

METHODOLOGICAL INSIGHTS INTO THE EFFECTS OF DIFFERENT MACROPHYTE STANDS ON THE ASSEMBLAGE STRUCTURE OF METAPHYTON IN LAKE TISZA (HUNGARY)

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Szalay, Gy., Nemes-Kókai, Zs., Csépes, E. I., Lukács, Á., T-Krasznai, E., Bácsi, I., T-Nagy, M., Borics, G. & B-Béres, V. (2025): Methodological insights into the effects of different macrophyte stands on the assemblage structure of metaphyton in Lake Tisza (Hungary). – *Studia bot. hung.* **56**(1): 25–46.

Abstract: Metaphyton is one of the least studied aquatic communities, and little emphasis has been placed on its research so far. Our aim was to investigate the qualitative and quantitative characteristics of metaphytic algae in different macrophyte stands and to identify the most suitable sampling method, as no standardized approach exists. Sampling was conducted in the Sarud Basin of Lake Tisza between June and August 2022, targeting coontail (*Ceratophyllum demersum*; submerged) and water caltrop (*Trapa natans*; floating) stands. Three methods were applied: grab sample (GS), benthic diatom protocol (DP), and a modified diatom protocol (MDP). We expected significant differences in community structure, habitat preference, and diversity across methods and plant types. Our findings confirmed that both structure and diversity differed depending on the sampling method. However, no compositional or diversity differences were observed between the algal assemblages inhabiting different plant stands, suggesting that both macrophyte types serve an equally important ecological function in Lake Tisza.

Key words: metaphyton, multi-purpose artificial lake, sampling methods, taxonomic diversity

INTRODUCTION

Just as healthy, natural ecosystems depend on diversity, so too does human society. However, the very activities that sustain human life are contributing to biodiversity loss (DÍAZ *et al.* 2006). Our current understanding of life's diversity on Earth is uneven: ecological and conservation research has traditionally focused on macroscopic organisms or species of direct relevance to human use, while aquatic communities – particularly microorganisms such as algae – remain significantly underrepresented (MEA 2003). In the field of conservation literature, freshwater biodiversity has received comparatively little attention, despite the fact that these ecosystems harbour exceptionally high species richness and are subject to more intense anthropogenic pressures than many other habitat types (STRAYER and DUDGEON 2010). At the same time, they are undergoing documented and inferred biodiversity declines on a scale and at a rate increasingly referred to as an 'invisible tragedy' unfolding beneath the water's surface (REID *et al.* 2019, RICHTER *et al.* 1997). Biodiversity is being lost at a rate that outpaces our understanding of it (TOKESHI and ARAKAKI 2012). Long-standing and pervasive threats to freshwater biota include habitat destruction, overexploitation, and biological invasions. In addition, emerging stressors such as climate change, microplastics, and novel pollutants have recently been recognised (DUDGEON *et al.* 2006, REID *et al.* 2019). Microorganisms are crucial for biodiversity assessment and also play an essential role in regulating and supporting ecosystem services, which are key to many provisioning services (NEE 2004). Microscopic algae are involved in approximately 20 different ecosystem services (B-BÉRES *et al.* 2023, NASELLI-FLORES and PADISÁK 2023). Their diversity in terms of size, morphology, primary and secondary metabolites is key to the efficiency of regulatory processes and the global stability of aquatic ecosystems (PTACNIK *et al.* 2008).

Habitat heterogeneity is a key factor in the functioning of aquatic ecosystems. It shapes species distributions and interactions and influences pivotal ecological processes (GIANUCA *et al.* 2017). Empirical evidence indicates a positive relationship between habitat diversity and species richness (BOLGOVICS *et al.* 2019, MUNGUIA *et al.* 2011), highlighting its importance for biodiversity conservation (SCHULER *et al.* 2017). Aquatic macrophytes create a three-dimensional and structurally complex habitat in the littoral zones of lakes, contributing to a wide range of physical, chemical, and biological interactions. Submerged, free-floating, and floating plant types have been shown to exert differing influences on phytoplankton dynamics (SCHEFFER 2004). These effects include modifications of light conditions and nutrient availability (DE TEZANOS and O'FARRELL 2014, HASLER and JONES 1949, KOLESZÁR *et al.* 2022), the provision of refuge for filter-feeding zooplankton (CHOI *et al.* 2014, JEPPESEN *et al.* 1997, TIMMS and MOSS 1984), and the release

of allelopathic compounds (HILT 2006, HILT and GROSS 2008, HOOTSMANS and BLINDOW 1994, KÖRNER and NICKLISCH 2002). These physical, chemical, and biological influences generate a series of microgradients within the aquatic vegetation, thereby facilitating the development of diverse microalgal communities. The habitat enclosed by macrophytes thus represents a distinct ecological niche that supports unique microalgal assemblages, collectively referred to as metaphyton. Metaphyton is distinct from both pelagic phytoplankton and benthic, substrate-associated communities (LUKÁCS *et al.* 2024). In freshwater ecosystems, these assemblages serve as important sources of propagules, contributing substantially to the high phytoplankton diversity observed in lakes and facilitating the dispersal of species from the littoral zone to open waters (MOSS and KARIM 1969). Submerged macrophytes can host rich and diverse algal communities that differ markedly from the phytoplankton found in the surrounding open water (KRASZNAI *et al.* 2010). The taxonomic composition of the macrophyte assemblage in a given water body strongly influences the structure and characteristics of the associated metaphytic community, including relative abundances of taxa, species richness, biomass, and overall diversity. Greater morphological complexity of macrophytes is generally associated with increased algal biomass and diversity, primarily due to enhanced niche availability (FERREIRO *et al.* 2013, HINOJOSA-GARRO *et al.* 2010, LEVI *et al.* 2017, PETTIT *et al.* 2016). However, several additional factors also influence the quality and composition of algal communities developing within macrophyte stands. These include colonization rate and duration (CASARTELLI and FERRAGUT 2018), as well as the age and structural characteristics of the macrophyte stand, such as leaf morphology (FERREIRO *et al.* 2013, LALONDE and DOWNING 1991, LAUGASTE and REUNANEN 2005, PETTIT *et al.* 2016, TÓTH 2013).

Lake Tisza (formerly known as the Kisköre Reservoir), with its area of 127 km² (12,700 ha) is the largest artificial and the second largest shallow lake in the Carpathian Basin. The site features a mosaic-like structure, composed of physiognomically distinct water bodies. The lake is generally divided into four primary basins and the main course of the Tisza River. The presence of cut-off meanders, oxbow lakes, elevated floodplain areas, and islands has led to the internal compartmentalisation of the reservoir area, even though the water level generally exceeds the elevation of some of these features. A levee ridge (high bank) runs through the reservoir area and follows the course of the Tisza River, separating the river from the other water bodies of the reservoir over a considerable stretch. To ensure a continuous supply of fresh water from the Tisza, twelve inlet-outlet channels (flushing channels) were constructed by cutting through this ridge. The primary function of Lake Tisza is water storage, mainly for flood control, water regulation, and agricultural irrigation. However, it also supports various recreational activities, including tourism, leisure, water sports, and fishing (KÓKAI *et al.*, 2019). Finally, it is a

site of high conservation importance, designated as a UNESCO World Heritage Site (UNESCO 1999), a Ramsar site, and part of the Natura 2000 network (WEB1, WEB2). Due to its rich and protected bird fauna, the reservoir is subject to eutrophication, which promotes the development of diverse aquatic vegetation.

Although the phytoplankton of the dammed section of the Tisza River and Lake Tisza has been studied since the 1970s (e.g. HAMAR 1987), and biomonitoring including benthic diatoms is currently carried out in accordance with the Water Framework Directive (EC 2000), knowledge of the structure of metaphytic algal communities and the factors driving their dynamics remains limited.

As there is no universally applied, standardised method for metaphyton sampling, the primary objective of this study was to identify the most suitable sampling technique. To this end, samples were collected from different macrophyte stands (floating and submerged) of Lake Tisza using three different methods: (1) by taking water samples from within the vegetation, (2) following the standard phytobenthos sampling protocol, and (3) using a modified version of the latter. We hypothesised that the samples collected using the three different sampling methods would (i) differ significantly in community structure and diversity, and (ii) show significant differences in the proportion of planktic, benthic, and metaphytic taxa. Furthermore, we hypothesised (iii) that the type of vegetation (floating or submerged) would influence the structure and biodiversity of the algal community. A more structurally complex macrophyte stand was expected to support a more diverse algal assemblage.

MATERIALS AND METHODS

Study area

The Sarud Basin was selected for the investigation of the metaphyton (Fig. 1). The total area of the basin is 23.19 km², of which 5.02 km² is covered by marsh and other aquatic vegetation, and 18.17 km² by open water surface. At the peak of the vegetation period, the surface coverage by floating macrophytes is approximately 15%. In 2022, the most common and dominant aquatic plant species in the Sarud Basin were *Ceratophyllum demersum* (coontail), *Nymphoides peltata* (yellow floating heart), and *Phragmites australis* (common reed), with their stands reaching 25–50% coverage (abundance-dominance value = 3). The species with 5–25% coverage (abundance-dominance value = 2) included *Hydrocharis morsus-ranae* (European frogbit), *Lemna minor* (common duckweed), *Najas marina* (spiny naiad), and *Najas minor* (lesser naiad), *Potamogeton perfoliatus* (clasping-leaf pondweed), *Trapa natans* (water caltrop), *Typha angustifolia* (narrowleaf cattail), and *Utricularia vulgaris* (common bladderwort) (CSÉPES *et al.* 2022).



Fig. 1. Location of Lake Tisza on the map of Hungary, highlighting the Sarud Basin with the sampling areas. The red circle marks the water caltrop (*Trapa natans*), the blue one marks the coontail (*Ceratophyllum demersum*) sampling area.

Sampling setup and identification

In 2022, a total of 18 metaphyton samples were collected on three occasions: in June, July, and August. As part of the National Laboratory for Water Science and Water Safety project – which, among other objectives, examines the ecological impacts of *Trapa natans* management in the Kisköre Reservoir – metaphyton assemblages associated with stands of *T. natans* were investigated here. To address our research questions and test the hypotheses, samples were also collected from *Ceratophyllum demersum* stands. This species was one of the most abundant macrophytes in the Sarud Basin in 2022 (see above). Furthermore, the submerged growth form, leaf morphology, and structural traits of *C. demersum* differ significantly from those of *T. natans*.

As mentioned above, three sampling methods were used: grab sampling (GS), the benthic diatom sampling protocol (DP), and the modified diatom sampling protocol (MDP).

1. Grab sample (GS): Water samples were collected using a sampling jug from three different points within each stand of macrophytes. The sampling depth was approximately 20–30 cm, and the distance between sampling points depended on the extent of the *Ceratophyllum demersum* and *Trapa natans* patches, but did not exceed 2–2.5 m. The samples were then pooled in a single container to create a composite sample. An aliquot of approximately 250 ml was then retained from this composite sample for microscopic analysis.

2. Benthic diatom sampling protocol (DP): This method is based on the EN 13496 (2014) protocol and the national guide (Ács *et al.* 2020). During each sampling event, five *Trapa natans* rosettes were removed from the macrophyte stand. Five to eight leaves were collected from each rosette, taking care to exclude any that had been persistently and extensively exposed above the water surface. Only the leaf rosettes were examined; the stems and roots were excluded from the analysis. In the case of *Ceratophyllum demersum*, at least five plants were removed from each macrophyte stand. In all cases, the basal, sediment-covered sections were cut off. To eliminate loosely attached algal species, the specimens of *C. demersum* and the rosettes of *T. natans* were shaken two to four times during collection. The collected samples of each plant type were pooled into a single container and thoroughly rinsed with boiled, cooled tap water. After thorough homogenisation, a 20 ml subsample was retained for microscopic analysis.

3. Modified diatom sampling protocol (MDP): This method differed from the previous one (DP) in that the aquatic plants were not shaken after being removed from the water. The plants, which were still dripping wet, were placed directly into the storage container. This increased the likelihood of including weakly attached benthic species, as well as planktic and metaphytic algal taxa that were associated with, or occurred among, the macrophytes.

As there is no established or standardised method for investigating metaphyton, the samples were analysed using the Utermöhl method (UTERMÖHL 1958) for phytoplankton, in accordance with the European standard (EN 15204) and the protocol described by Ács *et al.* (2020). The samples were preserved with Lugol's solution until the samples achieved a cognac-like colour. Analysis was performed using a Leica DMIL inverted plankton-counting microscope at 600× magnification. For samples with high algal density and substantial debris content, analyses were conducted using 5×, 8×, 10× or 30× dilutions. These dilutions were prepared using a mixture of tap water and Lugol's solution. Identification was carried out at species or genus level using the following identification books: COESEL and MEESTERS (2007), Ettl (1983), GRIGORSZKY *et al.* (1999), HUBER-PESTALOZZI (1950), KOMÁREK (2013), KOMÁREK and ANAGNOSTIDIS (1998,

2005), KRAMMER and LANGE-BERTALOT (1997*a, b*, 2004*a, b*), NÉMETH (1997), SCHMIDT and FEHÉR (1998–1999, 2001), STARMACH (1985).

Data processing and analyses

Algal taxa were classified into three habitat groups as planktic, benthic or metaphytic according to PADISÁK *et al.* (2009) and the REBECCA database (MOE *et al.* 2008).

Taxa richness was used to express the number of taxa (Taxa_S). To compare the ‘true diversity’ of the assemblages, effective Shannon’s H (effSH) was calculated following JOST (2006), as applied in previous studies (BECK and SCHWANGHART 2010, MORRIS *et al.* 2014, STUART-SMITH *et al.* 2013). Both taxa richness and effective Shannon’s H were calculated using PAST software (version 4.17; HAMMER *et al.* 2001). With regard to the calculation of functional diversity, Rao’s quadratic entropy (RaoQ) (RAO 1982) was performed using Canoco 5.0; TER BRAAK and ŠMILAUER 2002).

To assess the influence of sampling methods and the growth forms of aquatic plant stands on the taxonomic and habitat group composition of assemblages, non-metric multidimensional scaling (NMDS; Canoco 5.0; TER BRAAK and ŠMILAUER 2002) was performed using species abundance and trait community weighted mean (CWM) matrices. The CWM matrix was created by calculating the mean values of the habitat groups in the assemblages, with the relative abundances of the taxa taken into account. All taxa were included in the NMDS analyses; however, only dominant taxa (relative abundance > 0.03) are displayed in the figures. Following the NMDS, permutational multivariate analysis of variance (PERMANOVA) was applied to test for statistically significant differences in community composition (ANDERSON 2001). To identify characteristic taxa and habitat groups associated with the various sampling methods and plant stands, indicator species analyses (ISA) were carried out based on taxa relative abundances and the CWM values of habitat groups (DUFRÊNE and LEGENDRE 1997). Both PERMANOVA and ISA analyses were conducted using PAST software (version 4.17; HAMMER *et al.* 2001).

To test differences in diversity indices, method types and plant stands were used as fixed factors, similarly to the taxonomic and habitat group analyses. The Shapiro–Wilk test was applied to assess the distribution (normal or non-normal) of the variables. For normally distributed data, Welch’s test or one-way ANOVA was used, while for non-normally distributed data, the Mann–Whitney or Kruskal–Wallis test was applied to compare diversity metrics across sampling methods and plant growth forms. All analyses were performed using PAST software (version 4.17; HAMMER *et al.* 2001).

RESULTS

In this study, we identified a total of 288 taxa from the two plant stands (submerged and floating) using the three sampling methods (Appendix 1, electronic supplement). Of these, 232 were identified at the species level and 56 at the genus or higher taxonomic level. The taxonomic composition of the species found was as follows: 65 Bacillariophyceae, 56 Sphaeropleales, 40 Cyanobacteria, 30 Euglenophyta, 26 Trebouxiophyceae, 25 Desmidiaceae, 12 Cryptophyceae, 6 Volvocales, 4 Chrysophyceae, 4 Dinophyta, 4 Mediophyceae, 3 Coscinodiscophyceae, 3 Eustigmatophyceae, 3 Xanthophyceae, 2 Ulotrichales, 2 Zygnematales, 1 Klebsormidiales, 1 Oedogoniales, and 1 Tetrasporales taxon. In 90% of the samples, a total of eight taxa were identified (at least 16 samples). These were *Aulacoseira distans* (Ehrenberg) Simonsen, *Euastrum denticulatum* F. Gay, *Nitzschia paleacea* (Grunow) Grunow, *Scenedesmus ecornis* (Ehrenberg) Chodat, *Scenedesmus quadricauda* (Turpin) Brébisson, *Stephanocyclus meneghinianus* (Kützinger) Kulikovskiy, Genkal et Kociolek, *Tetradesmus lagerheimii* M. J. Wynne et Guiry, and *Tetraedron minimum* (A. Braun) Hansgirg.

Based on the habitat preference of each algae species, we have classified the taxa into three distinct categories: planktic, benthic, and metaphytic. Planktic algae constituted the largest trait, with 176 taxa, in addition 74 taxa were benthic, and 38 were metaphytic. Metaphytic group were the least represented, both in terms of taxon number and relative abundance, occurring in individual samples between 1.2% (GS_TR07) and 5.6% (MDP_TR08) of the time. In contrast, the relative abundance of planktic and benthic organisms varied widely, ranging from 13.1% (MDP_CE07) to 94.3% (GS_TR06) for planktic and from 2.5% (GS_TR06) to 84.9% (MDP_CE07) for benthic (Fig. 2).

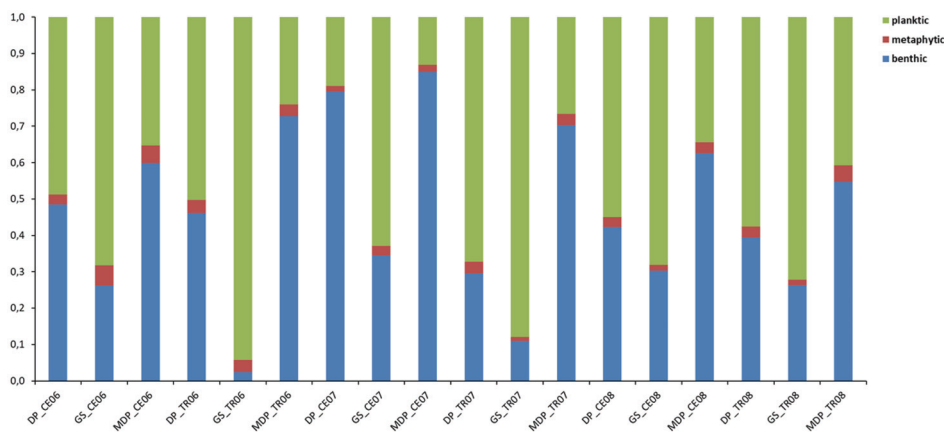


Fig. 2. The percentage relative abundance of planktic, metaphytic, and benthic taxa per sample.

Sampling methods

Of the 288 species identified, a total of 194 taxa were found in the Grab samples (GS), 206 in the Benthic diatom sampling protocol-based samples (DP), and 176 in the Modified diatom sampling protocol-based samples (MDP). A total of 104 taxa were identified across all three sampling types. In contrast, 47 taxa were found exclusively in GS, 38 taxa in DP, and 19 taxa in MDP. The number of taxa found using only two methods was the highest in the case of the DP and MDP methods (37) and the lowest in the case of the GS and MDP methods (16) (Fig. 3).

All 24 dominant taxa were found in the DP and MDP samples, while 21 dominant taxa were found in the GS samples. Taxa exhibiting relative abundance between 1 and 5% were found in similar proportions in all three methods: 69 taxa in the GS samples, 71 taxa in the DP samples, and 65 taxa in the MDP samples. Taxa with relative abundance of less than 1% accounted for approximately 50% of the taxa found, with 104 taxa in the GS samples, 111 taxa in the DP samples, and 87 taxa in the MDP samples.

With regard to the distribution of habitat groups according to the three sampling methods, it is evident that GS samples exhibited a higher proportion of planktic taxa and a lower proportion of benthic taxa. No significant differences

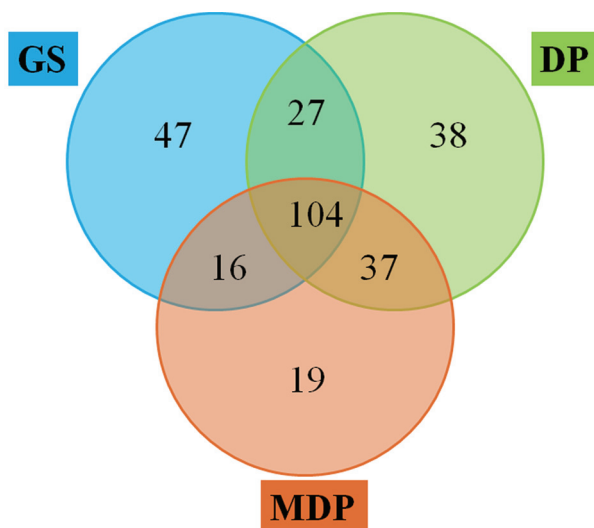


Fig. 3. Venn diagram shows the distribution of taxa identified in samples taken using the three sampling methods, according to the number of common and unique taxa. Blue = grab samples (GS); green = benthic diatom sampling protocol-based samples (DP); and brown = modified diatom sampling protocol-based samples (MDP).

were observed between the composition of DP and MDP samples, nor in the proportion of metaphytic taxa. 37 benthic (19.1%), 23 metaphytic (11.9%), and 131 planktic taxa were identified in the GS samples (69%). 59 benthic (28.7%), 25 metaphytic (12.1%), and 122 planktic (59.2%) taxa were identified in the DP samples. 54 benthic (30.7%), 19 metaphytic (10.8%), and 103 planktic (58.5%) taxa were identified in the MDP samples. However, examining the total relative abundance of habitat groups in the different sampling method categories, clear differences were revealed. While the relative abundance of planktic (P) taxa in the GS samples was 75.6%, and that of benthic (B) taxa was 21.8%, the ratio was 49.6% P: 47.6% B in the DP samples and 29% P: 67.5% B in the MDP samples. The relative abundance of metaphytic taxa was low for all three methods (GS: 2.6%, DP: 2.9%, MDP: 3.4%). Following the ISA analyses, a significant correlation was identified between the sampling method and the occurrence of 23 taxa in GS samples, 6 taxa in DP samples, and 20 taxa in MDP samples. Focusing on the dominant taxa, the analyses revealed that planktic species were the most indicative in GS samples including *Coelastrum microporum* Nägeli, *Lemmermannia tetrapedia* (Kirchner) Lemmermann, *Monoraphidium contortum* (Thuret) Komárková-Legnerová, and *Stephanocyclus meneghinianus* (Kützing) Kulikovskiy, Genkal et Kociolek. In contrast, in MDP samples, benthic species were the most indicative including *Cymbella* sp. small, *Fragilaria* sp., *Navicula capitatoradiata* H. Germain ex Gasse, *Navicula cryptotenella* Lange-Bertalot, and *Navicula* sp. Finally, no dominant indicator species were found in the DP samples.

The NMDS analyses revealed a distinct difference in taxa and habitat groups between sampling methods (Fig. 4). The PERMANOVA analysis confirmed that these differences were significant ($p = 0.0003$ and $p = 0.0002$). However, the pair-wise analysis of the taxonomic composition revealed that only the GS samples were distinct from the DP and MDP samples. In contrast, the pair-wise analyses revealed significant differences in all the three habitat groups.

No differences were found in taxonomy-based metrics (Taxa_S: $p = 0.25$; effSH: $p = 0.30$) or in habitat group-based metrics (RaoQ: $p = 0.10$) between the three sampling methods. However, a significant difference was observed in the functional diversity of the DP and GS assemblages ($p = 0.035$).

Plant stands – submerged and floating

Of the 288 species identified, 222 were found on the *Ceratophyllum demersum* and 237 on the *Trapa natans* stands, of which 51 were unique to the *C. demersum* and 66 to the *T. natans*, with 171 taxa found on both plant stands. We considered those taxa to be dominant that were present in at least one sample with a relative abundance higher than 5%. A total of 24 taxa were identified as dominant,

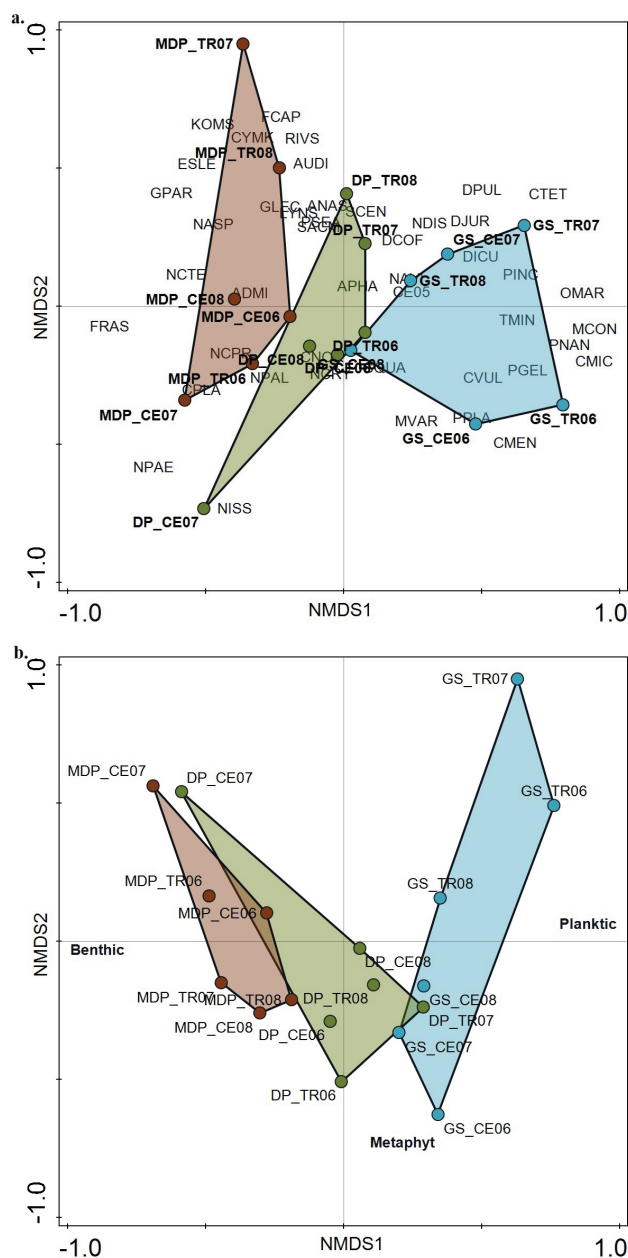


Fig. 4. The NMDS visualisation of samples taken by different sampling methods according to (a) taxonomic and (b) habitat group composition. Blue = grab samples (GS); green = benthic diatom sampling protocol-based samples (DP); and brown = modified diatom sampling protocol-based samples (MDP).

of which 22 were found in both plant stands, while 2 were unique to *T. natans* (*Fragilaria capucina* Desmazières and *Rivularia* sp.). The taxonomic composition of the dominant species was as follows: 12 Bacillariophyceae, 4 Sphaeropleales, 3 Trebouxiophyceae, 2 Coscinodiscophyceae, 2 Cyanobacteria, and 1 Mediophyceae. Concurrently, 85 taxa attained a relative abundance of between 1 and 5% on at least one occasion, of which 74 were identified in both plant stands, 3 were found exclusively on the coontrail, and 8 were present only in the *T. natans* population. Their taxonomic composition was also more diverse than that of taxa with a relative abundance higher than 5%: The following taxa were identified: 24 Sphaeropleales, 18 Bacillariophyceae, 15 Cyanobacteria, 9 Trebouxiophyceae, 8 Cryptophyceae, 3 Desmidiaceae, 1 Chrysophyceae, 1 Dinophyta, 1 Euglenophyta, 1 Eustigmatophyceae, 1 Mediophyceae, 1 Oedogoniales, 1 Ulotracheales, and 1 Volvocales. A significant proportion of the taxa identified, 179 in total, had a relative abundance of less than 1%. It is noteworthy that the majority of unique taxa (104 out of 117) were among these rare taxa.

A total of 222 taxa were identified from the *C. demersum* stand, with 57 classified as benthic, 28 as metaphytic, and 138 as planktic. A total of 22 taxa were dominant, while 78 taxa had a relative abundance of 1–5% and 123 taxa had a relative abundance of less than 1%. The Indicator Value analysis revealed that 8 taxa were indicative of *C. demersum*. These were: *Cryptoglena skujae* Marin et Melkonian, *Gonium pectorale* O. F. Müller, *Nitzschia acicularis* (Kützinger) W. Smith, *Nitzschia palea* (Kützinger) W. Smith, *Nitzschia paleacea* (Grunow) Grunow, *Nitzschia* spp. (32–64 × 4–8 µm), *Stephanocyclus meneghinianus* (Kützinger) Kulikovskiy, Genkal et Kociolek, and *Surirella librile* (Ehrenberg) Ehrenberg. Of the 8 indicator taxa, 4 were dominant, 1 had a relative abundance of 1–5%, 3 had a relative abundance of less than 1%, and 50–50% were benthic and planktic.

The *T. natans* stand was found to be slightly more species-rich than the *C. demersum* stand, with a total of 237 taxa identified, including 62 benthic, 30 metaphytic, and 145 planktic species. Our analysis identified 24 dominant taxa, 82 taxa with a relative abundance of 1–5%, and 131 taxa with a relative abundance of less than 1%. Among these 6 were identified as being indicative of *T. natans*. The following species are recognised: *Crucigenia fenestrata* (Schmidle) Schmidle, *Dictyosphaerium ehrenbergianum* Nägeli, *Lemmermannia tetrapedia* (Kirchner) Lemmermann, *Monoraphidium minutum* (Nägeli) Komárková-Legnerová, *Planktolynghya contorta* (Lemmermann) Anagnostidis et Komárek, and *Scenedesmus ecornis* (Ehrenberg) Chodat. All 6 indicator species are planktic, of which 1 was dominant, 4 had a relative abundance of 1–5%, and 1 had a relative abundance of less than 1%.

We also examined the differences between the taxonomic and habitat group composition of plant stands using NMDS visualisation (Fig. 5). However, we found no significant differences in either composition. This was confirmed

by PERMANOVA analysis ($p = 0.1143$ for taxonomic composition, $p = 0.2521$ for habitat group analysis).

In terms of biodiversity, no differences were found in taxonomy-based metrics (Taxa_S: $p = 0.40$; effSH: $p = 0.14$) or in habitat group-based metrics (RaoQ: $p = 0.48$) between the two plant samples.

DISCUSSION

In contrast to phytoplankton, metaphyton provides a habitat for benthic and epiphytic algae, both in terms of quality and quantity (KRASZNAI *et al.* 2010). Furthermore, it serves as a potential propagule source for planktic habitats (LUKÁCS *et al.* 2024). Therefore, recognising its ecological importance is essential for understanding the functioning of the lake ecosystem. The primary aim of this study was to identify the most effective sampling method for collecting metaphyton from submerged and floating macrophyte stands, and to assess whether the type of plant stand influences the composition and diversity of the associated algal assemblages. Using three different methods, a diverse metaphytic algal assemblage was identified in the Sarud Basin.

Sampling methods

The results of our study partially supported our first hypothesis (significant differences in the composition of assemblages but no differences in the diversity metrics), however, they rejected the second hypothesis (no difference in proportion of planktic, benthic, and metaphytic algae). Based solely on the number of taxa detected, the DP method proved to be the most effective. However, in the case of the grab sampling (GS) method, a greater number of taxa were unique to that sampling approach. More than one-third of the taxa (36.1%) were detected irrespective of the sampling method employed, while an equal proportion demonstrated sensitivity to only one particular method. Based on taxonomic composition, the DP method exhibited the highest overlap with the other two sampling methods.

The sensitivity of the sampling methods to habitat groups, based on their total relative abundances, showed significant differences: while the GS method was more sensitive to planktic elements and the MDP method to benthic ones, the DP method exhibited a similar level of sensitivity to both trait groups. Due to their low relative abundance, metaphytic taxa did not show significant differences between the sampling methods. Nevertheless, the highest sum-relative abundance of metaphytic algae was observed with the MDP method (MDP_TR08), whereas the highest number of taxa was recorded in samples collected

using the DP method (DP_TR06). A similar pattern was observed among the dominant indicator species, with planktic taxa being indicative of the GS samples, while benthic taxa were indicative of the MDP samples. It should be noted that planktic elements would have been expected to occur in higher proportions in the MDP samples. However, due to the two- to three-order magnitude difference in individual counts between planktic and benthic algae, and the extensive dilution required for sample processing, planktic taxa with low abundances were likely undetected.

Surprisingly, the DP method was found to be the most effective of the three sampling methods for collecting metaphyton, as it exhibits similar sensitivity to both planktic and benthic elements, unlike the MDP method. This method, *i.e.*, the DP, produces the highest number of taxa and appears to be the most representative for sampling both the water space among macrophytes and the organisms attached to the plant surfaces. These results appear to contradict the logical assumption that the MDP method would show greater sensitivity to both planktic and metaphytic taxa. In the MDP protocol, the vegetation used as substrate is not shaken, which should allow algal species inhabiting the water between plants, as well as taxa weakly attached to plant surfaces, to appear more abundantly in the samples. In contrast, the DP method involves shaking the plant to collect only the true benthic community. The detached plants are then rinsed with clean, boiled tap water or distilled water to remove the attached taxa. Samples obtained using either method must be diluted for microscopic analysis, which greatly reduces the likelihood of detecting rare taxa. In the case of the MDP method, however, the water between the plants is presumably very turbid and rich in debris. This often requires stronger dilution than with the DP method, which further reduces the probability of detecting rare species. This may explain why the MDP method is more strongly biased towards benthic taxa than the DP method.

It is also important to emphasise that the DP method is slightly less sensitive to planktic elements than the GS method, meaning some rare planktic taxa may be not detected. Although our study provides useful insights into the diversity and structure of the metaphyton, we cannot conclude with certainty that the combined use of the DP and GS methods reliably captures the entire metaphytic community of a habitat. A more extensive research effort involving a wider variety of lake types and stands of macrophytes would be necessary to draw such general conclusions. However, within the two stands of macrophytes investigated here, the combined application of these methods appeared to recover a large proportion of the taxa inhabiting the metaphyton, even when considering the limitations of the microscopic processing protocol (*i.e.*, the absence of targeted species searches).

Plant stands – submerged and floating

Contrary to our hypothesis, no significant differences were found in taxonomic composition or habitat group structure between *Ceratophyllum demersum* and *Trapa natans* stands (rejecting H3). Based on the selected macrophyte stands, our results also do not support the findings of FERREIRO *et al.* (2013), which suggested that higher morphological complexity of macrophytes (i.e., presence or absence of thorns, their number and/or the importance of edges; in this case, *C. demersum*) leads to higher algal community diversity. NEMES-KÓKAI *et al.* (2024) also demonstrated a significant difference in the algal assemblages associated with different macrophyte stands (floating, submerged, and emergent), based on investigations carried out between 2016 and 2019. It is important to note, however, that both FERREIRO *et al.* (2013) and NEMES-KÓKAI *et al.* (2024) investigated a benthic diatom community, the microscopic analysis of which differs from the identification method applied in our study. However, the two plant stands differed markedly in the composition of indicator species and in the habitat preferences of those species. While only planktic species were identified as indicators for *T. natans*, the indicator species associated with *C. demersum* included both planktic and benthic taxa, with the latter being more numerous. This pattern is likely due to the tendency of planktic species to settle on the floating leaves of *T. natans*, while the submerged foliage of *C. demersum* provides a suitable microhabitat for benthic diatoms. With regard to specifically metaphytic algae, their relative abundance and diversity did not differ significantly between the two macrophyte stands. While the highest taxon richness was found in a *Trapa* sample (DP_TR06), the highest sum-relative abundance (GS_CE06) and relative abundance (*Peridinium* sp.; GS_CE06) were recorded in the *C. demersum* stand.

These findings suggest that both types of macrophyte stands play an important role in sustaining the algal assemblages of Lake Tisza. Their similar assemblage structure indicates that samples collected from different vegetation types (floating or submerged) within the same year can be compared and evaluated meaningfully. However, further research is needed to determine whether inter-annual variation also occurs in the metaphyton associated with different macrophyte stands, as observed in benthic diatom assemblages.

CONCLUSIONS

We investigated the metaphyton assemblage of Lake Tisza with the aim of identifying the most suitable sampling method for efficiently collecting high-quality algal samples from different types of macrophyte stands, including both submerged and floating vegetation. The results obtained partially supported our

hypothesis (H1), demonstrating that both the community structure and, to a certain extent, the diversity of samples collected by different methods varied. The findings highlighted that, considering the practical difficulties of microscopic processing, the DP method – originally developed for benthic diatom sampling – is the most suitable for collecting metaphyton samples. The different sampling methods demonstrated varying sensitivity to planktic and benthic algae; however, no significant differences were identified in the number or relative abundance of metaphytic taxa (rejecting H2). No compositional or diversity-related differences were observed between the different macrophyte stand types (rejecting H3), further supporting the conclusion that both vegetation types play an important and equally valuable ecological role within the aquatic ecosystem of Lake Tisza.

* * *

Acknowledgements – I would like to express my gratitude for Judit Padisák, who started me on my algology career, was my diploma work supervisor during my university studies, and recommended me for my current job, where I could further expand my knowledge. The research presented in the article was carried out within the framework of the Széchenyi Plan Plus program with the support of the RRF 2.3.1 212022 00008 project (GySz, ECs, MTN, ZsNK, ÁL, VBB). The project was financially also supported by the National Research, Development and Innovation Office – NKFIH FK 132 142 (VBB) and NKFIH KKP 144068 (ÁL, VBB).

Összefoglaló: A metafiton a legkevésbé vizsgált vízi életközösségek egyike, kutatására eddig kevés hangsúlyt helyeztek. Célunk az volt, hogy feltárjuk a metafitikus algák minőségi és mennyiségi jellemzőit különböző vízinövény-állományokban, valamint meghatározzuk a mintavételükre legalkalmasabb módszert, mivel szabványosított módszer jelenleg nem létezik. A mintavételekre 2022 júniusa és augusztusa között került sor a Tisza-tó Sarudi-medencéjében érdes tócsagaz (*Ceratophyllum demersum*; alámerült) és sulyom (*Trapa natans*; úszó) állományokban. Három módszert alkalmaztunk: merítéses mintavétel (GS), bentikus kovaalga-mintavételi módszer (DP), valamint annak módosított változata (MDP). Feltételeztük, hogy jelentős különbségeket tapasztalunk a közösségszerkezetben, az élőhely-preferenciában és a diverzitásban a módszerek és növényfajták között. Eredményeink megerősítették, hogy a közösségszerkezet és a diverzitás valóban különbözik a választott mintavételi módszertől függően. Ugyanakkor az algaközösségek fajösszetételében és diverzitásában nem találtunk különbséget a különböző növényállományok között, ami arra utal, hogy mindkét vízi növény típus egyformán fontos ökológiai szerepet tölt be a Tisza-tóban.

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(submitted: 31.07.2025; accepted: 18.09.2025)