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Features that matter: studying how phytoplankton drives zooplankton community functional traits

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Abstract Freshwater phytoplankton and zooplankton are complex and diverse communities which greatly contribute to the functioning of freshwater ecosystems, constituting a path of nutrient cycling. The relationships of these communities are often driven by species' functional traits, such as defensive features and grazing adaptations. The aim of the present work was to study if the functional traits of phytoplankton (primary producers) promote specific traits of zooplankton (consumers). We calculated community weighted mean (CWM) of a trait of phytoplankton and zooplankton communities and constructed decision trees to study the relationships between the functional traits of both communities. We found that specific functional traits of zooplankton were most significantly promoted by size and shape of algal particles, followed by potential toxicity and spines possession, which had limited, however still important effects. Armor possession and motility of algae were found not to be promoting any functional traits of zooplankton. Easy-to-handle algal particles promoted greater variability of zooplankton's functional traits, while large, hard to manage algal particles (often characteristic for cyanobacteria) promoted zooplankton taxa bearing more specialized functional traits. Our study shows that phytoplankton functional traits can be considered as a biotic filter, leading to the selection of advantageous functional traits among zooplankton community.

Keywords Plankton ecology · Phytoplankton–zooplankton interactions · Freshwater food webs · Functional traits · Community weighted mean · Decision trees

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Introduction

Phytoplankton–zooplankton interactions have been a concern of numerous studies, and various study frameworks have been employed (Ger et al., 2014). One of the frequently asked questions has been: 'who eats whom?' and how the organic matter passes through the ecosystem. Classical approaches were based on taxonomical classifications or body sizes of planktonic animals and identification of their food sources, however such predictions have not always fairly depicted the reality (Bogdan & Gilbert, 1984). The method was enhanced with the use of clearance and ingestion rates of major taxonomical groups of zooplankton and morphological groups of

phytoplankton (Colina et al., 2016). This was a step towards a trait-based approach, which is assumed to be crucial in the recognition of the function of the zooplankton community (Litchman et al., 2013).

Phytoplankton–zooplankton interactions are responsible for one of the fundamental processes of the energy flow from primary producers (algae) to higher trophic levels. Seasonal pattern of functioning of aquatic ecosystems described as the Plankton Ecology Group (PEG) model (Sommer et al., 1986, 2012) assumes the succession of different algal groups in the phytoplankton community through an annual cycle. According to the PEG model, in eutrophic water bodies the zooplankton community develops with slight temporal delay after the phytoplankton community, then the phytoplankton may be considered as a driver of complex interactions. Grazing by zooplankton and grazing resistance of phytoplankton lead to 'dynamic equilibrium' of plankton communities (Scheffer et al., 2003). The base for species interactions are their functional traits which characterize the type, strength and direction of the interactions (McGill et al., 2006).

Studying such complex communities requires the employment of a method capable of defining an optimal living strategy under given, inconstant circumstances. Such an approach is the analysis of the Community Weighted Mean of a trait (CWM; Lavorel et al., 2008; Muscarella & Uriarte, 2016). The employment of this tool is advantageous in studying the traits' interactions of different communities, including cross-trophic level interactions, which may act as a biotic filter in a process of assembling a local community of organisms (Poff, 1997). Different phytoplankton species may bear traits such as large size as a particle (i.e. maximum linear dimension—MLD), armor-like features (e.g., silicified cell walls) or the ability to produce toxins, whose purpose is the reduction of grazing pressure of zooplankton (Colina et al., 2016).

Recently observed climatic changes and increasing anthropopressure are major threats for the functioning of numerous ecosystems, including freshwater ones, which are particularly vulnerable (Vörösmarty et al., 2010). Simultaneously with changes of aquatic ecosystems, the phytoplankton–zooplankton interactions will be altered (Ger et al., 2016; Teodosio & Barbosa, 2020). A certain point of interest—which appears to be remarkable in the face of climate changes—are predictions of proliferation and intensification

of cyanobacterial blooms in freshwater ecosystems (Paerl & Paul, 2012; Havens et al., 2019). Since cyanobacteria are considered as a poor-quality food and they may have numerous negative effects on zooplankton communities, the dominance of their functional traits (e.g. large cell colonies, thick solitary filaments or filament aggregations, toxicity; Ger et al., 2016) in the phytoplankton community may severely affect nutrient cycling in freshwater ecosystems (Huisman et al., 2018). To completely understand the consequences of global changes, special attention should be paid to the processes which are fundamental in the functioning of particular ecosystems, such as primary producer—consumer interactions in freshwater ecosystems.

Here, we analyze how CWM of phytoplankton may drive CWM of zooplankton. The assumption of the study was that CWM reflects the optimal living strategy (i.e., most eligible functional trait) under certain circumstances. We claim that such an approach is a proxy for studying interactions of phytoplankton–zooplankton communities. We hypothesized that specific functional traits of phytoplankton endorse specific functional traits of zooplankton. Functional traits studies of planktonic communities, however debated, still have some knowledge gaps (Sodré & Bozelli, 2019), on which we focused in our work. We studied relationships between phytoplankton morphology (i.e. functional traits characterizing defenses against grazing) and features outlining zooplankton grazing adaptations and routines. Furthermore, our study focuses on proto- and metazooplankton, while the majority of studies focus only on metazooplankton (Ger et al., 2016). In present study we aim to enhance the knowledge in this field. We employed decision trees (classification trees for qualitative traits and regression trees for quantitative traits) to test whether and, if so, which functional traits of phytoplankton promote which functional traits of zooplankton.

Materials and methods

Sampling was conducted in two week interval during the period from April to October of year 2017 in four waterbodies located in the vicinity of Kraków (southern Poland): oxbow lakes Tyniec 1 (50° 01′ 47″ N, 19° 49′ 39.8″ E; area: 5.75 ha) and Tyniec 2

(50°01′28.1″ N, 19°48′47.7″ E; area: 8.56 ha), and artificial ponds Podkamycze 1 (50° 05′ 11″ N, 19° 50′ 01.6″ E; area: 16.82 ha), and Podkamycze 2 (50° 04′ 59.6″ N, 19° 50′ 05.4″ E; area: 17.28 ha). All of the waterbodies are shallow (max. depth 1.5–3 m), eutrophic, stagnant and polymictic. The phytoplankton community structure of studied waterbodies was typical for eutrophic lakes. Diatoms (*Aulacoseira* spp., *Cyclotella* sp.) dominated in spring, and cyanobacteria (*Aphanizomenon flos-aquae* Ralfs ex Bornet& Flahault 1886—especially in ponds, *Microcystis aeruginosa* (Kützing) Kützing—in all of the waterbodies) started to develop since beginning of summer, creating blooms in period from August to October. Chlorophytes (*Desmodesmus* spp., *Scenedesmus* spp., *Pediastrum* spp.), euglenophytes (*Euglena* spp., *Trachelomonas* spp.) and dinophytes (*Ceratium hirudinella* (O.F. Müller) Dujardin, *Peridinium* spp.) were present in the phytoplankton frequently, occasionally dominating the community, especially in oxbow lakes. Spring zooplankton community was dominated mainly by ciliates: *Opercularia* sp. and *Vorticella* sp. in ponds, and *Coleps hirtus* (O.F. Müller, 1786) Nitzsch, 1827 and *Coleps spetai* Foissner, 1984 in oxbow lakes. Mentioned species were also present in late spring to autumn samples, however they did not reached as high biomasses as cladocerans (*Bosmina longirostris* O.F. Müller, 1785, *Daphnia* spp.). Rotifers (*Asplanchna priodonta* Gosse, 1850; *Brachionus angularis* Gosse, 1851) and copepods (*Cyclops strenuus* Fischer, 1851; *Eudiaptomus gracilis* G.O. Sars, 1863) dominated ocasionally.

Biological samples were collected from a depth of 1 m, from the volume of 10 L, concentrated with planktonic nets (mesh sizes: 10 μm for phytoplankton and protozooplankton and 50 μm for metazooplankton) and fixed with Lugols' solution (phytoplankton and protozooplankton) and formaldehyde (metazooplankton). Totally 56 samples (N = 56) were collected. Taxonomic composition was identified under light microscope in chambers of volume 0.5 ml for phytoplankton and metazooplankton and 1 ml for protozooplankton. Taxa were identified with the use of keys listed in Wilk-Wozniak (2009) for phytoplankton and Krztoń et al. (2019) for meta- and protozooplankton. Biomass of phytoplankton was calculated as a biovolume by comparing the specimens with their geometrical shapes (Rott, 1981). Biomass of protozooplankton was calculated according to Persson &

Ekbohm (1980), Putt & Stoecker (1989), Jerome et al. (1993), Wiackowski et al. (1994) and Menden-Deuer & Lessard (2000), and metazooplankton according to Cummins et al. (1969), Dumont et al. (1975), Bottrell et al. (1976) and Ruttner-Kolisko (1977)

Juvenile stages of copepods were not included into analyses, due to difficulties of their identification as species and limited knowledge on their specific feeding traits. Each of the identified taxa were characterized with their functional traits. The following phytoplankton traits were used: 1. Size as a particle (numeric trait, largest dimension of a solitary cell or colony, depending on the taxa life form; mean value on the basis of at least 50 cells/colonies measurement); 2. Shape as a particle (categorical trait, geometrical characteristics of a solitary cell or colony, depending on the taxa life form); 3. Potential toxicity (binary trait, potential ability of the taxa to produce toxins); 4. Motility (binary trait, ability of the taxa to active swimming); 5. Armor (binary trait, occurrence of armor-like morphological structures, e.g., plates or silica in the taxa cell wall); 6. Spines (categorical trait, occurrence of spines or horns). Proto- and metazooplankton were characterized with: 1. Body length (numeric trait, mean value on the basis of measurement of at least 50 specimens of each species); 2. Potential food source (categorical trait, ability to feed on one or multiple food sources—bacteria, algae or animal prey); 3. Feeding type (categorical trait; method of food particles uptake by the taxa); 4. Optimal food particle size (numeric trait; based on morphology of taxa feeding structures and its body length), according to Hansen et al. (1994) and Branstrator (1998). Information on the specific functional traits of the phytoplankton and zooplankton taxa is provided in Supplementary Tables A and B.

CWM was calculated on basis of taxa functional traits and biomass with the use of the "FD" package for R and R Studio statistical software (R Core Team, 2020). CWM was calculated separately for zooplankton and phytoplankton community. CWM for numerical traits was calculated as the biomass-weighted mean value of the trait values of all taxa present in the community. CWM for binary and categorical traits were calculated as a dominating trait identity inherent to single or multiple taxa in which cumulative biomass dominated in the sample (Gulati & Demott, 1997). Trait identity dominating in the CWM is treated as an optimal living strategy.

Analyses of the functional trait interactions were conducted with the use of Decision Trees ("rpart" package; Therneau et al., 2015). The calculated CWM of each of the functional traits of the zooplankton community were used as predicted variables in the analysis, while the CWM of phytoplankton traits were used as independent variables. Four unique decision trees were created, one for each of the zooplankton traits; numeric traits (body length and optimal food particle size) were predicted as regression trees, while values of categorical traits (potential food source and feeding type) were predicted as classification trees. The importance of each phytoplankton trait in predicting zooplankton traits was identified as "Variable importance" (a measure proposed by (Therneau et al., 2015) in the construction of each of the decision trees. The importance was scaled between 1 – 100 values (minimal–maximal importance). Decision trees with phytoplankton traits' CWM as predictors for zooplankton traits' CWM are treated as a proxy for the interactions of both communities, with an emphasis on the phytoplankton community as a biotic filter (Poff, 1997) for the zooplankton community.

Results

In the analysed biological samples, a total of 102 taxa of algae and 81 taxa of planktonic animals were identified. Mean size ("*size as a particle*" trait) of algae forming the studied communities was 15.547 μm, ranging from 3.476 to 41.234 μm (standard deviation—SD: 9.19 μm),. The most common shape ("*shape as a particle*" trait) of algae was spherical colony (dominating in 27 samples) followed by cylindric colony (dominating in 18 samples). Discoid, ellipsoid and filamentous forms were found most abundant in three samples each, and cylindric forms and flat colonies in one sample each. Taxa without the ability of cyanotoxin production ("*toxicity*" trait) prevailed in 34 samples, while potentially toxic taxa prevailed in 22 samples. Motile ("*motility*" trait) algae taxa dominated in one sample; 55 samples were dominated by non-motile algae. Six of the analysed samples were dominated by taxa possessing armor-like, defensive morphological features ("armor" trait), and the remaining 50 samples were dominated by armorless taxa. Spineless algae ("*spines*" trait) prevailed

in 44 of the analysed samples, and spine-possessing algae, prevailed in 12 samples; taxa possessing horns did not prevailed in any sample.

The body length trait of zooplankton communities found in the studied samples ranged from 34.41 to 3 609.65 μm (mean: 753.29 μm, SD: 639.89 μm). Optimum food particle size of planktonic animals ranged from 3.875 μm to 360.664 μm (mean: 45.487 μm, SD: 63.37 μm). The highest number of samples was dominated by algivorous animals ("*food source*" trait, 17 samples). Taxa able to feed both on algae and bacteria prevailed in 14 samples, and bacterivorous taxa prevailed in 13 samples. Six samples were dominated by taxa able to feed on algae and animal prey, four samples were dominated by predatory taxa, and two by omnivorous taxa. Most frequently abundant the food uptake mechanism ("*feeding type*" trait) was the ciliate-suspension feeding type, found in 21 samples. *Daphnia*-type filtering mechanism dominated in 10 samples, ambush feeding in 9 samples and feeding-current mechanism in 7 samples. *Bosmina*-type filtering animals were found to be most abundant in five samples, tactile feeding cladoceran *Leptodora kindtii* Focke, 1844 in 3 samples, and rotifer-suspension feeders were most abundant in one sample.

Considering the assumptions of our study, the most important phytoplankton traits found to be discriminating mean zooplankton body size were size of algal particles and shape of algal particles (in order of importance; Table 1). These two traits were used to build the decision tree (Fig. 1). Smallest animals dominance were supported by flat colonies and discoid and filamentous forms of algae (mean body size of animal in node: 316 μm, SD: 285 μm, 12% of observations; Fig. 1), by cylindrical colonies of size ranging from 7.3 to 20 μm (mean body size of animal in node: 370 μm, SD: 300 μm, 9% of observations; Fig. 1), and by cylindrical and ellipsoid forms and cylindrical and spherical colonies of size and larger than 26 μm (mean body size of animal in node: 457 μm, SD: 310 μm, 12% of observations; Fig. 1). Moderate body sizes of the zooplankton community were promoted by cylindrical colonies smaller than 7.3 μm (mean body size of animal in node: 671 μm, SD: 281 μm, 21% of observations; Fig. 1), and ellipsoid forms and spherical colonies of size ranging from 7.6 to 20 μm (mean body size of animal in node: 680 μm, SD: 203 μm, 20% of observations; Fig. 1). The largest animals were promoted by cylindrical and

Table 1 Importance of particular phytoplankton community traits (variable importance) in the construction of decision trees for each of the zooplankton community traits

Predicted zooplankton community trait	Phytoplankton community trait used in the tree construction	
	Trait	Importance
Body length	**Size as a particle**	**56**
	Shape as a particle	**18**
	Potential toxicity	10
	Armor	10
	Motility	5
	Spines possession	3
Optimum food particle size	**Size as a particle**	**69**
	Potential toxicity	**16**
	Shape as a particle	**15**
	Spines possession	< 1
Food source	**Size as a particle**	**50**
	Shape as a particle	**31**
	Spines possession	8
	Potential toxicity	7
	Armor	2
	Motility	1
Feeding type	**Size as a particle**	**48**
	Shape as a particle	**24**
	Spines possession	**13**
	Potential toxicity	8
	Armor	6
	Motility	2

Phytoplankton traits in bold (the highest importance) were used for construction of the particular decision trees

ellipsoid forms and cylindrical and spherical colonies of sizes: 1. ranging from 20 to 22 µm (mean body size of animal in node: 1 766 µm, SD: 1601 µm, 5% of observations; Fig. 1), and 2. Ranging from 22 to 26 µm (mean body size of animal in node: 1 183 µm, SD: 813 µm, 14% of observations; Fig. 1), and by ellipsoid forms and spherical colonies smaller than 7.6 µm (mean body size of animal in node 1 545 µm, SD: 629 µm, 5% of observations; Fig. 1).

The decision trees explaining optimum food particle size of the planktonic animals were constructed with three functional traits of phytoplankton community (in order of importance; Table 1): size as a particle, potential toxicity, and shape as a particle (Fig. 2). The lowest optimum food size (mean particle size in node: 19 µm, SD: 12 µm, 20% of observations; Fig. 2) was found to be supported by a dominance of algal particles of size and larger than 26 µm. The highest optimum food size (mean particle size in node: 196 µm, SD: 233 µm, 4% of observations; Fig. 2) was found to be supported by a dominance of non-toxic algal particles of size ranging from 20 to 26 µm. The analysis showed that toxic algal particles larger than 25 µm also promoted animals feeding on large particles (mean particle size in node: 169 µm, SD: 122 µm, 5% of observations; Fig. 2), while toxic particles of size ranging between 20 and 25 µm supported animals with relatively low food size optimum (mean particle size in node: 43 µm, SD: 7 µm, 9% of observations; Fig. 2). Small-sized optimum food particles were also supported by cylindrical and flat colonies and discoid and filamentous particles smaller than 20 µm (mean particle size in node: 27 µm, SD: 17 µm, 38% of observations; Fig. 2), and spherical colonies of size ranging from 8.2 to 20 µm (mean particle size in node: 33 µm, SD: 11 µm, 18% of observations; Fig. 2). Moderate optimum food size was supported by a dominance of ellipsoid food particles smaller than 20 µm (mean particle size in node: 90 µm, SD: 83 µm, 4% of observations; Fig. 2.), and algae organized in spherical colonies of size lower than 8.2 µm (mean particle size in node: 76 µm, SD: 89 µm, 4% of observations; Fig. 2).

The analysis showed that most important phytoplankton functional trait affecting zooplankton food source was size as a particle followed by shape as a particle (Tab 1). These were the only traits used to build the decision tree explaining zooplankton food source variability (Fig. 3). Bacterivorous (able to feed on bacteria and/or seston) animals were supported by discoid and filamentous food particles smaller than 8.7 µm (4% of observations; Fig. 3), discoid, ellipsoid, filamentous particles and flat colonies larger than 8.7 µm (11% of observations; Fig. 3.), and cylindrical particles and cylindrical and spherical colonies of algae of sizes 15 – 19 µm (7% of observations; Fig. 3). Algivorous animals were found to be supported by cylindrical and spherical colonies and ellipsoid food particles of four different size classes: 1. lower than 5.4 µm (4% of observations; Fig. 3); 2. ranging between 8.7 and 12 µm (7% of observations; Fig. 3); 3. ranging between 19 and 23 µm (11% of observations; Fig. 3) and 4. of size and larger than 26 µm (11% of observations; Fig. 3). Zooplankton taxa able to feed effectively, both with bacteria and algae, were found to be supported by only one set of
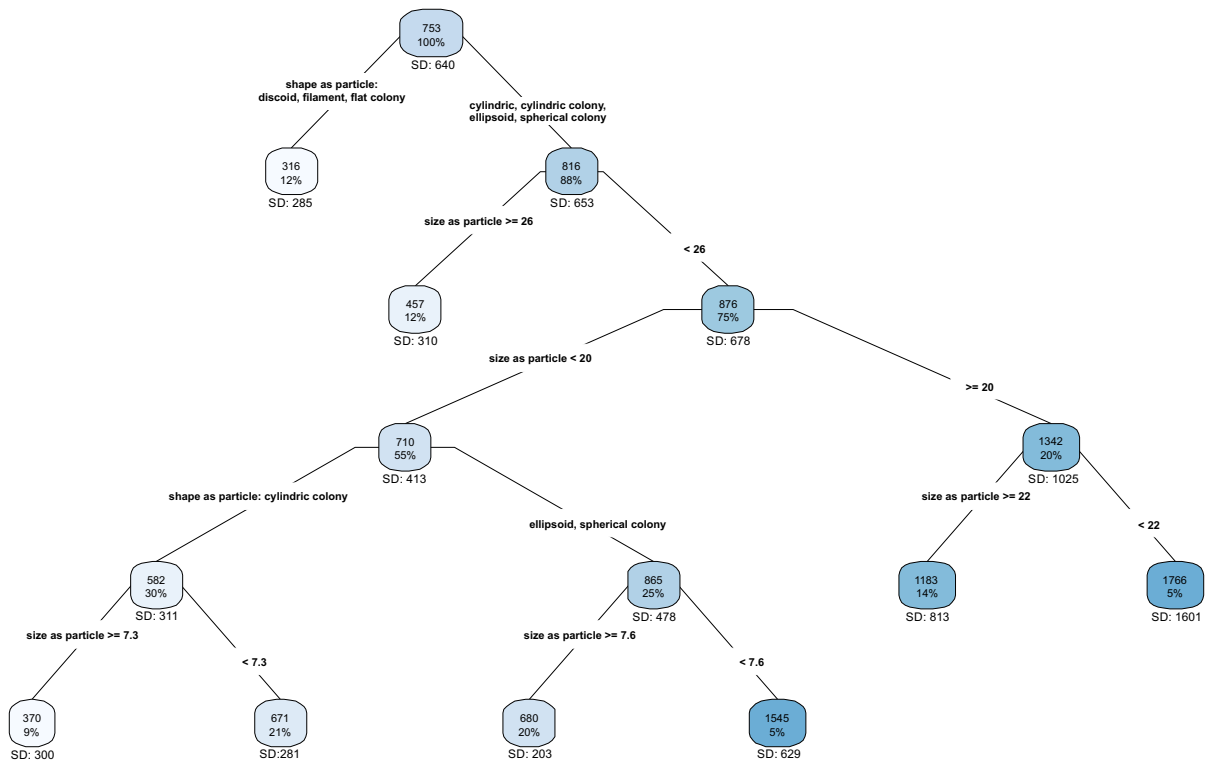
Fig. 1 Decision tree (regression tree) for zooplankton body length predicted by functional traits of phytoplankton community. Information on branches: trait values of the phytoplankton species used in the split. Values in brackets: mean zooplankton body length in a particular leaf (µm) and the percentage share of observations (% of N); SD (below bracket)—standard deviation in particular leaf (µm). Colors: Light/dark tones of blue represent small/large body sizes of zooplankton taxa. The darker the tone, the larger the body sizes

phytoplankton traits (29% of observations; Fig. 3): cylindrical and spherical colonies and ellipsoid food particles of size ranging between 5.4 and 8.7 µm. Animals able to feed both on algae and animal prey were found prevailing under dominance of algae of cylindrical shape and organized as cylindrical and spherical colonies, with sizes: 1. ranging between 12 and 15 µm (7% of observations; Fig. 3) and 2. ranging between 23 and 25 µm (4% of observations; Fig. 3). Predatory taxa were supported only under high abundance of cylindrical and cylindrical and spherical-organized algae of size and greater than 25 µm (7% of observations; Fig. 3). The analysis indicated that omnivorous animals were not related to any of the phytoplankton traits.

Zooplankton feeding type was found to be supported by three functional traits of phytoplankton in following order of significance: size as a particle, shape as a particle, and spines occurrence (Table 1).

The decision tree explaining zooplankton feeding type variability was constructed with the use of the above-mentioned phytoplankton functional traits (Fig. 4). Ciliate-type suspension feeders dominance were corresponding high abundance of discoid, filamentous, and flat colony-organized algae of all sizes (12% of observations; Fig. 4). Ciliate-type suspension feeders were also promoted by cylindrical, ellipsoid, and cylindrical colony- and spherical colony-organized algae of sizes: 1. ranging 8.7–20 µm (20% of observations, Fig. 4); and 2. larger than 26 µm (12% of observations; Fig. 4). *Bosmina*-type filtration feeders were related to spine possessing, cylindrical, ellipsoid, and cylindrical and spherical colonies of algae smaller than 5.5 µm (5% of observations; Fig. 4). *Bosmina*-type filtrators were also found to be prevailing under dominance of same morphological forms of spineless algae of sizes ranging 7.3–8.7 µm (7% of observations; Fig. 4).
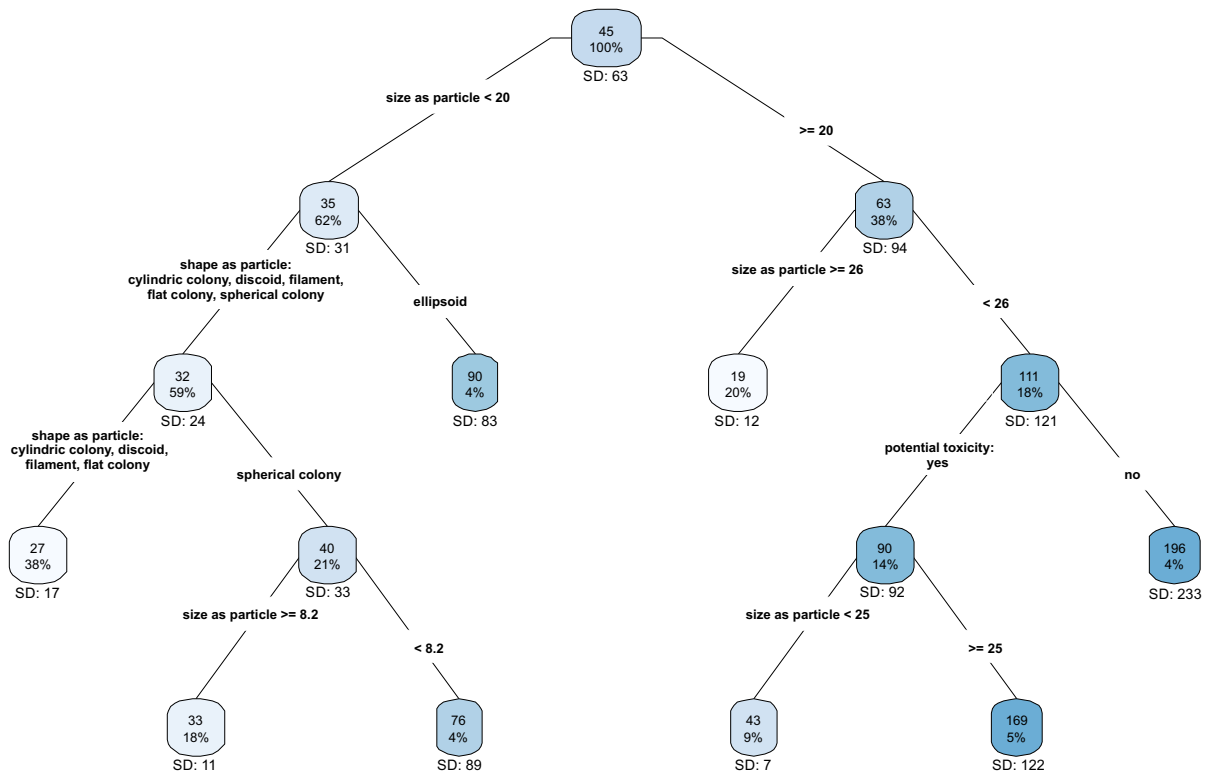
Fig. 2 Decision tree (regression) for zooplankton optimal food particle size predicted by the functional traits of the phytoplankton community. Information on branches: trait values of the phytoplankton species used in the split. Values in brackets: mean zooplankton optimal food size in a particular leaf (µm) and the percentage share of observations (% of N); SD (below bracket)—standard deviation in particular leaf (µm). Colors: Light/dark tones of blue represent small/large optimal food particle size of zooplankton taxa. The darker the tone, the larger the optimal food particle sizes

Similar circumstances (cylindrical, ellipsoid, and cylindrical and spherical colonies of spineless algae smaller than 7.3 cylindrical, ellipsoid, and cylindrical and spherical colonies of algae) were found to support dominance of *Daphnia*-type filtrators (9% of observations; Fig. 4). High abundances of ambush feeding animals was related to spine possessing cylindrical, ellipsoid, and cylindrical and spherical colonies of algae of sizes: 1. ranging from 5.5 to 7.3 µm (11% of observations; Fig. 4); 2. ranging from 20 to 25 µm (12% of observations; Fig. 4). Tactile feeding type was found to be supported only by a dominance of cylindrical, ellipsoid, and cylindrical and spherical colony-organized algae of size and greater than 25 µm (7% of observations; Fig. 4). The domination of feeding current-feeders and rotifer-type suspension-feeders was found not to be related to any of the phytoplankton functional traits.

Discussion

General pattern

Functional traits, at a level of individuals, define species' characteristics such as resource acquisition, growth and the ability to survive (McGill et al., 2006). In an extension to the ecosystem scale, the functional traits of species may affect some ecosystem processes (Violle et al., 2007). Phytoplankton—zooplankton interactions take effects both ways: zooplankton grazers tend to overcome phytoplankton defense mechanisms/structures (Ger et al., 2016), while phytoplankton develop adaptations to resist grazing (Lürling, 2021). According to the PEG model, zooplankton community is controlled by primary producers (i.e. food availability) and predatory pressure of higher trophic levels (e.g. fish). However, the development
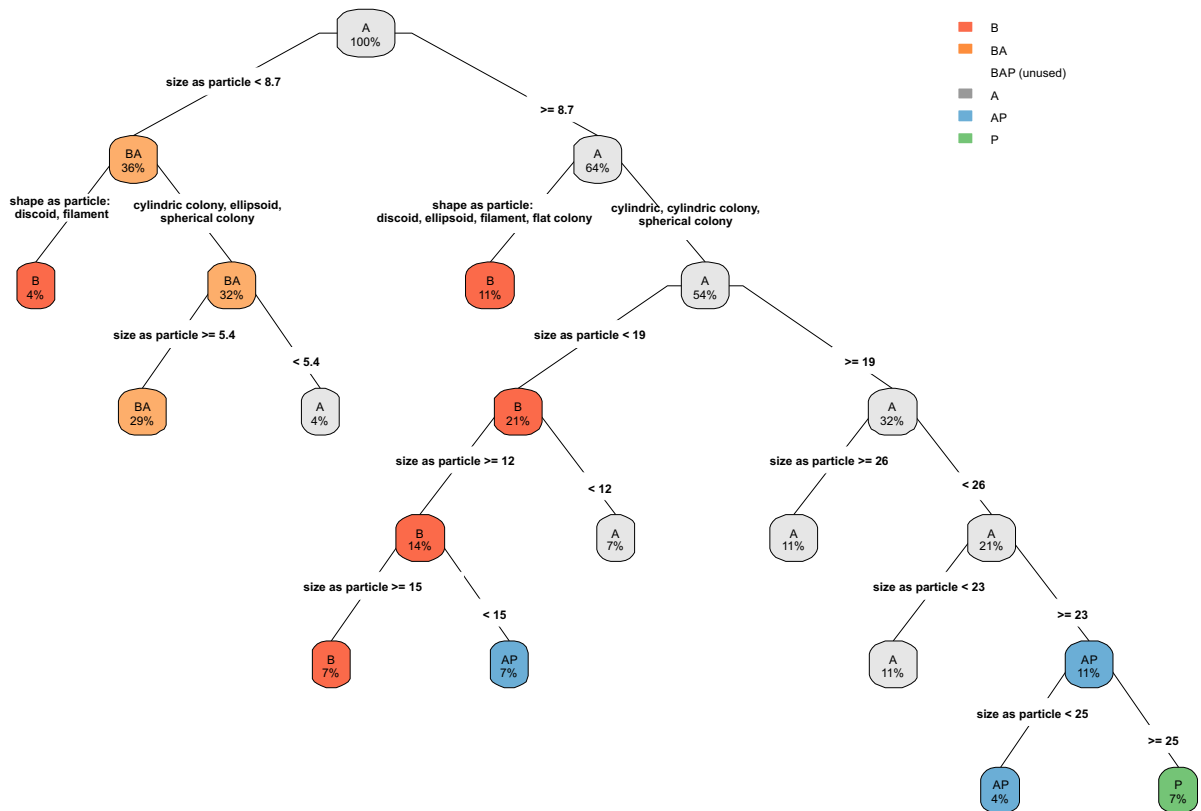
Fig. 3 Decision tree (classification tree) for the zooplankton food source predicted by the functional traits of the phytoplankton community. Information on branches: trait values of the phytoplankton species used in the split. Values in brackets: zooplankton food source dominating in a CWM particular leaf and the percentage share of observations (% of N). Abbreviations: B—bacteria and/or seston feeders, BA—bacteria and/or seston and algae feeders, BAP—omnivores, A—algaevores, AP—algae and animal prey feeders, P—predators

of zooplankton is a response to increase of algal food availability (Sommer et al., 1986, 2012), therefore the assumption of the study was that, the phytoplankton functional traits can directly and indirectly determine zooplankton functional traits. Resources acquired by primary producers are transferred to higher trophic levels through complex predator–prey interaction, which lead to the selection of specific traits in the community (Spitz et al., 2014).

Our results demonstrated that phytoplankton functional trait, which was remarkably important in zooplankters' traits determination, was the size of the algal cell as a food particle (MLD). In decision trees constructed in this study we encountered some small differences between branches (few μm), where the split was based on size of algal particles. Biological significance of this results may be limited, however considering the morphology of

structures responsible for food uptake in zooplankton, they appear to be noteworthy. For instance, small cladocerans *Bosmina* spp and *Chydorus* spp. are specialized in feeding on very fine food particles (1.5–5 μm and 0.4–2 μm respectively; Geller & Müller, 1981). In such case, even the minor difference in food particle size may be crucial. '*Size as a particle'* was the most important feature in supporting all of four considered zooplankton functional traits. This result corroborates with the study of Gliwicz (1990), who showed that one of most efficient filter-feeders—cladocerans of genus *Daphnia*—fail to control blooms of filamentous species of cyanobacteria when food particles size exceeds effective food size spectrum defined by animal body size. The performance of *Daphnia*-type filtrators may be also affected by thickness of filaments (Wejnerowski et al., 2015) and the proportion of
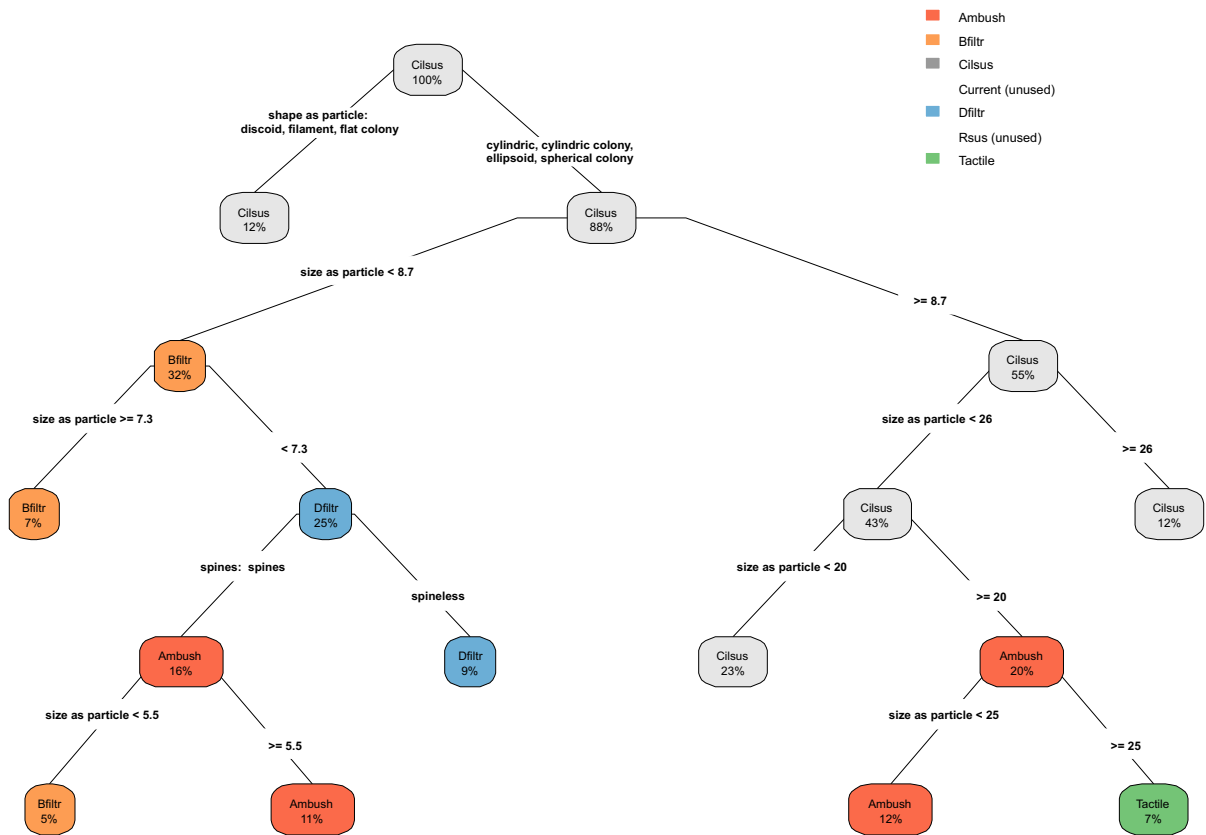
Fig. 4 Decision tree (classification tree) for zooplankton feeding type predicted by the functional traits of the phytoplankton community. Information on branches: trait values of the phytoplankton species used in the split. Values in brackets: zooplankton feeding type dominating in a CWM particular leaf and the percentage share of observations (% of N).

Abbreviations: Ambush—ambush-feeding, Bfiltr—*Bosmina*-type filtration, Cilsus—Ciliate-type suspension feeding, Current—feeding current feeders, Dfiltr—*Daphnia*-type filtration, *R-sus*—rotifer-type suspension feeding (rotifers with *Malleate*, *Malleoramate* and *Incaudate* Trophi), Tactile—prey hunting mode characteristic for *Leptodora kindtii*

cyanobacterial filaments in the food mixture (Panosso & Lürling, 2010).

Beside the size of particles, also their shape is considered as significant factor affecting grazers (Gulati & Demott, 1997). The shape of particles was the second most important functional trait of phytoplankton affecting zooplankters' functional traits (in three out of four created decision trees). Furthermore, Gulati and Demott (1997) argued that grazers may be deterred by some defensive features of phytoplankton. The results of our study indicated that the mentioned features were presence of spines and potential toxicity.

Admitting the importance of each of the functional traits, an insight into the traits' identity is necessary for an understanding of the biotic filtering process in plankton communities. Below, we address four issues that we encountered during interpreting the decision trees: 1. "Fine particles, handy shapes"—circumstance of the food web, where the phytoplankton community consisted of easy-manageable food particles, characteristic for spring—early summer phytoplankton bloom with a high share of diatoms and green algae; 2. "Large, troublesome chunks"—the period of the vegetation season where the food web is being dominated by large particles formed by, for instance, chroococcal and/or filamentous cyanobacteria, which might produce toxins; 3. "Lucky losers"—functional traits of zooplankters which were found highly abundant in zooplankton community CWM but were not used in the construction of decision trees; these traits are considered unaffected by

phytoplankton biotic filtering; 4. "Expendable features"—functional traits of phytoplankton found highly abundant in phytoplankton community CWM, but not used in the construction of decision trees; theses traits are not considered a significant factor in the shaping of the zooplankton community.

Fine particles, handy shapes

The Plankton Ecology Group model (Sommer et al., 2012) assumes that spring peak of phytoplankton development is followed by slightly delayed zooplankton grazing peak. The spring stage is dominated by small, edible phytoplankton species which promotes high-efficiency grazers (Sommer et al., 2012). Our results demonstrated that the size of easily-manageable for algaevorous food particles is generally smaller than 20 μm, with singular observations exceeding this value. Particles of this size and easy to manage shapes (cylindric colonies – diatoms and ellipsoid cells – green algae) and relatively small spherical colonies were found to be promoting zooplankters of different size classes (four leaves with mean body sizes: 370 μm, e.g. *Chydorus sphaericus* O. F. Müller, 1776; 671 and 680 μm, e.g. *Diaphanosoma brachyurum* Liévin, 1848 and 1 545 μm, e.g. *Eudiaptomus gracilis*). Therefore, we assume such food particles are an appropriate food source for the majority of zooplankters, however, according to the results, animals of medium body sizes (approx. body length 671–680 μm, e.g. *Diaphanosoma brachyurum*) seem to be most beneficial. These body sizes might provide the best trade-off between energy acquired from food and expended for metabolism and respiration (Kiørboe, 2011; Litchman et al., 2013). Moreover fine, edible particles created a broad niche space, promoting zooplankters able to feed on diverse food sources. The smallest particles (< 8.7 μm) supported the development of mainly bacterio-algaevorous animals, and animals which feed only on bacteria or small algae. These niches, considering the size of the particles, are related to each other and partially overlapped, especially in cladocerans (Gophen et al., 1974; Bogdan & Gilbert, 1984), rotifers (Arndt, 1993) and ciliates (Rassoulzadegan et al., 1988). Larger, but still easy-manageable particles, ranging between 8.7 and 19 μm, were also found to be promoting bacterivorous animals and algaevorous animals, and also algaevorous taxa able to feed with animal prey. A

similar range of particle size (5 to 15 μm) were found by Agasild et al. (2007) to be the most important edible algal food size for zooplankters dominating in an eutrophic lake. Heterotrophic bacteria development, linked to decaying organic matter (White et al., 1991), constitutes a niche for bacterivores, such as ciliates, which may serve as a food source for copepods (Jack & Gilbert, 1997; Laybourn-Parry et al., 2011). The contribution of ciliates, accumulating carbon by grazing on primary producers, in copepods' diet may be significant, considering the fact that copepods are ineffective in feeding on small food particles (smaller than 5–10 μm; Sommer et al., 2012). In fact, we found that small particles (5.5–8.7 μm) were related to ambush feeding (characteristic for copepods), however this result may be an indirect effect of copepods feeding on developing simultaneously ciliates (Cilsus—ciliate type suspension feeding) promoted by slightly larger particles (size 8.7–20 μm). This may be also supported by fact that we found the spherical colonies of similar size (smaller than 8.2 μm) supporting a relatively large size of optimal food particles (mean size in a node: 76 μm), which corresponds to a better energetic tradeoff for ambush feeding copepods (Hansen et al., 1994).

According to our results, small algal particles have a significant effect on promotion of certain zooplankton functional traits. The strength of this effect might underestimated, since possible underrepresentation of < 10 μm algal particles, due to sampling with planktonic net of 10 μm mesh size. Nevertheless, even underrepresented, < 10 μm algal particles still dominated in substantial part of samples ("size as a particle" trait range from 3.476 to 41.234 μm, with mean value 15.547 μm). We find this result consistent with already existing body of literature (e.g. Agasild et al., 2007), and therefore, considerable factor in supporting certain zooplankton functional traits.

Small, manageable particles, beside fitting the size spectrum of numerous zooplankton species, still possess some features that grant them some grazing defense; therefore, these features may also shape functional traits distribution in the zooplankton community. We found that the above-mentioned ambush-feeders were supported by spine-possessing algae. The animals might be not affected by grazing defenses due to the possibility of choosing alternative—animal prey (Kiørboe, 2011). However, spine-possessing algae supported *Bosmina*-type filtrators

(*Bosmina* spp.). *Bosmina* spp. feeding apparatus is specialized for small particles uptake, and enables them to feed on bacteria (Geller & Müller, 1981). On the other hand, we also found *Bosmina* spp. supported by slightly larger, spineless algal food particles of various shape. The ability to graze various foods enables *Bosmina* spp. to compete with larger, generalist grazers—*Daphnia* spp. (DeMott, 1982). Our results show that *Bosmina* spp. and *Daphnia*-type filtrators cover similar niches (similar food particles shapes and sizes), however the factor segregating them may be the presence of defensive structures (spines) in food particles. We found *Daphnia*-type filtrators dominating under high abundances of spineless forms of algae. The result is questionable in the face of the study of Mayeli et al. (2005), who experimentally showed that spines developed by the green alga *Scenedesmus quadricauda* (*Desmodesmus quadricauda* (Chodat) S.S. An, T. Friedl&E. Hegewald) were an effective defense against *Ceriodaphnia dubia* Richard, 1894, but not against *Daphnia pulex* Leydig, 1860 (both species are *Daphnia*-type filtrators). The factor which appeared to be crucial in interactions studied by Mayeli et al. (2005) was the body size of grazers: the larger *Daphnia pulex* was able to graze on spine-possessing *Scenedesmus* (now genus *Desmodesmus*) more efficiently than smaller *Ceriodaphnia dubia*. According to the study of Mayeli et al., (2005), the body sizes of *Daphnia*-type filtrators found in our field samples did not grant them the ability to overcome algal defensive features.

Large, troublesome chunks

Phytoplankton species have developed numerous strategies and features whose ecological function is defense against grazing, both by specialist and generalist grazers (Lürling, 2021). According to Litchman and Klausmeier (2008), functional traits linked to predator avoidance, among others, are cell size, cell shape and coloniality, which matches our findings. We found that hard to manage particles, such as discoid and filamentous particles and flat colonies, supported quite a narrow group of zooplankton functional traits: small body sizes, bacteria feeding, ciliate-type suspension feeders (all three traits characteristic for ciliates).

Ciliates contribution into energy flow in the aquatic food webs is considerable (Christoffersen et al., 1990;

Kalinowska, 2004; Zingel et al., 2007). Beside the ability of fluxing bacterial carbon, ciliates may consume some troublesome particles as, for instance, large-sized filamentous and colonial cyanobacteria (Porter et al., 1979). In our study algaevorous taxa and Ciliate-type suspension feeders were supported by algal particles larger than 26 μm. Also, algal particles larger than 26 μm supported the lowest mean optimal food particle size (19 μm), what corresponds to high share of ciliates in the zooplankton community. The inedible for metazooplankton algal biomass is grazed by ciliates, which become a prey for predators of higher trophic levels (Ger et al., 2014; Wilk-Woźniak, 2020). According to our results, large algal particles, of different shapes (among others—spherical colonies characteristic for cyanobacteria) also supported large bodied animal taxa (mean body sizes in plot leaves: 1 183 and 1 766 μm, e.g. *Acanthocyclops venustus* Norman and Scott, 1906; *Cyclops vicinus* Uljanin, 1875; *Daphnia galeata* G. O. Sars 1864; *D. longispina* O. F. Müller, 1776). Furthermore, large algal particles promoted taxa feeding on algae (both eukaryotic algae and prokaryotic cyanobacteria), predatory taxa, and taxa able to feed both on algae and animal prey. Moreover, promoted food uptake methods among zooplankton were ambush and tactile feeding characteristic for predatory taxa. The highest mean optimal food particle sizes (169 and 196 μm) were also promoted by large algal particles.

Such duality: support of predatory and algaevorous taxa by large algal particles—requires a closer look. The occurrence in zooplankton of large, algaevorous taxa in circumstances where phytoplankton community is dominated by large algal species may suggest the dominance of large bodied cladocerans (which may manage large algal particles; Mayeli et al., 2005) or calanoid copepods, able to avoid large algal particles (DeMott & Watson, 1991). Also, the promotion of large predatory taxa indicates that energy transfer to the higher trophic levels may be elongated by an extra trophic level. Promotion of predators and algaevores by large algal particles can be explained with potential toxicity of algae. Potentially toxic, large algal particles of size 20–25 μm supported large optimal food size of zooplankton (43 μm) characteristic for predatory and predatory and/or algaevorous copepods. This result also suggests an increase of importance of copepods in energy transfer.

In addition we found that large algal particles promoted high values of optimal food particle size in zooplankton community (CWM optimal food particle size: 169 μm and 196 μm). High standard deviation in these nodes of the decision tree (Fig. 2.) suggests cooccurrence of species possessing small optimal food particle size (e.g. ciliates) and large optimal food particle size (predatory cladoceran—*Leptodora kindtii*). *L. kindtii* is recognized to prey on numerous planktonic species, including large copepods and cladocerans (Branstrator & Lehman, 1991), what lead to decrease of predatory pressure of crustaceans on small species, e.g. ciliates. Our results (high mean values and high standard deviations of CWM optimal food particle size in zooplankton community) suggest indirect support of small taxa by *L. kindtii.*

Our results show that domination of food web by large-sized and potentially toxic particles (characteristic for cyanobacteria) may force elongation of the trophic chain in freshwater food webs by promotion of predatory zooplankters. Considering the fact that each trophic level consumes a considerable amount of energy for respiration and metabolism (Gaedke et al., 2002; Kath et al., 2018; Moustaka-Gouni & Sommer, 2020), the efficiency of energy transfer to the highest trophic levels may be drastically decreased due to elongation of the trophic chain with one additional level. In the face of climate changes and anthropogenic eutrophication of the environment, cyanobacterial blooms are predicted to proliferate and intensify. Study of Taranu et al. (2015) clearly demonstrates that cyanobacteria pigments concentration in northern hemisphere lakes sediments significantly increased since 1800, including more rapid increase since 1945. This is an effect of increasing temperature and nutrient availability caused by human activity. Further increase of temperature will cause extension of period of cyanobacterial bloom (earlier development of cyanobacteria and their longer persistence), larger biomass production (higher growth rates at elevated temperature) and expansion of blooms towards higher latitudes (Visser et al., 2016).

Lucky losers

Two feeding types (rotifer-type suspension and feeding currents feeding) were found to be highly abundant in CWM, but were not included in decision trees. Rotifer-type suspension feeders were

found dominating only in one sample, but were not related to any of the phytoplankton functional traits. Rotifer-type suspension feeders, although widely distributed and strongly contributing to freshwater ecosystem functioning (Pace & Orcutt, 1981), may be suppressed by larger crustaceans. They are less efficient than large cladocerans (MacIsaac & Gilbert, 1989) and can be grazed by predatory copepods (Brandl, 2005). Feeding current feeders prevailed in 7 samples, however this feeding type was also not included in decision tree. Calanoid copepods which use this mechanism to acquire food particles are characterized by high food selectivity (DeMott, 1988), then the defensive traits of the phytoplankton might have been overcome by selective feeding ability. In addition, algae not possessing any defensive features did not supported feeding current feeders. Feeding currents are less effective at high and medium concentrations of food particles, therefore calanoid copepods might have been outcompeted by cladocerans (Richman & Dodson, 1983). The only "*food source*" trait which was not used in the building of decision trees was omnivory. Omnivores are advantageous under different states of food availability and may outcompete specialist species (Wootton, 2017). Considering such flexibility of omnivores and the results of our study, we conclude that phytoplankton traits may have limited effect on omnivores performance.

Expendable features

We found motile algae prevailing in only one sample CWM, however it was not included into any decision tree. Motility of algae may be considered as an effective escape behavior, however only against certain grazing strategies (Pančić & Kiørboe, 2018). According to DeMott & Watson (1991) ambush feeding cyclopoid copepod prefer motile prey, while feeding current-forming calanoid copepod show no preferences toward motile nor non-motile prey. Motile algae are common inhabitants of eutrophic waterbodies (Paerl et al., 2001) contributing zooplankton diet (DeMott & Watson, 1991), but our results do not allow us to state if motility of the prey was a factor supporting any specific zooplankton functional traits.

Silicified cell walls and thecal plates are recognized as defensive features in numerous species of algae (DeMott, 1995; Hamm et al., 2003; Reynolds, 2006). In the present study, these structures were used

as an "*Armor*" trait of phytoplankton taxa, however we found this trait not supporting any specific zooplankton functional traits. Zooplankton is a heterogenous community formed by diverse taxa representing distinct life strategies, which may affect cross-trophic level interactions (Litchman et al., 2013; Krztoń & Kosiba, 2020). For instance, DeMott (1995) found that *Daphnia* spp. are able to ingest "hard" (armored) prey such as diatoms and dinoflagellates, however, they prefer "soft" particles (green algae, gelatinous dinoflagellates) when available. Furthermore, Levine et al. (1999) found that different fractions of planktonic animals—microzooplankton (< 200 μm) and macrozooplankton (> 200 μm)—are able to utilize different types of armored algae (diatoms and dinoflagellates, respectively), what explains our results.

Conclusions

Functional traits are features of organisms which drive their interactions within and across trophic level within the ecosystem. An understanding of these interactions enhances recognition of ecosystem health and external processes threatening it (Meunier et al., 2017). Our study focused on the interactions of functional traits among freshwater planktonic food webs depicting different circumstances of the food web. We found that easy-to-handle algal particles (linked to domination of small eukaryotic algae—e.g. chlorophytes) promoted greater variability of zooplankton functional traits possessed by the taxa whose niches partially overlapped. Moreover, the prevalence of the phytoplankton community by large particles of problematic shapes and/or potential ability of toxin production (traits characteristic for cyanobacteria) promoted planktonic animals bearing some specialized traits—small bacterivores (ciliates), large predators (predatory cyclopoid copepods and cladoceran *Leptodora kindtii*), and adapted algaevores (*Daphnia* spp.). On the other hand, our study indicates specialized zooplankton traits which are likely to be independent of circumstances—omnivores (e.g. rotifers of genus *Asplanchna*), feeding current generating copepods (calanoid copepods) and suspension feeding rotifers (e.g. *Brachionus* spp., *Keratella* spp.). Finally, our study demonstrated that some functional traits of the phytoplankton, beside contributing to the performance of the taxa, such as motility (e.g.

euglenophytes) or armor (diatoms, dinophytes), did not support any functional traits of the zooplankton.

According to our results, the phytoplankton community may be considered as a biotic filter (sensu Poff, 1997) for the zooplankton community. Seasonally changing environmental circumstances drive succession in the phytoplankton community, whose functional traits lead to the selection of zooplankton taxa bearing advantageous functional traits. A peculiar circumstance of aquatic food webs is the dominance of cyanobacteria, which bear specific functional traits, that discourage zooplankton grazers. Our results suggest that these functional traits may drive the promotion of adapted herbivores or the increase of importance of small bacterivores—planktonic predators link, what may have several consequences for the functioning of aquatic food webs in the predicted scenarios of climate change and cyanobacterial blooms proliferation.

Data availability Dataset used in statistical analyses is available and can be downloaded from the open-source repository: https://github.com/wmkrzt/cwmtraits.git.

Declarations

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

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