Zmiany różnorodności funkcjonalnej zooplanktonu jako odpowiedź na zakwity sinicowe

Changes in functional diversity of zooplankton triggered by cyanobacterial bloom

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Streszczenie

Zmiany klimatyczne oraz postępująca eutrofizacja, będące skutkami działalności człowieka, wywierają silny wpływ na środowisko naturalne. Prowadzą one do zaniku siedlisk i wymierania gatunków, co przekłada się na obniżenie różnorodności biologicznej, w tym także niezwykle istotnego jej komponentu – różnorodności funkcjonalnej. Koncepcja różnorodności funkcjonalnej zakłada, że każdy gatunek posiada cechy funkcjonalne (morfologiczne, fizjologiczne, behawioralne, historii życia), które charakteryzują jego rolę w procesach ekosystemowych, takich jak np. obieg pierwiastków, czy sposób w jaki wchodzi on w interakcję z innymi organizmami zasiedlającymi dany ekosystem. Obniżenie różnorodności funkcjonalnej w wyniku opisywanych globalnych zmian może powodować osłabienie procesów zachodzących w ekosystemie.

Środowiskami, które są szczególnie narażone na opisywane, globalnie zachodzące zmiany są ekosystemy słodkowodne. Przewiduje się, że ocieplenie klimatu oraz wzmożona eutrofizacja, promować będą (zwłaszcza w północnej hemisferze), częstsze występowanie zakwitów sinic (*Cyanobacteria*). Prognozuje się również, że czas trwania zakwitu będzie coraz dłuższy, a sam jego przebieg intensywniejszy (większa biomasa sinic; większe koncentracje toksyn uwalnianych do środowiska wodnego). Przełoży się to na drastyczne obniżenie jakości wody, co z kolei będzie negatywnie wpływać na wszystkie organizmy zasiedlające ekosystemy słodkowodne, w tym zwierzęta planktonowe.

Celem rozprawy doktorskiej było zbadanie wpływu zakwitu sinic i jego intensywności na wybrane komponenty różnorodności funkcjonalnej zespołu zooplanktonu płytkich zbiorników wodnych. Badania obejmowały analizę zależności pomiędzy cechami funkcjonalnymi fitoplanktonu i zooplanktonu, ze szczególnym uwzględnieniem cech funkcjonalnych sinic (**Artykuł nr 1**), oraz analizę zależności pomiędzy biomasą sinic, a liczebnością grup funkcjonalnych zespołu zooplanktonu (**Artykuł nr 2**) oraz wybranymi wskaźnikami różnorodności funkcjonalnej (**Artykuł nr 3**). Zastosowanie w badaniach metod opartych na cechach funkcjonalnych gatunków i analizie zmian różnorodności funkcjonalnej zespołu pozwoliło na szczegółowe zobrazowanie zależności fitoplankton – zooplankton, ze szczególnym uwzględnieniem roli sinic w tych relacjach.

Zrozumienie zmian zachodzących w zespołach organizmów, ich cechach oraz różnorodności funkcjonalnej jest kluczowe dla poszerzenia wiedzy o procesach ekosystemowych, takich jak np. obieg pierwiastków. Takie podejście w ostatnich latach zdobywa uznanie w badaniach ekologii zespołów organizmów, choć jest nieczęste w badaniach ekologii planktonu. Moja rozprawa doktorska stanowi

znaczący wkład w rozwój tematyki badawczej dotyczącej różnorodności funkcjonalnej zespołów zooplanktonu w ekosystemach słodkowodnych.

Summary

Human-driven climatic changes and growing eutrophication heavily affect natural environment. They lead to habitat loss and species extinction, and therefore to loss of biodiversity, as well as, it's most important component – functional diversity. The concept of functional diversity assumes that every species bear functional traits (morphological, physiological, behavioral, life history), which outline its role in ecosystem processes, such as cycle of elements, or a manner how it interacts with other organisms dwelling the ecosystem. The loss of functional diversity caused by mentioned global changes may cause weakening of ecosystem processes.

Habitats, which are particularly vulnerable for global changes are freshwater ecosystems. It is anticipated that predicted climate change and growing eutrophication will promote (especially in northern hemisphere), more frequent cyanobacterial blooms. The predictions also assume that periods of cyanobacterial blooms persistence will be extended, and the bloom itself will be intensified (larger biomass of cyanobacteria created, higher concentrations of cyanotoxins released to the environment). This will lead to drastic deterioration of water quality, therefore having negative effects on organisms dwelling freshwater ecosystems, including zooplankton.

The aim of the dissertation was to examine the effects of cyanobacterial bloom and its intensity on particular components of functional diversity of zooplankton community of shallow water bodies. The study included analyses of relationships of functional traits of phytoplankton and zooplankton, with particular emphasis on the functional characteristics of cyanobacteria (**Article 1**), as well as dependencies between cyanobacteria biomass and density of functional groups of zooplankton (**Article 2**) and selected indexes of functional diversity (**Article 3**). Trait-based approach and analysis of changes of functional diversity allowed for detailed depiction of phytoplankton – zooplankton relationships, with emphasis on role of cyanobacteria.

Understanding of changes in organismal communities, their functional traits and functional diversity is crucial for extending the knowledge on ecosystem processes, such as cycle of elements. Recently, such approach is gaining appreciation in community ecology studies, however is limited in plankton ecology studies. My dissertation constitutes a solid contribution in development of the research topic of functional diversity of zooplankton communities dwelling freshwater ecosystems.

Wstęp

Obserwowane obecnie globalne zmiany, takie jak ocieplenie klimatu, utrata siedlisk, czy wymieranie gatunków są efektem działalności człowieka. Skala zmian jest tak ogromna, że obecna epoka w dziejach Ziemi nazywana jest „Antropocenem" (Crutzen, 2006). Efektem zmian zachodzących w środowisku mogą być: modyfikacja fizjologii i cyklów życiowych, zmiany w rozmieszczeniu organizmów w środowisku (Hughes, 2000), a także utrata różnorodności biologicznej (Dudgeon, 2019) oraz niezwykle istotnego jej komponentu – różnorodności funkcjonalnej (Hansen i in., 2013). Koncepcja różnorodności funkcjonalnej zakłada, że każdy gatunek posiada cechy funkcjonalne (morfologiczne, fizjologiczne, behawioralne, historii życia), które charakteryzują jego rolę w procesach ekosystemowych, takich jak np. obieg pierwiastków w ekosystemie (Hébert i in., 2017), czy sposób w jaki wchodzi on w interakcję z innymi organizmami zasiedlającymi dany ekosystem (Litchman i Klausmeier, 2008; Litchman i in., 2013).

Różnorodność funkcjonalna opisywana jest przez szereg wskaźników, np. 1) bogactwo funkcjonalne (functional richness, Fric); 2. równomierność funkcjonalna (functional evenness, Feve); oraz 3) dywergencja funkcjonalna (functional divergence, Fdiv). Wskaźniki te opisują trzy niezależne, uzupełniające się aspekty różnorodności funkcjonalnej (Villéger i in., 2008). Analizowane i interpretowane razem bardziej szczegółowo opisują zmiany w środowisku, niż pojedynczy wskaźnik różnorodności biologicznej, które traktują wszystkie gatunki jako równo cenne (Mouchet, 2010; Sodré i in., 2017). Dodatkowo, zastosowanie cech funkcjonalnych w badaniach zespołu organizmów daje możliwość wyróżnienia grup funkcjonalnych. Grupa funkcjonalna definiowana jest jako zbiór gatunków posiadających podobne cechy, a co za tym idzie podobnie wpływających na funkcjonowanie ekosystemu (Tilman, 2001). Analiza wpływu czynnika na dynamikę liczebności grup funkcjonalnych (sumy liczebności wszystkich gatunków wchodzących w skład grupy funkcjonalnej) umożliwia określenie jak dany proces ekosystemowy (liczebność grupy funkcjonalnej wpływającej na jego przeprowadzenie) zmienia się w gradiencie danego czynnika.

Opisywane, globalne zmiany w środowisku naturalnym dotyczą wszystkich ekosystemów, jednak szczególnie zagrożone są ekosystemy słodkowodne (Sala i in., 2000), które pomimo że, stanowią zaledwie 0,8% powierzchni Ziemi, są środowiskiem życia ok. 6% gatunków (Dudgeon i in., 2006). Ekosystemy te świadczą również liczne usługi ekosystemowe (np. zaopatrzenie w wodę i żywność, funkcja rekreacyjna), których bezpośrednim beneficjentem jest człowiek (Harrison i in., 2010). Przyjmuje się, że zmiany klimatyczne oraz nadmierna eutrofizacja środowiska (zwiększanie dostępności nutrientów, m.in. azotu i fosforu) są dwoma głównymi procesami odpowiedzialnymi za negatywne zmiany w funkcjonowaniu ekosystemów słodkowodnych. Faworyzować one mogą nadmierny i

długotrwały rozwój sinic, które posiadają liczne, wykształcone przez 3,5 miliarda lat ewolucji mechanizmy, pozwalające na adaptację do zmieniających się warunków środowiskowych (Paerl i Huisman, 2009). Wysokie optimum termiczne sinic (często powyżej 25°C), pozwala im skutecznie konkurować z innymi grupami glonów, takimi jak okrzemki czy zielenice. Dodatkowo, niektóre gatunki sinic planktonowych charakteryzują się wysoką pławnością komórek, dzięki czemu zbierają się w najcieplejszej i najbardziej naświetlonej, podpowierzchniowej warstwie wody, gdzie ich biomasa tworzy wówczas gęsty kożuch ograniczający dostęp światła do niższych warstw wody (Paerl i Huisman, 2008). Dzięki tym adaptacjom, sinice wytwarzają dużą biomasę tworząc tzw. zakwity wody, będąc dominantami w zespole fitoplanktonu. Wyższa średnia roczna temperatura wody oraz dłuższy okres stratyfikacji termicznej kolumny wody, będące skutkiem zmian klimatycznych, prowadzić mogą do występowania wydłużonych okresów dominacji sinic w zbiornikach wodnych (Paerl i in., 2011). Czynnikiem dodatkowo zwiększającym ryzyko występowania zakwitów sinic jest eutrofizacja środowiska wodnego poprzez zwiększone wprowadzanie związków azotu i fosforu, których źródłem jest działalność człowieka (Xu i in., 2010). Wymienione procesy prowadzić mogą do proliferacji i intensyfikacji zakwitów sinic, w tym do występowania długotrwałych zakwitów, które prowadzić mogą do znacznego obniżenia jakości wody.

Dominacja sinic w składzie fitoplanktonu (zespole producentów), wywiera wpływ na skład zespołu zooplanktonu (zespół konsumentów), a co za tym idzie na wiele procesów zachodzących w ekosystemie (Paerl i Otten, 2013). Sinice posiadają pewne charakterystyczne cechy, dzięki którym mogą negatywnie wpływać na zwierzęta planktonowe. Jedną z nich jest zdolność produkcji toksyn, dzielących się na: neurotoksyny (anatoksyny, saksitoksyny), hepatotoksyny (mikrocystyny, nodularyny) oraz cytotoksyny, które mogą kumulować się w górę łańcucha pokarmowego (Codd i in., 2005). Drugą cechą jest morfologia komórek sinic - formy filamentowe (nitkowate) oraz kolonijne. Praca Wilsona i in. (2006) opierająca się na metaanalizie danych pochodzących z eksperymentów laboratoryjnych, dowodzi że zarówno filamenty jak i kolonie sinic mogą w sposób istotny obniżać kondycję wrotków oraz wioślarek. Zjawisko to, może być efektem mechanicznej interferencji długich filamentów lub rozległych kolonii sinic ze strukturami odpowiedzialnymi za pozyskiwanie pokarmu wymienionych grup zwierząt planktonowych (Bednarska i in., 2014, Wejnerowski i in., 2015). Badania nie wykazały wpływu morfologii sinic na kondycję widłonogów, jednocześnie wskazując na małą liczbę eksperymentów laboratoryjnych z użyciem tych organizmów. Sinice uważane są za niskojakościowy pokarm również ze względu na niską zawartość wielonienasyconych kwasów tłuszczowych (PUFA) oraz steroli, niezbędnych w diecie zwierząt planktonowych (Martin-Creuzburg i von Elert, 2009). Wszystkie wymienione wyżej aspekty, w sposób synergistyczny oddziaływać mogą na zespół zooplanktonu, prowadząc do selekcji gatunków posiadających przystosowania umożliwiające koegzystencję z

sinicami. Dominacja sinic będzie wspomagać rozwój gatunków odpornych na działanie toksyn sinicowych, gatunków odżywiających się selektywnie (również gatunki drapieżne), oraz potrafiących suplementować dietę, innymi niż fitoplankton, komponentami sieci troficznej (np. seston, bakterie; Ger i in., 2016). Gatunki posiadające mechanizmy detoksyfikacyjne (np. *Daphnia* spp.; Chislock i in., 2013), żerować mogą na komórkach sinic, wykorzystując niewielkie ilości wielonienasyconych kwasów tłuszczowych oraz steroli w nich zawarte, a także aminokwasy, węglowodany i białka oraz inne substancje odżywcze (Wilk-Woźniak, 2019). Rozwijająca się biomasa sinic stanowić może środowisko życia dla wirusów, wodnych grzybów (chytryd) oraz bakterii, a skomplikowane interakcje zachodzące pomiędzy nimi a sinicami, wpływać mogą na interakcje sinice - zooplankton. Infekcje wirusowe komórek sinic mogą powodować uwalnianie materii organicznej i detrytusu do środowiska, a także rozpadanie się długich filamentów na krótsze, które są łatwiejsze do konsumpcji (Wilk-Woźniak, 2019). Również chytrydy mogą pasożytować na komórkach sinic, w cyklu rozwojowym wytwarzając zoospory, które ze względu na wysoką wartość odżywczą stanowią atrakcyjne pożywienie dla zwierząt planktonowych (Kagami i in., 2014). Obumierająca biomasa sinic stanowi także substrat do rozwoju, dla bakterii, które również mogą być wykorzystywane jako pożywienie przez zwierzęta planktonowe (Wilk-Woźniak 2019).

Dotychczasowe prace dotyczące interakcji „sinice – zooplankton", w dużej części skupiały się na tzw. „ewolucyjnym wyścigu zbrojeń" (the evolutionary arms race, Ger i in., 2016). Zarówno badania terenowe jak i eksperymenty laboratoryjne licznie opisywały mechanizmy obronne sinic (toksyczność, morfologia komórek, itd.) oraz adaptacje zwierząt planktonowych pozwalające na żerowanie na sinicach (Ger i in., 2016). Ponadto, bardzo często jako modelowy organizm, do badań wykorzystywane były wioślarki (Cladocera) z rodzaju *Daphnia*, podczas gdy zwierzęta z innych grup takich jak orzęski (Ciliata), wrotki (Rotifera), widłonogi (Copepoda) były w tych badaniach pomijane (Ger i in., 2016). Wszystkie wyżej wymienione grupy zwierząt, tworzą razem zespół zooplanktonu, a posiadane przez poszczególne gatunki cechy funkcjonalne kształtują jego różnorodność funkcjonalną. Jest ona komponentem różnorodności biologicznej ściśle związanym z kluczowymi procesami zachodzącymi w ekosystemie, takimi jak obieg pierwiastków (węgla, azotu i fosforu; Díaz i Cabido, 2001; Gomes i in. 2019). Tworzące zakwit sinice prowadzić mogą do zmian różnorodności funkcjonalnej (Josué i in., 2019), a także do osłabienia obiegu pierwiastków w ekosystemie (Moustaka-Gouni i Sommer, 2020).

Cel badań

Celem rozprawy doktorskiej było **zbadanie wpływu zakwitu sinic i jego intensywności na wybrane komponenty różnorodności funkcjonalnej zespołu zooplanktonu płytkich zbiorników wodnych**. Badania obejmowały analizę zależności pomiędzy cechami funkcjonalnymi fitoplanktonu i zooplanktonu, ze szczególnym uwzględnieniem cech funkcjonalnych sinic, oraz analizę zależności pomiędzy biomasą sinic, a liczebnością grup funkcjonalnych zespołu zooplanktonu oraz wybranymi wskaźnikami różnorodności funkcjonalnej w dwóch typach zbiorników wodnych: 1) zbiornikach w których występują „krótkotrwałe" zakwity sinic (trwające nie dłużej niż miesiąc); 2) zbiornikach w których występują „długotrwałe" zakwity sinic (trwające dłużej niż trzy miesiące). W ramach opisywanych badań, weryfikowane były trzy hipotezy:

Hipoteza I: *Dominacja sinic w środowisku prowadzi do selekcji wyspecjalizowanych cech funkcjonalnych w zespole zooplanktonu* **(Artykuł 1: Krztoń, W., & Kosiba, J., & Wilk-Woźniak, E. (202x) Features that matter: studying how phytoplankton drives zooplankton community functional traits. Zaakceptowany do druku w Hydrobiologia)**

Podczas zakwitu sinic dochodzi do ich dominacji w składzie fitoplanktonu (zespole producentów), co wywiera wpływ na skład zooplanktonu (zespół konsumentów, Bolnick i in., 2011). Cechy funkcjonalne (wielkość, kształt i organizacja komórek np. w formie kolonii, toksyczność) dominujących sinic, mogą działać jak filtr biotyczny w procesie formowania lokalnego zespołu gatunków (Poff, 1997). Ze składu zooplanktonu eliminowane mogą być zwierzęta nie przystosowane do konsumowania sinic lub mające zdolność korzystania z innych niż fitoplankton, źródeł pokarmu. W konsekwencji zespół zooplanktonu zdominowany może zostać przez gatunki posiadające specyficzne cechy, umożliwiające im koegzystencję z sinicami.

Hipoteza II: *Zakwit sinic prowadzi do obniżenia liczebności grup funkcjonalnych zooplanktonu* **(Artykuł 2: Krztoń, W., & Kosiba, J. (2020). Variations in zooplankton functional groups density in freshwater ecosystems exposed to cyanobacterial blooms. Science of The Total Environment, 730, 139044.)**

Cechy funkcjonalne gatunku określają jego zdolność do radzenia sobie w środowisku życia (McGill i in., 2006). Gatunki posiadające podobne cechy tworzą grupy funkcjonalne, które pełnią określoną rolę w ekosystemie (Tilman, 2001). Zmieniające się warunki środowiskowe (będące np. efektem zmian klimatycznych) mogą istotnie wpływać na strukturę grup funkcjonalnych tworzących zespół organizmów, m.in. poprzez modyfikację liczebności gatunków tworzących poszczególne grupy funkcjonalne.

Obniżenie liczebności w danej grupie funkcjonalnej prowadzić może do ograniczenia jej roli w procesach ekosystemowych. Weryfikacja hipotezy pozwoli określić czy długotrwały zakwit sinic powoduje obniżenie liczebności lub całkowite wyeliminowanie, jednej lub wielu grup funkcjonalnych.

Hipoteza III: *Zakwit sinic powoduje spadek różnorodności funkcjonalnej zooplanktonu* **(Artykuł 3: Krztoń, W., Kosiba, J., Pociecha, A., & Wilk-Woźniak, E. (2019). The effect of cyanobacterial blooms on bio-and functional diversity of zooplankton communities. Biodiversity and Conservation, 28(7), 1815-1835.)**

Analiza zmian różnorodności biologicznej (opisywanych przez wskaźniki Shannona, Simpsona i bogactwa gatunkowego) nie daje pełnej informacji na temat zmian zachodzących w zespole zooplanktonu poddanym długotrwałym zakwitom sinic. Wskaźniki różnorodności biologicznej traktują wszystkie gatunki jako równocenne, niezależnie od funkcji jaką pełnią w ekosystemie (Mouchet, 2010). Analiza wartości wskaźników opisujących różnorodność funkcjonalną (bogactwo, równomierność i zróżnicowanie/dywergencja funkcjonalna; Villéger i in., 2008) pozwoli określić jak długotrwały zakwit sinic modyfikuje zakres i rozłożenie cech gatunków w zespole zooplanktonu.

Teren badań

Badania terenowe prowadzone były w latach 2014 i 2017. Próby pobierano dwa razy w miesiącu, w okresie od kwietnia do października z pięciu płytkich, eutroficznych zbiorników wodnych, zlokalizowanych w okolicy Krakowa (Fig. 1.). Trzy z badanych zbiorników to starorzecza Wisły: Tyniec 1 (50°01'47''N, 19°49'40''E), Tyniec 2 (50°01'28"N, 19°48'48"E) i Piekary (50°00'50''N 19°47'36''E). Pozostałe dwa zbiorniki to sztuczne stawy: Podkamycze 1 (50°05'11''N, 19°50'02''E) i Podkamycze 2 (50°04'60''N, 19°50'05''E).

Funkcjonowanie ekosystemów starorzeczy odbywa się zgodnie z naturalnym cyklem sezonowych zmian, charakterystycznym dla zbiorników eutroficznych. W ekosystemach tych, dominacja sinic tworzących zakwit zaznacza się w okresie lata i/lub jesieni. W zbiornikach sztucznych występują długotrwałe zakwity sinic, trwające od późnej wiosny do późnej jesieni.
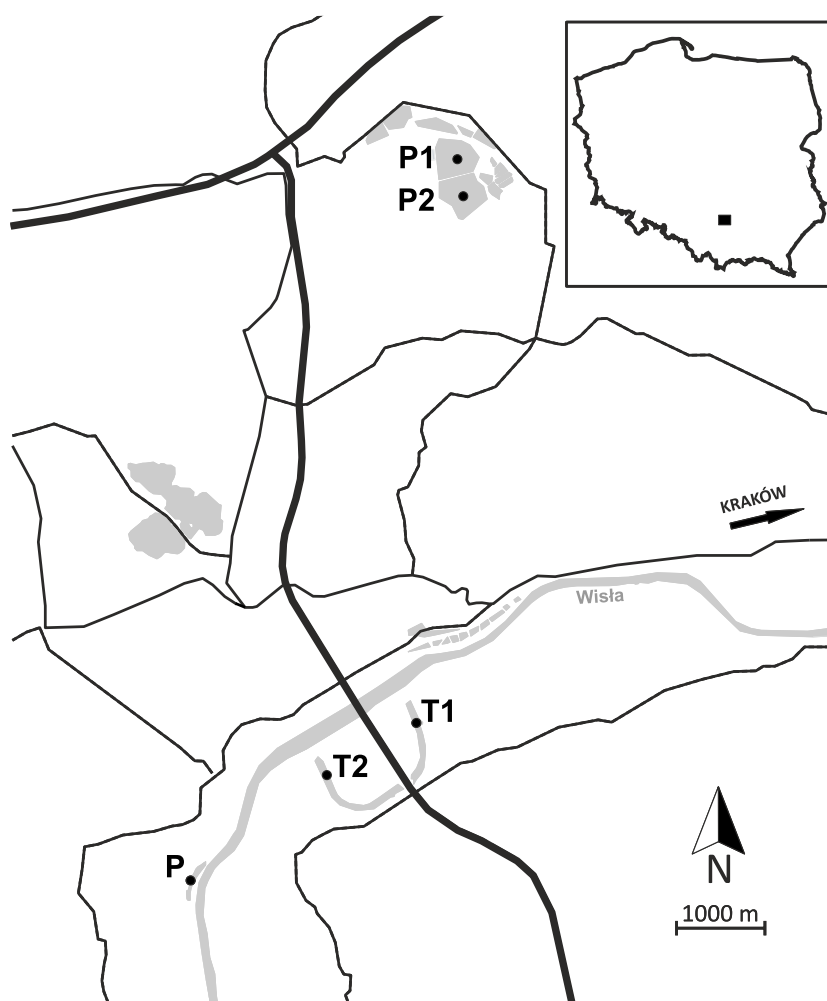

Fig. 1. Lokalizacja badanych zbiorników wodnych. P1 – Podkamycze 1, P2 – Podkamycze 2, T1 – Tyniec 1, T2 - Tyniec 2, P – Piekary.

Wyniki

W artykule nr 1 (Hipoteza I; Artykuł zaakceptowany do druku w Hydrobiologia) sprawdziłem, czy i jak cechy funkcjonalne fitoplanktonu determinują cechy funkcjonalne zooplanktonu. (Fig. 2.).
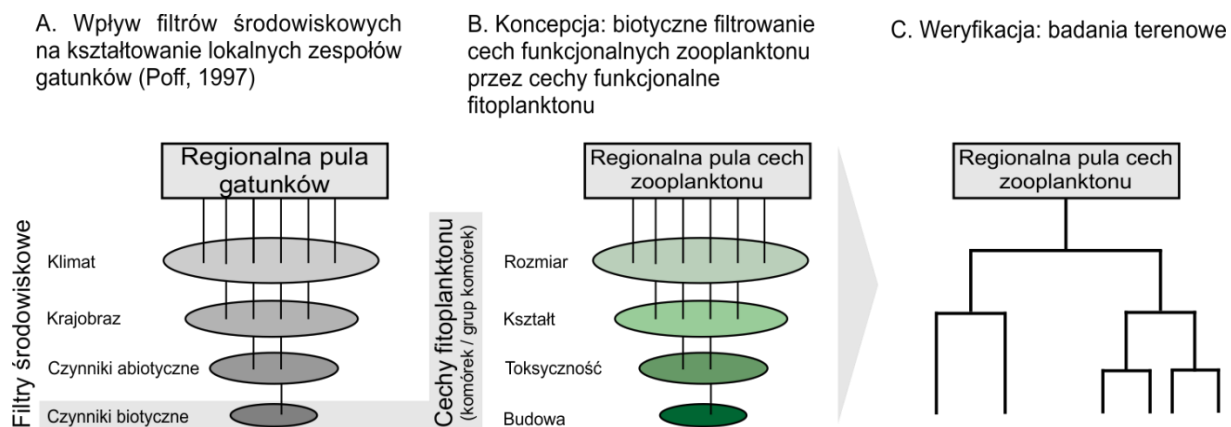

A. Wpływ filtrów środowiskowych na kształtowanie lokalnych zespołów gatunków (Poff, 1997)

B. Koncepcja: biotyczne filtrowanie cech funkcjonalnych zooplanktonu przez cechy funkcjonalne fitoplanktonu

C. Weryfikacja: badania terenowe

Fig. 2. Koncepcja filtrowania biotycznego cech funkcjonalnych zooplanktonu przez cechy funkcjonalne fitoplanktonu. Opracowane na podstawie Poff (1997).

W tym celu przeanalizowałem zależności pomiędzy średnią ważoną cech funkcjonalnych zespołu (Community Weighted Mean of Trait – CWM) obliczoną dla zespołów fitoplanktonu i zooplanktonu. Stworzyłem cztery drzewa decyzyjne – po jednym dla każdej z czterech, cech funkcjonalnych zooplanktonu: 1) długość ciała; 2) potencjalne źródło pokarmu; 3) sposób pobierania pokarmu; 4) optymalna wielkość cząsteczki pokarmu. CWM zooplanktonu została wykorzystane w drzewach decyzyjnych jako zmienna zależna, natomiast CWM fitoplanktonu – jako zmienna niezależna. Analizy wykazały, że najsilniejszy wpływ na cechy funkcjonalne zooplanktonu miały rozmiar i kształt komórek (lub grup komórek) fitoplanktonu, które wpływały istotnie na wszystkie cztery cechy zooplanktonu. Słabszy, ale wciąż istotny wpływ na cechy zooplanktonu miała potencjalna toksyczność komórek (lub grup komórek) modyfikująca optymalną wielkość cząsteczki pokarmu oraz obecność kolców, która wpływała na sposób pobierania pokarmu przez zwierzęta planktonowe. Obecność pancerza oraz zdolność ruchu nie wpływały istotnie na żadną z cech funkcjonalnych zooplanktonu. Analizy wykazały również, że dominacja CWM fitoplanktonu przez 'nieproblematyczne' cechy (małe rozmiary komórek, brak struktur obronnych, brak zdolności do produkcji toksyn), charakterystyczne dla glonów eukariotycznych promowały większą zmienność CWM zooplanktonu. Dominacja CWM fitoplanktonu przez cechy sinic (tj. duże rozmiary filamentów i kolonii, potencjalna toksyczność)

promowały cechy funkcjonalne charakterystyczne dla małych zwierząt bakteriożernych, dużych drapieżników oraz zwierząt glonożernych o dużych zdolnościach adaptacyjnych.

W artykule nr 2 (Hipoteza II; Science of The Total Environment, 2020) opisałem wpływ biomasy sinic oraz długości trwania zakwitu (zakwit krótko- i długotrwały) na liczebności zwierząt planktonowych w grupach funkcjonalnych. Na podstawie dostępnej literatury każdemu z gatunków obecnych w próbach zooplanktonu przydzieliłem cechy funkcjonalne, a następnie przy pomocy grupowania hierarchicznego (metoda Warda) wydzieliłem 6 grup funkcjonalnych zooplanktonu (Fig. 3.): 1) zwierzęta wszystkożerne, 2) bakterio-glonożerne wrotki, 3) pozostałe zwierzęta bakterio-glonożerne, 4) zwierzęta glonożerne, 5) zwierzęta drapieżne, 6) bakteriożerne orzęski.

Fig. 3. Dendrogram przedstawiający grupy funkcjonalne zooplanktonu wydzielone na podstawie cech funkcjonalnych gatunków (grupowanie hierarchiczne – metoda Warda)

Analiza z użyciem uogólnionych modeli liniowych (Generalized Linear Models - GLM) wykazała niższe liczebności wszystkich grup funkcjonalnych zooplanktonu w zbiornikach w których występowały długotrwałe zakwity sinic. Analiza wykazała też, że biomasa sinic negatywnie wpływała na liczebności

wszystkich grup funkcjonalnych w zbiornikach w których występowały krótkotrwałe zakwity. W zbiornikach w których występowały długotrwałe zakwity, biomasa sinic negatywnie wpływała na liczebność zwierząt wszystkożernych (Grupa 1), bakteriożernych wrotków (Grupa 2) oraz pozostałych zwierząt bakterio-glonożernych (Grupa 3), a także pozytywnie na liczebność zwierząt glonożernych (Grupa 4), zwierząt drapieżnych (Grupa 5) oraz bakteriożernych orzęsków (Grupa 6).

Zarówno zmiany w CWM, jak i w liczebności grup funkcjonalnych w trakcie zakwitu sinic, prowadzić mogą do modyfikacji różnorodności biologicznej i funkcjonalnej zespołu zooplanktonu. **W artykule nr 3 (Hipoteza III; Biodiversity and Conservation, 2019)** opisałem jak biomasa sinic oraz długość trwania zakwitu sinic wpływają na różnorodność biologiczną oraz funkcjonalną zespołu zooplanktonu. Analizowana była zmienność trzech klasycznie używanych wskaźników różnorodności biologicznej: 1) bogactwo gatunkowe; 2) Indeks Simpsona (D); 3) Indeks Shannona (H), a także trzy wskaźniki różnorodności funkcjonalnej zaproponowane przez Villéger i in. (2008): 1) bogactwo funkcjonalne (functional richness, Fric); 2. równomierność funkcjonalna (functional evenness, Feve); oraz 3) dywergencja funkcjonalna (functional divergence, Fdiv). Analizy wykazały brak zmienności wskaźników D Simpsona i H Shannona, a co za tym idzie, brak zmienności różnorodności biologicznej zespołu zooplanktonu wraz ze wzrostem biomasy sinic i czasu trwania zakwitu. Zastosowanie miar różnorodności funkcjonalnej pozwoliło stwierdzić, że wyżej wymienione czynniki spowodowały zmiany w zespole zooplanktonu, jednak wymiarem tych zmian nie była klasyczna różnorodność biologiczna. Spadek bogactwa funkcjonalnego (Fric) i wzrost równomierności funkcjonalnej (Feve) spowodowany długotrwałym zakwitem wskazują, że masowy rozwój sinic odpowiedzialny jest za osłabienie roli zooplanktonu. Długotrwałe zakwity sinic mogą wpływać na wykorzystanie zasobów przez zooplankton i osłabiać naturalne procesy ekologiczne.

Podsumowanie

Funkcjonowanie ekosystemów słodkowodnych w znacznym stopniu zależne jest od zespołów fitoplanktonu (producentów pierwotnych) oraz zooplanktonu (konsumentów). Cechy funkcjonalne posiadane przez gatunki tworzące te zespoły charakteryzują ich różnorodność funkcjonalną oraz rolę w procesach ekosystemowych. W swoich badaniach wykazałem, że cechy funkcjonalne gatunków fitoplanktonu mogą determinować obecność w zespole zooplanktonu cech ułatwiających pobieranie określonego rodzaju pokarmu. Na szczególną uwagę zasługuje wpływ cech funkcjonalnych sinic, które promują gatunki zwierząt planktonowych posiadające pewne wyspecjalizowane cechy, co wykazałem w swoich badaniach (**Artykuł 1**). Przewiduje się, że następstwem obserwowanych obecnie zmian klimatycznych będą częstsze i dłużej trwające zakwity sinic oraz zwiększenie ich wpływu na ekosystemy słodkowodne. W swojej pracy wykazałem, że prowadzić to może do zmian w liczebnościach grup funkcjonalnych zwierząt planktonowych: 1. wzrostu liczebności grup posiadających cechy korzystne; oraz 2. obniżenia liczebności grup nieposiadających cech korzystnych (**Artykuł 2**). Konsekwencją jest obniżenie różnorodności funkcjonalnej (opisywanej przy pomocy wybranych wskaźników) zespołu zooplanktonu, oraz osłabienie procesów kluczowych dla funkcjonowania ekosystemu (**Artykuł 3**). Zastosowanie podejścia opartego na cechach funkcjonalnych i analizie różnorodności funkcjonalnej pozwoliło na szczegółowe zobrazowanie zależności fitoplankton – zooplankton, ze szczególnym uwzględnieniem roli sinic w tych relacjach. Dodatkowo podejście oparte na cechach funkcjonalnych stanowiło wspólny mianownik dla silnie zróżnicowanego, morfologicznie i taksonomicznie, zespołu zooplanktonu składającego się z protozooplanktonu (orzęski - Ciliata) i metazooplanktonu (wrotki – Rotifera, wioślarki – Cladocera i widłonogi - Copepoda). Takie podejście stanowi rzadkość w badaniach ekologii planktonu, tym samym moja praca stanowi znaczące poszerzenie dotychczasowej wiedzy w tej dziedzinie. Praca również wpisuje się w zyskujący na znaczeniu nurt, uwzględniający konieczność zastosowania cech funkcjonalnych w badaniach ekologii zespołów organizmów.

Literatura

Bednarska, A., Pietrzak, B., & Pijanowska, J. (2014). Effect of poor manageability and low nutritional value of cyanobacteria on *Daphnia magna* life history performance. Journal of Plankton Research, 36(3), 838-847.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., ... & Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. Trends in ecology & evolution, 26(4), 183-192.

Chislock, M. F., Sarnelle, O., Jernigan, L. M., & Wilson, A. E. (2013). Do high concentrations of microcystin prevent *Daphnia* control of phytoplankton?. Water research, 47(6), 1961-1970.

Codd, G. A., Morrison, L. F., & Metcalf, J. S. (2005). Cyanobacterial toxins: risk management for health protection. Toxicology and applied pharmacology, 203(3), 264-272.

Crutzen, P. J. (2006). The "anthropocene". In Earth system science in the anthropocene (pp. 13-18). Springer, Berlin, Heidelberg.

Díaz, S., & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. Trends in ecology & evolution, 16(11), 646-655.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C., ... & Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. Biological reviews, 81(2), 163-182.

Dudgeon, D. (2019). Multiple threats imperil freshwater biodiversity in the Anthropocene. Current Biology, 29(19), R960-R967.

Ger, K. A., Urrutia-Cordero, P., Frost, P. C., Hansson, L. A., Sarnelle, O., Wilson, A. E., & Lürling, M. (2016). The interaction between cyanobacteria and zooplankton in a more eutrophic world. Harmful algae, 54, 128-144.

Gomes, L. F., Pereira, H. R., Gomes, A. C. A. M., Vieira, M. C., Martins, P. R., Roitman, I., & Vieira, L. C. G. (2019). Zooplankton functional-approach studies in continental aquatic environments: a systematic review. Aquatic ecology, 53(2), 191-203.

Hansen, J., Kharecha, P., Sato, M., Masson-Delmotte, V., Ackerman, F., Beerling, D. J., ... & Zachos, J. C. (2013). Assessing "dangerous climate change": Required reduction of carbon emissions to protect young people, future generations and nature. PloS one, 8(12), e81648.

Literatura

Harrison, P. A., Vandewalle, M., Sykes, M. T., Berry, P. M., Bugter, R., de Bello, F., ... & Jongman, R. H. (2010). Identifying and prioritising services in European terrestrial and freshwater ecosystems. Biodiversity and Conservation, 19(10), 2791-2821.

Hébert, M. P., Beisner, B. E., & Maranger, R. (2017). Linking zooplankton communities to ecosystem functioning: toward an effect-trait framework. Journal of Plankton Research, 39(1), 3-12.

Hughes, L. (2000). Biological consequences of global warming: is the signal already apparent?. Trends in ecology & evolution, 15(2), 56-61.

Josué, I. I., Cardoso, S. J., Miranda, M., Mucci, M., Ger, K. A., Roland, F., & Marinho, M. M. (2019). Cyanobacteria dominance drives zooplankton functional dispersion. Hydrobiologia, 831(1), 149-161.

Kagami, M., Miki, T., & Takimoto, G. (2014). Mycoloop: chytrids in aquatic food webs. Frontiers in microbiology, 5, 166.

Litchman, E., & Klausmeier, C. A. (2008). Trait-based community ecology of phytoplankton. Annual review of ecology, evolution, and systematics, 39, 615-639.

Litchman, E., Ohman, M. D., & Kiørboe, T. (2013). Trait-based approaches to zooplankton communities. Journal of plankton research, 35(3), 473-484.

Martin-Creuzburg, D., & von Elert, E. (2009). Good food versus bad food: the role of sterols and polyunsaturated fatty acids in determining growth and reproduction of *Daphnia magna*. Aquatic ecology, 43(4), 943-950.

McGill, B. J., B. J. Enquist, E. Weiher, & M. Westoby, 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21: 178–185.

Mouchet, M. A., Villéger, S., Mason, N. W., & Mouillot, D. (2010). Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology, 24(4), 867-876.

Moustaka-Gouni, M., & Sommer, U. (2020). Effects of harmful blooms of large-sized and colonial Cyanobacteria on aquatic food webs. Water, 12(6), 1587.

Paerl, H. W., & Huisman, J. (2008). Blooms like it hot. Science, 320(5872), 57-58.

Paerl, H. W., & Huisman, J. (2009). Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. Environmental microbiology reports, 1(1), 27-37.

Paerl, H. W., Hall, N. S., & Calandrino, E. S. (2011). Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatic-induced change. Science of the total environment, 409(10), 1739-1745.

Paerl, H. W., & Otten, T. G. (2013). Harmful cyanobacterial blooms: causes, consequences, and controls. Microbial ecology, 65(4), 995-1010.

Poff, N. L., 1997. Landscape Filters and Species Traits: Towards Mechanistic Understanding and Prediction in Stream Ecology. Journal of the North American Benthological Society 16: 391–409.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., ... & Leemans, R. (2000). Global biodiversity scenarios for the year 2100. science, 287(5459), 1770-1774.

Sodré, E. D. O., Figueiredo-Barros, M. P., Roland, F., Esteves, F. D. A., & Bozelli, R. L. (2017). Complimentary biodiversity measures applied to zooplankton in a recovering floodplain lake. Fundamental and Applied Limnology, 279-298.

Sommer, U., Gliwicz, Z. M., Lampert, W., & Duncan, A. (1986). The PEG-model of seasonal succession of planktonic events in fresh waters. Archiv für Hydrobiologie, 106(4), 433-471.

Sommer, U., Adrian, R., De Senerpont Domis, L., Elser, J. J., Gaedke, U., Ibelings, B., ... & Winder, M. (2012). Beyond the Plankton Ecology Group (PEG) model: mechanisms driving plankton succession. Annual review of ecology, evolution, and systematics, 43, 429-448.

Tilman, D. (2001). Functional diversity. Encyclopedia of biodiversity, 3(1), 109-120.

Villéger, S., Mason, N. W., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology, 89(8), 2290-2301.

Wejnerowski, L., Cerbin, S., & Dziuba, M. K. (2015). Thicker filaments of *Aphanizomenon gracile* are more harmful to *Daphnia* than thinner *Cylindrospermopsis raciborskii*. Zoological Studies, 54(1), 2.

Wilk-Woźniak, E. (2019). An introduction to the 'micronet'of cyanobacterial harmful algal blooms (CyanoHABs): cyanobacteria, zooplankton and microorganisms: a review. Marine and Freshwater Research, 71(5), 636-643.

Wilson, A. E., Sarnelle, O., & Tillmanns, A. R. (2006). Effects of cyanobacterial toxicity and morphology on the population growth of freshwater zooplankton: Meta-analyses of laboratory experiments. Limnology and Oceanography, 51(4), 1915-1924.

Xu, H., Paerl, H. W., Qin, B., Zhu, G., & Gaoa, G. (2010). Nitrogen and phosphorus inputs control phytoplankton growth in eutrophic Lake Taihu, China. Limnology and Oceanography, 55(1), 420-432.

Artykuł 1

Krztoń, W., & Kosiba, J., & Wilk-Woźniak, E. (202x) Features that matter: studying how phytoplankton drives zooplankton community functional traits. (Przyjęty do druku w Hydrobiologia, IF = 2.694, 100 pkt MNiSW)

Title: 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

Statements and Declarations:

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 meters), 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 1m, 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.

Table 1. Importance of particular phytoplankton community traits (variable importance) in the construction of decision trees for each of the zooplankton community traits. Phytoplankton traits in bold (the highest importance) were used for construction of the particular decision trees.

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; Tab. 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 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).

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.

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; Tab. 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).

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.

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 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.

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

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 (Tab. 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). 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 – 7.3 μm (11% of observations; Fig. 4); 2. ranging from 20 – 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.

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*

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 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 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. Also, 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.

Acknowledgements

References

Agasild, H., P. Zingel, I. Tõnno, J. Haberman, & T. Nõges, 2007. Contribution of different zooplankton groups in grazing on phytoplankton in shallow eutrophic Lake Võrtsjärv (Estonia). Hydrobiologia 584: 167–177.

Arndt, H., 1993. Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates) - a review. 16.

Bogdan, K. G., & J. J. Gilbert, 1984. Body size and food size in freshwater zooplankton. Proceedings of the National Academy of Sciences 81: 6427–6431.

Bottrell, H., A. Duncan, Z. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson, & T. Weglenska, 1976. A review of some problems in zooplankton production studies. NORWEGIAN JOURNAL OF ZOOLOGY 419–456.

Brandl, Z., 2005. Freshwater copepods and rotifers: predators and their prey In Herzig, A., R. D. Gulati, C. D. Jersabek, & L. May (eds), Rotifera X: Rotifer Research: Trends, New Tools and Recent Advances, Proceedings of the Xth International Rotifer Symposium, held in Illmitz, Austria, 7–13 June 2003. Springer Netherlands, Dordrecht: 475–489, https://doi.org/10.1007/1-4020-4408-9_49.

Branstrator, D. K., 1998. Predicting diet composition from body length in the zooplankton predator *Leptodora kindti*. Limnology and Oceanography Wiley Online Library 43: 530–535.

Branstrator, D. K., & J. T. Lehman, 1991. Invertebrate predation in Lake Michigan: Regulation of *Bosmina longirostris* by *Leptodora kindtii*. Limnology and Oceanography 36: 483–495.

Christoffersen, K., B. Riemann, L. R. Hansen, A. Klysner, & H. B. Sørensen, 1990. Qualitative importance of the microbial loop and plankton community structure in a eutrophic lake during a bloom of cyanobacteria. Microbial Ecology 20: 253–272.

Colina, M., D. Calliari, C. Carballo, & C. Kruk, 2016. A trait-based approach to summarize zooplankton–phytoplankton interactions in freshwaters. Hydrobiologia 767: 221–233.

Cummins, K. W., R. R. Costa, R. E. Rowe, G. A. Moshiri, R. M. Scanlon, & R. K. Zajdel, 1969. Ecological Energetics of a Natural Population of the Predaceous Zooplankter *Leptodora kindtii* Focke (Cladocera). Oikos [Nordic Society Oikos, Wiley] 20: 189–223.

DeMott, W. R., 1982. Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina*. Limnology and Oceanography 27: 518–527.

DeMott, W. R., 1988. Discrimination between algae and artificial particles by freshwater and marine copepods. Limnology and Oceanography 33: 397–408.

DeMott, W. R., 1995. The influence of prey hardness on *Daphnia*'s selectivity for large prey. In Larsson, P., & L. J. Weider (eds), Cladocera as Model Organisms in Biology. Springer Netherlands, Dordrecht: 127–138.

DeMott, W. R., & M. D. Watson, 1991. Remote detection of algae by copepods: responses to algal size, odors and motility. Journal of Plankton Research 13: 1203–1222.

Dumont, H. J., I. Van de Velde, & S. Dumont, 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia 19: 75–97.

Gaedke, U., S. Hochstädter, & D. Straile, 2002. Interplay Between Energy Limitation and Nutritional Deficiency: Empirical Data and Food Web Models. Ecological Monographs 72: 251–270.

Geller, W., & H. Müller, 1981. The filtration apparatus of Cladocera: Filter mesh-sizes and their implications on food Selectivity. Oecologia 49: 316–321.

Ger, K. A., L.-A. Hansson, & M. Lürling, 2014. Understanding cyanobacteria-zooplankton interactions in a more eutrophic world. Freshwater Biology 59: 1783–1798.

Ger, K. A., P. Urrutia-Cordero, P. C. Frost, L.-A. Hansson, O. Sarnelle, A. E. Wilson, & M. Lürling, 2016. The interaction between cyanobacteria and zooplankton in a more eutrophic world. Harmful Algae 54: 128–144.

Gliwicz, Z., 1990. Why Do Cladocerans Fail to Control Algal Blooms?. Hydrobiologia 200–201: 83–97.

Gophen, M., B. Z. Cavari, & T. Berman, 1974. Zooplankton Feeding on Differentially Labelled Algae and Bacteria. Nature 247: 393–394.

Gulati, R., & W. Demott, 1997. The role of food quality for zooplankton: remarks on the state-of-the-art, perspectives and priorities. Freshwater Biology 38: 753–768.

Hamm, C. E., R. Merkel, O. Springer, P. Jurkojc, C. Maier, K. Prechtel, & V. Smetacek, 2003. Architecture and material properties of diatom shells provide effective mechanical protection. Nature 421: 841–843.

Hansen, B., P. K. Bjornsen, & P. J. Hansen, 1994. The size ratio between planktonic predators and their prey. Limnology and Oceanography 39: 395–403.

Havens, K., G. Ji, J. Beaver, R. Fulton, & C. Teacher, 2019. Dynamics of cyanobacteria blooms are linked to the hydrology of shallow Florida lakes and provide insight into possible impacts of climate change. Hydrobiologia 829:.

Huisman, J., G. A. Codd, H. W. Paerl, B. W. Ibelings, J. M. H. Verspagen, & P. M. Visser, 2018. Cyanobacterial blooms. Nature Reviews Microbiology 16: 471–483.

Jack, J. D., & J. J. Gilbert, 1997. Effects of Metazoan Predators on Ciliates in Freshwater Plankton Communities1. Journal of Eukaryotic Microbiology 44: 194–199.

Jerome, C. A., D. J. S. Montagnes, & F. J. R. Taylor, 1993. The Effect of the Quantitative Protargol Stain and Lugol's and Bouin's Fixatives On Cell Size: A More Accurate Estimate of Ciliate Species Biomass. Journal of Eukaryotic Microbiology 40: 254–259.

Kalinowska, K., 2004. Bacteria, nanoflagellates and ciliates as components of the microbial loop in three lakes of different trophic status. Polish Journal of Ecology 1:, https://www.infona.pl//resource/bwmeta1.element.agro-article-53b02532-5fec-4012-ae80-5fa7e6f92126.

Kath, N. J., A. Boit, C. Guill, & U. Gaedke, 2018. Accounting for activity respiration results in realistic trophic transfer efficiencies in allometric trophic network (ATN) models. Theoretical Ecology 11: 453–463.

Kiørboe, T., 2011. How zooplankton feed: mechanisms, traits and trade-offs. Biological Reviews 86: 311–339.

Krztoń, W., & J. Kosiba, 2020. Variations in zooplankton functional groups density in freshwater ecosystems exposed to cyanobacterial blooms. Science of The Total Environment 730: 139044.

Krztoń, W., J. Kosiba, A. Pociecha, & E. Wilk-Woźniak, 2019. The effect of cyanobacterial blooms on bio- and functional diversity of zooplankton communities. Biodiversity and Conservation 28: 1815–1835.

Lavorel, S., K. Grigulis, S. McIntyre, N. S. G. Williams, D. Garden, J. Dorrough, S. Berman, F. Quétier, A. Thébault, & A. Bonis, 2008. Assessing functional diversity in the field – methodology matters!. Functional Ecology 22: 134–147.

Laybourn-Parry, J., B. A. Abdullahi, & S. V. Tinson, 2011. Temperature-dependent energy partitioning in the benthic copepods *Acanthocyclops viridis* and *Macrocyclops albidus*. Canadian Journal of Zoology NRC Research Press Ottawa, Canada, https://cdnsciencepub.com/doi/abs/10.1139/z88-397.

Levine, S. N., M. A. Borchardt, M. Braner, & A. d. Shambaugh, 1999. The Impact of Zooplankton Grazing on Phytoplankton Species Composition and Biomass in Lake Champlain (USA-Canada). Journal of Great Lakes Research 25: 61–77.

Litchman, E., & C. Klausmeier, 2008. Trait-Based Community Ecology of Phytoplankton. Annual Review of Ecology Evolution and Systematics 39: 615–639.

Litchman, E., M. D. Ohman, & T. Kiørboe, 2013. Trait-based approaches to zooplankton communities. Journal of Plankton Research 35: 473–484.

Lürling, M., 2021. Grazing resistance in phytoplankton. Hydrobiologia 848: 237–249.

MacIsaac, H. J., & J. J. Gilbert, 1989. Competition between rotifers and cladocerans of different body sizes. Oecologia 81: 295–301.

Mayeli, S. M., S. Nandini, & S. S. S. Sarma, (2005). The efficacy of *Scenedesmus* morphology as a defense mechanism against grazing by selected species of rotifers and cladocerans. Aquatic Ecology 38(4): 515-524.

McGill, B. J., B. J. Enquist, E. Weiher, & M. Westoby, 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21: 178–185.

Menden-Deuer, S., & E. J. Lessard, 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnology and Oceanography 45: 569–579.

Meunier, C. L., M. Boersma, R. El-Sabaawi, H. M. Halvorson, E. M. Herstoff, D. B. Van de Waal, R. J. Vogt, & E. Litchman, 2017. From Elements to Function: Toward Unifying Ecological Stoichiometry and Trait-Based Ecology. Frontiers in Environmental Science Frontiers 5:, https://www.frontiersin.org/articles/10.3389/fenvs.2017.00018/full.

Moustaka-Gouni, M., & U. Sommer, 2020. Effects of Harmful Blooms of Large-Sized and Colonial Cyanobacteria on Aquatic Food Webs. Water Multidisciplinary Digital Publishing Institute 12: 1587.

Muscarella, R., & M. Uriarte, 2016. Do community-weighted mean functional traits reflect optimal strategies?. Proceedings of the Royal Society B: Biological Sciences 283: 20152434.

Pace, M. L., & J. D. Orcutt, 1981. The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community1. Limnology and Oceanography 26: 822–830.

Paerl, H. W., R. S. Fulton, P. H. Moisander, & J. Dyble, 2001. Harmful Freshwater Algal Blooms, With an Emphasis on Cyanobacteria. The Scientific World JOURNAL 1: 76–113.

Paerl, H. W., & V. J. Paul, 2012. Climate change: Links to global expansion of harmful cyanobacteria. Water Research 46: 1349–1363.

Pančić, M., & T. Kiørboe, 2018. Phytoplankton defence mechanisms: traits and trade-offs. Biological Reviews 93: 1269–1303.

Panosso, R., & M. Lürling, 2010. *Daphnia magna* feeding on *Cylindrospermopsis raciborskii*: the role of food composition, filament length and body size. Journal of Plankton Research 32: 1393–1404.

Persson, G., & G. Ekbohm, 1980. Estimation of dry weight in zooplankton populations: Methods applied to crustacean populations from lakes in the Kuokkel area, northern Sweden. Archiv für Hydrobiologie 89: 225–246.

Poff, N. L., 1997. Landscape Filters and Species Traits: Towards Mechanistic Understanding and Prediction in Stream Ecology. Journal of the North American Benthological Society 16: 391–409.

Porter, K. G., M. L. Pace, & J. F. Battey, 1979. Ciliate protozoans as links in freshwater planktonic food chains. Nature Nature Publishing Group 277: 563–565.

Putt, M., & D. K. Stoecker, 1989. An experimentally determined carbon : volume ratio for marine "oligotrichous" ciliates from estuarine and coastal waters. Limnology and Oceanography 34: 1097–1103.

R Core Team, (2020). R: a language and environment for statistical computing [Internet]. R Foundation for Statistical Computing.

Rassoulzadegan, F., M. Laval-Peuto, & R. W. Sheldon, 1988. Partitioning of the food ration of marine ciliates between pico- and nanoplankton. Hydrobiologia 159: 75–88.

Reynolds, C. S., 2006. The Ecology of Phytoplankton. Cambridge University Press.

Richman, S., & S. I. Dodson, 1983. The effect of food quality on feeding and respiration by *Daphnia* and *Diaptomus*. Limnology and Oceanography 28: 948–956.

Rott, E., 1981. Some results from phytoplankton counting intercalibrations. Schweizerische Zeitschrift für Hydrologie 43: 34–62.

Ruttner-Kolisko, A., 1977. Suggestions of biomass calculation of plankton rotifers. Archiv fr Hydrobiologie Beiheft. Ergebnisse der Limnologie 8: 7176.

Scheffer, M., S. Rinaldi, J. Huisman, & F. J. Weissing, 2003. Why plankton communities have no equilibrium: solutions to the paradox. Hydrobiologia 491: 9–18.

Sodré, E. de O., & R. L. Bozelli, 2019. How planktonic microcrustaceans respond to environment and affect ecosystem: a functional trait perspective. International Aquatic Research 11: 207–223.

Sommer, U., R. Adrian, L. De Senerpont Domis, J. J. Elser, U. Gaedke, B. Ibelings, E. Jeppesen, M. Lürling, J. C. Molinero, W. M. Mooij, E. van Donk, & M. Winder, 2012. Beyond the Plankton Ecology Group (PEG) Model: Mechanisms Driving Plankton Succession. Annual Review of Ecology, Evolution, and Systematics 43: 429–448.

Sommer, U., Z. Gliwicz, W. Lampert, & A. Duncan, 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. Archiv. Fur Hydrobiologie 106:.

Spitz, J., V. Ridoux, & A. Brind'Amour, 2014. Let's go beyond taxonomy in diet description: testing a trait-based approach to prey–predator relationships. Journal of Animal Ecology 83: 1137–1148.

Taranu, Z. E., I. Gregory-Eaves, P. R. Leavitt, L. Bunting, T. Buchaca, J. Catalan, I. Domaizon, P. Guilizzoni, A. Lami, S. McGowan, H. Moorhouse, G. Morabito, F. R. Pick, M. A. Stevenson, P. L. Thompson, & R. D. Vinebrooke, 2015. Acceleration of cyanobacterial dominance in north temperate-subarctic lakes during the Anthropocene. Ecology Letters 18: 375–384.

Teodosio, M. A., & A. M. B. Barbosa, 2020. Zooplankton Ecology. CRC Press.

Therneau, T., B. Atkinson, B. Ripley, & M. B. Ripley, 2015. Package 'rpart.' Available online: cran. ma. ic. ac. uk/web/packages/rpart/rpart. pdf (accessed on 20 April 2016) .

Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, & E. Garnier, 2007. Let the concept of trait be functional!. Oikos 116: 882–892.

Visser, P. M., J. M. H. Verspagen, G. Sandrini, L. J. Stal, H. C. P. Matthijs, T. W. Davis, H. W. Paerl, & J. Huisman, 2016. How rising CO_2 and global warming may stimulate harmful cyanobacterial blooms. Harmful Algae 54: 145–159.

Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. R. Liermann, & P. M. Davies, 2010. Global threats to human water security and river biodiversity. Nature 467: 555–561.

Wejnerowski, L., S. Cerbin, & M. K. Dziuba, 2015. Thicker filaments of *Aphanizomenon gracile* are more harmful to *Daphnia* than thinner *Cylindrospermopsis raciborskii*. Zoological Studies 54: 2.

White, P., J. Kalff, J. Rasmussen, & J. Gasol, 1991. The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. Microbial ecology 21: 99–118.

Wiackowski, K., A. Doniec, & J. Fyda, 1994. An empirical study of the effect of fixation on ciliate cell volume. Marine microbial food webs 8: 59–69.

Wilk-Wozniak, E., 2009. Zmiany populacyjne w zbiorowiskach glonow planktonowych oraz ich strategie zyciowe w warunkach ekosystemow wodnych sztucznie zmienionych. Studia Naturae - 55: 1–132.

Wilk-Woźniak, E., 2020. An introduction to the 'micronet' of cyanobacterial harmful algal blooms (CyanoHABs): cyanobacteria, zooplankton and microorganisms: a review. Marine and Freshwater Research CSIRO PUBLISHING 71: 636–643.

Wootton, K. L., 2017. Omnivory and stability in freshwater habitats: Does theory match reality?. Freshwater Biology 62: 821–832.

Zingel, P., H. Agasild, T. Nõges, & V. Kisand, 2007. Ciliates are the Dominant Grazers on Pico- and Nanoplankton in a Shallow, Naturally Highly Eutrophic Lake. Microbial Ecology 53: 134–142.

Table 1. Importance of particular phytoplankton community traits (variable importance) in the construction of decision trees for each of the zooplankton community traits. Phytoplankton traits in bold (the highest importance) were used for construction of the particular decision trees.

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

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.

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.
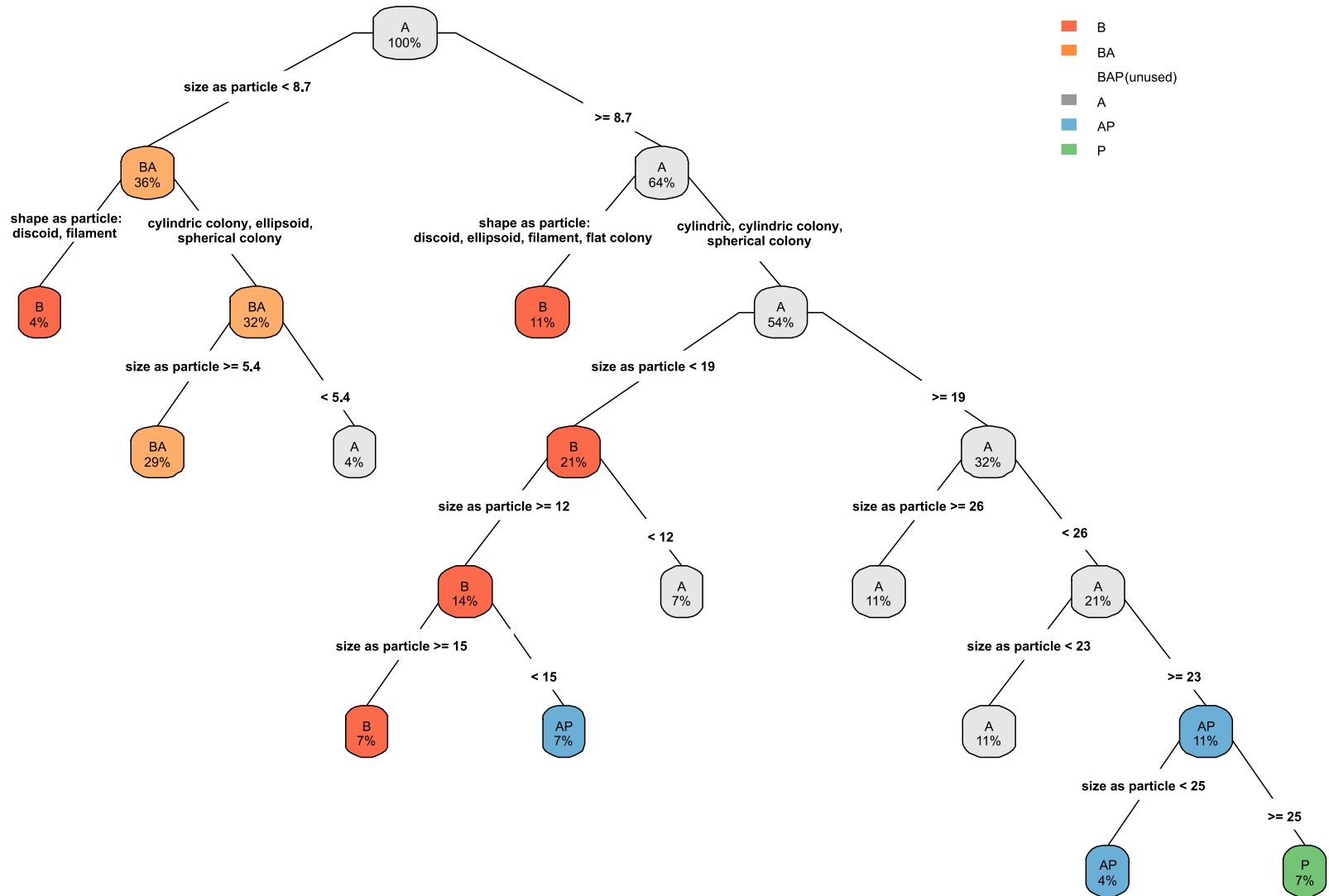
Fig. 3. Decision tree (classification tree) for the zooplankton food source predicted by the functional traits of the phytoplankton community. Information on branches: trait values of the phytoplankton species used in the split. Values in brackets: zooplankton food source dominating in a CWM particular 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
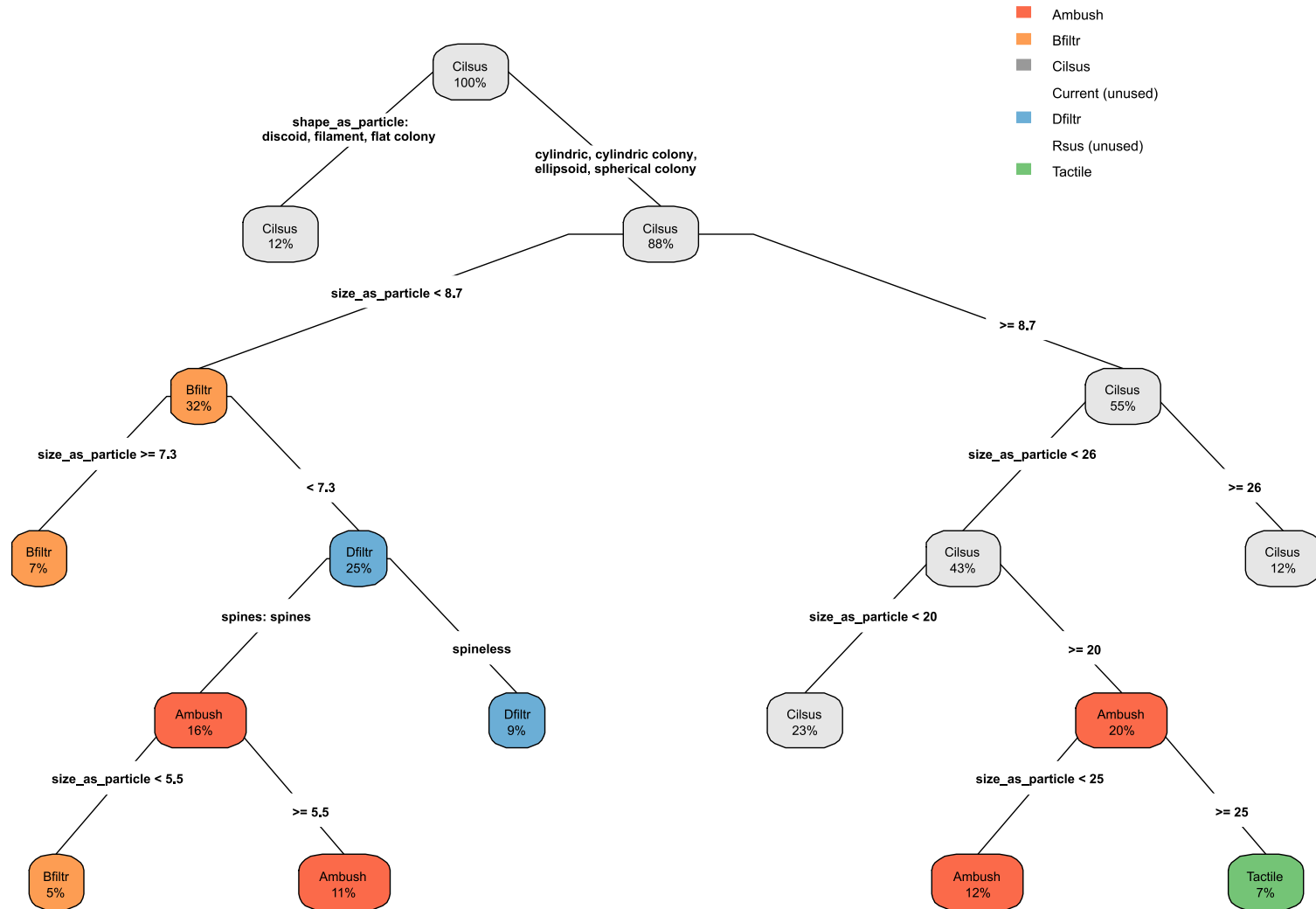
Fig. 4. Decision tree (classification tree) for zooplankton feeding type predicted by the functional traits of the phytoplankton community. Information on branches: trait values of the phytoplankton species used in the split. Values in brackets: zooplankton feeding type dominating in a CWM particular 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*

Artykuł 2

Krztoń, W., & Kosiba, J. (2020). Variations in zooplankton functional groups density in freshwater ecosystems exposed to cyanobacterial blooms. Science of The Total Environment, 730, 139044. (IF = 7.963, 200 pkt MNiSW)

Artykuł 3

Krztoń, W., Kosiba, J., Pociecha, A., & Wilk-Woźniak, E. (2019). The effect of cyanobacterial blooms on bio-and functional diversity of zooplankton communities. Biodiversity and Conservation, 28(7), 1815-1835. (IF = 2.935, 100 pkt MNiSW)

Artykuł 3

ORIGINAL PAPER

The effect of cyanobacterial blooms on bio- and functional diversity of zooplankton communities

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Abstract

Global biodiversity decline is believed to be caused by high anthropopressure. Particularly vulnerable habitats are freshwater ecosystems, which are hotspots of biodiversity. The threat to these ecosystems are cyanobacterial blooms, which tend to proliferate in the face of climate changes. Cyanobacteria development and dominance affect the whole food web, especially the zooplankton community. We used three classical biodiversity indexes (species richness, Simpson's Diversity Index and Shannon Diversity Index) and three functional diversity indexes (functional richness, functional evenness and functional divergence) to study the impact of cyanobacterial bloom on the zooplankton community. The study was conducted in water bodies with a different period of bloom duration (short-lasting blooms vs. long-lasting blooms) in order to determine the impact of the proliferated blooms on the aquatic ecosystems. Use of functional diversity indexes allowed for identifying changes that can be overlooked by classical biodiversity indexes. We conclude that cyanobacterial bloom involves modifications of functional trait space of studied communities and, in consequence, functioning of aquatic ecosystems.

Keywords Aquatic ecology · Biodiversity · Ecosystem functioning · Trait-based approach

Introduction

It is widely accepted that the current geological period is called 'Anthropocene' due to human activity (Crutzen 2006). High anthropopressure leads to the loss of global biodiversity known as the 'Sixth extinction' (Barnosky et al. 2011). Because of that, all ecosystems are threatened, but the freshwaters experience declines in biodiversity far greater than the terrestrial one. Covering only 0.8% of the Earth's surface, these ecosystems support almost 6% of species (Dudgeon et al. 2006).

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The high risk and threat to freshwater ecosystems are from cyanobacterial blooms. Thanks to numerous adaptations e.g., higher temperature optimum compared to other phytoplankton groups (Paerl and Huisman 2008), cyanobacteria tend to develop better in a changing world and phenomena such as global warming, heat waves and eutrophication (e.g. O'neil et al. 2012). Developing in mass, cyanobacteria create phenomena called water 'blooms' which impact many aspects of aquatic ecosystems, affecting the processes conducted by organisms dwelling in these habitats (Havens 2008). A particularly vulnerable group to cyanobacterial blooms is zooplankton, which is inseparably related to phytoplankton.

Planktonic animals may be affected by the presence of cyanobacteria in many ways (Ger et al. 2016). Cyanobacterial blooms are believed to be a stress that cause a decrease of biodiversity in water ecosystems due to numerous inhibitory effects on zooplankton (Paerl and Otten 2013) as, for example, toxins production (Tillmanns et al. 2008) or poor nutritional values or morphology (Wilson et al. 2006). Large colonies or long trichomes cause difficulties in the nourishing of animals and may cause mechanistic damages of feeding apparatus (Wejnerowski et al. 2015). In such a way, bloom events may affect the functioning of freshwater ecosystems by modification of zooplankton biodiversity (Kosiba et al. 2018). Some studies indicate that the stability of freshwater ecosystems (Thompson and Shurin 2012) is related to the higher biodiversity of zooplankton, however the complexity of processes in ecosystems imply difficulties in predicting loss of biodiversity.

The studies of Barnett et al. (2007) and Litchman et al. (2013) suggest that use of trait-based methods may improve our understanding of the processes determining the diversity of zooplankton communities. Biodiversity is clearly related to ecosystem functioning (Hooper et al. 2005), however not simply by species richness and composition but via their functional traits which influence ecological processes (Schmera et al. 2017). Classically-used indexes for measurement of biodiversity treat all of the species and individuals as equal (Mouchet et al. 2010), which leads to an underestimation of aspects of diversity which affect ecosystem properties (Diaz and Cabido 2001). Biodiversity–ecosystem functioning relationships could be more precisely studied with the use of functional diversity indexes that are based not only on species composition and abundances but also on their functional traits (Villéger et al. 2008). Functional traits characterise species morphology, physiology and behaviour, referring directly to species' role in the ecosystem (Litchman et al. 2013). Diversity analyses measured by trait-based indexes allow for improving the understanding of the relation between biodiversity and ecosystem functioning (Mouchet et al. 2010; Vaughn 2010; Hooper et al. 2012; Tilman et al. 2014).

One of the most crucial traits of the species is the body length, since it represents multiple correlated traits. Body length determines the amount of energy allocated in the specimen, its feeding rate, food particle (or prey) size, metabolism rate, etc. Another important trait is the species food source, characterising where the species uptakes energy from. The food source of all species in the community is also crucial for ecosystem functioning since it influences the food web structure and interactions between trophic groups (Litchman et al. 2013). Beside the food source, also the feeding type appears to be necessary both to species performance and the ecosystem functioning. Every feeding type (i.e., encountering food particles and capturing them) has its implications and trade-offs, and different strategies may be beneficial under different ecosystem conditions.

The above-mentioned traits of zooplankton may be used to define the functional trait space of the community, and functional diversity indexes are a tool used to describe the space. Linked and interpreted together, functional and biological diversity indexes provide more complementary information about the fitness of the ecosystem (Mouchet et al. 2010).

Therefore, the aim of our study was to: (1) measure and compare the bio- and functional diversity of zooplankton; (2) find if bio- and functional diversity indexes correlate with each other; (3) examine the effect of short- and long-lasting cyanobacterial blooms and the effect of cyanobacterial biomass on the zooplankton community in small, shallow, eutrophic water bodies. We hypothesised that prolonged bloom events trigger changes by decreasing the bio- and functional diversity of freshwater zooplankton. We used functional diversity indexes as a support for classical biodiversity measures to study the effect of cyanobacterial bloom on the zooplankton communities. Serving as food for fish and many other organisms related to water habitats, planktonic animals are crucial for the functioning of aquatic ecosystems.

Materials and methods

Study area

The study was conducted in four water bodies in the area of Cracow (Southern Poland, Table 1), two of them are oxbow lakes of the Vistula River (Piekary and Tyniec), and two are artificial ponds (Podkamycze 1 and Podkamycze 2). The studied water bodies are described precisely in Kosiba et al. (2018). Cyanobacterial blooms occurred in all of the studied reservoirs. The following definition of 'bloom' was applied: "a marked visible discoloration of the water that is caused (predominantly) by cyanobacteria" (Huisman et al. 2018). An additional factor which we measured and used as a complementation of the aforementioned definition is chlorophyll *a* concentration. According to Nebaeus (1984), chlorophyll *a* concentration over 20 µg L^{-1} is treated as a bloom.

In the oxbow lakes, the bloom (visible discoloration of water and chlorophyll *a* concentration higher than 20 µg L^{-1}) occurred from one up to 3 months (August–October)—we define them as 'short-lasting blooms'. In ponds, the blooms were present for 5 months (June–October); we define them as 'long-lasting blooms'. Further microscopic analyses confirmed that the blooms were created by cyanobacteria.

Sampling

All samples were collected from a central (deepest) point of each water body, from May to October 2014, at a depth of 1 m. Basic physico-chemical parameters (water temperature, conductivity, pH, chlorophyll a, oxygen saturation), and depth were measured in situ with a YSI 6600 V2 Multiparameter Probe, and the water transparency with Secchi disc. Biological samples consisted of phytoplankton, protozooplankton (ciliates) and metazooplankton (rotifers, cladocerans, copepods). One set of samples consisted of physico-chemical and biological samples collected simultaneously. In total, 64 sets of samples were collected: 24 sets from water bodies with short-lasting blooms, and 40 sets from water bodies with long-lasting blooms. Samples for biological analysis were collected from a volume of 10 L of water (based on two 5 L replicates), concentrated with planktonic net (10 µm for phytoplankton and ciliates and 50 µm for metazooplankton) and fixed (Lugol's solution for the phytoplankton and ciliates, and 4% formaldehyde for the metazooplankton). Qualitative and quantitative analyses of the biological samples were performed using a Nikon H550L light microscope under the magnification of 40–400×in chamber (0.5 mL for the phytoplankton, 1 mL for the ciliates and 0.5 mL for the metazooplankton). The cyanobacteria

Table 1 Basic information about the studied water bodies

	Piekary	Tyniec	Podkamycze 1	Podkamycze 2
Geographical coordinates	50°00′50.1″N, 19°47′35.7″E	50°01′47″N, 19°49′39.8″E	50°05′11″N, 19°50′01.6″E	50°04′59.6″N, 19°50′05.4″E
Area (ha)	1.56	5.75	16.82	17.28
Max. depth (m)	4.0	3.0	3.0	2.5
Cyanobacteria biomass (mean) (mg L^{-1})	0.11	4.65	1.13	1.40
Cyanobacteria share (mean) (%)	1.6	25.2	74.2	63.9
Species of cyanobacteria creating bloom	Oscillatoria tenuis, Dolichospermum planctonicum, D. spiroides, Microcystis wesenbergii	Aphanocapsa sp., Microcystis aeruginosa, M. ichthyoblabe, M. wesenbergii, Woronichinia naegeliana, Aphanizomenon sp.	Aphanizomenon flos-aque, M. aeruginosa	Aphanizomenon flos-aque, M. aeruginosa

were identified with the use of keys (Komárek 2013; Komárek and Anagnostidis 1998, 2005) and their biomass was calculated as a biovolume by comparing the specimens with their geometrical shapes (Rott 1981). The zooplankton species were identified with the use of keys: Foissner and Berger (1996) and Foissner et al. (1999) for the protozooplankton and Ejsmont-Karabin et al. (2004) and Błędzki and Rybak (2016) for the metazooplankton. The density of the zooplankton was calculated based on multiple counts (3 subsamples for the protozooplankton and 5 subsamples for the metazooplankton), and recalculated to ind L^{-1}.

Statistical analyses, biodiversity and functional diversity indexes calculation

Three biodiversity indexes were measured: species richness (SR), Simpson's Diversity Index (D) and Shannon's Diversity Index (H). Species richness (SR) was calculated as the number of species in the community. Simpson's and Shannon's indexes were calculated in R (R Core Team 2018) with the use of the 'vegan' package (Oksanen et al. 2013). We chose Shannon's (H) index due to its popularity as a general biodiversity measure and Simpson's (D) index as a measure of evenness (relative abundance) of species.

To describe the functional diversity of the studied zooplankton communities we used three functional diversity indexes: functional richness (Fric), functional evenness (Feve) and functional divergence (Fdiv). The Fric index describes the amount of trait space filled by the community, the Feve index describes how even is the abundance of the species distributed in the functional trait space, and the Fdiv index describes the degree of differentiation of functional traits among the community (Mason et al. 2005; Villéger et al. 2008).

The functional diversity indexes were calculated on the basis of species density and their functional traits. We chose three functional traits of each species: mean body length (BL), potential food source (FS) and feeding type (FT). They were calculated in R (R Core Team 2018) with the use of the 'FD' package (Laliberté and Legendre 2010; Laliberté et al. 2014).

BL was calculated as the mean body length of adult specimens of each species found in the zooplankton samples, and it is the only quantitative trait we used. FS was specified as a qualitative trait on the basis of available literature (see Appendix 1). We conducted a review of published works (with the use of Web of Science, Google Scholar and Scopus) in order to describe the FS trait value for each zooplankton species identified in the biological samples. Each species diet (i.e., potential food source) was described by one, up to three categories: bacterivorous and/or detitivores (B), algaevorous (A) and predator (P). FS is crucial for each species since it represents the trophic position and type of food consumed.

FT, as well as FS, was specified on the basis of the available literature as a qualitative trait. We qualified the species from our samples into four groups with final subcategories used in the analyses. The first group are suspension feeders with three subcategories: R-suspension feeders (Rsus—rotifers, with *Malleate*, *Malleoramate* and *Incaudate* Trophi); C-suspension feeders (Csus—copepods, both ambush-feeders and feeding-current feeders); and Cil-suspension feeders (Cilsus—ciliates, sieving food particles through ciliary structures) (Fenchel 1980; Kiørboe 2011; Ejsmont-Karabin et al. 2004). The second group are filter-feeders, divided into: *Bosmina*-type filtration (Bfil—where filtration takes place in a horizontal position); *Chydorus*-type filtration (Cfil—scrapping food particles from surfaces, characteristic for Chydorids); and *Daphnia*-type filtration (Dfil—where filtration takes place in a vertical position). In the Dfil subcategory we gathered animals which Barnett et al. (2007) treated as *Daphnia*-type and *Sida*-type filtration feeders given the similarity of these two filtration types (Barnett et al. 2007). The third group are piercers,

consisting of rotifers with *Virgate* Trophi, which feed by sucking out the prey's cell content (de Oliveira Sodré et al. 2017). The fourth group are tactile feeders, specified only for one species—the predatory cladoceran *Leptodora kindtii* (Herzig and Auer, 1990).

In order to test the correlation among the biological and functional diversity indexes of the zooplankton community—principal component analysis (PCA) was performed, and to test the effect of cyanobacterial biomass, the effect of short- or long-lasting cyanobacterial bloom and the interaction of both factors on biological and functional diversity indexes of zooplankton community—generalised linear model (GLM) analysis was performed. Statistical analyses were conducted with R (R Core Team 2018) with the use of 'stats' (Generalized Linear Models—GLM; R Core Team 2018), 'FactoMineR' (Principal components analysis—PCA; Lê et al. 2008) and 'factoextra' (visualisation of the result of PCA analysis; Kassambara and Mundt 2017) packages.

Results

Cyanobacterial blooms

Blooms occurred in all of four studied water bodies, however they differed with duration and species forming bloom. In the oxbow lakes, the blooms were present from August to October, while in the ponds they were present from June to the end of October. In the Piekary oxbow lake, the bloom was formed by *Oscillatoria tenuis, Dolichospermum planctonicum*, *D. spiroides* and *Microcystis wesenbergii*. In the Tyniec oxbow lake, the bloom was formed by *Aphanocapsa* sp., *Microcystis aeruginosa*, *M. ichthyoblabe*, *M. wesenbergii*, *Woronichinia naegeliana* and *Aphanizomenon* sp. In the Podkamycze 1 and Podkamycze 2 water bodies, the blooms were formed by *Aphanizomenon flos-aque* and *Microcystis aeruginosa*. During the bloom, the biomass of cyanobacteria in the reservoirs with short-lasting blooms ranged from 0.04 to 12.83 mg L^{-1} (mean 3.24 mg L^{-1}), and from 0.06 to 9.23 mg L^{-1} (mean 1.69 mg L^{-1}) in reservoirs with long-lasting blooms.

Biological and functional diversity of zooplankton

In the studied reservoirs, 71 taxa of planktonic animals were found in total: 15 ciliates, 24 rotifers, 13 copepods and 19 cladocerans. Two juvenile stages of copepods were also found.

We found that zooplankton richness (SR) was higher (mean value for the entire season and particular months) in water bodies where short-lasting cyanobacterial blooms occurred. However, the variance and range of SR was higher in the artificial ponds with long-lasting cyanobacterial blooms (Fig. 1a, Table 2).

Simpson's Evenness Index (D, mean value) was only slightly lower in reservoirs with long-lasting blooms (Table 2), and also the mean values for particular months were lower in June, August, September and October in such reservoirs (Fig. 1b).

Shannon Diversity Index (H) showed marginally higher mean value and variance in reservoirs with long-lasting cyanobacterial blooms (Table 2). Throughout the season we found mean values of H index slightly higher in water bodies where long-lasting cyanobacterial blooms occurred in June, September and October.

Fric mean value was higher in the water bodies with short-lasting blooms, however mean values of Feve and Fdiv were higher in the water bodies with long-lasting blooms
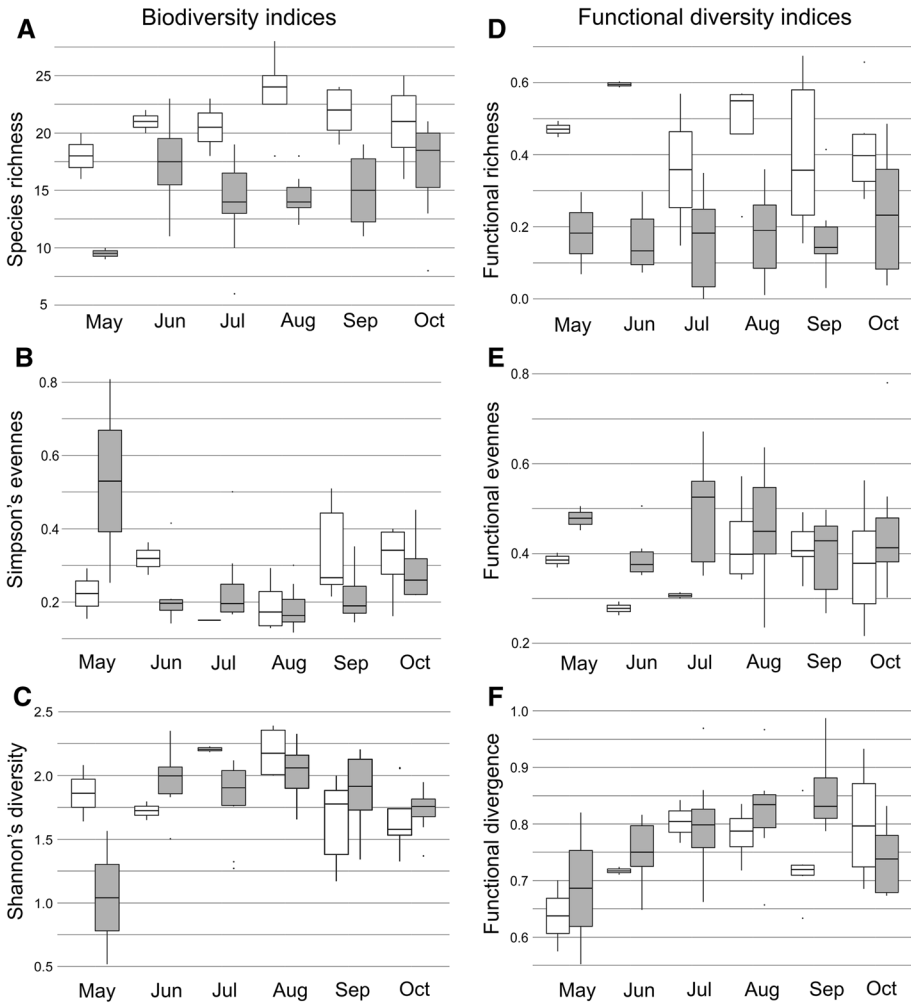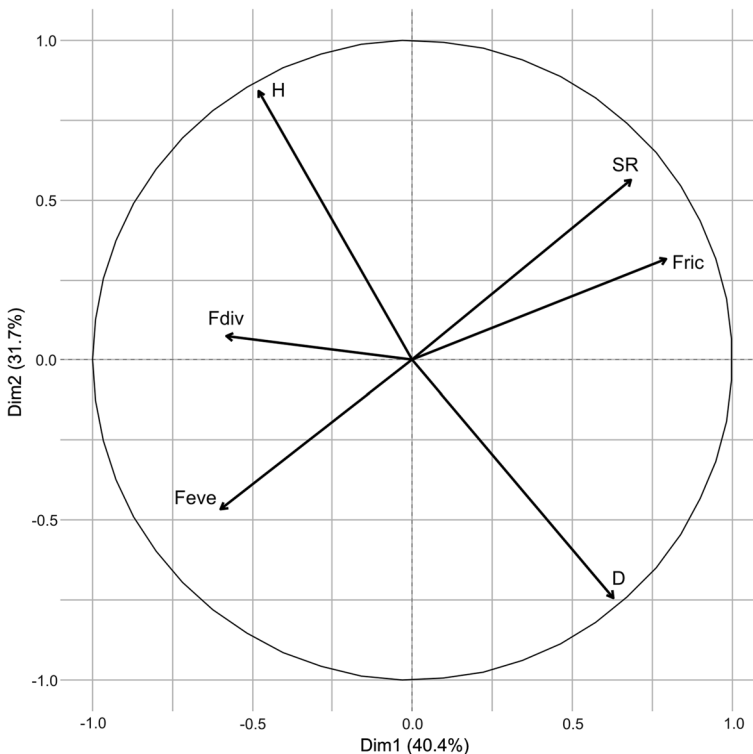
Fig. 1 Box plots for biological and functional diversity indexes during the season: **a** Species richness (SR); **b** Simpson's evenness (D); **c** Shannon's diversity (H); **d** functional richness (Fric); **e** functional evenness (Feve); **f** functional divergence (Fdiv). The horizontal lines represent median, the boxes represent 1st and 3rd percentiles, the vertical lines represent range, and the points represent outliers. The white boxes represent values of each index for the water bodies where short-lasting blooms occurred, the grey boxes represent values for water bodies where long-lasting blooms occurred

(Table 2). The mean values of Fric in particular months were also higher in water bodies with short-lasting blooms in comparison to water bodies with long-lasting blooms (Fig. 1d). Feve and Fdiv showed higher mean values in particular months in water bodies with long-lasting blooms (Fig. 1e and f).

PCA analysis showed that SR was positively correlated to Fric. Both of these indexes were negatively correlated to the Feve index. Shannon's (H) and Simpson's (D) indexes were correlated negatively to each other, and did not show correlation with other indexes. The analysis showed that the Fdiv index did not correlate to the other indexes (Fig. 2).

Table 2 Values of indexes of diversity calculated for the zooplankton community in the reservoirs with short and long-lasting cyanobacterial bloom

	Short-lasting blooms		Long-lasting blooms	
	Range (mean)	Variance	Range (mean)	Variance
Species richness (SR)	16–28 (21.29)	9.17	6–23 (15.05)	14.92
Simpson evenness (D)	0.129–0.51 (0.279)	0.012	0.117–0.81 (0.245)	0.015
Shannon diversity (H)	1.171–2.391 (1.811)	0.112	0.518–2.349 (1.892)	0.119
Functional richness (Fric)	0.148–0.674 (0.433)	0.026	8.3E−7–0.485 (0.186)	0.018
Functional evenness (Feve)	0.216–0.572 (0.382)	0.008	0.236–0.781 (0.448)	0.013
Functional divergence (Fdiv)	0.575–0.933 (0.760)	0.007	0.552–0.987 (0.787)	0.008

Fig. 2 PCA for biological and functional diversity indexes values in the studied reservoirs. The cumulative explained variation (for axis 1 and 2) is 72.12%. *SR* species richness, *D* Simpson's evenness, *H* Shannon's diversity, *Fric* functional richness, *Feve* functional evenness, *Fdiv* functional divergence

GLM showed that SR in ponds with long-lasting cyanobacterial blooms was significantly lower ($p < 0.001$) compared to SR in ponds with short-lasting blooms (Tables 2 and 3). However, the analysis did not show significant differences for both types of ecosystems, neither for the D nor for the H indexes (Tables 2 and 3). For the functional diversity indexes, GLM showed: the Fric index significantly lower in ponds

Table 3 The results of GLM analysis conducted for biodiversity and functional diversity indexes against the length of cyanobacterial bloom (factor), biomass of cyanobacteria and the interaction of cyanobacteria biomass and length of bloom

Predictor	Estimate	Std. error	T	p
Species richness (SR)				
Short-lasting bloom (intercept)	20.676	0.874	23.671	**<0.001**
Cyanobacteria biomass	0.240	0.201	1.192	0.238
Long-lasting bloom	−4.871	1.082	−4.503	**<0.001**
Cyano×long-lasting bloom	−0.837	0.331	−2.532	**<0.05**
Simpson's evenness (D)				
Short-lasting bloom (intercept)	0.276	0.031	8.955	**<0.001**
Cyanobacteria biomass	0.001	0.007	−0.186	0.853
Long-lasting bloom	−0.026	0.038	0.679	0.499
Cyano×long-lasting bloom	−0.005	0.012	0.414	0.681
Shannon diversity (H)				
Short-lasting bloom (intercept)	1.797	0.088	20.475	**<0.001**
Cyanobacteria biomass	0.005	0.020	0.264	0.793
Long-lasting bloom	0.047	0.109	0.428	0.670
Cyano×long-lasting bloom	−0.017	0.033	−0.508	0.614
Functional richness (Fric)				
Short-lasting bloom (intercept)	0.494	0.034	14.692	**<0.001**
Cyanobacteria biomass	−0.024	0.008	−3.067	**<0.01**
Long-lasting bloom	−0.284	0.042	−6.814	**<0.001**
Cyano×long-lasting bloom	0.004	0.013	0.323	0.748
Functional evenness (Feve)				
Short-lasting bloom (intercept)	0.353	0.026	13.438	**<0.001**
Cyanobacteria biomass	0.011	0.006	1.854	0.069
Long-lasting bloom	0.090	0.032	2.767	**<0.01**
Cyano×long-lasting bloom	−0.007	0.010	−0.722	0.473
Functional divergence (Fdiv)				
Short-lasting bloom (intercept)	0.743	0.022	34.356	**<0.001**
Cyanobacteria biomass	0.007	0.005	1.355	0.181
Long-lasting bloom	0.029	0.027	1.068	0.290
Cyano×long-lasting bloom	0.006	0.008	0.685	0.496

The p values in bold are statistically significant

with long-lasting cyanobacterial blooms ($p < 0.001$), and the Feve index significantly higher in ponds with long-lasting cyanobacterial blooms ($p < 0.01$) in comparison to the waters with short-lasting blooms. No statistical differences were showed between the Fdiv index of both types of ecosystems (Tables 2 and 3).

GLM showed the biomass of cyanobacteria affected (Table 3): SR in waters with long-lasting blooms ($p < 0.05$), Fric in waters with short-lasting blooms ($p < 0.001$) and Feve in waters with long-lasting blooms ($p < 0.01$).

Discussion

The biodiversity of aquatic ecosystems has been intensively studied over the last decades (Fryer 1980; Gee et al. 1997; Dudgeon et al. 2006). Traditional biodiversity indexes have come in for criticism because they treat all species and individuals equally (Mouchet et al. 2010). This is the reason why a new approach—measuring diversity using functional traits of species—has been proposed (Tilman 2001; Villéger et al. 2008). The range of species functional traits (functional trait space) characterise the species roles in the ecosystem processes, which is useful for studying communities of numerous and diverse species (Loreau et al. 2001; Hooper et al. 2005). Such a community is zooplankton, consisting of crustaceans (cladocerans and copepods), rotifers and ciliates, which differ in many aspects (body size and morphology, feeding behaviour etc.). The choice of traits used in the study became limited since each of traits had to be well described for every species. Petchey and Gaston (2006) defined the choice of functional traits as a critical for studying functional diversity. The traits have to refer to the most important features of the species which are responsible for their impact on the food web and ecosystem processes. Therefore, the possible limitation of the study is joining calanoid (feeding-current feeders) and cyclopoid (ambush-feeding feeders) copepods under the single Csus feeding trait. However, the aim of the study was not to distinguish which traits of zooplankton are associated with the cyanobacterial bloom, but to test how the bloom modify the trait space of the community. Here, the Csus trait represents not only the mechanism of food uptake but also the ability of selective feeding.

Among freshwater food webs, interactions between trophic levels are often more relevant than interactions between organisms occupying the same trophic level (Woodward 2009). Therefore, the zooplankton community may be limited by both bottom-up (food availability) and top-down (fish predation) effects (Gliwicz 2002). The observed effects of predatory pressure of fish are narrowing the size spectrum of the zooplankton community, causing the elimination of large bodied crustaceans, and switching the community towards rotifer domination (Reissig et al. 2006). The study we carried out did not consider detailed fish abundance (predatory pressure). Nevertheless, on the basis of the consultations with authorities of the Polish Angling Association and owner of the ponds, we can estimate the fish pressure on a similar level in all of the water bodies, so potential differences in top-down control may be negligible.

Studying biodiversity–ecosystem functioning relations are important for predicting how multispecies systems respond to stress factors. In this study, we used classical and trait-based methods to learn how the cyanobacterial bloom affect the bio- and functional diversity of zooplankton.

What did the traditional indexes show?

Using traditional indexes of diversity we found that only species richness (SR) showed the differences between ecosystems with short and long-lasting blooms. In ecosystems with short-lasting blooms, we found a higher number of species compared to those with long-lasting blooms. This might support the conclusions of Ger et al. (2014) that more intensive and prolonged cyanobacterial blooms triggers selection of better adapted species and, as a consequence, in such waters the number of species decreases.

Shannon's (H) and Simpson's (D) indexes showed a similar distribution of values in both types of water ecosystems. However, a broader range and a slightly larger variation of indexes in ponds with long-lasting blooms indicate higher fluctuation throughout the season. The comparable mean values of the indexes in both types of water bodies may be an effect of changes of zooplankton composition without loss of biodiversity (Bouvy et al. 2001).

What did the functional diversity indexes show?

Functional richness (Fric) values were lower in the water bodies with long-lasting cyanobacterial blooms during the entire season. This result indicates the limited ecological function of the community (Ger et al. 2014), which the authors explain as a selection of better-adapted species by prolonged blooms. According to Mason et al. (2005), lower Fric may suggest, however, that some of the resources in the environment are available, but that they are unused, which leads to the presence of niche space gaps. Since aquatic habitats are susceptible to invasions, these gaps may represent an opportunity for invaders (Lozon and MacIsaac 1997; Dukes 2001; Mason et al. 2005). Additionally, we found that functional evenness (Feve) of the zooplankton community was higher in the water bodies with long-lasting cyanobacterial blooms. According to Woodward (2009), evenness is the exception in nature (among freshwater ecosystems) and dominance is the rule. The fact that a long-lasting bloom forces more even distribution of traits in the zooplankton community (also understood as a lesser domination of one species in the community; Villéger et al. 2008) suggests that prolonged cyanobacteria domination is a driver of the weakening of natural processes. Our results corroborate with the study of Josué et al. (2018), who found cyanobacterial dominance reducing Functional dispersion of the zooplankton community (leading to the occurrence of species possessing similar functional traits) which may limit the zooplankton role in an ecosystem.

Lower Fric and Feve in the water bodies with long-lasting blooms suggest that the events force changes among available niches. Since a zooplankton community consists of species diversified in many aspects, there is a clear resource niche differentiation among every habitat they dwell in (Wilson 1990). Resources may become limited during the cyanobacterial bloom (Havens 2008), affecting also the differentiation of the niches. We did not find significant difference in Fdiv (functional divergence) values in water bodies with different types of bloom, which indicates that the length of the bloom did not affect the differentiation of the niches. We explain this phenomenon as the ability of the species in the community to adapt to the circumstances of resources shortage by switching to an alternative food source.

Do the bio- and functional diversity indexes correlate?

In order to check if traditional biodiversity indexes and functional diversity indexes are complementary, we used PCA analysis. A positive correlation of species richness (SR) and functional richness (Fric) showed that both of them are related to each other. The positive correlation between SR and Fric index may be implied by construction of the Fric index (Mason et al. 2005). Both of these indexes showed a negative correlation to the Feve index, suggesting that higher species richness and functional richness (Fric) were connected to domination of the community by a particular species.

Negative correlation between the Shannon (H) and Simpson (D) indexes was found, but they did not correlate with any other indexes. It is clear that these indexes provide information on how the community is diversified (H index), and how evenly the species are distributed (D index) among the community. Lack of correlation with functional evenness (Feve) and functional divergence (Fdiv) clearly showed that trait-based indexes provide some other information than classical biodiversity measures. They describe the functional trait space of the community, which is possible due to the incorporation of species functional traits into the indexes (Villéger et al. 2008). Furthermore, no correlation of functional divergence (Fdiv) with other indexes is explained by the fact that traits distribution in the community is not dependent on species richness and any other aspects of traditional understanding of diversity.

The effect of cyanobacterial blooms on bio- and functional diversity

During the bloom, cyanobacteria dominate freshwater ecosystems, developing a large amount of biomass which is poorly available for grazers as a food. This may promote the development of some more selective species (ciliates, rotifers, cladocerans), effectively feeding on an alternative food source such as bacteria (Zöllner et al. 2003; Arndt 1993; Brendelberger 1991; Geller and Müller 1981). Such interactions in the microbial food web induce modifications of the zooplankton composition and, as a consequence, a set of functional traits of the community. Thanks to the use of functional diversity measures, our study shows that different aspects of functional diversity were affected by cyanobacterial bloom.

The GLM showed that the species richness (SR) was not affected by increasing cyanobacterial biomass in water bodies with short-lasting blooms, but it was affected in water bodies with long-lasting cyanobacterial blooms. Short-lasting blooms are natural phenomena, and the increase of cyanobacterial biomass in natural cycles may not trigger rapid changes of zooplankton biodiversity. On the other hand, the lack of changes in SR might be explained as replacement of the species i.e., the decline of more vulnerable and the development of better adapted species. However, the negative effect of cyanobacterial biomass on Fric was found, but only in water bodies with short-lasting blooms. Such an effect represents the limitation of trait values, which is an effect of the inadequacy of cyanobacteria as a food source (Bednarska et al. 2014). We explain no effect of cyanobacterial biomass on Fric in reservoirs with long-lasting blooms as an adaptation of the community of these water bodies for prolonged bloom circumstances. The differences in the effects of the interaction of long-lasting bloom and cyanobacterial biomass (negative on SR and no effect on Fric) suggests that despite the disappearance of some species, the trait space remained unchanged. It can be explained as a fact of the existence of the community assembled of species adapted to circumstances of prolonged blooms. Furthermore, the increase of cyanobacterial biomass did not significantly affect the values of classically-used biodiversity indexes (Simpson's D and Shannon's H). Such a result is contrary to what we expected due to the fact that cyanobacterial blooms may be harmful for the entire food web (Paerl et al. 2001; Hansson et al. 2007). Nevertheless, recently there is increasing number of reports demonstrating that cyanobacteria–zooplankton interactions are more complicated, and genetic changes of both cyanobacteria and planktonic animals might change the mutual response (Wilk-Woźniak 2019).

We found cyanobacterial biomass effect on Feve on the border of significance in water bodies with short-lasting cyanobacterial blooms. This indicates that in some circumstances

cyanobacterial biomass could modify the Feve towards more even distribution of the species in the functional trait space. Our results coincide with the study of Massicotte et al. (2014), who found a negative correlation of chlorophyll *a* concentration and Feve of the zooplankton community, which may be interpreted as a bottom-up effect of phytoplankton assemblage. No effect of cyanobacterial biomass on Fdiv (in both types of reservoirs) suggests that their unsuitability as a food source does not enhance species traits distribution in the community. During the season we noticed the highest values of Fdiv from July to September in reservoirs with prolonged blooms, and in October in reservoirs where short-lasting blooms occurred. The highest values of Fdiv were associated with the highest percentage share of cyanobacteria in total phytoplankton biomass. These observations suggest that cyanobacteria may cause an enhancement of the traits towards extreme values, however lack of statistical evidence does not confirm that conclusion. Lack of significant effects of cyanobacterial biomass on both Feve and Fdiv indexes might be explained by the diversity of cyanobacteria. The size, shape (filamentous and chroococcal) and other functional traits of cyanobacterial cells provide different niche spaces for zooplankton. Including this issue into the analyses may reveal numerous associations of zooplankton and cyanobacteria traits which will be helpful in an understanding of the interactions of the aforementioned groups.

Conclusions

Functional diversity indexes are a reliable supplementation for traditional biodiversity indexes. They provide a set of additional information about the functional trait space of studied community, and allow for tracking changes which are undetectable by classic biodiversity measures. Simpson's D and Shannon's H indexes showed no loss of biodiversity of zooplankton caused by an increase of cyanobacterial biomass and duration of the bloom. Use of functional diversity measures allowed for concluding that the aforementioned factors involved changes among the community, however the dimension of the changes was not the classical biodiversity, but the functional trait space of the community. A decrease of functional richness (Fric) and an increase of functional evenness (Feve) caused by long-lasting bloom show that massive cyanobacteria development are responsible for the limitation of the role of the zooplankton community. A functional approach (i.e., measuring the functional trait space and its features) revealed that proliferated blooms may affect resource use by the zooplankton community and weaken the natural ecological processes and functioning of freshwater ecosystems.

Appendix 1

See Table 4.

Table 4 Functional traits of zooplankton species identified in the samples collected from the studied water bodies

Species	Food source	Feeding type	Body length (μm)	References
Ciliata				
Aspidisca sp.	B	Cilsus	40	Foissner and Berger (1996), Fenchel (1980)
Codonella cratera	A	Cilsus	60	Foissner and Berger (1996), Fenchel (1980)
Coleps hirtus	BA	Cilsus	50	Foissner and Berger (1996), Fenchel (1980)
Coleps spetai	A	Cilsus	65	Foissner and Berger (1996), Fenchel (1980)
Epistylis sp.	B	Cilsus	120	Foissner and Berger (1996), Fenchel (1980)
Non identified ciliate	B	Cilsus	95	Foissner and Berger (1996), Fenchel (1980)
Paramecium sp.	BA	Cilsus	98	Foissner and Berger (1996), Fenchel (1980)
Small scuticociliata	B	Cilsus	20	Foissner and Berger (1996), Fenchel (1980)
Stentor sp.	BA	Cilsus	500	Foissner and Berger (1996), Fenchel (1980)
Strobilidium sp.	BA	Cilsus	20	Foissner and Berger (1996), Fenchel (1980)
Strombidium sp.	BA	Cilsus	30	Foissner and Berger (1996), Fenchel (1980)
Tintinidium sp.	A	Cilsus	150	Foissner and Berger (1996), Fenchel (1980)
Vorticella campanula	BA	Cilsus	75	Foissner and Berger (1996), Fenchel (1980)
Vorticella convalaria	B	Cilsus	70	Foissner and Berger (1996), Fenchel (1980)
Vorticella sp.	B	Cilsus	60	Foissner and Berger (1996), Fenchel (1980)
Rotifera				
Asplanchna priodonta	BAP	Rsus	380	Chang et al. (2010), Ejsmont-Karabin et al. (2004), Kiørboe (2011)
Brachionus angularis	BAP	Rsus	144	Arndt (1993), Ejsmont-Karabin et al. (2004), Kiørboe (2011)
Brachionus calyciflorus	BAP	Rsus	270	Starkweather and Kellar (1983), Arndt (1993), Ejsmont-Karabin et al. (2004), Kiørboe (2011)
Brachionus diversicornis	BAP	Rsus	442	Arndt (1993), Ejsmont-Karabin et al. (2004), Kiørboe (2011)
Brachionus quadridentatus	BAP	Rsus	250	Arndt (1993), Ejsmont-Karabin et al. (2004), Kiørboe (2011)
Brachionus rubens	BAP	Rsus	210	Arndt (1993), Ejsmont-Karabin et al. (2004), Kiørboe (2011)
Brachionus urceolaris	BAP	Rsus	180	Arndt (1993), Ejsmont
Filinia longiseta	BA	Rsus	145	Arndt (1993), Ejsmont

Table 4 (continued)

Species	Food source	Feeding type	Body length (μm)	References
Gastropus minor	A	Piercer	125	Wilk-Wozniak et al. (2001), Ejsmont-Karabin et al. (2004), de Oliveira Sodré et al. (2017)
Kellicotia longispina	BA	Rsus	378	Arndt (1993), Wilk-Wozniak et al. (2001), Ejsmont-Karabin et al. (2004), Kiørboe (2011)
Keratella cochlearis	BA	Rsus	137	Arndt (1993), Wilk-Wozniak et al. (2001), Ejsmont-Karabin et al. (2004), Kiørboe (2011)
Keratella quadrata	BA	Rsus	283	Arndt (1993), Wilk-Wozniak et al. (2001), Ejsmont-Karabin et al. (2004), Kiørboe (2011)
Keratella tecta	BA	Rsus	103	Arndt (1993), Wilk-Wozniak et al. (2001), Ejsmont-Karabin et al. (2004), Kiørboe (2011)
Lecane sp.	BA	Rsus	90	Serrania-Soto et al. (2011), Ejsmont-Karabin et al. (2004), Kiørboe (2011)
Pompholyx sulcata	BA	Rsus	98	Ooms-Wilms (1997), Ejsmont-Karabin et al. (2004), Kiørboe (2011)
Polyarthra longiremis	BA	Piercer	138	Bogdan and Gilbert (1982), Arndt (1993), Ejsmont-Karabin et al. (2004), de Oliveira Sodré et al. (2017)
Polyarthra major	BA	Piercer	156	Work and Havens (2003), Ejsmont-Karabin et al. (2004), de Oliveira Sodré et al. (2017)
Polyarthra minor	BA	Piercer	83	Bogdan and Gilbert (1982), Arndt (1993), Ejsmont-Karabin et al. (2004), de Oliveira Sodré et al. (2017)
Polyarthra remata	BA	Piercer	141	Bogdan and Gilbert (1982), Arndt (1993), Ejsmont-Karabin et al. (2004), de Oliveira Sodré et al. (2017)
Polyarthra vulgaris	BA	Piercer	117	Bogdan and Gilbert (1982), Arndt (1993), Ejsmont-Karabin et al. (2004), de Oliveira Sodré et al. (2017)
Synchaeta pectinata	BAP	Piercer	271	Arndt (1993), Wilk-Wozniak et al. (2001), Ejsmont-Karabin et al. (2004), de Oliveira Sodré et al. (2017)
Trichocerca capucina	A	Piercer	318	Wilk-Wozniak et al. (2001), Ejsmont-Karabin et al. (2004), de Oliveira Sodré et al. (2017)
Trichocerca cylindrica	A	Piercer	316	Wilk-Wozniak et al. (2001), Ejsmont-Karabin et al. (2004), de Oliveira Sodré et al. (2017)
Trichocerca similis	BA	Piercer	179	Wilk-Wozniak et al. (2001), Ejsmont-Karabin et al. (2004), de Oliveira Sodré et al. (2017)
Cladocera				
Alona protzi	BA	Cfiltr	400	Geller and Müller (1981), Barnett et al. (2007)
Alona affinis	BA	Cfiltr	760	Geller and Müller (1981), Barnett et al. (2007)
Bosmina longirostris	BA	Bfiltr	372	DeMott (1982), Barnett et al. (2007)
Chydorus latus	BA	Cfiltr	350	Geller and Müller (1981), Barnett et al. (2007)
Chydorus sphaericus	BA	Cfiltr	259	Geller and Müller (1981), Barnett et al. (2007)

Table 4 (continued)

Species	Food source	Feeding type	Body length (μm)	References
Eubosmina longispina	BA	Bfiltr	334	Geller and Müller (1981), Barnett et al. (2007)
Eubosmina longicornis	BA	Bfiltr	1350	Geller and Müller (1981), Barnett et al. (2007)
Eubosmina coregoni	A	Bfiltr	411	Geller and Müller (1981), Barnett et al. (2007)
Eubosmina gibbera	BA	Bfiltr	447	Geller and Müller (1981), Barnett et al. (2007)
Eurycercus lamellatus	BA	Cfiltr	950	Smirnov (1962), Barnett et al. (2007)
Daphnia ambigua	A	Dfiltr	1115	Work and Havens (2003), Barnett et al. (2007)
Daphnia cucullata	BA	Dfiltr	830	Geller and Müller (1981), Barnett et al. (2007)
Daphnia cristata	A	Dfiltr	730	Geller and Müller (1981), Barnett et al. (2007)
Daphnia galeata	A	Dfiltr	875	Geller and Müller (1981), Barnett et al. (2007)
Daphnia longispina	BA	Dfiltr	1391	Kankaala (1988), Barnett et al. (2007)
Daphnia magna	BA	Dfiltr	1500	Geller and Müller (1981), Barnett et al. (2007)
Diaphanosoma brachyurum	BA	Dfiltr	724	Knoechel and Holtby (1986), Barnett et al. (2007)
Moina micrura	BA	Dfiltr	480	Niswati et al (2005), Barnett et al. (2007)
Leptodora kindtii	P	Tactile	5080	Błędzki and Rybak (2016), Herzig and Auer (1990)
Copepoda				
Nauplius	BA	Csus	240	Wilk-Woźniak et al. (2001), Roff et al. (1995), Kiørboe (2011)
Copepodid	BAP	Csus	472	Dussart and Defaye (2001), Work and Havens (2003), Kiørboe (2011)
Acanthocyclops trajani	P	Csus	970	Hopp and Maier (2005), Kiørboe (2011)
Acanthocyclops robustus	P	Csus	1073	Roche (1987), Kiørboe (2011)
Acanthocyclops venustus	P	Csus	916	Hopp and Maier (2005), Kiørboe (2011)
Cyclops vicinus	AP	Csus	1296	Hopp and Maier (2005), Kiørboe (2011)
Cyclops abyssorum	AP	Csus	1465	Błędzki and Rybak (2016), Hopp and Maier (2005), Kiørboe (2011)
Cyclops strenuus	AP	Csus	1527	Makino and Ban (1998), Kiørboe (2011)
Eurytemora affinis	A	Csus	1400	Engström et al. (2000), Kiørboe (2011)
Eudiaptomus gracilis	A	Csus	1211	Wilk-Woźniak et al. (2001), Kiørboe (2011)
Metacyclops gracilis	A	Csus	907	Farhadian (2012), Kiørboe (2011)

Table 4 (continued)

Species	Food source	Feeding type	Body length (μm)	References
Mesocyclops leuckartii	AP	Csus	1073	Hopp and Maier (2005), Kiørboe (2011)
Thermocyclops dybowskii	AP	Csus	865	Hopp and Maier (2005), Kiørboe (2011)
Thermocyclos oithonoides	AP	Csus	920	Hopp and Maier (2005), Kiørboe (2011)
Thermocyclops crassus	AP	Csus	797	Hopp and Maier (2005), Kiørboe (2011)

A Algae, *B* Bacteria, *P* Predator, *Cilsus* Ciliate-type suspension feeding, *Csus* Copepod-type suspension feeding, *Bfiltr* B-type filtration, *Cfiltr* C-type filtration , *Dfiltr* D-type filtration, *Piercer* Rotifers with *Vigrate* Trophi, *Rsus* Rotifer-type suspension feeding (rotifers with *Malleate*, *Malleoramate* and *Incaudate* Trophi), *Tactile* Prey hunting mode characteristic for *Leptodora kindtii*

References

Arndt H (1993) Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates)—a review. In: Gilbert JJ, Lubzens E, Miracle MR (eds) Rotifer symposium VI. Developments in hydrobiology, vol 83. Springer, Dordrecht

Barnett AJ, Finlay K, Beisner BE (2007) Functional diversity of crustacean zooplankton communities: towards a trait-based classification. Freshw Biol 52(5):796–813

Barnosky AD, Matzke N, Tomiya S, Wogan GO, Swartz B, Quental TB, Marshall C, McGuire JL, Lindsey EL, Maguire KC, Mersey B (2011) Has the Earth's sixth mass extinction already arrived? Nature 471(7336):51

Bednarska A, Pietrzak B, Pijanowska J (2014) Effect of poor manageability and low nutritional value of cyanobacteria on Daphnia magna life history performance. J Plankton Res 36(3):838–847

Błędzki LA, Rybak JI (2016) Freshwater crustacean zooplankton of Europe: Cladocera & Copepoda (Calanoida, Cyclopoida) key to species identification, with notes on ecology, distribution, methods and introduction to data analysis. Springer, New York

Bogdan KG, Gilbert JJ (1982) Seasonal patterns of feeding by natural populations of Keratella, Polyarthra, and Bosmina: clearance rates, selectivities, and contributions to community grazing. Limnol Oceanogr 27(5):918–934

Bouvy M, Pagano M, Troussellier M (2001) Effects of a cyanobacterial bloom (Cylindrospermopsis raciborskii) on bacteria and zooplankton communities in Ingazeira reservoir (northeast Brazil). Aquat Microb Ecol 25(3):215–227

Brendelberger H (1991) Filter mesh size of cladocerans predicts retention efficiency for bacteria. Limnol Oceanogr 36(5):884–894

Chang KH, Hideyuki DOI, Nishibe Y, Nakano SI (2010) Feeding habits of omnivorous Asplanchna: comparison of diet composition among Asplanchna herricki, A. priodonta and A. girodi in pond ecosystems. J Limnol 69(2):209–216

Crutzen PJ (2006) The "anthropocene". In: Ehlers E, Krafft T (eds) Earth system science in the anthropocene. Springer, Berlin, pp 13–18

de Oliveira Sodré E, Figueiredo-Barros MP, Roland F, de Assis Esteves F, Bozelli RL (2017) Complimentary biodiversity measures applied to zooplankton in a recovering floodplain lake. Fund Appl Limnol/Arch Hydrobiol 190(4):279–298

DeMott WR (1982) Feeding selectivities and relative ingestion rates of Daphnia and Bosmina. Limnol Oceanogr 27(3):518–527

Dıaz S, Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16(11):646–655

Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard AH, Soto D, Stiassny ML, Sullivan CA (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biol Rev 81(2):163–182

Dukes JS (2001) Biodiversity and invasibility in grassland microcosms. Oecologia 126:563–568

Dussart BH, Defaye D (2001) Introduction to the Copepoda. Guide to the identification of the microinvertebrates of the continental waters of the world, No. 16

Ejsmont-Karabin J, Radwan S, Bielańska-Grajner I (2004) Rotifers. Monogononta-atlas of species. Polish freshwater fauna. University of Łódź, Łódź, pp 77–447

Engström J, Koski M, Viitasalo M, Reinikainen M, Repka S, Sivonen K (2000) Feeding interactions of the copepods Eurytemora affinis and Acartia bifilosa with the cyanobacteria Nodularia sp. J Plankton Res 22(7):1403–1409

Farhadian O (2012) Culture of cyclopoid copepod Metacyclops gracilis fed on Scenedesmus quadricauda at different oxygen concentrations. Iran Sci Fish J 1(78):123–132

Fenchel T (1980) Suspension feeding in ciliated protozoa: structure and function of feeding organelles. Arch Protistenkd 123(3):239–260

Foissner W, Berger H (1996) A user-friendly guide to the ciliates (Protozoa, Ciliophora) commonly used by hydrobiologists as bioindicators in rivers, lakes, and waste waters, with notes on their ecology. Freshw Biol 35(2):375–482

Foissner W, Berger H, Schaumburg J (1999) Identification and ecology of limnetic plankton ciliates. Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft, München

Fryer G (1980) Acidity and species diversity in freshwater crustacean faunas. Freshw Biol 10(1):41–45

Gee JH, Smith BD, Lee KM, Griffiths SW (1997) The ecological basis of freshwater pond management for biodiversity. Aquat Conserv 7(2):91–104

Geller W, Müller H (1981) The filtration apparatus of Cladocera: filter mesh-sizes and their implications on food selectivity. Oecologia 49(3):316–321

Ger KA, Hansson LA, Lürling M (2014) Understanding cyanobacteria-zooplankton interactions in a more eutrophic world. Freshw Biol 59(9):1783–1798

Ger KA, Urrutia-Cordero P, Frost PC, Hansson LA, Sarnelle O, Wilson AE, Lürling M (2016) The interaction between cyanobacteria and zooplankton in a more eutrophic world. Harmful Algae 54:128–144

Gliwicz ZM (2002) On the different nature of top-down and bottom-up effects in pelagic food webs. Freshw Biol 47(12):2296–2312

Hansson LA, Gustafsson S, Rengefors K, Bomark L (2007) Cyanobacterial chemical warfare affects zooplankton community composition. Freshw Biol 52(7):1290–1301

Havens KE (2008) Cyanobacteria blooms: effects on aquatic ecosystems. In: Hundell HK (ed) Cyanobacterial harmful algal blooms: state of the science and research needs. Springer, New York, pp 733–747

Herzig A, Auer B (1990) The feeding behaviour of *Leptodora kindti* and its impact on the zooplankton community of Neusiedler See (Austria). Hydrobiologia 198(1):107–117

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S et al (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75(1):3–35

Hooper DU, Adair EC, Cardinale BJ, Byrnes JE, Hungate BA, Matulich KL et al (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486(7401):105

Hopp U, Maier G (2005) Implication of the feeding limb morphology for herbivorous feeding in some freshwater cyclopoid copepods. Freshw Biol 50(5):742–747

Huisman J, Codd GA, Paerl HW, Ibelings BW, Verspagen JM, Visser PM (2018) Cyanobacterial blooms. Nat Rev Microbiol 16(8):471–483

Josué II, Cardoso SJ, Miranda M, Mucci M, Ger KA, Roland F, Marinho MM (2018) Cyanobacteria dominance drives zooplankton functional dispersion. Hydrobiologia 831:149–161

Kankaala P (1988) The relative importance of algae and bacteria as food for *Daphnia longispina* (Cladocera) in a polyhumic lake. Freshw Biol 19(3):285–296

Kassambara A, Mundt F (2017) Factoextra: extract and visualize the results of multivariate data analyses. R package version 1.0. 4. 2017

Kiørboe T (2011) How zooplankton feed: mechanisms, traits and trade-offs. Biol Rev 86(2):311–339

Knoechel R, Holtby LB (1986) Cladoceran filtering rate: body length relationships for bacterial and large algal particles. Limnol Oceanogr 31(1):195–199

Komárek J (2013) Süßwasserflora von Mitteleuropa, Bd. 19/3: Cyanoprokaryota. 3. Teil/3rd part: Heterocytous Genera. In: Büdel B, Gärtner G, Krienitz L, Schagerl M, von Gegründet PA (eds) Süßwasserflora von Mitteleuropa. Spektrum Academischer Verlag, Heidelberg

Komárek J, Anagnostidis K (1998) Cyanoprokaryota. 1. Chroococcales. Süsswasserflora von Mitteleuropa. Bd. 19(1):548S

Komárek J, Anagnostidis K (2005) Cyanoprokaryota 2. Teil: Oscillatoriales. Süsswasserflora von Mitteleuropa 19/2

Kosiba J, Krztoń W, Wilk-Woźniak E (2018) Effect of microcystins on proto-and metazooplankton is more evident in artificial than in natural waterbodies. Microb Ecol 75(2):293–302

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305

Laliberté E, Legendre P, Shipley B (2014) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12

Lê S, Josse J, Husson F (2008) FactoMineR: an R package for multivariate analysis. J Stat Softw 25(1):1–18

Litchman E, Ohman MD, Kiørboe T (2013) Trait-based approaches to zooplankton communities. J Plankton Res 35(3):473–484

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294(5543):804–808

Lozon JD, MacIsaac HJ (1997) Biological invasions: are they dependent on disturbance? Environ Rev 5(2):131–144

Makino W, Ban S (1998) Diel changes in vertical overlap between *Cyclops strenuus* (Copepoda; Cyclopoida) and its prey in oligotrophic Lake Toya, Hokkaido, Japan. J Mar Syst 15(1–4):139–148

Mason NW, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111(1):112–118

Massicotte P, Frenette JJ, Proulx R, Pinel-Alloul B, Bertolo A (2014) Riverscape heterogeneity explains spatial variation in zooplankton functional evenness and biomass in a large river ecosystem. Landsc Ecol 29(1):67–79

Mouchet MA, Villéger S, Mason NW, Mouillot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Funct Ecol 24(4):867–876

Nebaeus M (1984) Algal water-blooms under ice-cover: with 1 figure and 2 tables in the text. Int Ver Theor Angew Limnol 22(2):719–724

Niswati A, Murase J, Kimura M (2005) Effect of application of rice straw and compost on the bacterial communities associated with *Moina* sp. in the floodwater of a paddy soil microcosm: estimation based on DGGE pattern and sequence analyses. Soil Sci Plant Nutr 51(4):565–571

O'neil JM, Davis TW, Burford MA, Gobler CJ (2012) The rise of harmful cyanobacteria blooms: the potential roles of eutrophication and climate change. Harmful Algae 14:313–334

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'hara RB et al. (2013) Package 'vegan'. Community ecology package, version, 2(9)

Ooms-Wilms AL (1997) Are bacteria an important food source for rotifers in eutrophic lakes? J Plankton Res 19(8):1125–1141

Paerl HW, Huisman J (2008) Blooms like it hot. Science 320(5872):57–58

Paerl HW, Otten TG (2013) Harmful cyanobacterial blooms: causes, consequences, and controls. Microb Ecol 65(4):995–1010

Paerl HW, Fulton RS, Moisander PH, Dyble J (2001) Harmful freshwater algal blooms, with an emphasis on cyanobacteria. Sci World J 1:76–113

Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol Lett 9(6):741–758

Reissig M, Trochine C, Queimaliños C, Balseiro E, Modenutti B (2006) Impact of fish introduction on planktonic food webs in lakes of the Patagonian Plateau. Biol Conserv 132(4):437–447

Roche KF (1987) Post-encounter vulnerability of some rotifer prey types to predation by the copepod *Acanthocyclops robustus*. In: Rotifer Symposium IV. Springer, Dordrecht, pp. 229–233

Roff JC, Turner JT, Webber MK, Hopcroft RR (1995) Bacterivory by tropical copepod nauplii: extent and possible significance. Aquat Microb Ecol 9(2):165–175

Rott E (1981) Some results from phytoplankton counting intercalibrations. Schweiz Z Hydrol 43(1):34–62

Schmera D, Heino J, Podani J, Erős T, Dolédec S (2017) Functional diversity: a review of methodology and current knowledge in freshwater macroinvertebrate research. Hydrobiologia 787(1):27–44

Serrania-Soto CR, Sarma SSS, Nandini S (2011) Studies on comparative population growth of some species of the rotifer Lecane (Rotifera). J Environ Biol 32(4):523

Smirnov NN (1962) *Eurycercus lamellatus* (OF Müller) (Chydoridae, Cladocera): field observations and nutrition. Hydrobiologia 20(3):280

Starkweather PL, Kellar PE (1983) Utilization of cyanobacteria by *Brachionus calyciflorus*: *Anabaena* flos-aquae (NRC-44-1) as a sole or complementary food source. In: Biology of Rotifers. Springer, Dordrecht, pp. 373–377

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Thompson PL, Shurin JB (2012) Regional zooplankton biodiversity provides limited buffering of pond ecosystems against climate change. J Anim Ecol 81(1):251–259

Tillmanns AR, Wilson AE, Pick FR, Sarnelle O (2008) Meta-analysis of cyanobacterial effects on zooplankton population growth rate: species-specific responses. Appl Limnol/Arch Hydrobiol 171(4):285–295

Tilman D (2001) Functional diversity. Encycl Biodiv 3(1):109–120

Tilman D, Isbell F, Cowles JM (2014) Biodiversity and ecosystem functioning. Annu Rev Ecol Evol 45:471–493

Vaughn CC (2010) Biodiversity losses and ecosystem function in freshwaters: emerging conclusions and research directions. Bioscience 60(1):25–35

Villéger S, Mason NW, Mouillot D (2008) New multidimensional functional diversity indexes for a multifaceted framework in functional ecology. Ecology 89(8):2290–2301

Wejnerowski L, Cerbin S, Dziuba MK (2015) Thicker filaments of Aphanizomenon gracile are more harmful to Daphnia than thinner *Cylindrospermopsis raciborskii*. Zool Stud 54(1):2

Wilk-Woźniak E (2019) An introduction to the 'micronet' of cyanoHABs: cyanobacteria, zooplankton and microorganisms. A review. Mar Freshwater Res.

Wilk-Wozniak E, Pociecha A, Bucka H (2001) Phytoplankton–zooplankton interactions, size relations and adaptive responses. A short review. Int J Ecohydrol Hydrobiol 4(1):511–517

Wilson JB (1990) Mechanisms of species coexistence: twelve explanations for Hutchinson's 'Paradox of the plankton': evidence from New Zealand plant communities. N Z J Ecol 13:17–42

Wilson AE, Sarnelle O, Tillmanns AR (2006) Effects of cyanobacterial toxicity and morphology on the population growth of freshwater zooplankton: meta-analyses of laboratory experiments. Limnol Oceanogr 51(4):1915–1924

Woodward GUY (2009) Biodiversity, ecosystem functioning and food webs in fresh waters: assembling the jigsaw puzzle. Freshw Biol 54(10):2171–2187

Work KA, Havens KE (2003) Zooplankton grazing on bacteria and cyanobacteria in a eutrophic lake. J Plankton Res 25(10):1301–1306

Zöllner E, Santer B, Boersma M, Hoppe HG, Jürgens K (2003) Cascading predation effects of Daphnia and copepods on microbial food web components. Freshw Biol 48(12):2174–2193