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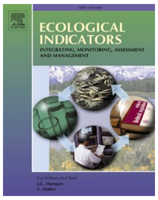

Contrasting the ecology of planktonic crustaceans from freshwaters: Insights from stable isotopes ($\delta^{13}C$, $\delta^{15}N$)

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ABSTRACT

We examined the feeding ecology of planktonic crustaceans at three waterbodies situated across a latitudinal gradient in Europe (Croatia, Poland, Lithuania) using stable isotope measurements ($\delta^{13}C$, $\delta^{15}N$) in animal tissues. Relative, lake-specific values of $\delta^{15}N$ showed that in all lakes, calanoid copepods occupied the highest trophic position, while *Daphnia* sp. and *Diaphanosoma* sp. were located closer to primary producers with Cyclopoid copepods located between these groups. We found a negative correlation between C:N ratio (proxy for lipid content) and $\delta^{15}N$, which indicates lipid content declined with the trophic level of the animals. Employment of stable isotope-based approach allows better recognition of trophic linkages than could be inferred from classical methods, and therefore our results contribute improvement of management strategies developed for aquatic ecosystems.

1. Introduction

Climate change and other anthropogenically induced factors are clear threats to ecosystem function and are flagship phenomena of the ‘Anthropocene’ era. Seasonal increases in temperature, precipitation and extreme weather events, interact with human-driven habitat transformations rendering both aquatic and terrestrial ecosystems vulnerable (Hughes, 2000; Sala et al., 2000). By the end of 21st century up to 66 % of lakes globally may experience shifts in thermal regime (Maberly et al., 2020), leading to shifts in taxonomical and functional structure of ecological communities, which will likely affect key ecological processes, such as energy flow through the food web (Yvon-Durocher et al., 2017).

In pelagic freshwater food webs, the energy flow strongly relies on planktonic crustaceans, which are considered ‘energy dissipators’ (Jones & Grey, 2011). Filter-feeding cladocerans of genus *Daphnia* are considered the keystone freshwater grazers, however importance of opportunistic, ambush or feeding-current foraging copepods should not be diminished, as eutrophication strengthens coupling between proto- and metazooplankton (Ger et al., 2016). This coupling is evident during periods of cyanobacterial dominance in the food web, when higher abundance of both, small-bodied bacterivores and predatory metazooplankton grazing them, leads to elongation of the trophic chain (Koski et al., 2002; Krztoń et al., 2022). This, in turn, decreases the efficiency of energy transfer in the food web, since each trophic level consumes a substantial amount of energy for metabolism and respiration (Kath et al., 2018; Moustaka-Gouni & Sommer, 2020).

Climate change and predicted shifts in thermal regimes threatening freshwaters highlight the need for greater understanding of the functioning of these ecosystems in the changing world (Maberly et al., 2020).

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We studied planktonic crustacean communities, in three shallow, eutrophic lakes from different regions in Europe during the cyanobacterial blooms. We used naturally occurring stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) which can provide key information on species diets and their trophic position in the food webs (reviewed by Fry, 2006). We hypothesized that relative trophic positions of Calanoid copepods, Cyclopoid copepods, *Daphnia* sp., *Diaphanosoma* sp. exhibit uniform pattern in the food webs of studied lakes. Furthermore, we assumed existence of two alternative pathways of energy flow (phytoplankton – algaevorous crustaceans vs. protozooplankton – predatory crustaceans links; Hart et al., 2000; Sommer et al., 2012; Segovia et al., 2015), and the fact that trophic transfer efficiency in freshwater food webs is limited (Karpowicz et al., 2021). Thus, we hypothesized that relative trophic position of the animals determines their carbon:nitrogen ratio (C:N) ratio, which is a proxy for the lipid content in their tissues (Syväranta & Rautio, 2010).

2. Materials and methods

Our study was conducted in three small, shallow eutrophic European lakes (Table 1), representing different thermal regimes (Maberly et al., 2020): 1) Lake Sakadaš – northern warm (NW) in southern Europe (Croatia), 2) Lake Tyniec – northern temperate (NT) in central Europe (Poland), and 3) Lake Gineitiškės – northern cool (NC) in northern Europe (Lithuania). To standardize the seasonal succession conditions of the communities among lakes sampling was conducted in 2019, in the period of the highest abundance of cyanobacteria (Lake Sakadaš: mid-September; Lake Tyniec: mid-July, Lake Gineitiškės: mid-August). The choice of lakes and sampling period minimized differences in habitat type among lakes and emphasized more the effect of biogeographic zone. Integrated samples were collected from 0.5 m below the surface to 0.5 m above the lake bottom, using dedicated sampler (Mantzouki et al., 2018). All environmental and biological samples were collected using the same method, at the same time and in the same place of each lake. Transparency of water was measured *in situ* using Secchi disc. Water temperature, pH and conductivity were measured *in situ* using YSI ProDSS probe. Mean minimum and mean maximum air temperatures for each lake were determined from weatherspark.com database.

Samples for chlorophyll *a* concentration were filtered through glass-fibre filter (Whatman GF/F type), frozen at −20 °C and analyzed according to Komarkova (1989). Trophic State Index (TSI) of lakes was calculated based on chlorophyll *a* concentration, according to Carlson (1977). Samples for ions concentration (NO_3, NH_4, PO_4) were collected *in situ* and analyzed using a Dionex ion chromatograph (DIONEX, IC25 Ion Chromatograph; ICS-1000, Sunnyvale, CA, USA).

Table 1
Basic information about studied waterbodies.

Lake	Gineitiškės (NC)	Tyniec (NT)	Sakadaš (NW)
Latitude	54°44′16.1″N	50°01′28.1″N	45°36′40.0″N
Longitude	25°11′06.6″E	19°48′47.7″E	18°48′06.0″E
Area [ha]	15	8.6	13
Mean depth [m]	5	1.5	2.5
Secchi depth [m]	0.5	0.4	0.5
TSI*	74	64	70
Average air temperature [°C] yearly (min–max)	2.75–10.08	4.75–12.92	6.50–16.58
Water temperature** [°C]	20.97	21.3	21.20
Conductivity** [μS/cm]	257.42	1512.43	564.29
NO3** [mg/L]	<0.10	0.11	0.29
NH4** [mg/L]	0.71	0.10	0.18
PO4** [mg/L]	0.016	0.018	0.017

* Trophic State Index (based on chlorophyll *a* concentration).
**The weekly average when samples were collected.

Integrated samples of phyto- and zooplankton were concentrated using a plankton net with a mesh size of 10 μm and 50 μm, respectively. Cyanobacteria were identified under the Nikon H550L light microscope, using identification keys (Komarek & Anagnostidis, 1999, 2005; Komarek, 2013). Density and biomass of crustacean zooplankton were analyzed using light microscope, in a 0.5 mL chamber, based on 5 counts. Planktonic crustaceans were identified using Bledzki & Rybak (2016) key. Samples for the analyses of stable isotopes of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and the elemental carbon:nitrogen ratio (C:N) were prepared by isolating planktonic crustaceans specimens from samples collected in the field by vertical hauls of the 50 μm mesh plankton net. Animals of four groups (Calanoid copepods, Cyclopoid copepods, *Daphnia* sp., *Diaphanosoma* sp.; not identified to the level of species) were isolated under light microscope separately from each lake. At least 100 adult specimens per sample were isolated. In total, for all three lakes 54 samples were prepared: 13 Calanoid copepods samples (absent in NW lake, 6 from NT lake, 7 from NC lake), 19 Cyclopoid copepods samples (7 from NW lake, 5 from NT lake, 7 from NC lake), 9 *Daphnia* sp. (absent in NW lake, 2 from NT lake, 7 from NC lake) samples and 13 *Diaphanosoma* sp. (7 from NW lake, 6 from NT lake, absent in NC lake) samples. Samples were dried at 60°C for 48 h and stored in Eppendorf tubes. Analyses of stable isotopes were performed at the Stable Isotope Laboratory of the Institute of Geological Sciences, Polish Academy of Sciences, Warsaw, Poland, using a Flash 1112 HT elemental analyzer (Thermo Scientific) coupled to Delta V Advantage IRMS (Thermo Scientific) with continuous flow mode and He carrier gas. Stable isotope values are reported in delta (δ) notation as parts per thousand (‰) deviation from Viena PeeDee Blemnite (VPDB) for ^{13}C and atmospheric AIR for $\delta^{15}N$. The results of duplicate analysis were calibrated with three international standards USGS 41a (L-glutamic acid, $\delta^{13}C = +36.55 \pm 0.08$ ‰, $\delta^{15}N = +47.55 \pm 0.15$ ‰), USGS 40 (L-glutamic acid, $\delta^{13}C = -26.389 \pm 0.042$ ‰, $\delta^{15}N = -4.5 \pm 0.1$ ‰) and IAEA 600 (caffeine, $\delta^{13}C = -27.771 \pm 0.043$ ‰, $\delta^{15}N = +1.0 \pm 0.2$ ‰). As an internal laboratory standard to control for instrument drift, we used USGS 65 (glycine, $\delta^{13}C = -20.29 \pm 0.04$ ‰, $\delta^{15}N + 20.68 \pm 0.06$ ‰). The precision of measurements (1σ) and reproducibility were generally better than ± 0.1 ‰ for $\delta^{13}C$ and ± 0.3 ‰ for $\delta^{15}N$, respectively. To calculate the C:N ratio the same standards were used, the C:N ratio was estimated with accuracy ± 0.1. Planktonic crustaceans contain lipids, which are depleted in ^{13}C leading to lower $\delta^{13}C$ values. So, we corrected for differential lipid content using the elemental C:N ratio according to Syväranta & Rautio (2010).

All statistical analyses and data visualizations were performed with R V.4.2.2 and R Studio statistical software. We used $\delta^{13}C$ and $\delta^{15}N$ measurements to describe the structure of isotopic niches of each crustacean community. Differences of $\delta^{13}C$, $\delta^{15}N$ and C:N among studied lakes were tested with use of Generalized Linear Models (GLMs); pairwise comparisons (contrasts) of variables between lakes were tested with ‘emmeans’ function (‘emmeans’ R package). Fitting 40 % Stable Isotope Bayesian Ellipses was performed with ‘SIBER’ R package for groups of crustaceans with at least three observations per group. Correlations of C:N ratio and $\delta^{15}N$ were tested using linear models (LMs).

3. Results

Cyanobacterial blooms were dominated by: *Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová & Cronberg (NW), *Microcystis aeruginosa* (Kützing) Kützing (NT), *Pseudoanabaena limnetica* (Lemmermann) Komárek, *Planktolyngbya limnetica* and *Microcystis aeruginosa* (NC).

Planktonic crustacean community of NW lake consisted mainly of Cyclopoid copepods (approx. 40 % of total density and 75 % of total biomass) and *Diaphanosoma* sp. (approx. 50 % of total density and 20 % of total biomass). The crustacean community of NT lake was dominated by Cyclopoid copepods, contributing to approx. 65 % of total density and 60 % of total biomass. *Diaphanosoma* sp. constituted approx. 15 % of total density and approx. 10 % of total biomass. *Daphnia* sp. and Calanoid copepods each accounted for only 5 % of the total density, but their contribution in total biomass was different: approx. 5 % in the case of *Daphnia* sp. and approx. 20 % in the case of Calanoid copepods. In NC lake, Cyclopoid copepods contributed to approx. 50 % of the density and biomass of crustacean zooplankton. *Daphnia* sp. accounted for approx. 30 % of the total density and 20 % of the total biomass. Calanoid copepods accounted for 5 % of the total density and total biomass of planktonic crustaceans, and *Diaphanosoma* sp. accounted for approx. 1 % of the total density and biomass of the crustacean community.

Analyses showed substantial variation in values of δ^{13}C and δ^{15}N in tissues of crustacean zooplankton and strong isotopic separation of samples among lakes (Fig. 1., Supplementary Table 1). Values of δ^{13}C and δ^{15}N for each lake are presented in Supplementary Table 2. The differences of both isotope values between lakes were significant, and are presented in Supplementary Tables 3 and 4. Values of δ^{13}C in the NW lake samples were lowest among studied lakes, while the highest were found in NC lake (Fig. 1., Supplementary Table 1). Highest values of δ^{15}N were found in NT lake and the lowest values in NC lake.

Highest mean values of δ^{15}N were found in tissues of Calanoid copepods (present in NT and NC lakes Fig. 1., Supplementary Table 1). Cyclopoid copepods were present in all three lakes and their δ^{15}N values were the most variable among studied groups of crustaceans. Cladocerans of genus *Diaphanosoma* (found in NW and NT) and *Daphnia* (found in NT and NC lakes) were characterized with relatively low δ^{15}N values compared to copepods in each lake.

Stable Isotope Bayesian Ellipses (40 %) were applied to the following groups: 1) Calanoid copepods, cyclopoid copepods and *Daphnia* sp. from NC lake; 2) Calanoid copepods, cyclopoid copepods and *Diaphanosoma* sp. from NT lake; and 3) cyclopoid copepods from NW lake. We found that the Bayesian ellipses did not overlap between any groups of studied animals (Fig. 1.). The C:N ratio of zooplankton showed no statistically significant differences among lakes (Supplementary Table 5). The highest values of C:N ratio was found in *Daphnia* sp. and *Diaphanosoma* sp. samples while the lowest ones in calanoid copepods samples.

Linear models set up for each lake separately showed negative relationship of zooplankton δ^{15}N and the C:N ratio (Fig. 2., Supplementary Table 6). The models showed this effect was strongest in the NW lake (estimate: −0.423 of C:N ratio per 1 ‰ δ^{15}N increase, $R^2 = 0.775$, $p < 0.01$). The estimate of models was slightly weaker for NT (−0.216, $R^2 = 0.28$, $p < 0.05$) and NC (−0.279, $R^2 = 0.717$, $p < 0.001$) lakes.

4. Discussion

Through the use of stable isotope measurements, we were able to infer ecological niches of planktonic crustaceans based on proxy isotopic niche space and patterns in bivariate isotope space. We found that crustaceans were separated in δ^{13}C gradient, from highly negative values in NW lake (mean value: −35.8 ‰), through intermediate values in NT lake (mean value: −25.8 ‰) to least negative values in NC lake (mean value: −20.5 ‰). The grazers' δ^{13}C values are strongly influenced by δ^{13}C of their food source, which can be highly variable (−34.4 to −5.9 ‰ in case of phytoplankton; Vuorio et al., 2006). Furthermore, additional variation in δ^{13}C values of crustacean zooplankton can be induced by dietary intakes of methane-originating carbon (δ^{13}C often < -50 ‰; Whiticar, 1999) or respired CO_2 which is depleted in ^{13}C, and can alter δ^{13}C values of food web components (Zimmer et al., 2020). Consequently, source of variation of δ^{13}C among studied lakes is difficult to infer, and would require additional studies concerning measurements of δ^{13}C values of primary producers (bacteria, algae). Within lakes, δ^{15}N showed the highest trophic position was occupied by Calanoid copepods. These animals use feeding currents and are able to feed on animal prey as well as on algal food (Koski et al., 2002; Kiørboe, 2011a). Our results indicated high rates of predation in Calanoid copepods despite they are more efficient at capturing prey without an ability for evasion (i.e. algae; Kiørboe, 2011a, 2011b). In contrast to calanoids, cyclopoid copepods are ambush feeders, attacking prey detected within their perception range, which is particularly effective for capturing motile prey (Kiørboe, 2011a, 2011b). Animal prey is preferred by cyclopoids, but they are still able to utilize phytoplankton (Hopp & Maier, 2005). Our results reflect their ability to forage on diverse food

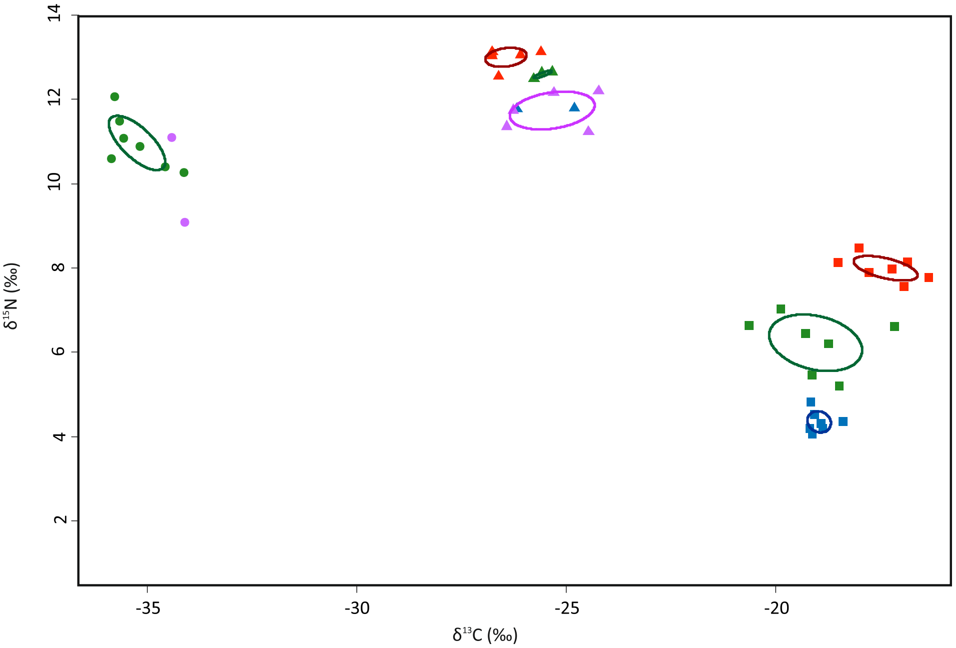

Fig. 1. Scatterplot for δ^{13}C and δ^{15}N values in analyzed planktonic crustaceans. Colors: red – calanoid copepods; green – cyclopoid copepods; blue – *Daphnia* spp.; purple – *Diaphanosoma* spp. Shapes: square – lake Gineitiškės (NC)); triangle – Tyniec oxbow lake (NT); circle – lake Sakadaš (NW); Ellipses – Bayesian ellipses fitted for δ^{13}C and δ^{15}N values in analyzed samples with minimal size: $N \geq 3$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

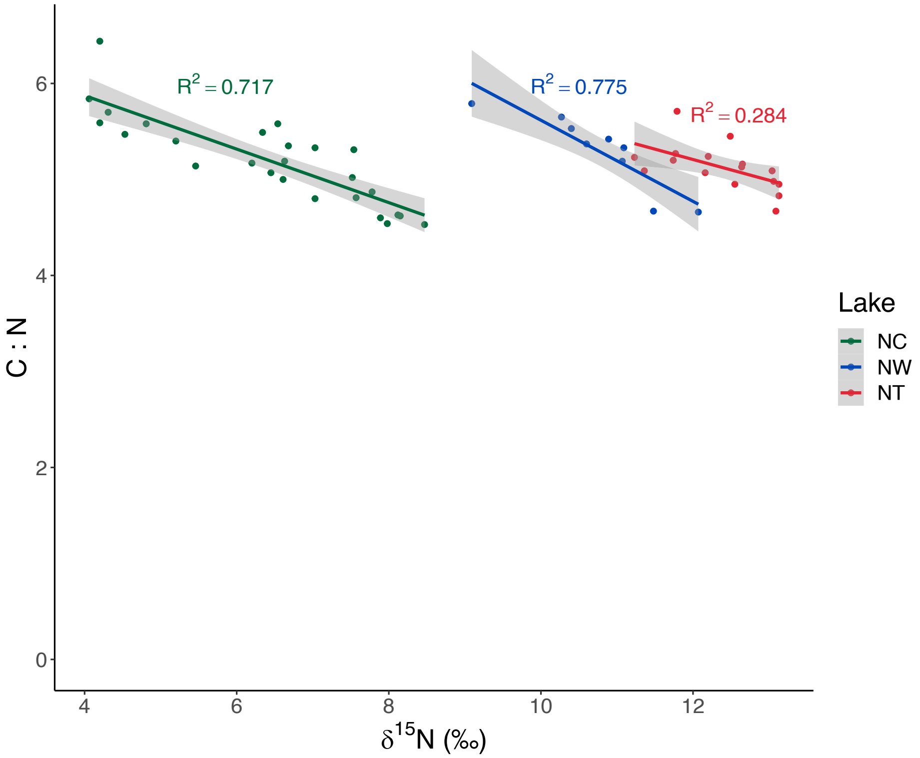

Fig. 2. Linear regression of δ^{15}N (independent variable) and C:N ratio (dependent variable) in studied lakes. Colors: green – lake Gineitiškės (NC); red – Tyniec oxbow lake (NT); blue – lake Sakadaš (NW). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

web components, as we found cyclopoid copepods occupying a trophic position between calanoid copepods and *Diaphanosoma* and/or *Daphnia* in the NT and NC lakes. Cladocerans *Daphnia* sp. and *Diaphanosoma* sp. occupied the lowest trophic positions in the studied lakes (lowest δ^{15}N values in each lake). Filter feeding, used by *Daphnia* and *Diaphanosoma* is efficient for consumption of bacteria and algae (Barnett et al., 2007), so the close trophic proximity of these animals to primary producers was expected, and in fact it has been demonstrated by the results of this study.

The C:N ratio can be treated as a proxy for lipid content in zooplankton, due to the positive correlation between these variables (Syväranta & Rautio, 2010). The diet of planktonic crustaceans strongly determines the profile of accumulated lipids since these animals acquire the lipids almost exclusively from ingested food (McLaskey et al., 2024). We did not find any statistically significant differences in C:N ratio between studied groups of crustacean zooplankton, which is contrary to findings of Persson & Vrede (2006), who demonstrated that zooplankton taxa differed in PUFA content and composition. However, we found a negative relationship between the C:N ratio and δ^{15}N values in crustacean zooplankton tissues, suggesting that lipid content decreased with relative trophic level of these animals. Specifically, animals situated closer to the primary producers (*Daphnia* and *Diaphanosoma*) in the food web contained higher amounts of lipids, than copepods which are more likely to utilize animal prey. This in turn, agrees with findings of Persson & Vrede (2006), who concluded that differences in PUFA content among zooplankton taxa can affect energy transfer in the food web, as PUFA content is crucial for development of numerous fish species. Furthermore, our results agree with the findings of Kainz et al. (2004), who found that polyunsaturated fatty acid content increased from seston through micro- to mesozooplankton and dropped in macrozooplankton. This result is of great importance to the overall energy transfer from primary producers to the highest trophic levels since a substantial part of the energy at each trophic level is allocated by the organisms into metabolism, respiration, etc. (Sommer et al., 2002) and only ∼10 % is transferred further (Pauly & Christensen, 1995). Moreover, Barneche et al. (2021) demonstrated that with temperature increase by 4 °C, the energy transfer can be up to 56 % less efficient. Results of this study support their findings, as we found that δ^{15}N had the strongest negative effect on the C:N ratio in lake functioning under warmest thermal regime (NW lake). Our findings are supported by Calderini et al. (2023) and Wu et al. (2021) who concluded that warming leads to decrease of polyunsaturated fatty acids (PUFA) in algal species. Another consequence of increasing water temperature is prolonged occurrence and/or domination of phytoplankton community by cyanobacteria. Cyanobacteria contain low amounts of omega-3 PUFAs, which potentially leads to decreasing availability of PUFA for consumers (Strandberg et al., 2015). Cladocerans are a group particularly exposed for such disruption, since they acquire majority of energy (up to 94 %) from phytoplankton (Galloway et al., 2014), while copepods tend to cover larger spectrum of available food sources (Kiørboe, 2011a). This explains not only the differences in total amount of stored lipids, but also the differences in lipid profile of the animals and seasonal fluctuations of abovementioned parameters (McMeans et al., 2015). The tranfer of PUFAs from phytoplankton to zooplankton is crucial for fish community development (Grosbois et al., 2022), therefore the decline of lipid content with increasing trophic level, being the consequence of predicted shifts in the thermal regimes of freshwater systems (Maberly et al., 2020), is potentially highly disrupting.

Our study was carried out in three lakes only, so the extrapolation of our conclusions to other lakes is limited. Nevertheless, using δ^{13}C and δ^{15}N measurements in planktonic crustacean tissues, we demonstrated functional-trait-dependent, within-community partitioning of isotopic niches among calanoid copepods, cyclopoid copepods, *Daphnia* sp. and *Diaphanosoma* sp. Results showed that employment of stable isotope-based approach allows better recognition of trophic linkages than could be inferred from classical methods. The multidimensionality of environmental changes which freshwater ecosystems are subjected to is hard to overestimate. Interacting phenomena such as climate change, eutrophication and switches in phyto- and zooplankton compositions are believed to alter the functioning of freshwater food webs and therefore we encourage more investigations of key planktonic communities using measurements of stable isotopes. By incorporating data from lakes across various latitudes, we will enhance and refine management strategies for aquatic ecosystems, allowing for more effective responses to environmental changes.

5. Statements and Declarations

CRediT authorship contribution statement

Wojciech Krztoń: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Edward Walusiak:** Resources, Investigation, Data curation. **Keith A. Hobson:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization. **Petar Žutinić:** Writing – review & editing, Validation, Project administration, Investigation, Data curation. **Marija Gligora Udovič:** Writing – review & editing, Validation, Project administration, Investigation, Data curation. **Antonija Kulaš:** Writing – review & editing, Validation, Investigation, Data curation. **Judita Koreivienė:** Writing – review & editing, Validation, Project administration, Investigation, Data curation. **Jur¯atė Karosienė:** Writing – review & editing, Validation, Project administration, Investigation, Data curation. **Beata Gebus-Czupyt:** Writing – review & editing, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Anita Galir Balkić:** Writing – review & editing, Validation, Project administration, Investigation, Data curation. **Filip Stević:** Writing – review & editing, Validation, Project administration, Investigation, Data curation. **Tanja Žuna Pfeiffer:** Writing – review & editing, Validation, Project administration, Investigation, Data curation. **Dubravka Špoljarić Maronić:** Writing – review & editing, Validation, Project administration, Investigation, Data curation. **Elżbieta Wilk-Woźniak:** Writing – review & editing, Writing – original draft, Validation, Supervision, Investigation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.112732.

Data availability

Data will be made available on request.

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