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Zooplankton functional diversity as a bioindicator of freshwater ecosystem health across land use gradient

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Zooplankton are critical indicators of pressures impacting freshwater ecosystems. We analyzed the response of zooplankton communities across different sub-catchment types—headwaters, natural, urban, urban-agricultural, and agricultural—within the Łyna river–lake system in Northern Poland. Using taxonomic groups and functional traits (body size, feeding strategies), we applied Partial Least Squares Regression (PLS-R) to elucidate the relationships between environmental conditions, land use, and zooplankton metacommunity structure. Two-Way Cluster Analysis (TWCA) identified local subsets with characteristic patterns, while Indicator Species Analysis (ISA) determined area-specific taxa. The natural river zone exhibited significant habitat heterogeneity and feeding niches, whereas urban areas created functional homogenization of zooplankton, dominated by small, broad-diet microphages. Agricultural areas promoted diversity among large filter feeders (Crustacea), active suctors (Rotifera), and amoebae (Protozoa). However, intensified agricultural activities, substantially diminished the zooplankton population, biomass, taxonomic richness, and overall ecosystem functionality. The impact of land cover change is more pronounced at small-scale sub-catchments than at the catchment level as a whole. Therefore, assessing these impacts requires detailed spatial and temporal analysis at the sub-catchment level to identify the most affected areas. This study introduces a new sub-catchment-based perspective on ecosystem health assessment and underscores the zooplankton's role as robust indicators of ecological change.

Keywords Catchment area, Community traits, Lotic ecosystem, Partial least squares regression, Zooplankton assemblage matrix

Species distribution patterns and the structure of riverine zooplankton communities align with metacommunity theory, which posits interconnected local communities shaped by environmental and spatial processes[1,2]. Biological conditions in rivers are primarily shaped by water flow and watershed impacts, with flow being the strongest determinant of river biocoenosis, affecting habitat construction, food conditions, and species' functional traits[3–5]. The watershed environment also influences water chemistry, thermal conditions, and species composition[6].

Zooplankton communities in lotic systems are less diverse than in standing waters due to food and reproductive limitations. Their presence in rivers often results from influxes from lakes, floodplains, or drift from tributaries, supported by the river continuum concept that describes gradual habitat and energy transformations along river courses[3,7]. Observations indicate increased zooplankton density in middle and lower river sections, with variations in crustacean presence, species diversity, and biomass across different zones influenced by environmental factors like flow and retention time[4,8–10].

The rapid generational turnover of planktonic animals facilitates their adaptation to river environments, responding sensitively to changes including temperature, turbidity, and pollution, despite zooplankton not being standard indicators for water quality under the EU Water Framework Directive[11–14]. Their role in the trophic chain links primary producers with higher-order consumers, making them crucial for river ecosystem functioning[15–18].

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The taxonomic and functional diversity of zooplankton serves as "ecosystem-focused Essential Biodiversity Variables (EBVs)" which are essential for analyzing community structures and understanding ecological niches within ecosystems[14,19,20]. The ecosystem attributes, according to EBV framework—the basis of biomonitoring programs worldwide presented by Pereira et al.[21], require priority attributes such as structural—(Ecosystem Structure) and functional attributes of the ecosystem (Ecosystem Function), as well as community-level abundance and diversity of organisms occurring within the ecosystem (Community Composition EBVs). The bioindicative value of zooplankton is significant in ecosystems facing anthropogenic threats like agriculture and urbanization, where they reflect impacts of physical and chemical changes on biocoenoses[2,19,22,23].

Anthropogenic activities lead to increased nutrient concentrations, affecting autotroph activity and reducing zooplankton diversity, favoring species with high environmental tolerance ("generalists"). Increased organic pollutants and altered nutrient levels result in a shift towards smaller rotifers and protozoans, with fewer specialist species[24,25]. The use of pheopigments as indicators provides insights into algal cell condition and zooplankton food quality, reflecting the impact of these environmental changes[26,27].

The aim of this study was to assess the variability in the zooplankton metacommunity of the Łyna River, the largest river in northeastern Poland, under the influence of diverse land use forms within its catchment. Prior studies have often focused on specific river segments impacted by environmental changes[14,22,23]. However, understanding the variability of zooplankton across the entire river course—encompassing a varied landscape influenced by a young glacial topography—presents a more complex and less explored challenge.

Our study required integration of multiparametric watershed-wide data according to the requirements of Water Framework Directive (WFD, 2000/60/EC), the primary legislation in EU setting out rules to halt deterioration in the status of water bodies and achieve good status for Europe's rivers, lakes and groundwater. Thus, our objective as to comprehensively investigate the dynamics of zooplankton variability in a lowland river ecosystem for the first time. Utilizing Partial Least Square Regression (PLS-R), we analyzed how land use variability within the watershed affects the zooplankton metacommunity. This analysis spans a 200 km postglacial river course, evaluating both the direct impacts of watershed management on water quality and the indirect effects on zooplankton dynamics.

Our hypotheses deal with environmental impacts on zooplankton ecological niches. We predict that the diverse land uses in the river catchment —ranging from natural to urban and urban-agricultural areas—affect the ecological traits and distribution patterns of the zooplankton. Specifically, we hypothesize that: (1) zooplankton communities are composed of localized subsets, each characterized by distinct distribution and co-occurrence patterns that reflect their specific environmental contexts; (2) environmental factors such as land use and water flow significantly influence the abundance and diversity of specialized indicator taxa.

Drawing on the urban tolerance hypothesis, we anticipate that urbanized areas will predominantly support generalist species with broad environmental tolerances, resulting in functional homogenization. In contrast, areas characterized by natural landscapes or reduced water flow are expected to support a higher diversity of specialist species, indicative of more varied habitat niches. Additionally, increased flow intensity is likely to restrict the available niche space, favoring species that are more competitive.

This comprehensive study of the Łyna River's zooplankton aims to evaluate the zooplankton structures across varying watershed conditions and their responses to anthropogenic pressures. By doing so, we seek to highlight the bioindicative value of zooplankton in monitoring the ecological health and environmental changes of freshwater ecosystems.

Results

Environmental characteristics

Land use influenced the variation of certain physical and chemical water parameters across five zones (I–V) along the Łyna River. Significant differences were observed in pH, electrical conductivity (EC), total inorganic carbon (TIC), turbidity, nutrient and organic matter concentrations, and chlorophyll pigments (Supplementary Table S1). Headwaters (zone I) were rich in inorganic ionic forms correlated with EC and TIC. A distinct gradient of organic matter in the water was observed along with the increased catchment area, marked by significant increases in concentrations of biological oxygen demand (BOD), total organic carbon (TOC), total nitrogen (TN), and total phosphorus (TP) (Supplementary Table S1). A significantly different and several times higher than the average level in the waters of the Łyna River, high concentrations of N-NO_3 and TN (3.15 mg/L and 3.43 mg/L, respectively) were observed in the headwaters. The average concentration of ammonia did not significantly differ across the individual catchment sections; however, increases in N-NH4, similar to orthophosphate, were associated with the urban section (zone III). The primary production size, measured by the total concentration of chlorophyll a, amounted to an average of 14.22 µg/L, varying along the river's course from 2.42 µg/L in the headwater section (zone I) to 20.66 µg/L in zone V. The proportion of pheophytin in the total chlorophyll a concentration ranged from 20% (zone II) to 80% (zone I), with an average of 44% for the Łyna River ecosystem. Water turbidity increased progressively along the river, from 1.61 NTU (zone I) to 7.34 NTU (zone V), with a sharp increase in the urban section (zone III) (Supplementary Table S1).

Zooplankton structure and diversity

In the zooplankton structure of the Łyna River, a total of 158 taxa and forms of zooplankton were identified, comprising 111 Rotifera, 23 Cladocera, 13 Copepoda (including juvenile stages of nauplii and copepodites), 10 Protozoa, and larval veliger stages of *Dreissena polymorpha* (Pallas, 1771). Rotifers constituted on average from 66.5% (zone I) to 85.3% (zone V) of the overall zooplankton density, and the most commonly were *Keratella cochlearis* (Gosse, 1851) and *Polyarthra longiremis* Carlin 1943, with average frequencies of 79.4% and 70.9%, respectively (Supplementary Table S2). Crustaceans accounted for an average of 16.7% (zone IV) to 68.6% (zone

II) of the overall zooplankton biomass. The nauplii larval stages of Copepoda were characterised by the highest frequency, appearing in 69.1% of the samples. Protozoa were primarily represented by the amoebae *Galeripora discoides* (Ehrenberg, 1843), *Codonella cratera* Leidy 1887, and *Difflugia* spp., with frequencies of 75.4%, 34.9%, and 32.8%, respectively. The share of protozoans in the overall zooplankton density ranged from 5.1% (zone II) to 28.8% (zone I).

The highest statistically significant ($p < 0.05$) average abundance (667 ind/L), biomass (1280.8 μg/L), and number of species (19) of zooplankton were recorded in the natural section (zone II). In contrast, the lowest values of abundance and biomass were noted at site 1 (15 ind/L and 7.7 μg/L, respectively), while the fewest species (10) of zooplankton were found at the most downstream location (zone V). Measures of zooplankton taxonomic diversity, expressed by the Margalef's species richness (d) index and Shannon's diversity index (H'), were highest in zone I and lowest in zone V, with values of 4.74 and 1.84 (zone I) and 2.38 and 1.66 (zone V), respectively. The Pielou's evenness index (J') reached the lowest average level of 0.603 in zone II, indicating the prolific development of a few species and an uneven quantitative proportion in the zooplankton communities of the natural zone (Fig. 1; Supplementary Table S2).

Habitat distribution patterns of zooplankton and characteristic species

In the zooplankton metacommunity of the Łyna River ecosystem, we identified local subsets and species characteristic of specific habitat niches within the sub-catchment type. A total of 35 zooplankton taxa and two developmental forms of Copepoda showed significant affinity for the designated five watershed zones. Headwaters (zone I) formed the most distinct habitat assemblage from other zones, with top indicators being *Scaridium longicaudum* (Müller, 1786) (IndVal = 12.3; $p = 0.0002$), *Monommata maculata* Harring & Myers, 1924 (IndVal = 6.3; $p = 0.015$), and Ciliata (IndVal = 8.3; $p = 0.014$). The influence of the natural watershed (zone II), grouping sites 2–4, reflected the most numerous and diverse pattern of the zooplankton assembly, consisting of 17 taxa of Rotifera and 9 taxa and forms of Crustacea, significant for the habitat according to the IndVal index (Fig. 2; Table 1). Key indicators for the natural habitat (IndVal > 20; $p \leq 0.0016$) included *Keratella tecta* (Gosse, 1851), *Asplanchna priodonta* Gosse, 1850, *Conochilus unicornis* (Rousselet, 1892), *Trichocerca capucina* (Wierzejski & Zacharias, 1893), *T. similis* (Wierzejski, 1893), *T. pusilla* (Lauterborn, 1898), *Gastropus stylifer* Imhof, 1891, *Bosmina longirostris* (O.F. Müller, 1785), *Eudiaptomus graciloides* (Lilljeborg, 1888), *Thermocyclops crassus* (Fischer, 1853) and nauplii and copepodite larvae of Copepoda. The urban zone (III) zooplankton community, forming a cohesive cluster of sites 5–9, included many taxa such as *Keratella ticinensis* (Callerio, 1920), *K. paludosa* (Lucks, 1912), *Colurella* spp., *Lepadella* spp., *Squatinella* spp., and *Plationus patulus* (Müller, 1786) (Fig. 2). However, none of the taxa had significant indicator value for this habitat. The urban-agricultural cluster (zone IV) grouped zooplankton assemblies of sites 10–14, represented by *Kellicottia longispina* (Kellicott, 1879), *Synchaeta* spp., *Trichocerca musculus* (Hauer, 1936), *Brachionus calyciflorus* Pallas, 1766, and *Alona* spp. (Fig. 2). Significant indicators ($p < 0.05$) characterizing the local habitat of zone 4 included rotifers of the genera *Cephalodella* (IndVal = 12.4), *Trichotria* (IndVal = 6.8), *Ascomorpha* (IndVal = 11.6), *Lecane* (IndVal = 9.5), and the protozoans *A. discoides* (IndVal = 37.0), *Centropyxis aculeata* (Ehrenberg, 1832) (IndVal = 7.7), and *Difflugia* spp. (IndVal = 9.0). The agricultural zone (V) zooplankton community included *Brachionus angularis* Gosse, 1851, *B. leydigii* Cohn, 1862, *Trichocerca rattus* (Müller, 1776), *Proales* sp., and *Alonella nana* (Baird, 1843), but only one species, *Brachionus urceolaris* (Müller, 1773) (IndVal = 6.1; $p = 0.03$), proved to be a characteristic and significant indicator of this habitat niche (Fig. 2; Table 1).

Spatial variability of zooplankton metacommunities

The increase in flow intensity correlated with sub-catchment size significantly differentiated the population of 21 taxa and naupliar forms of Copepoda (Supplementary Table S3), of which 11 belonged to the set of indicators for habitats of individual sub-catchment types (Table 1). Most taxa characteristic of upper segment habitats (section I and II), showed a negative correlation in population numbers along the river course, or this variability was not significant. The variability in population numbers of individual taxa, which was important for the structure of the metacommunity, was diverse (Supplementary Fig. S1). Trends in population number growth with sub-catchment area and flow were shown by 9 taxa, and a decrease in population numbers was observed by 12 taxa and nauplii.

Environmental and spatial variability of zooplankton functionality

The natural zone (II) significantly differed from the other sections in terms of zooplankton abundance and biomass (Fig. 1 A, B), affecting the density of all functional groups and main feeding guilds of zooplankton (Fig. 3A–H). In the zooplankton metacommunity, the small microphages (SMC) group was dominant, ranging from 59% (zone I) to 74% (zone III), corresponded to the type of trophy in Rotifera (Supplementary Fig. S2; Table S2). The increase in significance of actively feeding RAP species, particularly from the group of suctor rotifers in the urban-agricultural zone (IV), was statistically significant and differed from other watershed sections (Fig. 3C,G). The largest share (6%), across the entire Łyna ecosystem, of large microphages (LMC), primarily represented by filter feeders and scrapers as well as predatory species, was noted in zone II.

PLS-R analysis demonstrated the importance of explanatory variables significantly contributing to the response of zooplankton functional groups. The Variable Importance for Projection included phosphorus forms ($P\text{-}PO_4$, TP), primary production (Chl-*a*, Pheo/Chl-*a*), inorganic ionic forms (EC, TIC), surface water areas (Lake, Lake_cum, Water), and urban areas in the catchment (Build-ups) (Fig. 4). The most important predictor, based on the highest VID scores for three of the four functional groups, was the share of areas with high water retention, primarily provided by lakes (Lake_cum): LMC (VID = 0.880), STA (VID = 0.790), and SMC (VID = 0.619). The key predictor with a positive VID score for the RAP group was Chl-*a* (VID = 0.584). EC, TN, and the share of wetlands in the direct catchment were adversely associated with LMC and STA (Table 2).

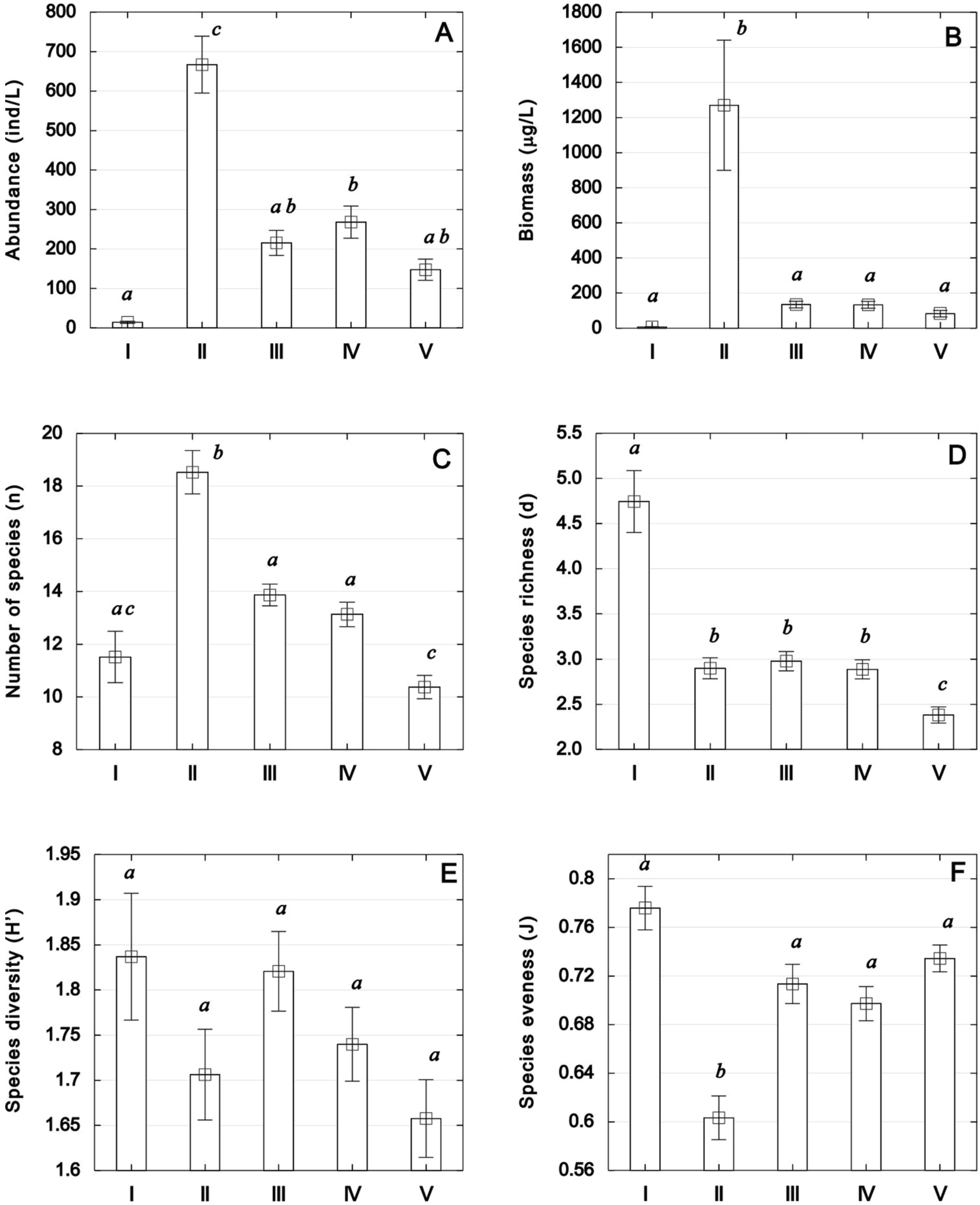

Figure 1. Abundance (ind/L), biomass (µg/L), number of species (n), species diversity (H'), species richness (d), and species eveness (J) of zooplankton in five zones along the Łyna River course, distinguished by land use. Statistically significant differences, indicated by superscripts, were determined using Tukey's post-hoc test following one-way ANOVA ($p < 0.05$).

A negative effect on SMC and RAP was detected for P-PO_4 (VID = − 0.663 and − 0.691, respectively), Pheo/Chl-*a* (VID = − 0.563 and − 0.586, respectively), and TP (VID = − 0.541 and − 0.547, respectively), (Table 2). All functional zooplankton groups were adversely associated with the share of urbanized areas in the catchment, phosphorus compounds (P-PO_4 and TP), and low phytoplankton quality (Pheo/Chl-*a*) (Fig. 4).

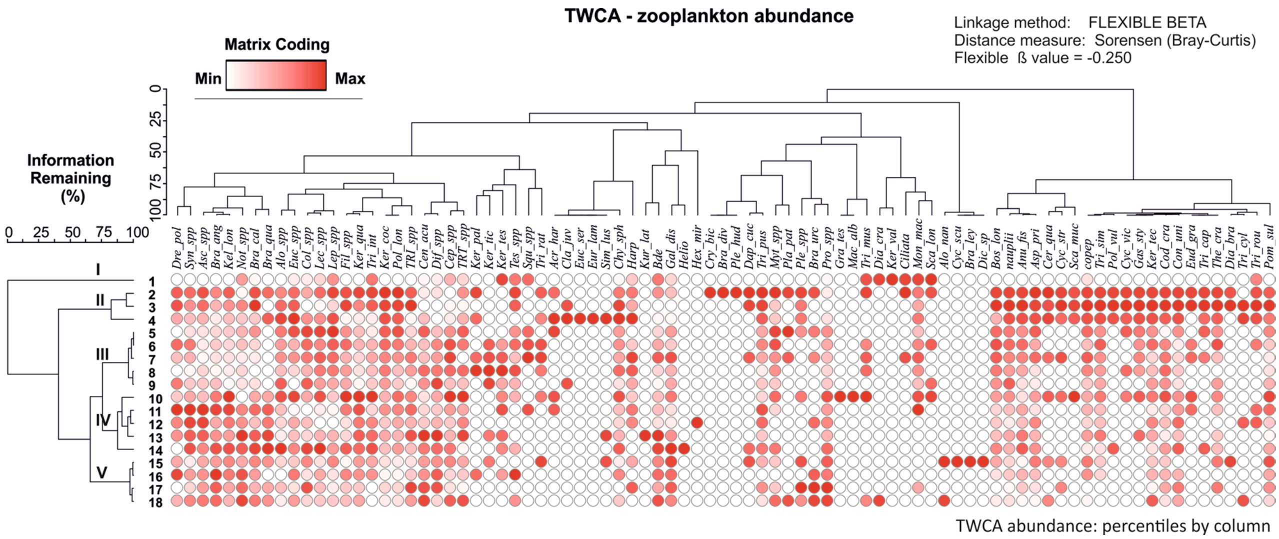

Figure 2. TWCA matrix of zooplankton grouping in 5 catchment zones of the Łyna River. Zooplankton species name abbreviations are explained in Supplementary Table S2.

Discussion

The results of this study demonstrated that watershed management conditions and water flow intensity are factors controlling the structural characteristics and accumulation patterns of zooplankton communities in the Łyna River, typical watercourse for postglacial areas of Mid-Eastern Europe. Rotifers predominated in the zooplankton metacommunity, a common trait in lotic environments due to their short generational cycles and ability to thrive in nutrient-poor river waters[3,28]. The qualitative structure of Rotifera was primarily composed of eurytopic species such as *Keratella cochlearis* and *Polyarthra longiremis*, which are often dominant in potamoplankton[11,12,29,30]. However, local subsets consisting of both the aforementioned generalists and specialist species showed a variability in their populations, correlated with land use form, catchment area, and flow intensity (Fig. 2, Supplementary Fig. S1).

The headwaters zone (I) differed from other river segments in terms of the lowest abundance, biomass, and species count of zooplankton. As emphasized by Ejsmont-Karabin and Kruk[31], upper stream biotic communities are highly susceptible to adjacent land use due to the large surface area in contact with the narrow, shallow river channel. Additionally, the small water flow and fast current of headwater sections result in varied abundances and specific zooplankton assemblages[30,31]. The headwaters section of the studied Łyna River, characterized by a forested setting, low water temperature, and significant shading, despite good organic matter resources (BOD), limited primary production (Chl-*a*) and resulted in a high proportion of pheophytin[26]. A high Pheo/Chl-*a* ratio, indicative of poor physiological state of phytoplankton[27,32] pointed to poor quality and/or availability of food, constraining all functional groups. The headwaters section of the Łyna River was represented by diverse but small populations of minute pelagic rotifers, aligning with findings by Ejsmont-Karabin and Kruk[31]. Specialised rotifers (RAP) *Monommata maculata* and *Scaridium longicaudum*, equipped with the best functionally active feeding methods and utilizing feeding guilds, best represented (IndVal) the upper river segment (Table 1).

The local zooplankton community in the natural zone (II) reflected a structure typically found in lentic—lacustrine ecosystems. High abundance and biomass of all taxonomic and functional groups of zooplankton, along with the subdominance of eutrophic species populations, are characteristics of potamoplankton communities in the outflow zones of lakes[8,9,28]. Lakes within river flow systems serve as refuges for numerous species with higher nutritional, thermal, and phenological requirements[12,18,29] simultaneously supplying the outflow zone with organic matter and phytoplankton[33]. Therefore, the local subset of zooplankton in the natural section was abundant and diverse both taxonomically and functionally, with a characteristic pattern of co-occurrence of indicator taxa of specific feeding guilds (Fig. 2). Representatives of all functional groups showed a highly positive correlational relationship (PLS) with areas of the catchment having high hydrological retention (SMC, LMC and STA) and concentrations of Chl-*a* (with a low proportion of Pheo) in the water (RAP), characterizing the natural section (II). These included crustaceans from Cyclopoida (e.g., *Cyclops* spp.; RAP), Calanoida (*Eudiaptomus graciloides*; STA), and pelagic and littoral Cladocera (e.g., *Simocephalus, Ceriodaphnia*; LMC). A similar finding was reported by Thorp and Mantovani[12], highlighting a positive correlation between crustacean density and hydrological retention (negative with flow velocity). The resource-rich outflow habitat (site 2 and 3) also provided optimal conditions for Rotifera species with varied functional traits (different trophic types), both from the "specialist" group (e.g. predator *A. priodonta*) and the common/"generalist" group (*K. cochlearis, P. longiremis*) (Supplementary Table S2). These characteristics of the zooplankton community in the outflow section are consistent with the findings of Braghin et al.[34], where the availability of food resources (Chl-*a*) on one hand increased the functional diversity of zooplankton and on the other led to the intense development of populations of highly competitive species (generalists). The strong dominance of *K. cochlearis* (38%), *P. longiremis* (14%), *K. tecta*, and nauplii larvae of Copepoda resulted in a low assessment of taxonomic diversity in zone II.

Taxa	Functional group	Feeding guilds	Site	Catchment zone	IndVal x ± SD	*p*	M–K test *p*	Trend
Rotifera								
Monommata maculata	RAP	Suctor	1	I	6.3 (2.8 ± 1.2)	0.0152		
Scaridium longicaudum	RAP	Suctor	1	I	12.3 (2.6 ± 1.3)	0.0002		
Anuraeopsis fissa	SMC	Filtration	2	II	13.3 (6.5 ± 2.4)	0.0196		
Asplanchna priodonta	RAP	Predator	2	II	31.7 (5.9 ± 2.1)	0.0002	0.045	↓
Brachionus diversicornis	SMC	Filtration	2	II	8.3 (4.0 ± 1.0)	0.0492		
Keratella cochlearis	SMC	Filtration	2	II	15.4 (9.3 ± 1.6)	0.0042	0.002	↓
Mytilina spp.	SMC	Filtration	2	II	7.4 (3.2 ± 1.3)	0.0116	0.005	↑
Ploesoma spp.	RAP	Suctor	2	II	12.5 (2.6 ± 1.4)	0.0028		
Polyarthra longiremis	RAP	Suctor	2	II	17.1 (7.9 ± 1.3)	0.0002	0.000	↓
Trichocerca pusilla	RAP	Suctor	2	II	21.4 (5.3 ± 2.0)	0.0002		
Trichocerca musculus	RAP	Suctor	2	II	10.2 (2.9 ± 1.4)	0.0002		
Conochilus unicornis	SMC	Filtration	3	II	33.8 (8.1 ± 3.3)	0.0002	0.002	↓
Gastropus stylifer	RAP	Suctor	3	II	26.4 (3.6 ± 1.6)	0.0002		
Keratella tecta	SMC	Filtration	3	II	35.6 (12.1 ± 3.6)	0.0002	0.001	↑
Polyarthra vulgaris	RAP	Filtration	3	II	16.7 (3.1 ± 1.5)	0.0002		
Pompholyx sulcata	SMC	Filtration	3	II	17.1 (4.9 ± 1.8)	0.0006		
Trichocerca capucina	RAP	Suctor	3	II	28.6 (3.0 ± 1.4)	0.0002		
Trichocerca cylindrica	RAP	Suctor	3	II	14.9 (4.9 ± 2.3)	0.0030	0.006	↑
Trichocerca similis	RAP	Suctor	3	II	26.9 (5.6 ± 2.2)	0.0002		
Cephalodella spp.	RAP	Suctor	10	IV	12.4 (5.4 ± 1.2)	0.0002		
Trichotria spp.	SMC	Filtration	10	IV	6.8 (3.8 ± 1.5)	0.0474		
Ascomorpha spp.	RAP	Suctor	11	IV	11.6 (7.9 ± 1.8)	0.0378	< 0.0001	↓
Lecane spp.	SMC	Filtration	14	IV	9.5 (6.0 ± 1.2)	0.0138	0.001	↑
Brachionus urceolaris	SMC	Filtration	17	V	6.1 (2.8 ± 1.5)	0.0304		
Crustacea								
Ceriodaphnia quadrangula	LMC	Filtration	2	II	9.9 (3.5 ± 1.8)	0.0080		
Daphnia cucullata	LMC	Filtration	2	II	15.4 (3.7 ± 2.0)	0.0004		
Cyclops strenuus	RAP	Raptorial	2	II	10.1 (2.6 ± 1.2)	0.0012		
Bosmina longirostris	LMC	Filtration	3	II	21.5 (8.9 ± 3.1)	0.0016	0.007	↓
Diaphanosoma brachyurum	LMC	Filtration	3	II	17.2 (2.6 ± 1.5)	0.0004		
Eudiaptomus graciloides	STA	Filtration	3	II	34.9 (3.0 ± 1.4)	0.0002		
Thermocyclops crassus	RAP	Raptorial	3	II	52 (3.7 ± 1.4)	0.0002		
Copepodites	LMC	Filtration	3	II	53.6 (5.2 ± 1.6)	0.0002		
Nauplii	SMC	Filtration	3	II	35.2 (8.8 ± 1.7)	0.0002	0.004	↓
Protozoa								
Ciliata			1	I	8.3 (2.9 ± 1.6)	0.0146		
Difflugia spp.			13	IV	9 (5.5 ± 1.4)	0.0230		
Centropyxis aculeata			13	IV	7.7 (4.5 ± 1.3)	0.0280		
Galeripora discoides			14	IV	37 (15.8 ± 3.0)	0.0002	0.001	↑

Table 1. Taxa characteristic of the habitats of Łyna river catchment sections. Indicator Value (IndVal), mean ± SD), and the trend of population size variability with the increasing area of the Łyna River catchment (Mann–Kendall test, $p < 0.05$).

Moving away from the natural habitat, zooplankton abundance, biomass, and species number decreased due to the river current's filtering impact, deteriorating habitat conditions, and fish predation[8,9,17,28]. In the urban zone (III), under the influence of the largest city on the river (Olsztyn), zooplankton abundance halved, and biomass nearly decreased tenfold. All functional groups were negatively correlated with urbanized areas, increased phosphorus and nitrogen compounds, decreased primary production, and increased Pheo/Chl-*a* ratio. This deterioration of habitat quality severely limits zooplankton in urbanized waters[22,23]. According to the urban tolerance hypothesis[35,36], the zooplankton community of the urban section was dominated (75%) by small microphages (SMC) from a pool of common rotifers (generalists) with broad environmental tolerance. The largest share in this group comprised small filter feeders from the genera *Keratella*, *Brachionus*, *Lecane*, and *Filinia*, which corresponds with the results of Frau et al.[19] and Mulani et al.[24]. The significance of LMC and RAP groups significantly declined, consistent with urbanization impacts on river catchment[25]. Thus, no indicators were found, characteristic of the local subset of section III (lack of IndVal indicators). Although these observations

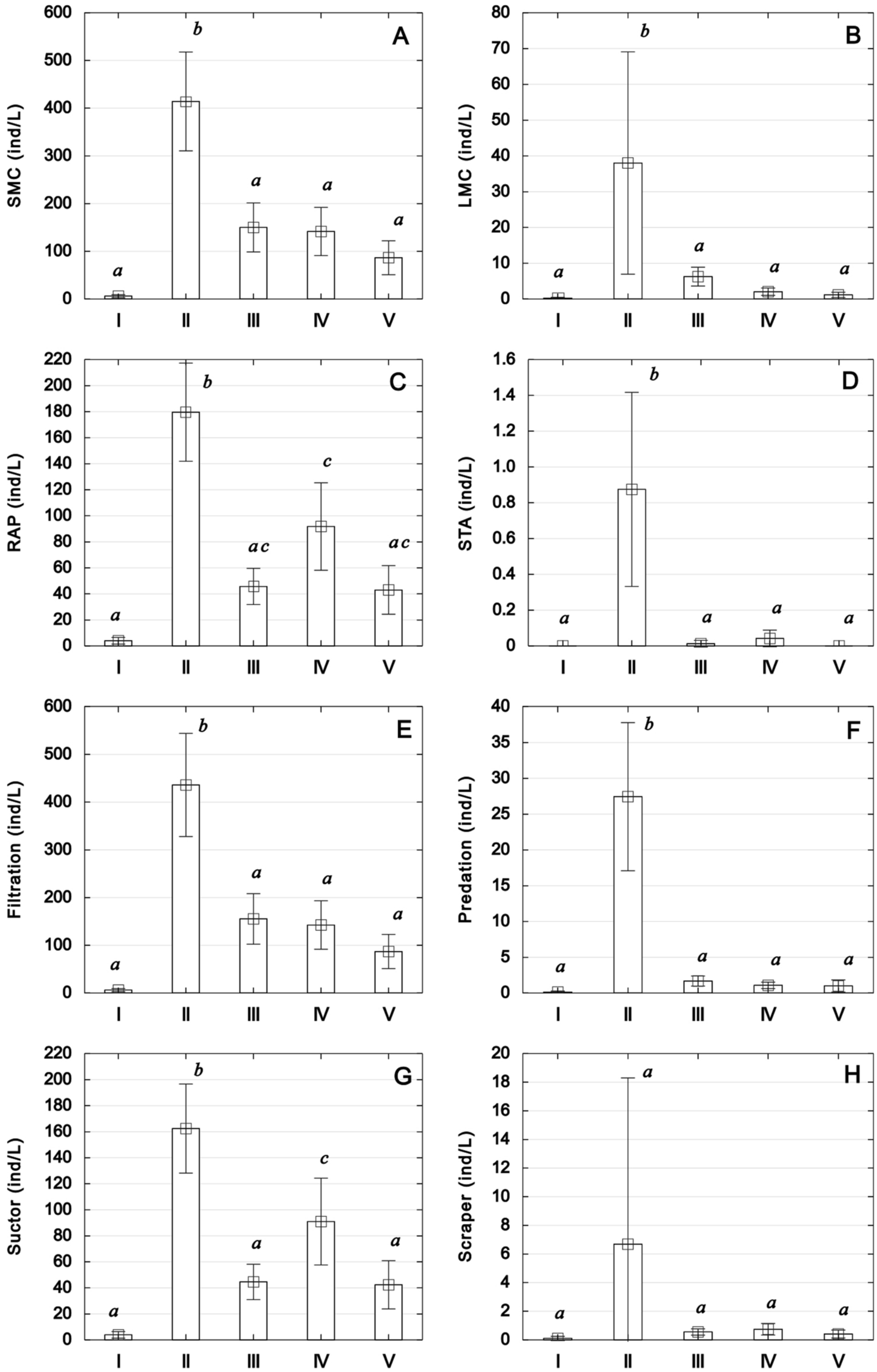

Figure 3. Functional groups (**A**–**D**) and feeding guilds of zooplankton (**E**–**H**) in five zones along the Łyna River course. Statistically significant differences, indicated by superscripts, were determined using Tukey's post-hoc test following one-way ANOVA ($p < 0.05$).

indicate an intensification of functional homogenization of zooplankton within the urban section, it should be noted that the dominant group of small filter feeders (SMC; *Brachionus angularis*, *B. calyciflorus*, *Conochilus unicornis*, *Keratella* spp., *Filinia* spp.) was "heterogeneous" in terms of a wide spectrum of food sources (detritus, bacteria, protozoans, algae). The ability to utilize various food sources, especially in the presence of poor quality

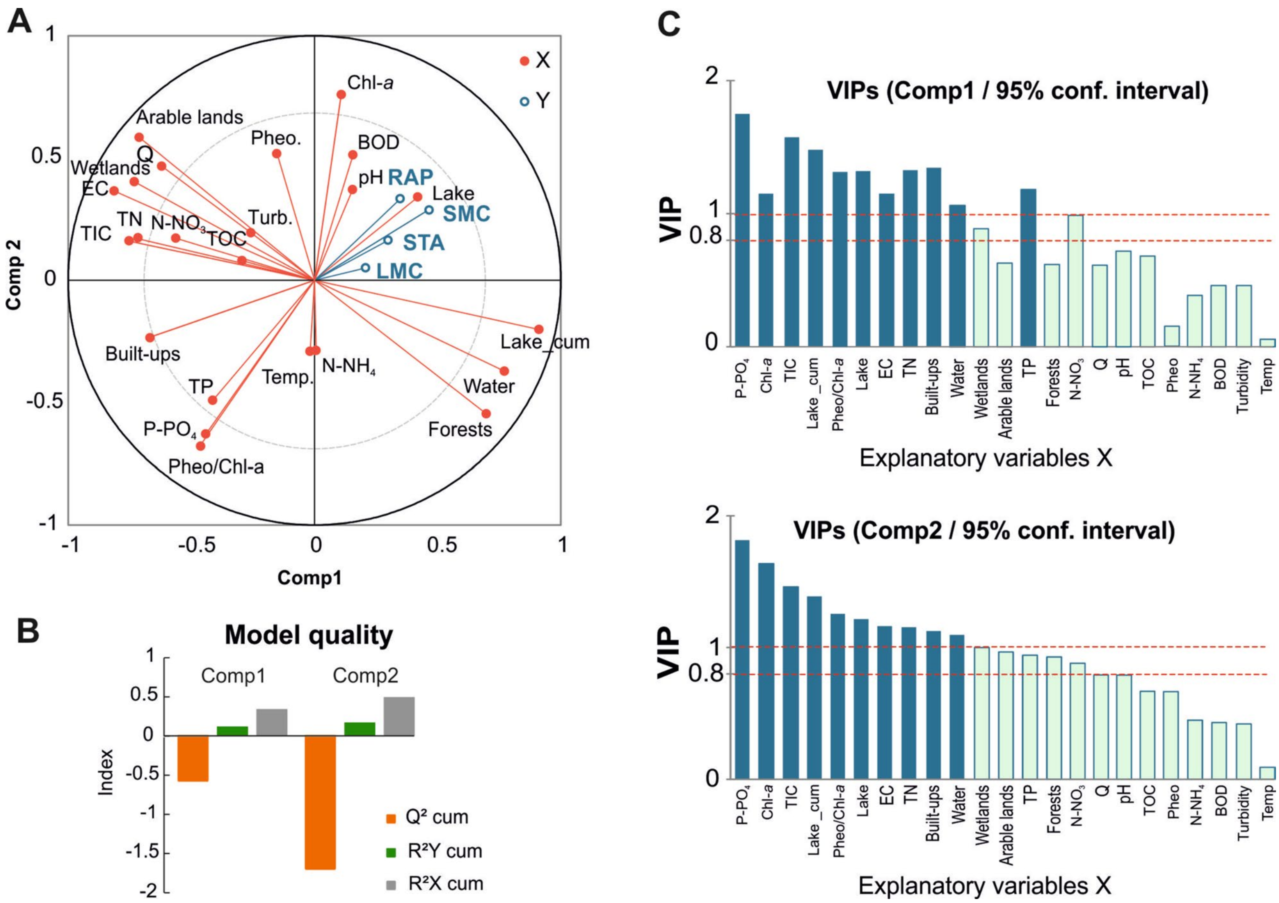

Figure 4. Partial least squares (PLS) regression biplot reflecting the effect of land-use classes and water quality parameters as the explanatory variables (X) on the zooplankton groups (Y). Inner dashed circle denotes correlation coefficient r = 0.75 (**A**). PLS-R model quality (**B**). VIPs (Variable Influence on Projection) for each explanatory variable of Component 1 and Component 2. VIP diagrams show relative importance of predictors. VIPs > 0.8, based on Wold's criteria[69], indicate that the predictor variable is considered to be significantly important to the corresponding dependent variable (**C**).

	SMC		**LMC**		**RAP**		**STA**	
	VID	**Component**	**VID**	**Component**	**VID**	**Component**	**VID**	**Component**
Positive	0.619	Lake_cum	0.880	Lake_cum	0.584	Chl-*a*	0.790	Lake_cum
			0.737	Water			0.648	Water
			0.604	Forests				
Negative	−0.663	P-PO_4	−0.732	EC	−0.691	P-PO_4	−0.638	TN
	−0.563	Pheo/Chl-*a*	−0.689	Wetlands	−0.586	Pheo/Chl-*a*	−0.624	EC
	−0.541	TP	−0.686	TN	−0.547	TP	−0.600	Wetlands
	−0.525	TN	−0.619	Arable lands			−0.579	P-PO_4
	−0.514	Built-ups	−0.589	TIC			−0.551	Built-ups
			−0.567	N-NO_3			−0.518	TIC
			−0.551	Built-ups				
			−0.525	Q				

Table 2. Discriminative components for each zooplankton functional group selected through the Variable Identification (VID) procedure (PLS-R) and listed in decreasing order of VID score (>\|0.5\|; n = 428). Positive VID scores indicate positively associated variables with the response variables, while negative scores indicate variables negatively associated with the response variables. More negative or positive scores suggest a stronger influence.

or scarcity of phytoplankton, is a phenomenon observed in anthropogenically disturbed ecosystems[37,38], including urbanised areas and results in the overlapping (interlocking) of niches[25].

The increasing catchment area, flow intensity, and volume of water, as well as the growth in the proportion of agriculturally used areas in the lower sections, significantly influenced the increase in water turbidity, mineral compounds (TIC), and EC. High turbidity, limiting the euphotic zone, can impact feeding efficiency and development of filtering zooplankton species[34,39,40]. On the other hand, mineral suspension particles, determining water turbidity, can also enhance the food pool by accumulating organic forms, thereby increasing zooplankton diversity[41,42]. As in the experiments of Mulani et al.[24] and Frau et al.[19], these factors favored rotifers from the families Brachionidae, Lecanidae, Trichocercidae, and Gastropodidae, but not LMC and STA.

The lower section of the Łyna River (zone IV) responded to improved food conditions with restored Crustacea structure, possibly due to reduced fish predation on Cladocera and adult Copepoda in turbid waters and expanded littoral vegetation zones providing habitat for littoral species (e.g. *Simocephalus, Graptoleberis*, *Kurzia, Pleuroxus*; Supplementary Table S2)[43–45]. Additionally, zone IV was characterised by an increase in Protozoa, and Rotifera from the actively feeding suctors roup (RAP: *Trichocerca*, *Polyarthra, Synchaeta*) at the expense of filter feeders (SMC), likely due to competition with LMC—Cladocera[46–49]. Indicator taxa for urban-agricultural habitats included rotifers from the genera *Ascomorpha*, *Cephalodella*, *Lecane*, and *Trichotria*, as well as protozoans from the amoeba group (*Galeripora, Difflugia, Centropyxis*).

The lower sections (IV and V) showed dominance by *Galeripora discoides* most likely due to increasing turbidity (suspended solid concentration), agricultural areas, but also the presence of hydraulic structures. As shown by Endler et al.[50], water levels, small hydropower plants, various elements, and structures impounding the river often become a substrate for the development of a "microbial film" and protozoans. Numerous populations of Protozoa are detached from the structural elements by the water current and complement the local zooplankton communities.

The study of the Łyna River highlights the pivotal role of watershed management and water flow intensity in shaping the health of its ecosystem, particularly through the structural characteristics and distribution patterns of zooplankton communities. These findings provide crucial insights for the assessment of ecosystem health, linking zooplankton community structure to environmental stressors. By addressing these key factors, it is possible to mitigate the adverse effects of anthropogenic pressures and promote the long-term health and sustainability of riverine environments.

Conclusions

The study of the Łyna River highlights the pivotal role of land use and water flow intensity in shaping the health of its ecosystem, particularly through the structural characteristics and distribution patterns of zooplankton communities. Our findings provide crucial insights for assessing ecosystem health by linking zooplankton community structure to environmental stressors. Increased primary production (rise in Chl-*a*), good quality food (decrease in Pheo/Chl-*a*), and enhanced water retention in the catchment fostered a heterogeneous habitat and diverse feeding guilds for all functional groups, particularly large microphages (LMC), the stationary suspension group (STA), and various specialized taxa. In contrast, urban watersheds limited habitat suitability for all functional groups, with only small filtering microphages from the generalist group, which have a broad food spectrum (detritophagous, bacteriophagous), showing resilience, thus supporting the urban tolerance hypothesis.

The semi-natural watershed (urban-agricultural) showed increased diversity in feeding guilds, greater variety of LMC, higher activity of suctor Rotifera (RAP), and more amoeboid Protozoa compared to the urban area. However, intensified agricultural pressure significantly reduced zooplankton abundance, biomass, and taxa diversity, impairing the habitat functionality of the lower river zone, which confirms our hypotheses. The impact of land cover change is more pronounced at small-scale sub-catchments than at the catchment level as a whole. Therefore, assessing land cover change impacts on both hydrological processes and biological components requires sufficient spatial and temporal detail at the sub-catchment level to identify the most impacted areas. While some existing conclusions are deepened, this study primarily presents a new sub-catchment-based perspective on ecosystem health assessment.

To preserve water quality and biodiversity, maintaining natural hydrological conditions and minimizing urban and agricultural runoff are priorities for sustainable water management. Effective watershed management strategies should focus on enhancing water retention in natural areas, reducing nutrient loading, and protecting riparian habitats to support resilient and healthy aquatic ecosystems. Addressing these key factors will help mitigate the adverse effects of anthropogenic pressures and promote the long-term health and sustainability of riverine environments.

Methods

Study area

The Łyna River is the main watercourse in northeastern Poland (53°26′28.4″N, 20°24′48.6″E; 54°37′14.8″N; 21°13′35.6″E), with a flow regime typical for temperate climate zones on the Central European plains. The total catchment area of the river is 7126 km^2, and its length is 264 km (Fig. 5). The geomorphology and hydrographic network of the area are products of the last glaciation, which occurred approximately 10,000 years before present (BP). The landscape is characterized by morainic hills and outwash plains, predominantly utilized for agriculture or covered with pine forests. Additionally, the region features numerous natural lakes of postglacial origin, which occupy 4.2% of the river catchment area. Flow-through lakes along the Łyna watercourse take as much as 15.9% of the total riverbed length, with a maximum of 54.11% in the upper part, contributing to the flow range attenuation and minimized the risk of floods. Average specific outflows amount to 5.5 L/s from 1 km^2[51]. Longitudinal riverbed gradients range from 0.05‰ to 10‰. Along the river's course, anthropogenic pressure

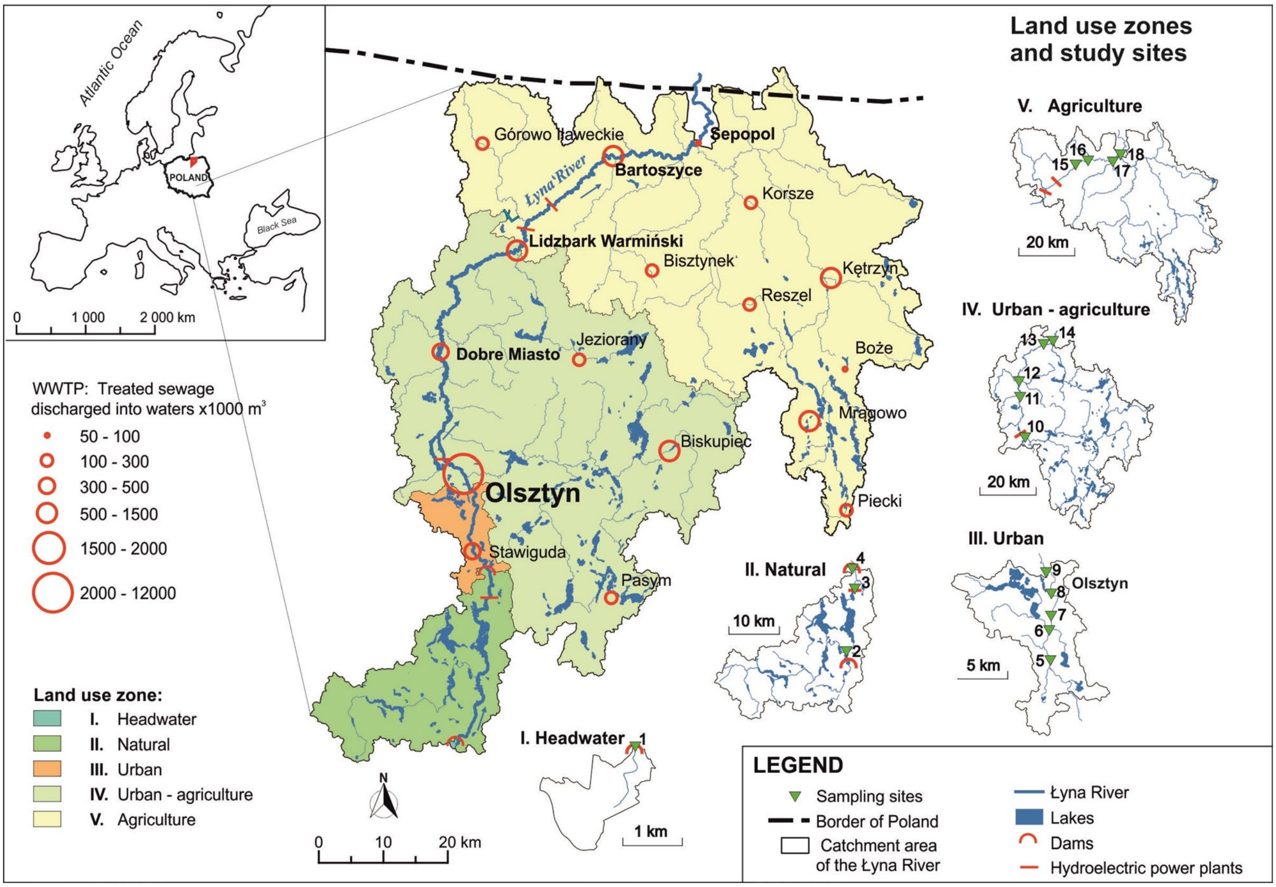

Figure 5. Location of the study area on the background of the Łyna River catchment.

increases[51]. In the south, the headwater catchment has a semi-natural character. Large areas are covered with forests growing on sandy outwash plains. The largest share of agriculturally used lands occurs in the lower part of the Łyna catchment, where the soils are primarily composed of moraine clays, as well as silty deposits suitable for agricultural development.

Due to the threats to the water quality of the Łyna catchment from land use, five zones (I-V) characteristic for various segments of the river were identified (Supplementary Table S4). Each zone was monitored for this hydrochemical and biological study. In total, 18 sampling sites were located along an approximately 200-km stretch of the river (Fig. 5). These sites represent characteristic sub-catchment types along the river: I: headwaters (site 1), II: natural (sites 2–4), III: urban (sites 5–9), IV: urban-agricultural (sites 10–14), and V: agricultural (sites 15–18).

Because the entire Łyna catchment, under EU Directive 91/271/EEC, is designated as an area sensitive to eutrophication due to pollution (N and P) from municipal sources, which cause deterioration of the riverine ecosystem health, maintaining a balance between nature conservation and economic needs is priority for the sustainable water management of the Warmia and Mazury region in NE Poland.

Sampling and analytical procedure

Zooplankton samples were collected one to two times per season—spring, summer, autumn, and winter—from 2019 to 2023. A total of 428 zooplankton samples were collected during the study period. Samples were collected using a 10-L sampler from a depth of approximately 20 cm below the water surface, at the central part of the riverbed.

Each collected sample of a volume of 20 L was filtered through a plankton net with 30 µm mesh size, preserved with Lugol's solution, and fixed in 4% formalin solution. Each sample was analysed in triplicate (sub-samples). Each time, 1 mL of the sample was analysed in the Sedgewick-Rafter chamber. Zooplankton were identified to the lowest possible taxonomic level (with the exception of juvenile Crustacea stages) under a Zeiss AXIO Imager microscope, using the methods described by Błędzki and Rybak[52], Radwan et al.[53], Koste[54], Rybak and Błędzki[55], and von Flössner[56]. The number of individuals among the zooplankton (ind/L) was estimated according to the Hansen's rule[57]. In order to determine the zooplankton biomass (µg/L), standard weights for rotifers were applied[53]. Regarding crustaceans and protozoa, particular organisms were measured under a microscope with a measuring lens at the maximum precision to 0.01 mm, using transmitted light. For the purpose of estimating biomass, it was assumed that the density of a zooplankton organism = 1. i.e. $1\ mm^3 = 1\ mg$[58]. Based on the results of the measurements, cubic volume of individuals was calculated, by comparing their shape to the basic geometrical solids.

Species diversity (Shannon diversity index, H′), and species evenness of zooplankton communities (Pielou's evenness index, J′) were analyzed with the use of MVSP 3.22 software[59] The species richness index (d) was calculated according to the formula of Margalef[60].

The functional variability of the zooplankton metacommunities was assessed in relation to feeding guilds, dependent of feeding strategy and body size of rotifer and crustacean species. On this basis, rotifer and crustacean species were classified into four groups: small microphagous (SMC), large microphagous (LMC), raptorials (RAP), and stationary/suspended (STA) feeders (Supplementary Table S2), according methods[61–64].

The SMC functional group included Rotifer's species with a malleate, malleoramate, or ramate trophi, that collect (filtration) multiple food items (*Anuraeopsis, Brachionus, Colurella, Conochilus, Euchlanis, Filinia, Hexarthra, Kellicottia, Keratella, Lecane, Lepadella, Mylitina, Notholca, Plationus, Platyias, Pompholyx, Proales, Squatinella, Testudinella, and Trichotria*), and Copepod's nauplii. The RAP functional group included Rotifer's genera with forcipate, incudate, or virgate trophi that show an active action (suctor, predator) to catch single food items (*Ascomorpha, Asplanchna, Cephalodella, Dicranophorous, Gastropus, Monommata, Ploesoma, Polyarthra, Scaridium, Synchaeta, and Trichocerca*), and all adult Cyclopoida. The LMC functional group included Cladocera species and copepodites Copepoda (Supplementary Table S2).

The physical and chemical parameters of water were analyzed in each zooplankton sampling site during each sampling event. Water temperature (°C), pH, dissolved oxygen (DO), turbidity (NTU), electrical conductivity (EC), were measured with the YSI 6600R2 calibrated multiprobe (Yellow Springs, OH, USA). Water samples were collected for laboratory analyses of total nitrogen (TN), nitrate nitrogen (N-NO_3), ammonium nitrogen (N-NH_4,), total phosphorous (TP), orthophosphate (P-PO_4), total organic carbon (TOC), total inorganic carbon (TIC), biochemical oxygen demand (BOD), chlorophyll *a* (Chl-*a*), and pheophytin (Pheo). Hydrochemical analyses were conducted in accordance with APHA-AWWA-WEF[65].

Hydrological data—daily river flows (Q, m^3/s) for the period from 2019 to 2023 for three gauging stations on the Łyna River: Olsztyn—Kortowo (site 7), Smolajny (site 12), and Sępopol (site 18) were provided by the Institute of Meteorology and Water Management (IMGW-PIB) in Poland. Flow data for other study sites was obtained using the Delft-3D wflow-sbm model, an open-source tool available at https://www.deltares.nl/en/software-and-data/products/wflow-catchment-hydrology[66].

In five distinguished research zones along the Łyna River, the following shares of land use forms were determined: forests, wetlands, arable land, build-up areas (Build-ups), and lakes. The part (%) of the riverbed lengh occupied by lakes was also determined (Lake cum) (Table S4). The share of land use forms in various parts of the Łyna river catchment was determined based on information on land cover/land use provided by the CORINE Land Cover (CLC2018) using the SCALGO Live® platform (www.scalgo.com).

Statistical procedures

Before analyses, the dataset was checked for normality using the Shapiro–Wilk test at $p < 0.05$. To evaluate general differences among five zones of the Łyna River, distinguished by land use, in terms of zooplankton abundance, biomass, species diversity, and characteristics of functional groups, analysis of variance one-way ANOVA, followed by a post-hoc Tukey HSD test ($p \leq 0.05$), was performed.

The specific zooplankton taxa for a given site were determined by indicator species analysis (ISA) using PC-ORD 6.0 (MjM Software, Gleneden Beach, Oregon, US). The ISA was calculated as the product of relative species abundance and frequency of occurrence to obtain a maximum indicator value (IndVal) for each species[67]. Indicator values range from 0 to 100. A value of 100 represents a perfect indicator species, i.e., a species that occurs exclusively in one group, is found in all samples in that group, and has a high relative abundance within that group. To group zooplankton species and sampling locations along the river course we employed Two-Way Cluster Analysis (TWCA) based on Bray–Curtis similarity. Prior to analysis, data were normalised to mitigate the influence of outliers.

Partial Least Squares Regression (PLS-R) analysis was performed to identify the impact of various environmental factors on the functional groups of zooplankton community along the river. PLS-R is a multivariate statistical technique that combines features from principal component analysis and multiple regression, particularly suited for ecological studies where the predictor variables are numerous and highly collinear[68]. It allowed us for the identification of the most influential factors on zooplankton distribution and abundance. We used rotifer and crustacean functional groups (SMC, LMC, RAP, and STA) as response (Y) variables, and environmental parameters (physical, chemical, and biological parameters) as predictor (X) variables.

To identify the most significant predictors, the Variable Importance in Projection (VIP) scores in the PLS-R model were used to assess the importance of each variable in explaining the variance in the response variables[69]. Variables X (predictors) with VIP scores > 1 were considered as more important than average in explaining the variance in the response variables across all the components of the PLS model. To enhance the selection of predictors (X) that are considered key drivers in the PLS-R model we applied Variable Identification (VID) technique. VID absolute value indicates the strength of the variable's influence on the model by identifying those that have a substantial impact on the response variable. In the interpretation of the PLS model, a VID score cut-off at 0.50 was considered indicative of an important variable, provided that the confidence interval for the standardized coefficient did not include zero. This condition ensures clarity regarding the direction and statistical significance of the variable's impact on the dependent variable. Positive VID scores indicate positively associated variables with particular zooplankton groups, while negative scores indicate an adverse relationship. The robustness of the PLS model was assessed through various diagnostic checks, including RMSE, MSE and the examination of the predictive relevance (Q^2) of the model. The PLS-R model analysis was performed using XLSTAT software, MS Excel add-ins statistical tool (www.xlstat.com).

Data availability

The datasets used and/or analysed during the current study available from the corresponding author on reasonable request.

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Author contributions
A.M.G. designed the research, conducted fieldwork, analyzed the zooplankton samples and water samples, planned and wrote the main manuscript text and prepared Figs. 1, 3, and Fig. S2. I.C. conducted fieldwork, analyzed hydrological and cachment data and prepared Fig. 5. K.G-L. conducted main statistical analysis (ISA, PLS-R, and TWCA) interpreted results and prepared Figs. 2, 4, and Fig. S1. All authors reviewed the manuscript.

Competing interests
The authors declare no competing interests.

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