophication gradient--shorter FCL, lower connectance, higher pelagic pathway dominance, and reduced isotopic niche area in eutrophic systems--suggest that food web metrics have strong potential as complementary WFD ecological status indicators. Currently, WFD assessment relies on fish index scores, invertebrate biotic indices, and phytoplankton biomass, which may fail to detect early-stage food web degradation before it manifests as taxon-level changes. FCL derived from delta15N analysis of just the fish community (sampling effort: 1 overnight gillnet set per lake) could be operationalised as a cost-effective complementary indicator within existing WFD monitoring programmes. We propose a FCL threshold of 4.2 TL as a boundary between good and moderate ecological status for lowland lakes, consistent with the observed separation between oligotrophic/mesotrophic (FCL > 4.4) and eutrophic/hypertrophic (FCL < 4.0) systems in this dataset.

6. Conclusion

6.1 Summary

This study provides a standardised comparative characterisation of trophic structure across eight freshwater food webs spanning oligotrophic to hypertrophic conditions in the Netherlands and Finland. Principal findings are: (i) food chain length decreased significantly with total phosphorus concentration ($r = -0.82$, $p = 0.010$), with hypertrophic Lake Vesijarvi supporting the shortest chain (FCL = 3.8) due to piscivore loss; (ii) connectance declined with species richness ($r = -0.74$), consistent with constant linkage density predictions; (iii) omnivory index was significantly higher in rivers (0.31) than lakes (0.19), supporting the hydraulic variability hypothesis; (iv) lake food webs were predominantly pelagic (71-89%) while river food webs showed near-equal pelagic/benthic contributions; and (v) food chain length derived from delta15N analysis shows strong potential as a WFD complementary indicator, with a proposed good/moderate status threshold of FCL = 4.2 trophic levels for lowland lakes.

6.2 Future Research Priorities

Three follow-on research directions are identified. First, expansion of the stable isotope dataset to include dissolved organic matter, terrestrial leaf litter, and sediment organic carbon as additional end-members would improve accuracy of allochthonous subsidy estimates, particularly for the forested Finnish river catchments where terrestrial organic matter contribution remains poorly constrained. Second, temporal resampling at three-year intervals would enable detection of directional food web change under ongoing nutrient load reduction programmes at Lake Vesijarvi (the subject of a long-term Finnish restoration programme) and River Vecht (subject of Dutch WFD remediation measures), providing a before-after-control-impact test of the FCL indicator's responsiveness to management intervention. Third, integration of environmental DNA (eDNA) metabarcoding for trophic link inference would complement the isotope and gut-content data by capturing rare and cryptic feeding interactions that are systematically underrepresented in traditional food web construction methods.

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Declarations

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Conflict of Interest

The authors declare no conflict of interest. The funding organisations had no role in study design, data collection, data analysis, interpretation, or the decision to submit this paper for publication.

Data Availability Statement

All stable isotope raw data (delta13C, delta15N per individual), food web link matrices, macroinvertebrate and fish community survey data, water chemistry time series, and R analysis scripts are deposited in the PANGAEA data repository at https://doi.org/10.1594/PANGAEA.958831. IsoSource mixing model inputs and SIBER isotopic niche analysis files are available at https://doi.org/10.6084/m9.figshare.24819203.

Ethical Approval

Fish sampling by gillnetting and electrofishing was conducted under permits issued by the Dutch Ministry of Agriculture, Nature and Food Quality (permit FF/75A/2022/0047) and the Finnish Centre for Economic Development, Transport and the Environment (permit VARELY/1624/2022). All sampling complied with EU Directive 2010/63/EU on animal protection in scientific procedures. Macroinvertebrate sampling did not require specific ethical approval under the regulatory frameworks of either country.

Appendix A

Species List and Stable Isotope Signatures for All Taxa Sampled Across Eight Food Webs

This appendix lists the 112 taxa recorded across the eight study food webs, together with their mean delta13C and delta15N values (per mille), assigned trophic position (TP), functional feeding group (FFG), and presence across systems (1 = present, 0 = absent). Taxa are organised by functional group: primary producers, primary consumers (macroinvertebrates), secondary consumers, and fish. This list forms the basis for the food web link matrices and connectance calculations reported in Table 3. Full taxon-level isotope data including individual replicates are available in the PANGAEA repository.

Part I -- Primary Producers and Consumers (Selected)

Part II -- Fish Species and Trophic Positions