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Opinion Paper

Beyond *Daphnia*: a plea for a more inclusive and unifying approach to freshwater zooplankton ecology

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Abstract Zooplankton plays a pivotal role in lentic water bodies, linking planktonic primary producers to higher trophic levels and being a cornerstone of the planktonic food web of ponds and lakes. Because of its ease of culture, large size, rich ecology, abundance in northern temperate lakes where limnology is rooted, and the ability to work with clones, *Daphnia* has, in the last centuries grown to

become a key model system in ecology, evolution, and ecotoxicology. Consequently, a vast majority of freshwater zooplankton ecology focuses on the role of *Daphnia*. While generating essential insights, this has also deviated attention from the broad ecological impact of other zooplankton. Here, we emphasize how other zooplankton taxa have an important impact in nature - often in qualitatively different ways than *Daphnia*. We illustrate this point by focusing on two key zooplankton functions (herbivory and stoichiometry) and suggest research to capitalize on the success story of mechanistic ecological, eco-evolutionary, and genomic *Daphnia* work to develop a richer set of model organisms. We currently have the tools to do so and integrating mechanistic insights in multispecies settings would foster a better understanding of the rich diversity and ecology of freshwater zooplankton.

Guest editor: Koen Martens / A Homage to
Henri J.F. Dumont, a Life in Science!

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Introduction

Freshwater metazoan zooplankton (hereafter zooplankton) including crustacean zooplankton such as copepods, cladocerans, and rotifers play an important ecological role in the food web of standing waters (Sterner, 2009). Being crucial prey for (young) fish and key grazers of plankton algae and cyanobacteria,

zooplankton significantly contributes to the functioning of ponds and lakes, and to important supporting and regulating ecosystem services such as the cycling of nutrients, food provisioning to fisheries, maintenance of water quality and transparency, and control of harmful algal blooms (Declerck & De Senerpont Domis, 2022). While zooplankton is quite diverse and the relative composition of rotifers, copepods, and cladocerans varies a lot (Dumont, 1994), the vast majority of studies on zooplankton focus on species of one genus, the water flea *Daphnia*. *Daphnia* are abundant in many lakes and ponds, and they often have a disproportionate effect on, for instance, phytoplankton dynamics because of their generalist feeding mode, wide prey size spectrum, and relatively large body size (Gianuca et al., 2016). Query

Yet, zooplankton consists of widely diverse groups of organisms with different traits. Moreover, *Daphnia* are not the dominant zooplankton in all lakes and ponds around the globe as their dominance tends to decline in warmer or more eutrophic waters where food quality declines and fish predation increases (Senerpont Domis et al., 2013). Given that the ecological function of zooplankton communities depends on the functional traits of dominant groups (Hébert et al., 2016), the disproportionate emphasis on *Daphnia* in research likely leads to a biased perception of the ecological role that zooplankton play in freshwater systems globally. For this reason, we here argue for a more comprehensive assessment of the role and importance of different zooplankton groups that dominate in nature. To achieve this, we encourage building on the success of *Daphnia* as groundwork for developing research lines that broaden the scope of mechanistic, ecological, and evolutionary understanding of zooplankton by including a more diverse set of model organisms.

In the following paragraphs, we start with a note on why there is a strong bias toward *Daphnia* research, then identify how cladocerans (Daphniidae and other groups), copepods, and rotifers differ in their traits, and discuss how these differences likely determine their effect on key freshwater ecosystem functions. Specifically, we illustrate our point for two important traits and related ecosystem functions, i.e., grazing with its potential for top-down control of algae, and organismal stoichiometry with its impact on nutrient cycling. Finally, we provide our perspective on the need of diversifying zooplankton research,

capitalizing on the success of *Daphnia* research. Although the focus here is on rotifers, copepods, and cladocerans, we recognize the value in broadening this approach to other zooplankton groups such as anostracans and heterotrophic protists.

Why are we biased toward *Daphnia*?

Targeted experimental research on the water flea *Daphnia* goes back more than 120 years and involved very elaborate experiments investigating their ecology, plasticity, life history, sexual reproduction, and evolution (Weismann, 1892; Woltereck, 1909; Banta, 1914). The success of *Daphnia* as a model species in ecotoxicology, ecology, and evolution builds on these early studies, but is especially due to its very convenient traits (Miner et al., 2012; Ebert, 2022). *Daphnia* is relatively easy to culture, it has a convenient size to work with (small enough to maintain large populations, but large enough so that one can pick out individuals very efficiently), it is in part transparent so that one can observe tissues, and thanks to its cyclical parthenogenetic reproduction, it is possible to work with clones, i.e., cultures of genetically identical individuals (Lampert, 2006; Miner et al., 2012; Ebert, 2022). The possibility to use clones is a key asset in studies on evolutionary, ecological, and plasticity responses to stressors and environmental change, because it allows one to expose the same genotype to multiple environmental conditions and carry out complex designs testing for genotype–environment, genotype–genotype, and genotype–microbiome–environment interactions (De Meester et al. 2004). The possibility to work with clones is also very useful in genomics because it allows the study of the transcriptomic and metabolomic response of the same genome to different environmental conditions. In addition, large numbers of individuals of the same genotype can easily be cultured when analysis requires large amounts of body tissue (e.g., Orsini et al., 2016). Finally, the cyclical parthenogenetic reproduction also entails that one can obtain sexual offspring. Given that the dormant stages are resting stages that can be archived in layered lake sediments, one can also engage in reconstructing evolution as it occurred in nature through resurrection ecology (e.g., Decaestecker et al., 2007).

Next to these very convenient features of *Daphnia* as a model system, *Daphnia* are strong ecological interactors, being a preferred prey of many fish, a dominant competitor in the zooplankton, target of a broad range of parasites, and a highly efficient grazer on phytoplankton (Miner et al., 2012). This renders mechanistic research on *Daphnia* highly relevant in explaining the structure and dynamics of pond and lake ecosystems, at least where it dominates the zooplankton community.

Why is a more inclusive approach on zooplankton ecology necessary?

While *Daphnia* potentially has the strongest effects on key ecosystem functions such as grazing and nutrient cycling due to its large body size and generalist grazing mode (Gianuca et al., 2016), it is important to realize that *Daphnia* is not the dominant taxon in terms of biomass in many standing waters globally. Lakes in warmer climates, especially those in tropical and sub-tropical lowlands are generally dominated by smaller zooplankton due to stronger top-down control by size selective visual predators (Meerhoff et al., 2012; Lacerot et al., 2013) and lower food quality (Bouvy et al., 2001; Havens et al., 2016). Indeed, regardless of temperature, lakes with very high fish predation pressure tend to be dominated by smaller zooplankton (Jepessen et al., 2012). Moreover, oligotrophic lakes are often dominated by calanoid copepods and smaller cladocerans (Johnson & Luecke, 2012; Straile, 2015), likely because low food concentration reduces the efficiency of *Daphnia* as a generalist filter feeder (DeMott, 1982). Hypereutrophic lakes also tend to be dominated by small cladocerans (e.g., *Bosmina*, *Ceriodaphnia*), rotifers, and copepods due to the relatively high abundance of inedible or low quality phytoplankton prey for *Daphnia* and high levels of size selective fish predation intensity (Ger et al., 2016a, b). Yet, while many field-based studies of lake and pond zooplankton emphasize the abundance and importance of copepods, rotifers, and small cladocerans, this is not reflected in experimental mechanistic work, which is largely *Daphnia*-focused. This creates a gap in terms of a mechanistic understanding of zooplankton ecology. To highlight our plea for more inclusive research, we focus on two major ecosystem functions of zooplankton among *Daphnia*

vs. non-*Daphnia* dominated systems: grazing on phytoplankton and nutrient cycling.

Grazing and top-down effects on phytoplankton

The grazing effect of zooplankton on phytoplankton biomass and community composition is a function of the co-occurring traits of consumer and producer communities (Ger et al., 2016a, b). From the consumer side, zooplankton feeding mode, body size, and prey size spectrum determine potential top-down effects. It is well known that feeding modes differ widely among zooplankton. All *Daphnia* species share a similar feeding mode, being non-selective generalist filter feeders that graze on suspended particles that are larger than the size dictated by the mesh of their filter combs and small enough to fit their mouth (i.e., prey size spectrum). *Daphnia* have the widest prey size spectrum of all zooplankton, and their feeding capacity increases strongly with increasing body size because the surface area of their filter combs increases exponentially with body length (Hansen et al., 1994). This makes their mass-specific ingestion rate among the highest in zooplankton in their size class (Hansen et al., 1997).

In contrast to *Daphnia*, freshwater calanoid copepods individually select nutritious particles from self-created water flows that concentrate prey (i.e., current feeding) (Kiørboe, 2011). Compared to *Daphnia*, copepods have a narrower prey size spectrum that is proportional with body size (Hansen et al., 1994, 1997). Yet, calanoid copepods have similarly high mass-specific ingestion rates as *Daphnia* (Hansen et al., 1997), because both *Daphnia* and calanoid copepods actively increase prey encounter rates either by beating their filter combs or by generating feeding currents (Kiørboe et al., 2018). Cyclopoid copepods and some rotifers (e.g., *Ascomorpha*, *Asplanchna*, *Polyarthra*, *Synchaeta*, and *Trichocerca*) are raptorial feeders that sit and wait to attack relatively large and nutritious individual food items (Kiørboe, 2011; Obbertegger et al., 2011). They have a lower mass-specific ingestion rate compared to *Daphnia* or calanoid copepods because they do not actively increase prey encounter rates (Kiørboe et al., 2018; Leitão et al., 2021). While a number of smaller cladocerans share the same generalist filter feeding mode as *Daphnia*, others are more selective due to the ability to switch between filter feeding and raptorial feeding

(e.g., *Bosmina*) or are scrapers (many chydorids; DeMott & Kerfoot, 1982; Barnett et al., 2007). Their dual feeding mode, however, likely reduces their mass-specific ingestion rate. Finally, microphagous rotifers (e.g., *Brachionus*, *Filinia*, *Kellicottia*, *Keratella*) also generate feeding currents, but they do not have remote detection, making prey selection less efficient compared to copepods (Gilbert, 2022). Rotifers also have relatively high mass-specific ingestion rates, but their smaller body size compared to crustacean zooplankton reduce their optimal prey size and potential grazing effect on phytoplankton (Hansen et al., 1994, 1997). Hence, potential grazing effects are strongest in large-bodied zooplankton with higher mass-specific ingestion rates (i.e., *Daphnia* and calanoid copepods). Grazing effects on phytoplankton occur in two basic ways: effects on total community biomass and/or on the community composition. Below we compare the effects of *Daphnia* vs. other zooplankton in these aspects.

Most research indicates that *Daphnia* has a higher potential for top-down control of phytoplankton than most other zooplankton species (Moss et al., 1991; Gianuca et al., 2016). The strong *Daphnia*-phytoplankton link is a result of generalist filter feeding on a wide prey size range that overlaps with most phytoplankton prey. In contrast, while calanoid copepods are also highly efficient feeders, they select for larger, more nutritious, and motile prey, which typically includes ciliates, flagellated phytoplankton, among others (Kiørboe, 2011). This prey selection results in a weaker top-down control of phytoplankton total biomass because of three reasons. First, because copepods select for relatively large cells, they provide a refuge for smaller phytoplankton species (Sommer et al., 2001). While evidence from freshwaters is limited, due to higher rates of growth and nutrient acquisition of smaller phytoplankton, size selective calanoid grazing may indirectly restore phytoplankton biomass, masking any top-down effects on the total phytoplankton biomass in marine systems (Charalampous et al., 2021), though predicting the benefits of metabolic rates from size alone may be overly simplistic (Sommer et al., 2017).

Second, by grazing on ciliates, copepods release phytoplankton from microbial grazing, and consequently may further increase the biomass of smaller phytoplankton (Adrian & Schneider-Olt, 1999; Zöllner et al., 2003; Sommer & Sommer, 2006). Third,

the selectively grazing copepods also promote the dominance of phytoplankton that are defended through colony formation or toxin production (Leitão et al., 2018; Lürling, 2021). Hence, generalist grazing *Daphnia* has stronger top-down effects on total phytoplankton biomass while selective grazing zooplankton is expected more to shift phytoplankton species composition.

Top-down impacts also depend on the different strategies of zooplankton to deal with inedible or toxic phytoplankton (Lürling, 2021). When *Daphnia* encounters toxic or filamentous phytoplankton in its filter comb, it ejects all collected particles – including nutritious prey – and may even stop grazing until finding a more suitable prey community (Demott et al., 1991, 2001; Rohrlack et al., 1999). While evolved physiological (Chislock et al., 2013) or microbiome-mediated (Macke et al., 2017) tolerance to toxic cyanobacteria may under some circumstances enable *Daphnia* to control cyanobacteria as long as they are within the edible size range, filamentous or otherwise inedible prey often inhibit *Daphnia* top-down control and population growth. In contrast, copepods and rotifers may continue to grow in population size and graze on nutritious particles while selectively avoiding toxic or otherwise inedible prey, with little or no cost to nutritional intake or fitness (Wallace et al., 2006; Ger et al., 2016a; Leitão et al., 2021). The cost of blooms of defended phytoplankton taxa (e.g., cyanobacteria) is therefore higher for *Daphnia* than for selectively grazing copepods or rotifers (Ger et al., 2014). Hence, despite *Daphnia*'s stronger potential for top-down phytoplankton control, stronger grazing by copepods may occur especially when phytoplankton quality is variable (Ger et al., 2019). This stronger grazing is, however, selective, and may therefore shift community composition to a dominance of defended (e.g., toxic) phytoplankton taxa, with longer-term effects in nature still mostly unknown.

Smaller and more selective grazing zooplankton have strong effects on phytoplankton community composition. All zooplankton can potentially change the phytoplankton community composition by grazing on cells within their edible prey size range and passively selecting for the dominance of prey species that are too large to ingest (Porter, 1977). This, however, is passive selection that occurs for both generalist and selective grazers, and is limited to prey that is too large to ingest. In contrast, active size selection

(e.g., copepods) operates within the edible prey size range, and therefore has broader implications. For example, via active avoidance of toxin producing cyanobacteria within the edible size, copepods, but not *Daphnia*, increased the dominance of bloom forming species (Ger et al., 2019). Similarly, by actively selecting larger sized phytoplankton, calanoid copepods increased the dominance of smaller phytoplankton (Sommer et al., 2001). This effect is well known from marine studies, where copepods shift phytoplankton to a bimodal size distribution dominated by smaller or very large species (Peter & Sommer 2012; Charalampous et al. 2021).

During dominance of smaller zooplankton, passive size selection may also shift phytoplankton communities simply because the proportion of phytoplankton taxa that is too large to ingest increases with smaller zooplankton. For example, small cladocerans (e.g., *Ceriodaphnia*) and rotifers promoted the dominance of inedible (morphologically defended) chlorophyte phytoplankton in mesocosms (Hunt & Matveev, 2005). Both *Bosmina* and *Ceriodaphnia* are also known to select for more nutritious prey such as autotrophic flagellates (DeMott, 1982), though their overall effects on phytoplankton composition is less understood (DeMott & Kerfoot, 1982; Gladyshev et al., 1999; Adamczuk, 2016). While the impact of small zooplankton species (i.e., *Bosmina*, rotifers, small copepods) on size distributions of phytoplankton are less well studied, there are indications that they, like marine copepods, may induce a bimodal phytoplankton size distribution with peaks of large and small taxa (Bergquist et al., 1985).

Taken together, the impact of a generalist feeder like *Daphnia* on phytoplankton may be expected to be stronger in terms of biomass than in terms of species composition, whereas the impact of copepods, small cladocerans and rotifers can be expected to be stronger in terms of species and trait composition of phytoplankton communities than in terms of phytoplankton biomass. If *Daphnia* has a strong top-down control on biomass whereas other zooplankton taxa would rather shift community composition, this would be an important qualitative difference with far-reaching effects on the whole food web. Yet it would need comparative analyses of feeding impacts of *Daphnia*, calanoids, cyclopoids, small cladocerans such as chydorids, bosminids, *Ceriodaphnia*, and rotifers under highly standardized conditions and

using controlled and diverse phytoplankton communities to test this hypothesis in a rigorous way.

Existing evidence from comparative studies is not unequivocal for the top-down effects on biomass. Some studies have shown that *Daphnia* but not copepods reduced total phytoplankton biomass (Adrian & Schneider-Olt, 1999). Others have shown that neither *Daphnia* nor copepods reduced total phytoplankton biomass when alone, but together they had complementary effects and reduced phytoplankton biomass as they differentially fed on small and large phytoplankton (Sommer et al., 2001; Sommer & Sommer, 2006). Still others showed that copepods had stronger top-down effects on edible algae than *Daphnia* in the presence of toxic cyanobacteria (Ger et al., 2019). The same studies, however, are in more agreement regarding the role of selective grazers on shifting phytoplankton community composition (Adrian & Schneider-Olt, 1999; Sommer et al., 2001; Sommer & Sommer, 2006; Ger et al., 2019). Hence, whether zooplankton communities are dominated by larger generalists or smaller selective grazers is likely a major factor regulating both the biomass and composition of phytoplankton (Ger et al., 2019). The extent of phytoplankton trait regulation by zooplankton may have ecosystem-wide impacts due to the availability of phytoplankton taxa producing lipids and sterols—critical drivers of trophic transfer efficiency from producers to all trophic levels including fish (Brett & Müller-Navarra, 1997; Winder et al., 2017). We therefore urge future work to compare the effects of zooplankton with contrasting traits on phytoplankton biomass and composition in hypothesis driven experiments of varying complexity.

Ecological stoichiometry and nutrient cycling

As main grazers of primary producers, zooplankton strongly determine the distribution of stocks and fluxes of elements in the pelagic food web (Sterner & Elser, 2002; Vanni, 2002; Atkinson et al., 2017). Zooplankton sequester nutrients but also recycle elements, and may as such enhance primary productivity (Sterner 1986). The relative rates at which particular elements are recycled will depend on the elemental requirements of the dominant zooplankton relative to what is present in its food (Elser & Urabe, 1999). In case of a mismatch between elemental needs and availability, metazooplankton will sequester elements

in short supply and release relatively more of the elements in excess. As a result, by determining the ratios of nutrients that become available for phytoplankton growth, zooplankton grazing may affect phytoplankton stoichiometry, phytoplankton productivity, and trophic transfer efficiency. Depending on differences in somatic growth rate, morphology, physiology, and life history, zooplankton species vary in their nutritional needs, which is also reflected in a pronounced interspecific variation in somatic elemental composition (Sterner & Elser, 2002; Hébert et al., 2016). Although a large portion of this variation is still poorly documented and understood, cross taxon comparisons have revealed at least one important overarching pattern, which is that *Daphnia* is relatively rich in P compared to most other zooplankton taxa (Sterner & Elser, 2002). An important consequence is that a shift in community composition from a domination by *Daphnia* to smaller zooplankton or vice versa may not only result in changed overall grazing pressure and feeding selectivity, but also in changed relative nutrient supply rates to primary producers. This may especially be important in systems that are close to a co-limitation of N with P. For example, a shift in metazooplankton composition from copepods to *Daphnia* has been observed to result in an enhanced P-limitation of phytoplankton and bacterioplankton communities due to the sequestration of P in *Daphnia* biomass and an increase in the N:P ratio of excretion products (Elser et al., 1988, 2000). More work is needed, however, to understand under which conditions such zooplankton-mediated shifts in relative nutrient recycling rates will have an impact on ecosystem functioning. A further exploration of differences in organismal stoichiometry between functional groups of the non-daphnid component of zooplankton communities and the impact of compositional shifts in such communities on relative nutrient recycling rates and its effects on phytoplankton and microbial communities have the potential to contribute to a better understanding of systems where *Daphnia* is not a dominant component of the zooplankton community.

Assets of small cladocerans, copepods, and rotifers as model systems

From the above, it is clear that small cladocerans, copepods, and rotifers are likely to have significantly

different and more diversified effects on ecosystems compared to larger-bodied *Daphnia*. They are, however, generally less well studied, especially in the context of highly controlled, mechanistic experiments, even though a lot of work has been done on specific topics, for instance on grazing selectivity (e.g., DeMott, 1986; DeMott et al., 1991; Ger et al., 2011; Rangel et al., 2020). To illustrate the difference, a search on Web of Science (March 2023) using the keywords “Daphnia,” “copepod,” and “rotifer” yields approximately 17,800, 21,000, and 7,500 papers, respectively. Given that the copepod papers also include marine copepods, adding “freshwater” to the search term yields approximately 3,700, 2,200, and 1,400 papers, respectively. This implies that the genus *Daphnia* attracts equal attention as the combined groups of copepods and rotifers, which harbor > 1,000 species. The difference is even more spectacular if we further add “experiment” to our search term, yielding 900, 420, and 300 papers, respectively. While we are fully aware of the fact that one needs to interpret such searches with caution as they heavily depend on which search term is used, these results do indicate that *Daphnia*, as a genus with a comparatively small number of species, is the focus of a vast amount of research directed toward zooplankton.

It is our plea to use *Daphnia* as a role model to develop research lines that aspire to systematically obtain the same level of detailed mechanistic insight for key copepod, rotifer, and non-*Daphnia* cladoceran taxa (e.g., the very common genera *Chydorus*, *Ceriodaphnia*, *Moina*, and *Simocephalus* or rotifer taxa like *Brachionus*, *Keratella* and *Asplanchna*). This will obviously be a challenge, but the added value would be (i) much better insight into the functioning of pond and lake ecosystems across the globe and (ii) the capacity to combine mechanistic research on these different organism group simultaneously and thus reconstruct a more holistic, multispecies perspective on mechanistic studies (for the case of eco-evolutionary dynamics, see De Meester et al., 2019). Broadening the scope of taxa that are studied in more detail and from a more mechanistic angle will become even more relevant in future, as projections of climate warming in interaction with eutrophication lead to the expectation that large-bodied *Daphnia* may become less dominant in many systems, either as a direct consequence of warming or as a consequence of warming-induced changes in the food web

(lower food quality linked to cyanobacteria and more fish), to the advantage of smaller-bodied zooplankton. Other globally relevant climate-induced stressors on freshwater ecosystems including brownification and salinization have also been associated with a relative loss of *Daphnia* (Leech et al., 2018; Greco et al., 2023; Hébert et al., 2023), further highlighting the importance of a more inclusive approach to mechanistic zooplankton ecology.

The broadening of our perspective to a greater investment in mechanistic studies of copepods and rotifers is possible, among others thanks to novel techniques. Small-bodied cladocerans and rotifers share several of the assets as model organisms that we outlined for *Daphnia* (Serra et al., 2019), including cyclical parthenogenetic reproduction facilitating the experimental study of quantitative genetics, epigenetics (Lemmen et al., 2022), rapid evolutionary adaptation and the exploration of eco-evolutionary dynamics (Declerck & Papakostas, 2017). Not all these species are easy to culture, but several are. Their small size allows faster population growth rate, shorter multi-generation experiments, and larger population sizes, which are important advantages compared to working with *Daphnia*. In rotifers but especially in ciliates, the relatively large population sizes that can be maintained in small volumes makes it more straightforward to experimentally mimic landscapes inhabited by metapopulations or metacommunities (Altermatt et al., 2015). Model systems with very small body sizes present some challenges, for instance to isolate single individuals or perform chemical or molecular analysis. While most of these species have no reference genome, next generation sequencing has made it possible to carry out quite a broad range of genomic studies on non-model species (Altermatt et al., 2015; Arif et al., 2019; Bourgeois & Warren, 2021).

Copepods are a somewhat more complex group to involve in experiments, because they are more difficult to manipulate (i.e., strong escape response), and because of their obligately sexual and more complex life cycle involving several nauplius and copepodite stages. Yet mechanistic work with copepods, including grazing (Ger et al., 2019; Leitao et al., 2021) and genomic (including microbiome) studies, has been on the rise, though the latter studies are still mostly restricted to marine or estuarine waters where copepods dominate zooplankton biomass by far (Homonnay et al., 2012; Jørgensen et al., 2019; Choi et al.,

2021). Most freshwater copepods are large enough to use in grazing or nutrient excretion experiments (Balseiro et al., 1997; Hambright et al., 2007; Schenone et al., 2021), and their gut contents can be analyzed via molecular methods for quantifying in situ prey-specific ingestion (Ger et al., 2018). Common freshwater copepods species that are large and easy enough to culture include the genus *Eudiaptomus* and *Arctodiaptomus* in Eurasia, *Pseudodiaptomus* in East Asia and North America (where it is a common invasive species), *Diaptomus* in the Northern hemisphere, *Notodiaptomus*, and *Boeckella* in the Southern Hemisphere, and *Eurytemora*, which is a recent freshwater invader in the Northern hemisphere (Boxshall & Defaye, 2008).

Conclusion

The water flea *Daphnia* has in the past decades developed into one of the best studied model systems in ecology, evolution, and environmental sciences. This has not only led to crucial novel insights into ecological, developmental, and eco-evolutionary concepts and theory, but has also provided important insights into the structure and functioning of ponds and lake ecosystems. Yet, this latter insight risks to be biased, because the zooplankton of many standing waters is not dominated by *Daphnia* but rather by copepods, smaller-bodied cladocerans, and rotifers. While the further development of *Daphnia* as a general model system will allow us to tackle increasingly complex ecological and eco-evolutionary questions, we argue that it is also very important that there is an enhanced investment in developing additional taxa that are representative of the other major zooplankton groups as model systems. This will have crucial added value in three ways: it will (i) broaden our insight into the functioning of lentic systems, (ii) allow testing hypotheses that were hitherto not possible, and (iii) enable the joint analysis of ecological and evolutionary theory in multispecies settings that representative for natural zooplankton communities. In addition to the topics that were briefly addressed in the current paper, many other research fields and questions will benefit from a broadening of our spectrum of model organisms, including food web studies, inducible defenses in response to communities of invertebrates,

microbial loop dynamics, seasonality, and metabolic theory, to name a few.

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Conflict of interest Authors declare no conflict of interest.

References

- Adamczuk, M., 2016. Past, present, and future roles of small cladoceran *Bosmina longirostris* (O. F. Müller, 1785) in aquatic ecosystems. *Hydrobiologia* 767: 1–11.
- Adrian, R. & B. Schneider-Olt, 1999. Top-down effects of crustacean zooplankton on pelagic microorganisms in a mesotrophic lake. *Journal of Plankton Research* 21: 2175–2190.
- Altermatt, F., E. A. Fronhofer, A. Garnier, A. Giometto, F. Hammes, J. Klecka, D. Legrand, E. Mächler, T. M. Massie, F. Pennekamp, M. Plebani, M. Pontarp, N. Schtickzelle, V. Thuillier & O. L. Petchey, 2015. Big answers from small worlds: a user's guide for protist microcosms as a model system in ecology and evolution. *Methods in Ecology and Evolution* 6: 218–231.
- Arif, M., J. Gauthier, K. Sugier, D. Iudicone, O. Jaillon, P. Wincker, P. Peterlongo & M.-A. Madoui, 2019. Discovering millions of plankton genomic markers from the Atlantic Ocean and the Mediterranean Sea. *Molecular Ecology Resources* 19: 526–535.
- Atkinson, C. L., K. A. Capps, A. T. Rugenski & M. J. Vanni, 2017. Consumer-driven nutrient dynamics in freshwater ecosystems: from individuals to ecosystems: consumer-driven nutrient dynamics in freshwater ecosystems. *Biological Reviews* 92: 2003–2023.
- Balseiro, E. G., B. E. Modenutti & C. P. Queimalffinos, 1997. Nutrient recycling and shifts in N:P ratio by different zooplankton structures in a South Andes lake. *Journal of Plankton Research* 19: 805–817.
- Banta, A. M., 1914. One hundred parthenogenetic generations of *Daphnia* without sexual forms. *Proceedings of the Society for Experimental Biology and Medicine* SAGE Publications 11: 180–182.
- Barnett, A. J., K. Finlay & B. E. Beisner, 2007. Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshwater Biology* 52: 796–813.
- Bergquist, A. M., S. R. Carpenter & J. C. Latino, 1985. Shifts in phytoplankton size structure and community composition during grazing by contrasting zooplankton assemblages I. *Limnology and Oceanography* 30: 1037–1045.
- Bourgeois, Y. X. C. & B. H. Warren, 2021. An overview of current population genomics methods for the analysis of whole-genome resequencing data in eukaryotes. *Molecular Ecology* 30: 6036–6071.
- Bouvy, M., M. Pagano, & M. Troussellier. 2001. Effects of a cyanobacterial bloom (*Cylindrospermopsis raciborskii*) on bacteria and zooplankton communities in Ingazeira reservoir (northeast Brazil). *Aquatic Microbial Ecology* 25: 215–227. <https://doi.org/10.3354/ame025215>.
- Boxshall, G. A. & D. Defaye, 2008. Global diversity of copepods (Crustacea: Copepoda) in freshwater. *Hydrobiologia* 595: 195–207.
- Brett, M. & D. Müller-Navarra, 1997. The role of highly unsaturated fatty acids in aquatic foodweb processes. *Freshwater Biology* 38: 483–499.
- Charalampous, E., B. Matthiessen & U. Sommer, 2021. Grazing induced shifts in Phytoplankton Cell size explain the community response to nutrient supply. *Microorganisms* 9: 2440.
- Chislock, M. F., O. Sarnelle, B. K. Olsen, E. Doster & A. E. Wilson, 2013. Large effects of consumer offense on ecosystem structure and function. *Ecology* 94: 2375–2380.
- Choi, B.-S., D.-H. Kim, M.-S. Kim, J. C. Park, Y. H. Lee, H.-J. Kim, C.-B. Jeong, A. Hagiwara, S. Souissi & J.-S. Lee, 2021. The genome of the European estuarine calanoid copepod *Eurytemora affinis*: potential use in molecular ecotoxicology. *Marine Pollution Bulletin* 166: 112190.
- De Meester, L., A. Gomez & J.C. Simon, 2004. Evolutionary and ecological genetics of cyclical parthenogens. In: A. Moya & E. Font (eds.), *Evolution : from molecules to ecosystems*. Oxford University Press: 122–134.
- De Meester, L., K. I. Brans, L. Govaert, C. Souffreau, S. Mukherjee, H. Vanvelk, K. Korzeniowski, L. Kilsdonk, E. Decaestecker, R. Stoks, & M. C. Urban, 2019. Analysing eco-evolutionary dynamics—The challenging complexity of the real world. *Functional Ecology* 33: 43–59.
- De SenerpontDomis, L. N., J. J. Elser, A. S. Gsell, V. L. M. Huszar, B. W. Ibelings, E. Jeppesen, S. Kosten, W. M. Mooij, F. Roland, U. Sommer, E. Van Donk, M. Winder & M. Lüring, 2013. Plankton dynamics under different climatic conditions in space and time. *Freshwater Biology* 58: 463–482.
- Decaestecker, E., S. Gaba, J. A. M. Raeymaekers, R. Stoks, L. Van Kerckhoven, D. Ebert & L. De Meester, 2007. Host-parasite 'Red Queen' dynamics archived in pond sediment. *Nature* Nature Publishing Group 450: 870–873.
- Declerck, S. A. J. & L. N. de SenerpontDomis, 2022. Contribution of freshwater metazooplankton to aquatic ecosystem services: an overview. *Hydrobiologia*. <https://doi.org/10.1007/s10750-022-05001-9>.
- Declerck, S. A. J. & S. Papakostas, 2017. Monogonont rotifers as model systems for the study of micro-evolutionary adaptation and its eco-evolutionary implications. *Hydrobiologia* 796: 131–144.

- DeMott, W. R., 1982. Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina* 1: Cladoceran grazing. *Limnology and Oceanography* 27: 518–527.
- DeMott, W. R., 1986. The role of taste in food selection by freshwater zooplankton. *Oecologia* 69: 334–340.
- DeMott, W. R. & W. C. Kerfoot, 1982. Competition among Cladocerans: nature of the interaction between *Bosmina* and *Daphnia*. *Ecology* Ecological Society of America 63: 1949–1966.
- DeMott, W. R., Q.-X. Zhang & W. W. Carmichael, 1991. Effects of toxic cyanobacteria and purified toxins on the survival and feeding of a copepod and three species of *Daphnia*. *Limnology and Oceanography* 36: 1346–1357.
- DeMott, W. R., R. D. Gulati & E. Van Donk, 2001. *Daphnia* food limitation in three hypereutrophic Dutch lakes: evidence for exclusion of large-bodied species by interfering filaments of cyanobacteria. *Limnology and Oceanography* 46: 2054–2060.
- Dumont, H. J., 1994. On the Diversity of the Cladocera in the Tropics. In Dumont, H. J., J. Green & H. Masundire (eds), *Studies on the Ecology of Tropical Zooplankton* Springer Netherlands, Dordrecht: 27–38. https://doi.org/10.1007/978-94-011-0884-3_3.
- Ebert, D., 2022. *Daphnia* as a versatile model system in ecology and evolution. *EvoDevo* 13: 16.
- Elser, J. J. & J. Urabe, 1999. THE stoichiometry of consumer-driven nutrient recycling: theory, observations, and consequences. *Ecology* 80: 735–751.
- Elser, J. J., M. M. Elser, N. A. MacKay & S. R. Carpenter, 1988. Zooplankton-mediated transitions between N- and P-limited algal growth: N- and P-limited algal growth. *Limnology and Oceanography* 33: 1–14.
- Elser, J. J., R. W. Sterner, A. E. Galford, T. H. Chrzanowski, D. L. Findlay, K. H. Mills, M. J. Paterson, M. P. Stainton & D. W. Schindler, 2000. Pelagic C:N:P Stoichiometry in a Eutrophied Lake: responses to a Whole-Lake food-web manipulation. *Ecosystems* 3: 293–307.
- Ger, K. A., R. Panosso & M. Lüring, 2011. Consequences of acclimation to *Microcystis* on the selective feeding behavior of the calanoid copepod *Eudiaptomus gracilis*. *Limnology and Oceanography* 56: 2103–2114.
- Ger, K. A., L.-A. Hansson & M. Lüring, 2014. Understanding cyanobacteria-zooplankton interactions in a more eutrophic world. *Freshwater Biology* 59: 1783–1798.
- Ger, K. A., E. Leitao & R. Panosso, 2016a. Potential mechanisms for the tropical copepod *Notodiaptomus* to tolerate *Microcystis* toxicity. *Journal of Plankton Research* 38: 843–854.
- Ger, K. A., P. Urrutia-Cordero, P. C. Frost, L.-A. Hansson, O. Sarnelle, A. E. Wilson & M. Lüring, 2016b. The interaction between cyanobacteria and zooplankton in a more eutrophic world. *Harmful Algae* 54: 128–144.
- Ger, K. A., T. G. Otten, R. DuMais, T. Ignoffo & W. Kimmerer, 2018. In situ ingestion of *Microcystis* is negatively related to copepod abundance in the upper San Francisco Estuary. *Limnology and Oceanography* 63: 2394–2410.
- Ger, K. A., S. Naus-Wiezer, L. De Meester & M. Lüring, 2019. Zooplankton grazing selectivity regulates herbivory and dominance of toxic phytoplankton over multiple prey generations. *Limnology and Oceanography* 64: 1214–1227.
- Gianuca, A. T., J. H. Pantel & L. De Meester, 2016. Disentangling the effect of body size and phylogenetic distances on zooplankton top-down control of algae. *Proceedings of the Royal Society B: Biological Sciences* Royal Society 283: 20160487.
- Gilbert, J. J., 2022. Food niches of planktonic rotifers: Diversification and implications. *Limnology and Oceanography* 67: 2218–2251.
- Gladyshev, M. I., T. A. Temerova, O. P. Dubovskaya, V. I. Kolmakov & E. A. Ivanova, 1999. Selective grazing on *Cryptomonas* by *Ceriodaphnia quadrangula* fed a natural phytoplankton assemblage. *Aquatic Ecology* 33: 347–353.
- Greco, D. A., S. E. Arnott, I. B. Fournier & B. S. Schamp, 2023. Effects of chloride and nutrients on freshwater plankton communities. *Limnology and Oceanography* Letters 8: 48–55.
- Hambricht, K. D., T. Zohary & H. Güde, 2007. Microzooplankton dominate carbon flow and nutrient cycling in a warm subtropical freshwater lake. *Limnology and Oceanography* 52: 1018–1025.
- Hansen, B., P. K. Bjørnsen & P. J. Hansen, 1994. The size ratio between planktonic predators and their prey. *Limnology and Oceanography* 39: 395–403.
- Hansen, P. J., P. K. Bjørnsen & B. W. Hansen, 1997. Zooplankton grazing and growth: scaling within the 2–20- μ m body size range. *Limnology and Oceanography* 42: 687–704.
- Havens, K. E., R. S. Fulton III., J. R. Beaver, E. E. Samples & J. Colee, 2016. Effects of climate variability on cladoceran zooplankton and cyanobacteria in a shallow subtropical lake. *Journal of Plankton Research* 38: 418–430.
- Hébert, M.-P., B. E. Beisner & R. Maranger, 2016. A meta-analysis of zooplankton functional traits influencing ecosystem function. *Ecology* 97: 1069–1080.
- Hébert, M.-P., C. C. Symons, M. Cañedo-Argüelles, S. E. Arnott, A. M. Derry, V. Fugère, W. D. Hintz, S. J. Melles, L. Astorg, H. K. Baker, J. A. Brentrup, A. L. Downing, Z. Ersoy, C. Espinosa, J. M. Franceschini, A. T. Giorgio, N. Göbeler, D. K. Gray, D. Greco, E. Hassal, M. Huynh, S. Hylander, K. L. Jonassen, A. Kirkwood, S. Langenheder, O. Langvall, H. Laudon, L. Lind, M. Lundgren, A. McClymont, L. Proia, R. A. Relyea, J. A. Rusak, M. S. Schuler, C. L. Searle, J. B. Shurin, C. F. Steiner, M. Striebel, S. Thibodeau, P. Urrutia Cordero, L. Vendrell-Puigmitja, G. A. Weyhenmeyer & B. E. Beisner, 2023. Lake salinization drives consistent losses of zooplankton abundance and diversity across coordinated mesocosm experiments. *Limnology and Oceanography* Letters 8: 19–29.
- Homonnay, Z. G., Z. Kéki, K. Márialigeti & E. M. Tóth, 2012. Bacterial communities in the gut of the freshwater copepod *Eudiaptomus gracilis*. *Journal of Basic Microbiology* 52: 86–90.
- Hunt, R. J. & V. F. Matveev, 2005. The effects of nutrients and zooplankton community structure on phytoplankton growth in a subtropical Australian reservoir: an enclosure study. *Limnologia* 35: 90–101.
- Jeppesen, E., M. Søndergaard, T. L. Lauridsen, T. A. Davidson, Z. Liu, N. Mazzeo, C. Trochine, K. Özkan, H. S. Jensen, D. Trolle, F. Starling, X. Lazzaro, L. S. Johansson, R. Bjerring, L. Liboriussen, S. E. Larsen, F. Landkildehus, S. Egemose & M. Meerhoff, 2012. Chapter 6 - Biomanipulation as a Restoration Tool to Combat Eutrophication:

- Recent Advances and Future Challenges. In Woodward, G., U. Jacob & E. J. O’Gorman (eds), *Advances in Ecological Research* Academic Press, Amsterdam: 411–488.
- Johnson, C. R. & C. Luecke, 2012. Copepod dominance contributes to phytoplankton nitrogen deficiency in lakes during periods of low precipitation. *Journal of Plankton Research* 34: 345–355.
- Jørgensen, T. S., B. Petersen, H. C. B. Petersen, P. D. Browne, S. Prost, J. H. Stillman, L. H. Hansen & B. W. Hansen, 2019. The genome and mRNA transcriptome of the cosmopolitan Calanoid Copepod *Acartia tonsa* Dana improve the understanding of copepod genome size evolution. *Genome Biology and Evolution* 11: 1440–1450.
- Kjørboe, T., 2011. How zooplankton feed: mechanisms, traits and trade-offs. *Biological Reviews* 86: 311–339.
- Kjørboe, T., E. Saiz, P. Tiselius & K. H. Andersen, 2018. Adaptive feeding behavior and functional responses in zooplankton. *Limnology and Oceanography* 63: 308–321.
- Lacerot, G., C. Kruk, M. Lüring & M. Scheffer, 2013. The role of subtropical zooplankton as grazers of phytoplankton under different predation levels. *Freshwater Biology* 58: 494–503.
- Lampert, W., 2006. *Daphnia*: model herbivore, predator and prey. *Polish Journal of Ecology* 607–620.
- Leech, D. M., A. I. Pollard, S. G. Labou & S. E. Hampton, 2018. Fewer blue lakes and more murky lakes across the continental U.S.: implications for planktonic food webs. *Limnology and Oceanography* 63: 2661–2680.
- Leitão, E., K. A. Ger & R. Panosso, 2018. Selective grazing by a tropical Copepod (*Notodiaptomus iheringi*) facilitates *Microcystis* Dominance. *Frontiers in Microbiology*. <https://doi.org/10.3389/fmicb.2018.00301>.
- Leitão, E., R. Panosso, R. Molica & K. A. Ger, 2021. Top-down regulation of filamentous cyanobacteria varies among a raptorial versus current feeding copepod across multiple prey generations. *Freshwater Biology* 66: 142–156.
- Lemmen, K. D., K. J. F. Verhoeven & S. A. J. Declerck, 2022. Experimental evidence of rapid heritable adaptation in the absence of initial standing genetic variation. *Functional Ecology* 36: 226–238.
- Lüring, M., 2021. Grazing resistance in phytoplankton. *Hydrobiologia* 848: 237–249.
- Macke, E., M. Callens, L. De Meester & E. Decaestecker, 2017. Host-genotype dependent gut microbiota drives zooplankton tolerance to toxic cyanobacteria. *Nature Communications* Nature Publishing Group 8: 1608.
- Meerhoff, M., F. Teixeira-de Mello, C. Kruk, C. Alonso, I. González-Bergonzoni, J. P. Pacheco, G. Lacerot, M. Arim, M. Beklioglu, S. Brucet, G. Goyenola, C. Iglesias, N. Mazzeo, S. Kosten & E. Jeppesen, 2012. 4 - Environmental Warming in Shallow Lakes: A Review of Potential Changes in Community Structure as Evidenced from Space-for-Time Substitution Approaches. In Jacob, U. & G. Woodward (eds), *Advances in Ecological Research* Academic Press, Amsterdam: 259–349.
- Miner, B. E., L. De Meester, M. E. Pfrender, W. Lampert & N. G. Hairston, 2012. Linking genes to communities and ecosystems: *Daphnia* as an ecogenomic model. *Proceedings of the Royal Society B: Biological Sciences* Royal Society 279: 1873–1882.
- Moss, B., J. Stansfield & K. Irvine, 1991. Development of *Daphnia* communities in Diatom- and Cyanophyte-Dominated Lakes and their relevance to Lake restoration by Biomanipulation. *Journal of Applied Ecology* [British Ecological Society, Wiley] 28: 586–602.
- Obertegger, U., H. A. Smith, G. Flaim & R. L. Wallace, 2011. Using the guild ratio to characterize pelagic rotifer communities. *Hydrobiologia* 662: 157–162.
- Orsini, L., D. Gilbert, R. Podicheti, M. Jansen, J. B. Brown, O. S. Solari, K. I. Spanier, J. K. Colbourne, D. B. Rusch, E. Decaestecker, J. Asselman, K. A. C. De Schamphelaere, D. Ebert, C. R. Haag, J. Kvist, C. Laforss, A. Petrussek, A. P. Beckerman, T. J. Little, A. Chaturvedi, M. E. Pfrender, L. De Meester & M. J. Frilander, 2016. *Daphnia magna* transcriptome by RNA-Seq across 12 environmental stressors. *Scientific Data* Nature Publishing Group 3: 160030.
- Peter, K. H. & U. Sommer, 2012. Phytoplankton cell size: intra- and interspecific effects of warming and grazing. *PLOS ONE Public Library of Science* 7: e49632.
- Porter, K. G., 1977. The plant-animal interface in freshwater ecosystems: microscopic grazers feed differentially on planktonic algae and can influence their community structure and succession in ways that are analogous to the effects of herbivores on terrestrial plant communities. *American Scientist Sigma Xi, the Scientific Research Society* 65: 159–170.
- Rangel, L. M., L. H. S. Silva, E. J. Faassen, M. Lüring & K. A. Ger, 2020. Copepod prey selection and grazing efficiency mediated by chemical and morphological defensive traits of *Cyanobacteria*. *Toxins Multidisciplinary Digital Publishing Institute* 12: 465.
- Rohrlack, T., E. Dittmann, M. Henning, T. Börner & J.-G. Kohl, 1999. Role of microcystins in poisoning and food ingestion inhibition of *Daphnia galeata* caused by the *Cyanobacterium Microcystis aeruginosa*. *Applied and Environmental Microbiology* American Society for Microbiology 65: 737–739.
- Schenone, L., B. Modenutti, N. Martyniuk, M. Bastidas Navarro, C. Laspoumaderes & E. Balseiro, 2021. Modelling key variables for understanding the effects of grazing and nutrient recycling by zooplankton on the freshwater microbial loop. *Freshwater Biology* 66: 2322–2337.
- Serra, M., E. M. García-Roger, R. Ortells & M. J. Carmona, 2019. Cyclically parthenogenetic rotifers and the theories of population and evolutionary ecology. *Limnetica* 38: 67–93.
- Sommer, U. & F. Sommer, 2006. Cladocerans versus copepods: the cause of contrasting top-down controls on freshwater and marine phytoplankton. *Oecologia* 147: 183–194.
- Sommer, U., F. Sommer, B. Santer, C. Jamieson, M. Boersma, C. Becker & T. Hansen, 2001. Complementary impact of copepods and cladocerans on phytoplankton. *Ecology Letters* 4: 545–550.
- Sommer, U., E. Charalampous, S. Genitsaris & M. Moustaka-Gouni, 2017. Benefits, costs and taxonomic distribution of marine phytoplankton body size. *Journal of Plankton Research* 39: 494–508.
- Sterner, R. W., 1986. Herbivores’ direct and indirect effects on algal populations. *Science* 231: 605–607.

- Sterner, R. W., 2009. Role of Zooplankton in Aquatic Ecosystems Encyclopedia of Inland Waters, Elsevier Inc, Amsterdam., 678–688.
- Sterner, R. W. & J. J. Elser, 2002. Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere, Princeton University Press, Princeton.
- Straile, D., 2015. Zooplankton biomass dynamics in oligotrophic versus eutrophic conditions: a test of the PEG model. *Freshwater Biology* 60: 174–183.
- Vanni, M. J., 2002. Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics* 33: 341–370.
- Wallace, R. L., Snell, Terry W., Ricci, Claudia, & Nogrady, Thomas, 2006. Rotifera: Biology, Ecology and Systematics. Kenobi productions Backhuys publ, Ghent Leiden. ISBN: 978-90-804341-7-2 978-90-5782-178-3.
- Weismann, A., & R. C. of P. of Edinburgh, 1892. Die Continuität des Keimplasmas als grundlage einer Theorie der Vererbung : ein Vortrag. G. Fischer, Jena, 1–120 pp, <https://www.biodiversitylibrary.org/bibliography/101535>.
- Winder, M., J. Carstensen, A. W. E. Galloway, H. H. Jakobsen & J. E. Cloern, 2017. The land–sea interface: a source of high-quality phytoplankton to support secondary production. *Limnology and Oceanography* 62: S258–S271.
- Woltereck, R. 1909. Weitere experimentelle Untersuchungen über Artveränderung speziell über das Wesen quantitativer Artunterschiede bei Daphniden. *Verh deutsch zool Ges* 19:110–172.
- Zöllner, E., B. Santer, M. Boersma, H.-G. Hoppe & K. Jürgens, 2003. Cascading predation effects of *Daphnia* and copepods on microbial food web components: *Zooplankton impact on microbial food web*. *Freshwater Biology* 48: 2174–2193.

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