

HOW DOES THE INVASIVE ZOOPLANKTON SPECIES AFFECT THE ZOOPLANKTON COMMUNITY IN SMALL AND SHALLOW WATERS? APPEARANCE AND DISTRIBUTION OF *SINODIAPTOMUS SARSI* (COPEPODA, CALANOIDA)

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Korponai, J., †Forró, L., Selmeczy, G. B., Vadkerti, E. & Padisák, J. (2025): How does the invasive zooplankton species affect the zooplankton community in small and shallow waters? Appearance and distribution of *Sinodiaptomus sarsi* (Copepoda, Calanoida). – *Studia bot. hung.* **56**(1): 111–132.

Abstract: During our study on small and shallow waters in Hungary, a new invasive species of copepod, *Sinodiaptomus sarsi* (Rylov, 1923), was found in our zooplankton samples collected in 2017. In Hungary, we found it in 17 lakes, with significant biomass in the 4th fishing lake on the outskirts of Püspökladány, Szénaréti-tó in Nyírbátor, the Fegyverneki-Holt-Tisza, and Lake Déli-tó in Gyopárosfürdő. As a result, we confirm that *Sinodiaptomus sarsi* has successfully established populations in Hungarian waters, yet we found no clear evidence that its presence has significantly altered the overall zooplankton community structure. As a selective filter feeder, it can potentially fulfil the functional role of native calanoid copepods in lentic ecosystems. However, its distribution may be restricted by its thermal requirements, which could confine its presence to specific habitats or seasons. *S. sarsi* appears to be an invasive and opportunistic member of Hungarian freshwater zooplankton, with its role and distribution likely determined by the interplay of temperature regimes, trophic state, and predator pressure. Monitoring its dispersion will be essential to detect potential shifts in population dynamics, particularly under changing climatic and eutrophication scenarios.

Key words: composition, feeding, Reynolds's functional groups, *Sinodiaptomus sarsi*, traits, zooplankton

INTRODUCTION

Humans significantly affect the environment. (DÍAZ *et al.* 2019). The demands of a growing human population have driven its impact on biota (KECK *et al.* 2025). Intensifying land use, resource depletion, environmental pollution, climate change, and globalisation threaten biodiversity. Globalisation not only exhausts natural resources but also increases the uniformity of biota. Diverse ecosystems are more resilient to disturbances like climate extremes, disease outbreaks, and invasive species. When biodiversity declines, ecosystems become more fragile and less able to adapt to environmental change. Human activities have extensively altered freshwater ecosystems, whose species loss rates rival those found in tropical forests (RICCIARDI and RASMUSSEN 1999). Besides species loss, alien species are among the most important, least controlled, and least reversible of human impacts on the freshwater (STRAYER 2010).

Invasive zooplankton species can restructure aquatic ecosystems, alter food webs, alter nutrient cycling, and replace native taxa in ecosystem functioning (HAVEL *et al.* 2015). Making their study is critical for understanding and mitigating human-induced biodiversity change. Zooplankton are crucial components of aquatic systems, transferring energy from primary producers to higher trophic levels (LAMPERT and SOMMER 2007).

The calanoid copepod *Sinodiaptomus sarsi* (Rylov, 1923) is native to East Asia and was originally described in fishponds and reservoirs in eastern China. Since then, the species has spread to western Asia and has been found in Turkey in the 1990s (GÜNDÜZ 1998). The first European record was from Sophia in Bulgaria, where it was from a fish tank (BLEDZKI and RYBAK 2016). However, its presence remained uncertain until 2016, when MYKITCHAK (2016) found it in Ukraine in the Carpathian Mountain region near the Slovakian border (MYKITCHAK 2018, MYKITCHAK and KOVAL 2018). Subsequently, the species was also reported from also Ukraine, from Kyiv (SVETLICHNY and SAMCHYSHYNA 2021), and Romania (BATTES *et al.* 2020).

MATERIALS AND METHODS

Study area and the measured variables

During the study, a total of 70 lakes were sampled. Due to a lack of environmental data, only 64 were assessed in this study (Fig. 1). All the visited lakes are located in Hungary (Central Europe), and their surface areas range between 0.08 and 102 ha. The depths at the sampling sites ranged from 0.8 to 14 m. The sampling sites were approached by a belly boat, and the depth of the lakes was measured with Deeper Smart Sonar Pro+. Sampling was con-

ducted during the summer (July–August) of 2017. Zooplankton samples were taken by a 12 L volume of a Schindler-Patalas plankton trap with a 65 μm mesh from two depths. Three replicates were taken from near the surface of the water, and the other three were taken from near the bottom. Then, the samples were integrated and preserved using Lugol's solution. Subsamples were taken, and a counting chamber was used for enumerating zooplankton under a Nikon Diaphot inverted microscope (1 ml subsamples for rotifers, 5 ml subsample for microcrustaceans). At least 100 specimens were counted for each zooplankton group (microcrustaceans and rotifers). Microcrustacean biomass was calculated based on weight-length regressions (DOWNING and RIGLER 1981), while rotifer biomass was assessed based on its biovolume. The length of the first 30 individuals of each microcrustacean species encountered in each sample was measured with an ocular micrometre. Biomass data were given in mg w.w. m^{-3} and introduced into all statistical analyses. Functional groups for zooplankton were determined based on their foraging strategies (Table 1). For the identification of zooplankton, we used BATTES *et al.* (2020), BLEDZKI and RYBAK (2016), GULYÁS and FORRÓ (1999), PODSHIVALINA and SHEVELEVA (2020), GÜNDÜZ (1998), SVETLICHNY and SAMCHYSHYNA (2021) for microcrustaceans, and BANCISI (1986, 1988) for rotifers.

The conductivity (COND, $\mu\text{S cm}^{-1}$), pH and water temperature (TEMP, $^{\circ}\text{C}$), and dissolved oxygen (DO, mg L^{-1}) were measured on site. Water samples were analysed for total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN), dissolved inorganic nitrogen (DIN) (as sum of nitriteN ($\text{NO}_2\text{-N}$),

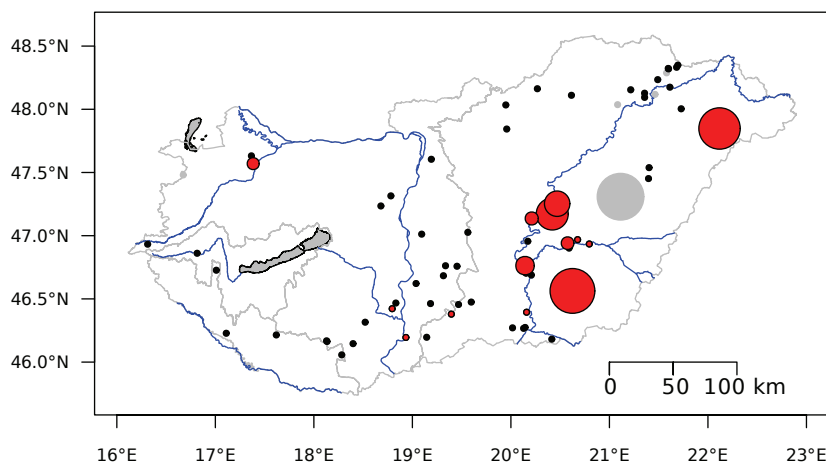


Fig. 1. Map of the sampling sites. (Dots represent the water bodies. Grey dots show those waters which are not involved in the statistical analyses. Red and black dots represent waters inhabited and uninhabited by *Sinodiaptomus sarsi*, respectively. The size of the dots refers to the biomass of *S. sarsi*).

Table 1. List of zooplankton species with functional groups.

Taxon name	Code	Traits	Groups
<i>Bosmina coregoni</i>	Bos_core	bacteria_feeder	Cladocera
<i>Bosmina longirostris</i>	Bos_long	bacteria_feeder	Cladocera
<i>Iliocryptus acutifrons</i>	Ili_acut	benthic_picker	Cladocera
<i>Iliocryptus agilis</i>	Ili_agil	benthic_picker	Cladocera
<i>Leptodora kindtii</i>	Lep_kind	large_predator	Cladocera
<i>Acropterus harpae</i>	Acr_harp	large_substratum scrapers	Cladocera
<i>Simocephalus vetulus</i>	Sim_vetu	littoral_large filterers	Cladocera
<i>Daphnia ambigua</i>	Dap_ambi	pelagic_large filterers	Cladocera
<i>Daphnia cucullata</i>	Dap_cucu	pelagic_large filterers	Cladocera
<i>Daphnia galeata</i>	Dap_gale	pelagic_large filterers	Cladocera
<i>Daphnia magna</i>	Dap_magn	pelagic_large filterers	Cladocera
<i>Daphnia parvula</i>	Dap_parv	pelagic_large filterers	Cladocera
<i>Diaphanosoma brachyurum</i>	Dia_brac	pelagic_non_daphnid filterers	Cladocera
<i>Moina brachiata</i>	Moi_brac	pelagic_small filterers	Cladocera
<i>Moina micrura</i>	Moi_micr	pelagic_small filterers	Cladocera
<i>Moina weismanni</i>	Moi_weis	pelagic_small filterers	Cladocera
<i>Ceriodaphnia laticaudata</i>	Cer_lati	small_littoral_daphnid filterers	Cladocera
<i>Ceriodaphnia pulchella</i>	Cer_pulc	small_littoral_daphnid filterers	Cladocera
<i>Ceriodaphnia quadrangula</i>	Cer_quad	small_littoral_daphnid filterers	Cladocera
<i>Ceriodaphnia reticulata</i>	Cer_reti	small_littoral_daphnid filterers	Cladocera
<i>Ceriodaphnia rotunda</i>	Cer_rotu	small_littoral_daphnid filterers	Cladocera
<i>Ceriodaphnia</i> sp.	Cer_sp.	small_littoral_daphnid filterers	Cladocera
<i>Alona rectangula</i>	Alo_rect	small_substratum scrapers	Cladocera
<i>Alonella excisa</i>	Alo_exc	small_substratum scrapers	Cladocera
<i>Alonella exigua</i>	Alo_exig	small_substratum scrapers	Cladocera
<i>Chydorus sphaericus</i>	Chy_spha	small_substratum scrapers	Cladocera
<i>Macrothrix hirsuticornis</i>	Mac_hirs	substratum scrapers	Cladocera
<i>Macrothrix laticornis</i>	Mac_lati	substratum scrapers	Cladocera
<i>Pleuroxus denticulatus</i>	Ple_dent	substratum scrapers	Cladocera
<i>Pleuroxus uncinatus</i>	Ple_unci	substratum scrapers	Cladocera
<i>Scapholebaris mucronata</i>	Sca_mucr	substratum scrapers	Cladocera
<i>Acanthocyclops robustus</i>	Aca_robu	large_omnivore	Copepoda
<i>Eudiaptomus gracilis</i>	Eud_grac	selective_filterer	Copepoda
<i>Sinodiaptomus sarsi</i>	Sin_sars	selective_filterer	Copepoda
<i>Nauplius calanoids</i>	Nau_cal	small_filterer	Copepoda
<i>Nauplius cyclopoids</i>	Nau_cyc	small_filterer	Copepoda
<i>Acanthocyclops robustus copepodite</i>	Aca_cop	small_omnivore	Copepoda
<i>Eucyclops serrulatus copepodite</i>	Euc_serr	small_omnivore	Copepoda
<i>Macrocyclus albidus copepodid</i>	Mac_albi	small_omnivore	Copepoda
<i>Mesocyclops leuckarti</i>	Mes_leuc	small_omnivore	Copepoda
<i>Thermocyclops crassus</i>	The_cras	small_omnivore	Copepoda
<i>Thermocyclops dybowski</i>	The_dybo	small_omnivore	Copepoda

Table 1. (continued)

Taxon name	Code	Traits	Groups
<i>Anuraeopsis fissa</i>	Anu_fiss	micro_filterer	Rotifera
<i>Bdelloidea</i> spp.	Bde_spp	micro_filterer	Rotifera
<i>Brachionus angularis</i>	Bra_angu	micro_filterer	Rotifera
<i>Brachionus budapestiensis</i>	Bra_buda	micro_filterer	Rotifera
<i>Brachionus calyciflorus</i>	Bra_caly	micro_filterer	Rotifera
<i>Brachionus diversicornis</i>	Bra_dive	micro_filterer	Rotifera
<i>Brachionus dorcas</i>	Bra_dorc	micro_filterer	Rotifera
<i>Brachionus elevatus</i>	Bra_elev	micro_filterer	Rotifera
<i>Brachionus falcatus</i>	Bra_falc	micro_filterer	Rotifera
<i>Brachionus fernandoi</i>	Bra_fern	micro_filterer	Rotifera
<i>Brachionus forficula</i>	Bra_forf	micro_filterer	Rotifera
<i>Brachionus leydigi</i>	Bra_leyd	micro_filterer	Rotifera
<i>Brachionus quadridentatus</i>	Bra_quad	micro_filterer	Rotifera
<i>Brachionus urceolata</i>	Bra_urce	micro_filterer	Rotifera
<i>Brachionus variabilis</i>	Bra_vari	micro_filterer	Rotifera
<i>Cephalodella gibba</i>	Cep_gibb	micro_filterer	Rotifera
<i>Cephalodella mucronata</i>	Cep_mucr	micro_filterer	Rotifera
<i>Cephalodella</i> sp.	Cep_sp	micro_filterer	Rotifera
<i>Collotheca</i> sp.	Col_sp	micro_filterer	Rotifera
<i>Colurella</i> spp.	Col_spp	micro_filterer	Rotifera
<i>Filinia limnetica</i>	Fil_limn	micro_filterer	Rotifera
<i>Filinia longiseta</i>	Fil_long	micro_filterer	Rotifera
<i>Filinia opoliensis</i>	Fil_opol	micro_filterer	Rotifera
<i>Hexarta intermedia</i>	Hex_inte	micro_filterer	Rotifera
<i>Keratella cochlearis</i>	Ker_coch	micro_filterer	Rotifera
<i>Keratella cochlearis-tecta</i>	Ker_coch	micro_filterer	Rotifera
<i>Keratella quadrata</i>	Ker_quad	micro_filterer	Rotifera
<i>Keratella serrulata</i>	Ker_serr	micro_filterer	Rotifera
<i>Keratella tropica</i>	Ker_trop	micro_filterer	Rotifera
<i>Keratella valga</i>	Ker_valg	micro_filterer	Rotifera
<i>Lecane bulla</i>	Lec_bull	micro_filterer	Rotifera
<i>Lecane closteroerca</i>	Lec_clos	micro_filterer	Rotifera
<i>Lecane cornuta</i>	Lec_corn	micro_filterer	Rotifera
<i>Lecane elsa</i>	Lec_elsa	micro_filterer	Rotifera
<i>Lecane hamata</i>	Lec_hama	micro_filterer	Rotifera
<i>Lecane ludwigi</i>	Lec_ludw	micro_filterer	Rotifera
<i>Lecane luna</i>	Lec_luna	micro_filterer	Rotifera
<i>Lecane lunaris</i>	Lec_luna	micro_filterer	Rotifera
<i>Lepadella acuminata</i>	Lep_acum	micro_filterer	Rotifera
<i>Lepadella dactyloseta</i>	Lep_dact	micro_filterer	Rotifera
<i>Lepadella patella</i>	Lep_pate	micro_filterer	Rotifera
<i>Lepadella rhomboides</i>	Lep_rhom	micro_filterer	Rotifera

Table 1. (continued)

Taxon name	Code	Traits	Groups
<i>Lepadella</i> sp.	Lep_sp	micro_filterer	Rotifera
<i>Lophocharis salpina</i>	Lop_salp	micro_filterer	Rotifera
<i>Mytilina acanthophora</i>	Myt_acan	micro_filterer	Rotifera
<i>Mytilina mucronata</i>	Myt_mucr	micro_filterer	Rotifera
<i>Platylabus patulus</i>	Pla_patu	micro_filterer	Rotifera
<i>Platylabus quadricornis</i>	Pla_quad	micro_filterer	Rotifera
<i>Polyarthra dissimulans</i>	Pol_diss	micro_filterer	Rotifera
<i>Polyarthra dolychoptera</i>	Pol_doly	micro_filterer	Rotifera
<i>Polyarthra euryptera</i>	Pol_eury	micro_filterer	Rotifera
<i>Polyarthra vulgaris</i>	Pol_vulg	micro_filterer	Rotifera
<i>Pompholyx complanata</i>	Pom_comp	micro_filterer	Rotifera
<i>Pompholyx sulcata</i>	Pom_sulc	micro_filterer	Rotifera
<i>Rotaria</i> spp.	Rot_spp	micro_filterer	Rotifera
<i>Squatinella mutica</i>	Squ_muti	micro_filterer	Rotifera
<i>Synchaeta oblonga</i>	Syn_oblo	micro_filterer	Rotifera
<i>Synchaeta</i> spp.	Syn_spp	micro_filterer	Rotifera
<i>Testudinella patina</i>	Tes_pati	micro_filterer	Rotifera
<i>Trichocerca capucina</i>	Tri_capu	micro_filterer	Rotifera
<i>Trichocerca cylindrica</i>	Tri_cyli	micro_filterer	Rotifera
<i>Trichocerca elongata</i>	Tri_elon	micro_filterer	Rotifera
<i>Trichocerca pusilla</i>	Tri_pusi	micro_filterer	Rotifera
<i>Trichocerca rattus</i>	Tri_ratt	micro_filterer	Rotifera
<i>Trichocerca similis</i>	Tri_simi	micro_filterer	Rotifera
<i>Trichocerca</i> spp.	Tri_spp	micro_filterer	Rotifera
<i>Asplanchna priodonta</i>	Asp_prio	micro_pred	Rotifera
<i>Asplanchna sieboldi</i>	Asp_sieb	micro_pred	Rotifera

nitrateN ($\text{NO}_3\text{-N}$), ammoniumN ($\text{NH}_4\text{-N}$), soluble reactive silica (Si), sulphate (SO_4^{2-}), chloride (Cl^-), carbonate (CO_3^{2-}), bicarbonate (HCO_3^-), and chemical oxygen demand (COD). TP and COD were expressed in $\mu\text{g L}^{-1}$, while the others were given in mg L^{-1} (see SELMECZY *et al.* 2023). Phytoplankton biomass was determined based on cell volumes from the most similar geometric forms and was sorted into Reynolds's functional groups (RFG) (see SELMECZY *et al.* 2023).

Land use types were employed based on the Corine Land Cover (CLC) database (European Union, Copernicus Land Monitoring Service 2018, European Environment Agency). Five categories were determined: urban areas, agricultural areas, forest and seminatural areas, wetlands, and water (see SELMECZY *et al.* 2023). Geographical environmental variables were compiled from the physical (watershed area (km^2), lake surface area (km^2)) and metadata (longitude, latitude, and altitude) of the lakes.

Statistical analyses

The constrained ordination method was selected, revealing the factors that can regulate or respond to the zooplankton community. Prior to any statistical analyses, all data were transformed. The biomass data were Hellinger transformed following LEGENDRE and GALLAGHER's (2001) suggestions, and their heterogeneity was checked by the *decorana* function of *vegan*. Since the gradient lengths were less than 4, the linear constrained ordination method, Redundancy Analysis (RDA), was applied. Water chemistry data were standardised to zero means and unit variances (z-transformation), while land-use cover was submitted to a square root transformation. Data analyses were carried out in the R environment 4.5.1 (R CORE TEAM 2025) with the following packages: *vegan* (OKSANEN *et al.* 2025), *maps* (BECKER *et al.* 2025) and *raster* (HIJMANS 2025). Environmental variables, which were introduced into RDA, were selected by the variance inflation factor. Variables with a VIF < 10 were submitted into RDA (BORCARD *et al.* 2011), and the significant environmental and land-use variables were selected with stepwise selection in an RDA model using the “ordistep” function. The “intersetcor” function of the *vegan* package was used for the calculation of correlation.

Procrustes analysis was used to investigate the degree of concordance between each pair of ordinations. Procrustes analysis rotates two ordinations to maximise the similarities between them by minimising the sum of their squared distances (GOWER 1971). The residuals of a Procrustes rotation reflect the extent of the changes in the position of assemblages in the ordination space. Residuals are high if the removal of *Sinodiaptomus sarsi* strongly modifies the structure of the assemblages. The Procrustes rotation was computed by means of the “procrustes” function in the *vegan* package (OKSANEN *et al.* 2025). Prior to the Procrustes analysis, Principal Component Analyses (PCA) were run on Hellinger-transformed zooplankton data. One PCA was applied to the entire data set, while the second was run on the data set from which the *S. sarsi* was removed.

RESULTS

Altogether, 108 taxa were found in the 70 lakes belonging to three taxonomic groups and 17 foraging traits (Table 1). Rotatoria was the richest taxonomic group with 68 taxa, followed by Cladocera with 31 taxa, while Copepoda was represented by only eight taxa. Biomass of zooplankton varied in a considerable interval (Fig. 7). The lowest zooplankton population (0.34 mg d.w. L⁻¹) was found in Bánya-tó near Tarcál village. The highest zooplankton biomass (39.83 mg d.w. L⁻¹) was recorded in the Cibakházi Holt-Tisza due to the mass production of *Brachionus diversicornis* rotifera (Fig. 7).

We found *Sinodiaptomus sarsi* (Rylov, 1923) in seventeen samples during the study. This species is new to the Hungarian fauna. Most of the lakes inhabited by this species are located in the eastern part of the Danube; only two occurrences have been recorded in the western part of Hungary with low biomass (Tolnai-Duna and Fábíán-tó in Bácskai-tó). Taxonomically, this species belongs to the Diaptomidae family of the Calanoida order of Crustacea. Large in size, the adults can reach 2 mm in length. Its density varied between 0.014 and 113.542 ind L^{-1} , while biomass varied between 0.001 and 3.889 mg L^{-1} . This species occurred with the highest biomass in the 4th fishing lake on the outskirts of Püspökladány. It occurred in significant biomass in three places (Déli-tó at Gyopárosfürdő, Szénaréti-tó at Nyírbátor, and Fegyverneki-Holt-Tisza, while its biomass was moderate in the rest of the lakes. This species can be easily identified by its morphological characteristics. Females carry a dorsal bulge on the 5th thoracic segment (Fig. 2). The second segment of exopodite of the fifth swimming leg (P5) of males ends in a lamellate thumb-like process (Fig. 4). Its endopodite reaches the apex of exopodite (Fig. 5). Females have spinules on both margins of the end claw of the fifth leg exopodite (Fig. 6).

Rotifer biomass varied between 0 and 22 mg d.w. L^{-1} , they took the highest part (36%) of the total zooplankton biomass. Rotifers were sorted into two foraging traits: micro filterers and micro predators. Micro filterers took a significant share of zooplankton; their biomass varied from 0 to 21 mg d.w. L^{-1} accounted for a little more than one third of the total zooplankton biomass. The most frequent micro filterers belonged to *Branchionus*, *Keratella*, *Pompholyx*, and



Fig. 2. General habitus of female *Sinodiaptomus sarsi* with egg sack. The red arrow points to the dorsal bulge on the 5th thoracic segment (40× magnification).



Fig. 3. Female of *Sinodiaptomus sarsi* with egg sacks with 100 $\times$ magnification. The red arrow indicates the dorsal bulge on the 5th thoracic segment.

Polyarthra genera, while micro predators were *Asplanchna* species, and it took only 1% of the total zooplankton biomass (Figs 7–8).

Copepod biomass accounted for the largest part (44%) of the total zooplankton biomass. Its biomass varied between 0 and 14 mg d.w. L⁻¹. Copepod species



Fig. 4. The left 5th swimming leg (P5) of a male of *Sinodiaptomus sarsi*. The red arrow shows the second segment of exopodite ending in a lamellate thumb-like process (100 $\times$ magnification).



Fig. 5. The right fifth swimming leg (P5) of a male of *Sinodiaptomus sarsi*. The red arrow shows the endopodite reaching the apex of exopodite (100× magnification).

can be sorted into two large foraging groups. Only the adult *Acanthocyclops robustus* (G. O. Sars, 1863) cyclopoid gave a large omnivore trait. The adults and immature copepodites of *Eudiaptomus gracilis* (Sars, 1863) and *Sinodiaptomus sarsi* calanoids were selective filterers, sharing even 5% of total biomass. Nauplii were grouped into small filterers. It took a small part (5%) of the zooplankton biomass.



Fig. 6. The fifth swimming leg (P5) of a female of *Sinodiaptomus sarsi* (400× magnification).

Thermocyclops crassus (Fischer, 1853) and copepodite stages of all other cyclopoids belonged to the small omnivores. The biomass of this group varied between 0 and 14 mg d.w L⁻¹, and it was another group which shared one-third (33%) of the total zooplankton biomass (Figs 7–8).

Cladoceran biomass gave the lowest part (20%) of the zooplankton biomass, varying between 0 and 11 mg d.w L⁻¹. Cladocerans were classified into eleven groups based on their feeding traits (Table 1). Cladocera species, which were represented by the highest biomass, can be sorted into four foraging trait categories: bacteria feeders represented by bosminids with 11% biomass, pelagic large filterers by daphnids with 4%, pelagic non-daphnia by only *Diaphanosoma brachyurum* (Liévin, 1848) with 2%, pelagic small filterers such as moinids with 2%, and littoral daphnid filterers as *Ceriodaphnia* species with 1% sharing (Figs 7–8).

RDA analyses revealed that environmental parameters explained only a small part of the zooplankton variances of either species structure or trait aspect (Table 2). Although latitude became the uniquely significant constrained variable for the composition of the zooplankton species (RDA1: explained variance = 0.0154, $F_{\text{pseudo}} = 1.9164$, $p = 0.014$, $r = 0.543$), neither the land use of the surroundings nor the geographical background of the lakes seemed to affect the zooplankton. This was proven because latitude lost its constraint; therefore, no constraining factor remained in the traits-geographical RDA (Table 2). Relationships between zooplankton and water quality, or phytoplankton, were significant in both approaches (Table 2). From the water quality variables, temperatures (temp), total phosphorus (TP), and dissolved oxygen (DO) were effective factors in the composition of zooplankton since these variables were significant in both species-water quality and trait-water quality ordinations (Table 3). The first three components were significant in species-water quality RDA (RDA1: explained variance = 0.0305, $F_{\text{pseudo}} = 4.1131$, $p = 0.001$, RDA2: explained variance = 0.0221, $F_{\text{pseudo}} = 2.9792$, $p = 0.004$; RDA3: explained variance = 0.0174, $F_{\text{pseudo}} = 2.3454$, $p = 0.016$). The first redundant component of this RDA presented the highest correlation with Cl⁻ ($r = -0.810$) and TP ($r = -0.779$), the second component of species-water quality RDA was correlated with DO ($r = -0.911$), while TEMP was the variable that explained variance significantly ($r = 0.846$) in the third component of this RDA. Regarding the traits and water quality, the first two components were significant in their RDA (RDA1: explained variance = 0.0178, $F_{\text{pseudo}} = 4.3382$, $p = 0.004$; RDA2: explained variance = 0.0127, $F_{\text{pseudo}} = 3.087$, $p = 0.026$), and DO, TEMP, and TP also proved significant explanatory variables. The first redundant component of this RDA presented the highest correlation with DO ($r = 0.804$), while the second component was correlated with TEMP ($r = -0.757$) and TP ($r = -0.700$). Since the first redundancy component (RDA1) of species and the second redundancy component (RDA2) of trait RDAs showed a high correlation with TP, and the correlation between the components (Spearman's $r = 0.674$,

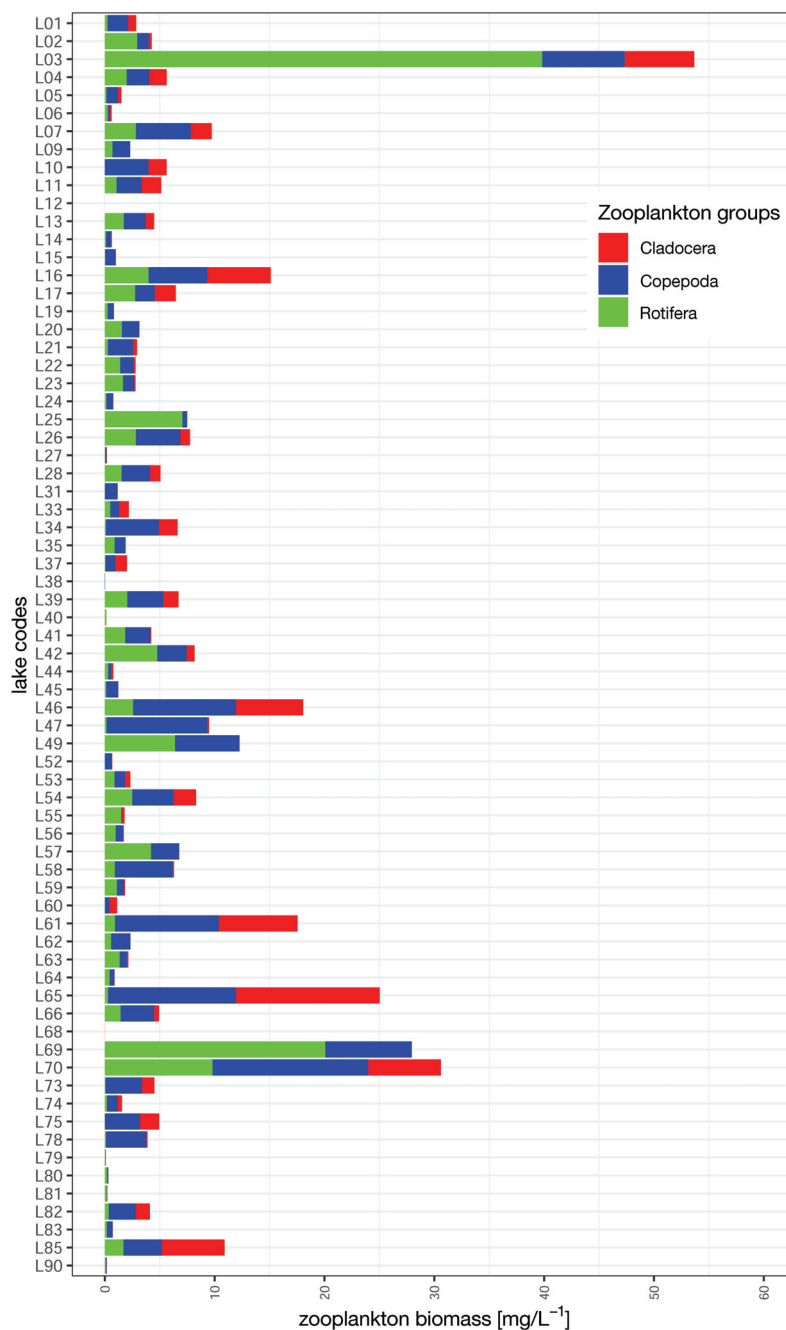


Fig. 7. Biomass of the main groups of zooplankton biomass of the studied lakes.

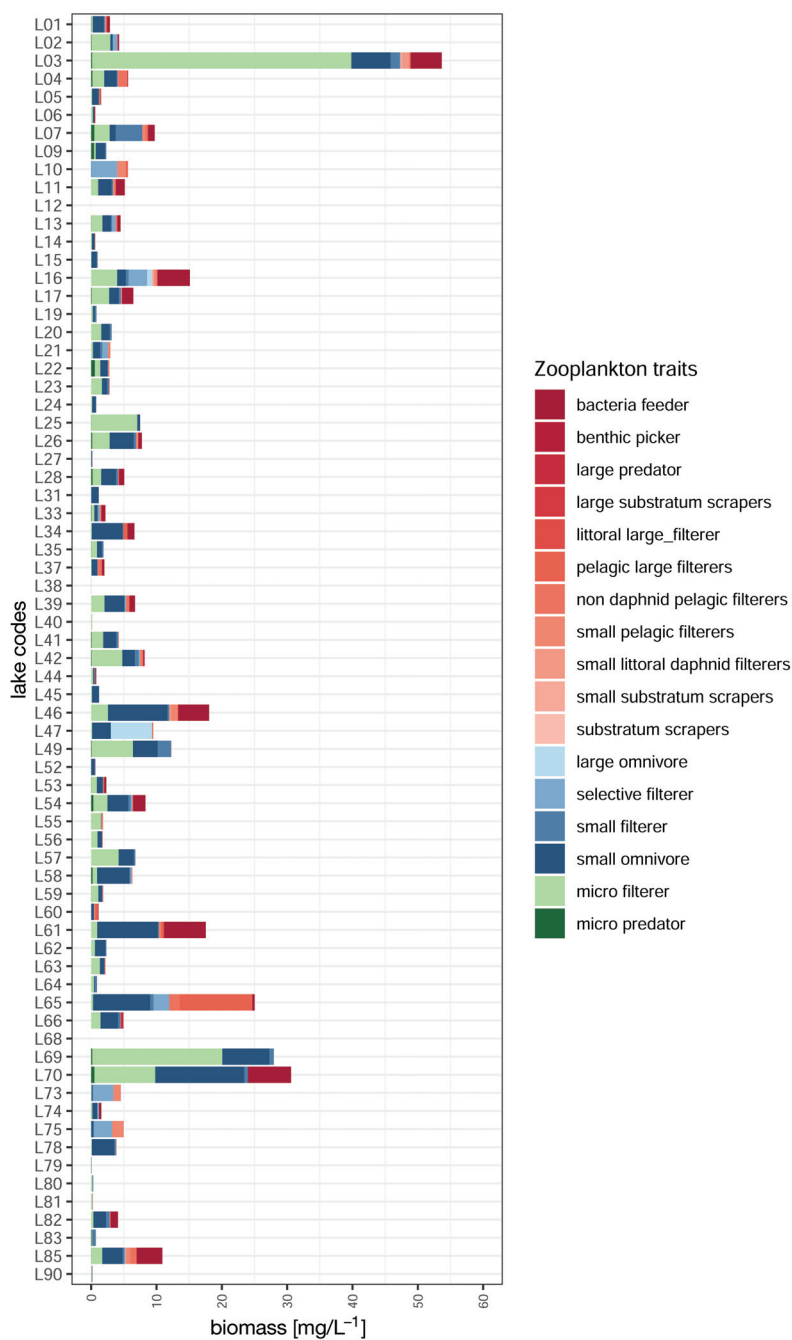


Fig. 8. Distribution of the biomass of zooplankton functional groups (feeding traits).

Table 2. Summary table of RDA results.

		Inertia	%	R ² _{adj}	F _{Pseudo}	p
Community						
water quality	total	0.5135	100	0.0908	2.5723	0.001
	constrained	0.0762	14.85			
	unconstrained	0.4372	85.15			
phytoplankton	total	0.5135	100	0.0843	2.4503	0.001
	constrained	0.0732	14.25			
	unconstrained	0.4403	85.75			
land use	total	0.5135	100	0	0	0
	constrained	0	0			
	unconstrained	0.5135	100			
geographical	total	0.5135	100	0.0143	1.9164	0.014
	constrained	0.0154	3			
		0.4981	97			
Feeding trait						
water quality	total	0.2835	100	0.0868	2.9957	0.001
	constrained	0.0369	13.03			
	unconstrained	0.2466	86.97			
phytoplankton	total	0.2835	100	0.108	2.9066	0.001
	constrained	0.0467	16.46			
	unconstrained	0.2368	83.54			
land use	total	0.2835	100	0	0	0
	constrained	0	0			
	unconstrained	0.2835	100			
geographical	total	0.2835	100	0	0	0
	constrained	0	0			
	unconstrained	0.2835	100			

S = 14228, p-value < 0.001) was high, the distribution of lakes was determined by the eutrophic gradient. Increasing component scores decreases trophic status.

The phytoplankton can also explain species and trait compositions of zooplankton since their relationship with zooplankton became significant in both species and trait RDAs (Table 2, Figs 9–10). In species-phytoplankton RDA, the first two components were significant (RDA1: explained variance = 0.0388, F_{pseudo} = 5.1966, p = 0.001; RDA2: explained variance = 0.0169, F_{pseudo} = 2.2670, p = 0.045). Four RFGs were proven to be effective factors in connection with zooplankton. The codons X1, SN, Y, and LM were significant with zooplankton species composition, while codons H1, X1, XPh, and T were with zooplankton trait (Table 3). The first redundant component of species RDA presented the highest correlation with codon X1 (r = 0.728), SN (r = - 0.643), and codon LM (r = 0.560), while the second component was correlated with codon Y (r = -0.938). In the traits and phytoplankton RDA, the first two redundant components were significant (RDA1: explained

variance = 0.0232, $F_{\text{pseudo}} = 5.7671$, $p = 0.002$; RDA2: explained variance = 0.0142, $F_{\text{pseudo}} = 3.5293$, $p = 0.035$), and X1 RFG kept its substantial explanatory variable status. However, the highest correlation was with the third RDA component ($r = 0.720$), although this component was insignificant ($\text{RDA3} = 0.0065$, $F_{\text{pseudo}} = 1.6303$, $p = 0.344$). In this RDA analysis, codons H1, XPh, and T also became substantial variables. The first redundant component of this trait-phytoplankton RDA was the strongest correlation with codon XPh ($r = -0.628$) and codon T ($r = -0.602$) groups, while the second component was correlated with codon H1 ($r = 0.723$).

DISCUSSION

Aquatic ecosystems are threatened in Hungary (BORICS *et al.* 2016). Nutrient enrichment, invasion of alien species, and water scarcity can be considered threatening factors. Hungarian aquatic fauna enriched with a new calanoid copepod species, *Sinodiaptomus sarsi* (Rylov, 1923). This species was first recorded in neighbouring Romania and Ukraine in 2020 (BATTES *et al.* 2020, PODSHIVALINA and SHEVELEVA 2020, SVETLICHNY and SAMCHYSHYNA 2021). In Europe, most

Table 3. Anova table.

		Df	Variance	F	p
Community					
water quality	Cl	1	0.024	3.223	0.003
	DO	1	0.022	3.004	0.002
	TP	1	0.016	2.147	0.013
	TEMP	1	0.014	1.915	0.018
	residual	59	0.437		
phytoplankton	X1	1	0.025	3.356	0.001
	SN	1	0.016	2.209	0.004
	Y	1	0.015	1.982	0.01
	LM	1	0.017		
	residual	59	0.44		
geographical	latitude	1	0.015	1.916	0.021
	residual	62	0.498		
Functional groups					
water quality	DO	1	0.014	3.481	0.003
	TEMP	1	0.013	3.14	0.013
	TP	1	0.01	2.365	0.04
	residual	60	0.247		
phytoplankton	H1	1	0.012	2.954	0.006
	X1	1	0.01	2.608	0.018
	XPh	1	0.012	3.035	0.005
	T	1	0.012	3.029	0.009
	residual	590.237			

known occurrences of *S. sarsi* are restricted to fishponds and urban lakes. All seventeen lakes in which *S. sarsi* was detected in Hungary are fishponds managed for angling. In four of the lakes – 4th-tó at Püspökladány, Szénaréti-tó at Nyírbátor, Fegyverneki Holt-Tisza at Fegyvernek, Déli-tó at Orosháza-Gyopárosfürdő – the biomass of *S. sarsi* exceeded 1 mg L⁻¹. Given that these lakes are separated by an average distance of approximately 100 km, the pattern strongly suggests that the species' spread is a byproduct of fish stocking.

Statistical analyses revealed that trophic conditions were the primary determinant of zooplankton community structure. Both taxonomic and functional approaches indicated that the lakes were arranged along the RDA1 axis.

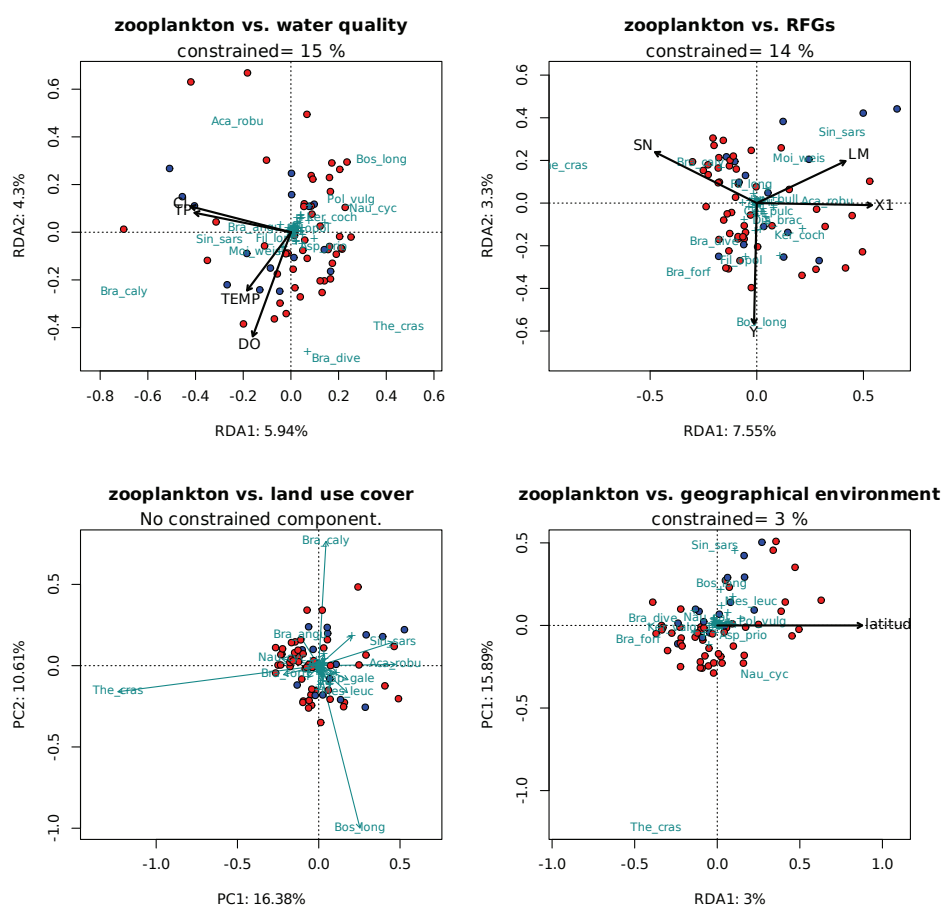


Fig. 9. Triplot of the redundancy analysis on zooplankton community with environmental variables: A = water quality; B = phytoplankton functional groups (RFG); C = the land use types; D = geographical metadata. (Red and blue dots represent sites with and without *Sinodiaptomus sarsi*, respectively).

Zooplankton community composition was mainly driven by limnological conditions (Figs 9–10). Although we assumed that land use would influence aquatic environments, no significant relationship was found between land use and zooplankton composition. However, species composition varied along a latitudinal gradient (Figs 9–10).

Zooplankton assemblages were associated with RFG codons characteristic of eutrophic to hypertrophic conditions, including X1, SN, Y, LM, XPh, and H1. Codons X1 and SN became significant variables in both taxonomic and functional analyses. The dissolved oxygen (DO), total phosphorus (TP), and temperature (TEMP) were also the significant explanatory variables.

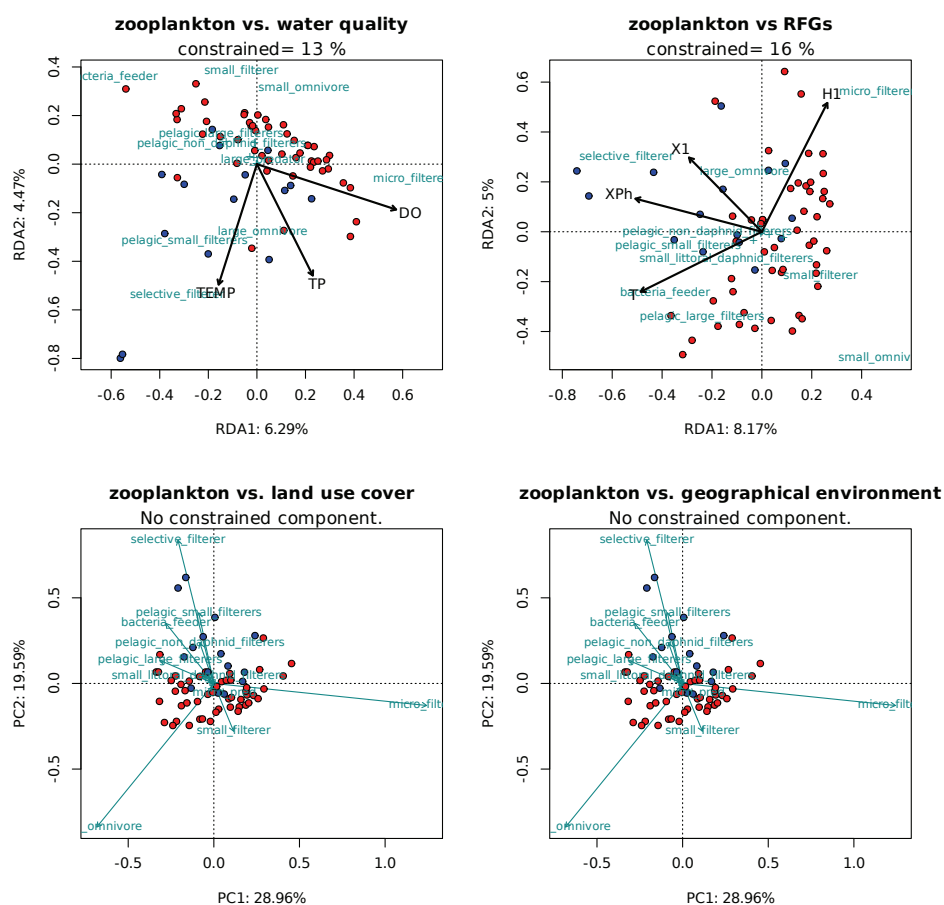


Fig. 10. Triplot of the redundancy analysis on zooplankton functional groups with environmental variables: A = water quality; B = phytoplankton functional groups (RFG); C = the land use types; D = geographical metadata. (Blue dots represent sites with *Sinodiaptomus sarsi*; red dots are sites without).

Total phosphorus acts as a primary driver of eutrophication (VOLLENWEIDER and KEREKES 1982); elevated daytime oxygen concentrations are a consequence of high primary production (WETZEL 2001), while temperature accelerates eutrophication processes (JEPPSEN *et al.* 2003, 2014, MOSS *et al.* 2009). Warmer environments tend to reduce organism body size (ATKINSON 1995, GIBERT and DELONG 2014, KORPONAI *et al.* 2020, ROBERTS *et al.* 2010), favouring the dominance of small-bodied zooplankters. Our observations confirmed this pattern: rotifers and small copepods, such as *Thermocyclops crassus*, and small cladocerans, such as *Moina* spp., were dominant in the samples from warmer waters (BLEDZKI and RYBAK 2016). This was further supported by the strong correlation of small pelagic filter feeders (*Moina* spp.) and selective filterers (calanoids) with the RDA2 component (Figs 9–10).

The thermophilic nature of *Sinodiaptomus sarsi* was also confirmed. Originally reported from subtropical regions of Asia, the species was later recorded in Central Asia (MYKITCHAK 2016, PODSHIVALINA and SHEVELEVA 2020, SVETLICHNY and SAMCHYSHYNA 2021), supporting the conclusion that it is thermophilous. RDA results corroborated this, as both temperature and *S. sarsi* also presented the highest correlation with the RDA3 component.

According to OECD classification (VOLLENWEIDER and KEREKES 1982), eutrophic conditions correspond to TP concentrations of 35–100 $\mu\text{g L}^{-1}$. TP concentrations in the studied lakes exceeded the lower limit of eutrophic status, and the zooplankton communities were characteristic of highly eutrophic waters. Our analyses further indicated that *Sinodiaptomus sarsi* prefers hypertrophic conditions, as evidenced by its strong negative correlation with the RDA1 axis, similar to TP. Alongside *S. sarsi*, *Brachionus calyciflorus* Pallas, 1766, and *Thermocyclops crassus* showed the highest negative correlations with RDA1, while *Bosmina longirostris* O. F. Müller, 1776 exhibited a strong positive correlation, suggesting a preference for lower trophic states.

Higher biomass of codon X1 was associated with copepods (selective filter feeders and small omnivores). Variation in the occurrence of other codons – SN, Y, LM, XPh, T, and H1 – can be attributed to heterogeneity among the lakes. In eutrophic lakes with fish, zooplankton communities are typically dominated by rotifers, small cladocerans, and copepods due to high predation pressure (BONECKER *et al.* 2011, CHRISTOFFERSEN *et al.* 1993, IGLESIAS *et al.* 2011, KORPONAI *et al.* 1997). The studied lakes, being managed for angling, experience significant fish predation, which is reflected in communities dominated by rotifers, small-bodied cladocerans (*Bosmina longirostris*, *Daphnia galeata*, *Moina* spp., *Diaphanosoma brachyurum*, *Chydorus sphaericus*), and copepods (*Eudiaptomus gracilis*, *Acanthocyclops robustus* and *Thermocyclops crassus*).

Along the eutrophication gradient, the hypertrophic status was associated with codon X1 (Figs 9–10). This association can be explained by the top-down effect of

fish, as fish predation promotes the dominance of rotifers and copepods, which are comparatively less efficient filter feeders (CHRISTOFFERSEN *et al.* 1993, JEPPESEN *et al.* 1997). The reduced grazing pressure exerted by zooplankton under these conditions facilitates the proliferation of members of codon X1. Codon SN was exclusively composed of *Raphidiopsis raciborskii* and represented the most important RFG among the phytoplankton (SELMECZY *et al.* 2023). H1 was represented by other nitrogen-fixing cyanobacteria (PADISÁK *et al.* 2009). Their appearance among the significant environmental factors indicated the nitrogen deficiency of the waters. The differing behaviours of the SN and H1 groups in the RDA analyses remain unclear; however, the functional approach underscores the significant role of rotifers, as micro-filter feeders, in shaping zooplankton community structure under eutrophic conditions.

In summary, our results indicate that *Sinodiaptomus sarsi* has successfully established populations in Hungarian waters, yet we found no clear evidence that its presence has no significantly altered the overall zooplankton community structure (Procrustes test: $r^2_{m12} = 0.04912$, $r = 0.9751$, $p < 0.001$, permutation = 999). As a selective filter feeder, it can potentially fulfil the functional role of native calanoid copepods in lentic ecosystems. However, its distribution may be restricted by its thermal requirements, which could confine its presence to specific habitats or seasons.

S. sarsi appears to be an invasive but opportunistic component of Hungarian freshwater zooplankton, with its long-term role likely determined by the interplay of temperature regimes, trophic state, and predator pressure. Continued monitoring will be essential to detect potential shifts in its population dynamics, particularly under changing climatic and eutrophication scenarios.

* * *

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Összefoglaló: A magyarországi kis és sekély vizekről végzett kutatásunk során egy új inváziós copepoda faj, a *Sinodiaptomus sarsi* (Rylov, 1923) került elő a 2017-ben gyűjtött zooplankton mintáinkból. Magyarországon több, fontos horgászvízben is megtaláltuk jelentős biomasszával. A

S. sarsi sikeresen megtelepedett a hazai kisvizekben, azonban nem találtunk egyértelmű bizonyítékot arra, hogy jelenléte jelentősen hatott volna a zooplankton közösség szerkezetére. Mivel szelektív szűrő szervezet, potenciálisan betöltheti az őshonos calanoid copepodák funkcionális szerepét a hazai tavi ökoszisztémákban, kiszorítva őket a planktonból. A *S. sarsi* a magyar édesvízi zooplankton inváziós és opportunistá tagja, szerepét és elterjedését valószínűleg a hőmérsékleti viszonyok, a trofikus állapot és a ragadozói nyomás kölcsönhatása határozza meg. Elterjedésének és populációdinamikájának figyelemmel kísérése elengedhetetlen lesz a faj ökológiájának megértéséhez. A változó éghajlati és trofikus környezet kedvez az inváziós fajok megjelenéséhez, amelyek negatívan hathatnak a lokális ökoszisztémákra, és így a közösségszerkezet megváltoztatásával a biodiverzitásra. Terjedésük nyomon követése és ökológiájuk megértése kulcsfontosságú a birtokos fajok negatív hatásának csökkentését igénylő cselekvések kidolgozásához.

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