



Review Paper

Contribution of freshwater metazooplankton to aquatic ecosystem services: an overview

Steven A. J. Declerck 

Lisette N. de Senerpont Domis 

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Abstract Although its role in the functioning of aquatic systems is widely recognized, the contribution of freshwater metazooplankton (metazoan plankton) to ecosystem services (ES) is seldom considered. Here we aim at providing a first overview of how this group contributes to ecosystem services according to the Millennium Ecosystem Assessment framework. We show that although metazooplankton hardly generates any provisioning services, it provides crucial support to the generation of other

services. Metazooplankton is important for fisheries because it forms an essential food item for the larval and juvenile stages of most freshwater fish and acts as a trophic link between phytoplankton and microbial communities and the fish community. Through its stoichiometric homeostasis and ability to feed on biochemically complementary food sources it may also act as a buffer against bottom-up effects of nutrient deficiencies in primary producers. Metazooplankton often has a crucial regulatory function by controlling phytoplankton growth and dissolved organic carbon, contributing to the quality of drinking and irrigation water supplies and of the underwater light climate. It provides attractive study material for didactic purposes and some taxa have served as model systems that have considerably aided progress in scientific disciplines, such as ecology, evolutionary biology, ecotoxicology, environmental, and biomedical sciences.

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S. A. J. Declerck (✉) · L. N. de Senerpont Domis
Department of Aquatic Ecology, Netherlands Institute of Ecology, Wageningen, The Netherlands
e-mail: s.declerck@nioo.knaw.nl

S. A. J. Declerck
Laboratory of Aquatic Ecology, Evolution and Conservation, Department of Biology, KU Leuven, Leuven, Belgium

L. N. de Senerpont Domis
Faculty of Geo-Information Science and Earth Observation, University of Twente, Enschede, The Netherlands

L. N. de Senerpont Domis
Faculty of Electrical Engineering, Mathematics and Computer Science, University of Twente, Enschede, The Netherlands

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Introduction

Metazooplankton (i.e., metazoan plankton or multicellular zooplankton) occupies a central position in the pelagic food web. By acting as conveyors of matter and energy, they form a crucial trophic link between primary producers and the heterotrophic

microbial food web on the one hand and the higher trophic levels such as fishes on the other hand. In addition, through grazing, metazooplankton has a major impact on the lower trophic levels and acts as important recycler of nutrients. Although the importance of these functions to aquatic systems is widely recognized, they are rarely discussed explicitly in the context of ecosystem services (ES), which are, according to the Millennium Ecosystem Assessment (MEA; Leemans & Groot, 2003), defined as the benefits that people obtain from ecosystems. There is a long tradition of ecological studies on the functional roles of metazooplankton (Hébert et al., 2017), but, with the exception of marine zooplankton (Lomartire et al., 2021), we are not aware of any overviews of how metazooplankton contributes to the broad range of important ecosystem services that aquatic systems provide. Possibly this is partly because they are an inconspicuous group due to their microscopic size. Probably more important is that they mainly contribute to regulating and supporting services (Potschin-Young et al., 2018), which are services that only indirectly contribute to the provisioning of goods (e.g., supply of good quality water for drinking and irrigation, resource base for fisheries) and the more visible cultural services (e.g., good water for swimming and recreational fishing). Metazooplankton is also difficult to manipulate directly through management measures unlike, for example, water quality or fish communities.

The purpose of this paper is to give an overview of the ways how metazooplankton contributes to the generation of ecosystem services in freshwater systems. Freshwater metazooplankton communities are primarily but not exclusively composed of microcrustaceans (copepods and cladocerans) and rotifers (monogononts and bdelloids). They also include other multicellular organisms, such as larvae of the phantom midge *Chaoborus*, large branchiopods, or freshwater jellyfish. They typically consist of multiple trophic levels, including primary, secondary (e.g., predatory copepods and cladocerans), and even tertiary consumers (e.g., *Chaoborus*). However, most species are omnivores with a diet based on phytoplankton, combined to varying degrees with detritus, heterotrophic protist, bacterial, or other metazooplankton prey (Brönmark & Hansson, 2018).

According to the MEA (Leemans & Groot, 2003) ecosystem services were originally classified into four

major categories: (1) provisioning services, which are “the products obtained from ecosystems, including food, fiber, fresh water and genetic resources”, (2) cultural services, which are “the non-material benefits people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation, and esthetic experience, including, knowledge systems, social relations, and esthetic values”, (3) regulating services, which are “the benefits obtained from the regulation of ecosystem processes”, including the regulation of climate, water, human diseases..., and finally, (4) the supporting services, which are indirectly beneficial to humans because they represent ecosystem processes that support all other ecosystem services. Since the development of the MEA, the ecosystem services approach has been standardized into the Common International Classification of Ecosystem Services (CICES) which provides the international standard for the classification of ecosystem services. CICES is built on the cascade conceptual framework by Potschin-Young et al. (2018), which captures the (non-linear) relationship between ecosystem structure and processes. This framework makes an additional distinction between supporting or intermediate services, and final services such as provisioning, regulating, and cultural services. In contrast to the supporting services, the latter have a more direct relationship with socio-economic systems, as they have a more direct impact on health and well-being of humans and often (but not always) can be expressed in monetary values. Following Potschin-Young et al. (2018) we have exemplified one possible pathway through which metazooplankton can contribute to ecosystem service provisioning (Fig. 1). Recognizing that there are more pluralistic manners through which nature and people interact than through direct benefits for mankind, more recently the nature futures framework (NFF) has been developed (Pereira et al., 2020). The NFF identifies 3 perspectives, i.e., nature for nature (nature having an intrinsic value), nature as culture (nature as part of a cultural landscape), and nature for society, the latter reflecting the more conventional ecosystem services approaches. Based on the latter views, metazooplankton also has an intrinsic value through its contribution to biodiversity and the functioning of aquatic ecosystems.

In line with the other contributions of this special issue we here examine the potential contribution of

The cascade model applied to a zooplankton mediated ES

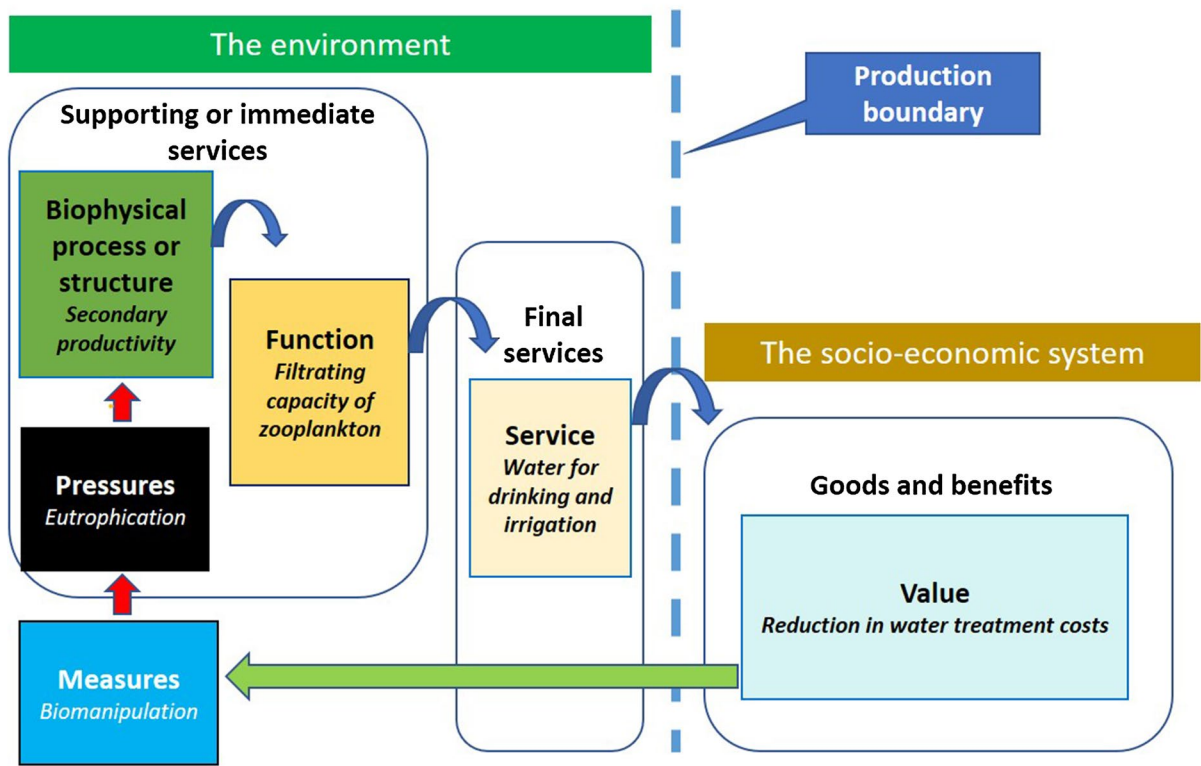


Fig. 1 Application of the cascade model by Potschin-Young et al. (2018) to an ES that is mediated by metazooplankton. The ecosystem service cascade model is a conceptual framework that outlines the key elements of the ecosystem services paradigm by identifying how specific biophysical processes such as secondary productivity influences an ecosystem function like filtration capacity of zooplankton. These supporting or immediate services will subsequently provide a final or provisioning service such as water for drinking and irriga-

tion. This in turn, affects the benefits a particular ecosystem service can provide for people, in this case reduction in water treatment costs. It links to the Driver-Pressures-State-Impact-Response (DPSIR) framework as conceptualized by the European Environmental Agency describing how perceived reductions or increases in benefits (Impact) can motivate measures (Responses) to reduce the pressures on the state of the environment

metazooplankton to ecosystem services for each ES category as defined by the MEA (Leemans & Groot, 2003). These contributions are identified on the basis of the scientific knowledge that is currently available about the functional roles that metazooplankton plays in freshwater ecosystems. We note that these contributions mainly reflect a potential. In any water body, the realization of this potential will, however, depend on the context shaped by food web structure and environment. As such, providing an encompassing overview of zooplankton-mediated ES per water body type, ecoregion, or climatic zone is beyond the scope

of our review. We rather provide a first overview of zooplankton-mediated ES and discuss the role of food web structure and environment as well as ways how ecosystem management may act upon them. In addition, we address the different routes through which metazooplankton may compromise services. The classification model for ecosystem services proposed by the MEA (Leemans & Groot, 2003) is not always applicable to metazooplankton and in some cases, we took a more liberal approach to its terminology or classification criteria to allow proper discussion of ecosystem services provided by this group.

Supporting services

Metazooplankton serves as a link between trophic levels

Metazooplankton supports fisheries

River and lacustrine-based freshwater fisheries provide a substantial fraction of human populations with locally sourced, low-cost protein, especially in regions with low food security (Amarasinghe & De Silva, 2015; McIntyre et al., 2016). Due to its central position in the pelagic food web and its role as food source for larval and juvenile fish, metazooplankton provides an important supporting function to this important ecosystem service. Metazooplankton consumes phytoplankton primary producers and several components of the microbial food web and serves as an essential food source for the larval and often also part of the juvenile development of the majority of freshwater fish species, irrespective of their adult feeding niche (Lazzaro, 1987; Fernando, 1994; Nunn et al., 2012). As a result, the availability of metazooplankton prey represents a crucial factor determining fish recruitment (Dettmers & Wahl, 1999; Cowan et al., 2000; Burrow et al., 2011). Larval and juvenile fish of various species in temperate lakes (e.g., European whitefish, *Coregonus lavaretus* (Linnaeus, 1758), Eurasian perch, *Perca fluviatilis* (Linnaeus, 1758) and burbot, *Lota lota* (Linnaeus, 1758) hatch in spring and move to the pelagic to forage on zooplankton or perform diurnal migrations between the pelagic and littoral zones (e.g., roach, *Rutilus rutilus* (Linnaeus, 1758) and bream, *Abramis brama* (Linnaeus, 1758). In contrast, fish larvae and juveniles of many other fish species mainly rely on the littoral habitat of shallow lakes, flood plains, and reservoirs, especially in the tropics (Fernando, 1994; Teixeira de Mello et al., 2009), and feed on metazooplankton, insects and other micro- and mesofauna. This also holds for many riverine species. Although the higher reaches of rivers do not provide suitable habitats to zooplankton, many of their fish populations depend strongly for their recruitment on littoral habitat in connected floodplains (Nunn et al., 2012). Typically, a shift in prey selectivity and diet composition takes place during the ontogenetic development. Small metazooplankton like rotifers form an important food source mainly for fish larvae (e.g., larvae of

cyprinids), whereas copepods and cladocerans form an important part of the diet of both larva and juveniles (Nunn et al., 2012). As fish juveniles grow and their gape size increases, their food preference shifts toward larger prey, such a large metazooplankton (*Daphnia*) and non-planktonic prey such as benthic and littoral macroinvertebrates or fish larvae (Mayer & Wahl, 1997).

Metazooplankton also forms a primary food base for specialized zooplanktivore fish, especially in large pelagic systems (e.g., stolothrissids of Lake Tanganyika, ‘barbs’ in Lake Tana (Dejen et al., 2006). However, most freshwater systems lack specialized planktivores and, with a few exceptions, productivity of such populations is relatively low and their global significance to fisheries limited (Fernando, 1994; Reynolds, 2008). Nevertheless, the importance of small pelagic fish as sustainable food source for local communities is increasingly recognized, especially in Africa (Kolding et al., 2019). In other functional groups, the relative importance of metazooplankton to the diet of adult fish is variable but tends to decrease toward smaller and shallower systems when access to other invertebrate prey from benthic and littoral origin increases (Vander Zanden et al., 2006; Reynolds, 2008). Fish populations may nevertheless feed opportunistically on zooplankton when present in high abundances (Townsend et al., 1986; Hoogenboezem et al., 1992) or when alternative food sources are temporarily scarce (Anton-Pardo & Adámek, 2015).

Use of metazooplankton in aquaculture

Metazooplankton is used as food supplement in aquaculture as a more sustainable alternative to traditional fish feed. Conventionally, fish in freshwater aquaculture are pulse fed using fish pellets consisting of fishmeal, oil, and/or cereal. The use of such pellets is unsustainable and leads to high nutrient discharge from aquaculture systems, with the industry looking for more environmentally friendly alternatives (Tóth et al., 2020). A meta-analysis comparing live food (i.e., metazooplankton) with compound food (such as aforementioned pellets) showed that fish larvae had 2.5 lower mortality risk when fed with live metazooplankton (Sales, 2011). The benefits of live metazooplankton food have also been identified for adult fish, such as carp, resulting in weight gain and higher

survival (Anton-Pardo & Adámek, 2015). Unlike fish pellets, live metazooplankton will not aggregate on the water surface or sediment out and thus remain available for visual predators such as fish larvae for longer periods (Conceição et al., 2010). Unfortunately, a complete substitution of inert diets such as fishmeal by live metazooplankton is often economically not viable and may involve operational risks (Tóth et al., 2020). Nevertheless, live food can complement the diet and contribute to a more sustainable aquaculture industry.

Metazooplankton acts as a link between the microbial food web and fish

As part of the microbial loop (Azam et al., 1983), metazooplankton may play an important role by shunting energy and nutrients from the microbial foodweb loop to the pelagic food chain. Heterotrophic bacteria grow on particulate and dissolved organic matter and are consumed by larger heterotrophic protists, such as nanoflagellates and ciliates. In contrast to metazooplankton, these microbial components are inaccessible as food to fish because of their small size. Metazooplankton, however, is a grazer of these microbial organisms (Jürgens, 2000; Schenone et al., 2021) and may as such act as a trophic link between the microbial food web and fish. Especially in nutrient-poor systems with low primary productivity and high allochthonous carbon input, metazooplankton may through this pathway provide the aquatic food chain with an important additional energy source (Taipale et al., 2008; Emery et al., 2015).

A potential disservice: metazooplankton as a vector of human pathogens

Zooplankton can also act as a vector of human pathogens and thus provide a potential disservice to humans. As zooplankters often perform diel vertical and horizontal migration, hitchhiking bacteria may be able to exploit favorable conditions in different parts of waterbodies (Grossart et al., 2010). Although this may facilitate the ES that are realized by microbial communities, it can also contribute to the wider distribution of human pathogens. To exemplify, *Vibrio cholerae* (Pacini, 1854) an infectious disease causing life-threatening diarrhea has been frequently associated with chitinous zooplankton, such as copepods,

rotifers, and cladocerans (Huq et al., 1983; de Magny et al., 2011). The One Health approach recognizes that reducing water-related exposure to human pathogens, such as through zooplankton vectors, requires the understanding of interactions between human, animal, and environmental health and identification of critical exposure pathways (O'Brien & Xagorarakis, 2019; de Senerpont Domis & Teurlincx, 2020). For zooplankton-mediated transfer, these critical pathways are often through the use of water for drinking and sanitation and likely require early detection through data-driven predictive modeling (O'Brien & Xagorarakis, 2019).

Metazooplankton acts as a buffer against nutritional deficiencies at the producer level

In addition to the trophic transfer of energy, metazooplankton also acts as a conveyer of other important nutrients to higher trophic levels, such as nitrogen (N) and phosphorus (P), as well as several biochemical substances produced by primary producers or microbial organisms, such as essential fatty acids, amino acids, sterols, and vitamins (Brett & Muller-Navarra, 1997; Müller-Navarra, 2008; Kainz et al., 2009). Depending on taxonomic composition and ambient environmental conditions, primary producers show strong variation in proportions of these constituents and deficiencies in biochemical substances may negatively impact not only metazooplankton productivity, but also the quality of metazooplankton as food for fish. Metazooplankton, however, may buffer such deficiencies in various ways. Although metazooplankton itself has no or only limited abilities to produce essential fatty acids or sterols (Müller-Navarra, 2008) it is believed to be able to complement nutrient deficiency of primary producers with nutrients from other food sources. For example, in addition to their potential toxicity and unpalatability (Ger et al., 2016), cyanobacteria are also poor in some essential biochemical substances, such as PUFA and sterols (Von Elert et al., 2003; Martin-Creuzburg et al., 2008). Metazooplankton is able to alleviate potential deficiencies associated with cyanobacterial blooms by grazing on protists such as heterotroph nanoflagellates and ciliates which are known to be able to biosynthesize PUFA and sterols de novo or by modifying short-chain PUFA into EPA and DHA (Bouvy et al.,

2001; Koski et al., 2002). Furthermore, nutrient deficiencies may also be complemented by essential nutrients originating from the mycoloop, a pathway in which nutrients from host cells are transferred to metazooplankton via the zoospores of parasitic chytrids (Kagami et al., 2004, 2014). Cyanobacteria and other large, non-edible phytoplankton suffer from chytrid infections. Grazing on freeliving zoospores produced by these infections may provide metazooplankton with sources of essential fatty acids that originate from the phytoplankton hosts and sterols that are produced *de novo* by the chytrids (Kagami et al., 2007; Agha et al., 2016; Gerphagnon et al., 2019). Metazooplankton may also be capable of mitigating potential nutritional deficiencies when C-sources from allochthonous origin predominate as energy source. These C-sources (tPOM, tDOM) and their associated communities of heterotrophic bacteria are poor in essential fatty acids and sterols. Metazooplankton may, however, alleviate these nutritional constraints by grazing on heterotrophic protists that are able to synthesize these components *de novo*. Through such trophic upgrading, metazooplankton enhances its own productivity and at the same time provides a richer and more balanced food source to higher trophic levels such as fish.

In addition, metazooplankton is also believed to alleviate the degree of stoichiometric mismatch between primary producers and higher trophic levels of consumers that may be caused by P- or N-limitation. The elemental composition of phytoplankton varies strongly in response to the availability of nutrients and light, whereas the composition of consumers is much more constant (Sterner & Elser, 2002). Metazooplankton has the ability to capture and retain limiting elements and eliminate excess elements by varying element-specific uptake, assimilation, and excretion rates (Meunier et al. 2014). This stoichiometric homeostasis of metazooplankton may provide a buffer against variation in the elemental composition of primary producers and as such stabilize trophic transfer efficiency (Golz et al., 2015). It should, however, be noted that such trophic upgrading has its limitations. The maintenance of homeostasis comes with the cost of resource loss and reduced productivity while its strength also has limits (Meunier et al., 2014; Zhou & Declerck, 2019). As such effects of

nutrient limitation may still travel up the food chain (Boersma et al., 2008).

A potential disservice: trophic transfer and biomagnification of pollutants and toxins

Although metazooplankton plays a role in trophic upgrading, it also plays a role in the trophic transfer and biomagnification of pollutants and toxins. Biomagnification by metazooplankton has been shown for a wide range of potential harmful substances, such as perfluorinated compounds (Xu et al., 2014) or heavy metals like mercury (Watras & Bloom, 1992; Pickhardt et al., 2005) and arsenic (Chen & Folt, 2000). In addition to the chemical–physical characteristics of the compound (Xie et al., 2015; Hoondert et al., 2020), the strength of biomagnification by metazooplankton has been suggested to depend on the trophic position of the species and its traits, e.g., lipid content, biomass, and the extent of vertical migration behavior (Le Jeune et al., 2012). Whereas, there is some evidence for biomagnification of cyanotoxins by zooplankton (Kozłowsky-Suzuki et al., 2012), biodilution seems to be the predominant process (Ibelings & Havens, 2008; da Ferrão-Filho & Kozłowsky-Suzuki, 2011; Papadimitriou et al., 2012).

Metazooplankton as a main recycler of elements

Because of its role as grazer on phytoplankton and the microbial plankton community, metazooplankton has a large impact on the distribution of stocks and fluxes of elements in the pelagic food web (Sterner & Elser, 2002; Vanni, 2002; Atkinson et al., 2017). By grazing producers, metazooplankton recycle elements and as such enhance primary productivity. Stimulation of primary productivity by nutrient recycling may even entirely compensate for metazooplankton grazing losses (Sterner, 1986). Conversely, during periods of sustained growth metazooplankton can also increase nutrient limitation of phytoplankton by sequestering limiting nutrients (Urabe et al., 1995).

Metazooplankton grazing may also affect phytoplankton stoichiometry by determining the ratios of nutrients that become available for phytoplankton growth. In case of stoichiometric mismatch, metazooplankton maintains stoichiometric homeostasis by sequestering elements in short supply and by releasing relatively more of the elements in excess. The

recycling rate of a particular element will thus depend on the elemental requirements of the dominant metazooplankton relative to what is present in its food (Elser & Urabe, 1999). Metazooplankton species differ in their somatic element composition (Sterner & Elser, 2002; Teurlinckx et al., 2017). Some species have a high P-content (e.g., *Daphnia*) with a low N:P ratio, while other species tend to have a low P-content and high N:P ratio (e.g., adult copepods, *Bosmina*). Hence, under certain circumstances (Andersen, 1997; Daufresne & Loreau, 2001), a shift in metazooplankton composition from e.g., copepods to *Daphnia* may result in an enhanced P-limitation for phytoplankton and bacteria 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). Such changes in the relative ability of nutrients may also alter the taxonomic and functional composition of phytoplankton communities (Attayde & Hansson, 1999; Hall, 2009) and potentially affect transfer efficiency of energy and nutrients to higher trophic levels.

Regulatory services

Water filtration: metazooplankton as a regulator of phytoplankton biomass and dissolved organic matter

Production of toxins by cyanobacteria may hamper drinking water supply and represent a threat to human and animal health (Chorus & Bartram, 1999; Westrick et al., 2010). In addition, the presence of large amounts of dissolved organic matter may interfere with drinking water provisioning, because they lead to an increased application of disinfection products that produce carcinogenic byproducts and because they increase the overall treatment costs due to higher coagulation demands (Sharp et al., 2006). Metazooplankton has the potential to increase the natural filtration capacity of surface waters, by reducing both dissolved organic matter levels (Salonen & Hammar, 1986) as well as the biomass of phytoplankton and microbial communities (Cyr & Pace, 1992).

The degree to which metazooplankton is able to control phytoplankton biomass depends strongly on the features of both communities (Ger et al., 2014; Colina et al., 2016). The ability of metazooplankton to suppress phytoplankton is largely dependent on its body size, feeding mode, prey selectivity, and

tolerance to cyanotoxins (Cyr & Curtis, 1999). Phytoplankton communities are often functionally very diverse and composed of groups that vary in size, morphology, palatability, and toxicity (Litchman & Klausmeier, 2008). The capacity of copepods and rotifers to reduce entire phytoplankton communities is generally limited because they do not graze all components of the phytoplankton, due to limitations in food particle size range and their selective feeding mode (Cyr & Curtis, 1999; Colina et al., 2016). As such, selective grazing on the small, edible phytoplankton component, and the recycling of their nutrients may even stimulate the growth of the inedible fraction of the phytoplankton community and induce harmful algal blooms (HAB's; Mitra & Flynn, 2006; Ger et al., 2014). In contrast, most pelagic cladocerans are nonselective filter feeders (Gophen & Geller, 1984). Their capacity to suppress phytoplankton is strongly determined by their body size given that body size determines the maximum ingestible food particle size (Burns, 1968; Cyr & Curtis, 1999). As a result, metazooplankton communities dominated by large cladocerans, especially large members of the genus *Daphnia*, have the potential to suppress phytoplankton biomass and prevent blooms of harmful toxic cyanobacteria, even under nutrient-rich conditions.

There are nevertheless several circumstances that potentially prevent metazooplankton from controlling phytoplankton biomass and HAB's. Predation by fish is a very common and important factor limiting grazing pressure of metazooplankton on phytoplankton (Shapiro & Wright, 1984; Carpenter et al., 1985), in temperate but especially also in subtropical and tropical lakes (Jeppesen et al., 2012; Meerhoff et al., 2012). Planktivorous fish are very efficient visual predators that feed selectively (Lazzaro 1987) and have the ability to suppress populations of large metazooplankton. Doing so they cause a shift in the metazooplankton community toward smaller size classes and functional groups with more selective feeding modes and a reduced ability to ingest large phytoplankton size classes (e.g., copepods, rotifers, small cladocerans). In addition, the ability of metazooplankton communities to exert top-down control on phytoplankton may strongly depend on its functional composition and be reduced if this community consist of a large share of large colonies or filaments, unpalatable (mucilaginous sheaths) or toxic taxa (Mitra &

Flynn, 2006; Ger et al., 2014; Lürling, 2021). Despite a large food particle size range, even large *Daphnia* are limited in the size of food particles they are able to ingest. Due to their aselective feeding large *Daphnia* may even be especially sensitive to the presence of toxic cyanobacteria or filaments that interfere with their food uptake (Ger et al. 2014, 2016). Nevertheless, there is evidence that *Daphnia* is able to prevent or suppress cyanobacterial blooms (Chislock et al., 2013a; Ekvall et al., 2014), depending on initial conditions and the degree of tolerance of *Daphnia* to toxins (Chislock et al., 2013b). High aselective grazing by metazooplankton may also favor small fast-growing phytoplankton cells over larger, more slowly growing cells or colonies and contribute to the edibility of the phytoplankton community.

Climate regulation: role of metazooplankton in carbon storage and generation of greenhouse gas emissions

Metazooplankton grazing may profoundly affect the biogeochemical cycling of C. Depending on the context, metazooplankton may contribute in very different, often opposing ways to the processes that determine the balance between C-capture and release and the contribution of different molecules (CO₂ and CH₄) to greenhouse gas emissions by freshwater systems. In oligotrophic boreal lakes with low primary productivity and high allochthonous C-input, metazooplankton has been found to increase emissions of the very potent greenhouse gas CH₄ by its grazing on methane-oxidizing bacteria (Devlin et al., 2015). In contrast, lakes with higher nutrient loading and primary productivity have the potential to act as C-sink (Schindler et al., 1997; Balmer & Downing, 2011; CO₂ emissions < 0). When not controlled by fish (Schindler et al., 1997; Atwood et al., 2013), metazooplankton grazing may reduce C-capture. However, by doing so it may also reduce C-enrichment and deoxygenation of the sediments and conversion of C-rich substances into methane. The processes that determine the C-balance in and greenhouse gas emissions by freshwater systems (i.e., the CO₂ equivalent balance) are determined by multiple interacting factors and processes, such as primary productivity, terrestrial C-inputs, eutrophication and temperature (Grasset et al., 2020), lake depth, stratification and

anoxia, bioturbation, and fish predation effects on zooplanktonic and benthic communities (Oliveira Junior et al., 2019; Colina et al., 2021). So far, not much attention has been given to the quantitative role of metazooplankton in these processes.

Provisioning services

Although metazooplankton supports fisheries by providing an essential food resource to fish (see ‘Supporting services’), they are not commonly considered for human consumption. Marine metazooplankton has been explored as a human food source in the past (Clarke & Bishop, 1948; Geiger, 1958) and is valued for its high lipid content and presence of anti-oxidants (Eysteinnsson et al., 2018). However, the technical challenges in terms of harvesting makes this at present not an economically and environmentally viable alternative to fish.

Cultural services

Educational value

The didactic values of metazooplankton were recognized as early as the middle of the last century (Sherman, 1962). The intriguing multiplicity of life forms in a metazooplankton sample appeals as a visual illustration of biodiversity and provides rewarding material for a hands-on introduction to community ecology (e.g., identification of species, calculation of biodiversity indices, demonstration of compositional responses of communities to natural and anthropogenic environmental gradients). Furthermore, especially the larger cladocerans (e.g., *Daphnia*, *Simonecephalus*) and rotifers (*Brachionus*) are very suitable for experiments because they are easy to grow and manipulate. These groups are also transparent, making them valuable study material for the life observation of functioning organs. In addition, they are easy to use in simple behavioral experiments (e.g., demonstration of predator avoidance behavior; optimal foraging) or experiments that illustrate the importance of trophic interactions (e.g., suppression of phytoplankton; the impact of selective grazing).

Contribution to scientific developments

Metazooplankton has contributed significantly to progress in scientific disciplines, such as ecology, evolutionary biology, and ecotoxicology. Cladocerans and rotifers in particular share a number of features that make them very amenable for experimentation, such as small body size, ease of culture and handling, and cyclic parthenogenetic reproduction (Seda & Petrusek, 2011; Declerck & Papakostas, 2017). Clonal reproduction permits individual genotypes to be maintained for many generations in the lab and be replicated in experiments, making it possible to easily tease apart genetic and plastic components of trait variation. Especially species of the genus *Daphnia* have played a key role in a number of scientific developments. *Daphnia* was one of the very few arthropods in the list of model species for biomedical research from the US National Institutes of Health and is no doubt the best studied aquatic invertebrate (Seda & Petrusek, 2011). Species such as *Daphnia pulex* (Leydig, 1860) and *Daphnia magna* (Straus, 1820) have also widely been used as a model organism in ecology and evolution (Peters & de Bernardi, 1987; Lampert, 2011; Seda & Petrusek, 2011), including the study of phenotypic plasticity (e.g., cyclomorphosis and predator-induced morphological defenses), gene expression, ecological genomics, epigenetics, behavior (e.g., vertical migration), the evolution of sex, aging, reproductive biology, and host–parasite and host–microbiome interactions (e.g., Cousyn et al., 2001; Ebert, 2005; Decaestecker et al., 2007; Shaw et al., 2008; Orsini et al., 2011; Harris et al., 2012; Miner et al., 2012; Macke et al., 2017). Due to its high sensitivity, *Daphnia* is also a very important model organism in ecotoxicology and stress ecology (Altshuler et al., 2011; Tkaczyk et al., 2021) and it has proven to be also very promising for studying microevolutionary adaptation to new, man-made systems such as the urban environment (Brans et al., 2017). In addition, a number of monogonont and bdelloid rotifers, especially from the genera *Brachionus* and *Adineta*, are widely used in ecological, evolutionary, ecotoxicological, and aging studies (e.g., Mark Welch & Meselson, 2000; Gómez et al., 2002; Fontaneto et al., 2009; Dahms et al., 2011; Flot et al., 2013; Declerck & Papakostas, 2017; Gribble & Mark Welch, 2017; Serra et al., 2019).

Indicator value

Metazooplankton has a lot of potential to contribute to a more effective monitoring and management of freshwater ecosystems because of their indicator value. Many studies have shown that metazooplankton is highly sensitive to a multitude of environmental factors (Jeppesen et al., 2011; Pinel-Alloul et al., 2021) that play at a wide range of different scales, e.g., eutrophication (Jeppesen et al., 2000; Muñoz-Colmenares et al., 2021), chemical pollutants (Sánchez-Bayo et al., 2011; Xiong et al., 2020), salinity (Bruce et al., 2009), acidification (Anas et al., 2013) and decalcification (Jeziorski et al., 2008), changes in land use (e.g., agriculture, residential development and urbanization; Gélinas & Pinel-Alloul, 2008; Schindler, 2009), or climate warming (Carter et al., 2017). Due to their central position in the food web and the fact that they are strongly influenced by both bottom-up and top-down mechanisms, features of metazooplankton communities also provide information regarding trophic interactions, such as degree of zooplanktivory by fish and invertebrate predators (Jeppesen et al., 2003; Gélinas & Pinel-Alloul, 2008; Bruce et al., 2010) and the ability of zooplankton to control phytoplankton biomass. Based on this knowledge, several potentially informative zooplankton-based indicators have been proposed (Jeppesen et al., 2011; Muñoz-Colmenares et al., 2021). Depending on their tolerance to specific environmental conditions, particular species or species groups may serve as indicators of certain water quality parameters (Anas et al., 2013). Alternatively, a community-based approach can be taken where indicators are based on, e.g., variation in species composition, ratios between specific taxa, total zooplankton biomass, biomass and population size structure of specific taxa or taxonomic groups or the biomass ratio among trophic levels (e.g., zooplankton to phytoplankton biomass ratio) (Jeppesen et al., 2011). Because the three major metazooplankton groups (rotifers, cladocerans, and copepods) comprise both many pelagic and macrophyte-associated taxa, the relative abundance of such taxa has also proven to be a useful indicator of the relative importance of pelagic versus littoral habitat in paleolimnological records (Davidson et al., 2007). However, caution is warranted when applying many of these indices along large environmental gradients, as region-specific circumstances may modify species responses, while the

presence of cryptic species may obscure relationships (Zettler et al., 2013). In order to remediate the consequences of such context dependence, large-scale validation and intercalibration is highly needed (Poi-kane et al., 2014) but lacking for metazooplankton. For example, the fact that zooplankton is not included as a Biological Quality Element in EU Water Framework Assessments has undoubtedly hampered the wide use of such indicators on the European continent (Jeppesen et al., 2011). This is unfortunate given that zooplankton is easy to sample and given that the analysis of its communities is a very cost-effective way to gain information on ecological status and functioning of freshwater systems compared to other groups (e.g., fish) while it also provides information complementary to that yielded by other groups (Davidson et al., 2010; Jeppesen et al., 2011). Zooplankton could potentially also be useful as indicator of specific ecosystem services. This approach has been operationalized for terrestrial species in agricultural landscapes (Birkhofer et al., 2018), but could be useful for aquatic systems if cause–effect relationships between the presence/absence of indicator species and the provisioning of certain ES would be substantiated.

Management of metazooplankton-derived ecosystem services

The degree to which a metazooplankton community will contribute to specific ecosystem services in a given water body will strongly depend on the ecological context. As explained above, the biomass and functional composition of the metazooplankton community will be strongly determined by nutrient loading and trophic state, predation regime, and the composition of phytoplankton and microbial communities. For this reason, metazooplankton cannot be considered as an ecosystem engineer according to the classical definition (Jones et al., 1994). From a management perspective it is nearly impossible to directly manipulate metazooplankton communities, in contrast to other groups, such as fish or, in some cases, also macrophytes. However, to achieve specific management goals the regulating and supporting functions performed by metazooplankton may still be enhanced through indirect manipulation. A nice example is provided by the restoration of eutrophic shallow lakes through food web manipulation

(“biomanipulation”). Biomanipulation (Shapiro & Wright, 1984; Perrow et al., 1997; Hansson et al., 1998; Jeppesen et al., 2012) is a technique that aims at the restoration of a clearwater stable state (Scheffer et al., 1993) characterized by transparent water, the absence of cyanobacterial blooms, and an extensive submerged aquatic vegetation. It usually involves the removal of planktivorous and benthivorous fish stocks, often combined with the introduction of piscivorous fish. One of the important mechanisms that contribute to the success of biomanipulation is the biomass increase of large metazooplankton due to the reduction in size selective zooplanktivory (Carpenter & Kitchell, 1993; Ekvall et al., 2014). By suppressing phytoplankton, metazooplankton contributes to a suitable light climate for submerged macrophyte growth, even under conditions of high nutrient loadings. Although biomanipulation has proven to be very successful in several cases, the long-term success of such intervention is largely determined by the extent to which the import of nutrients can be reduced and stocks of planktivorous and bottom-dwelling benthic fish can be kept under control (Gulati & Van Donk, 2002). In subtropical and tropical climate zones, the role of zooplankton as a factor mediating the restoration of shallow lakes is less certain, given the near absence of efficient herbivores, like *Daphnia*, and the high recovery potential of planktivore fish populations after fish removal. Compared to temperate regions, fish in warm climates tend to be smaller, more abundant, more omnivorous, and able to forage and recruit throughout the year (Lazzaro, 1997; Jeppesen et al., 2012; Meerhoff et al., 2012; Lacerot et al., 2013, 2021), which all results in a considerably higher and continuous predation pressure on zooplankton.

In contrast to lake restoration, aquaculture practices aim at supporting the function of metazooplankton as food for fish through the addition of fertilizers (Green, 2015). Fertilizers boost primary productivity and hence the resource base of metazooplankton. Obviously, such management will trade off with the grazing function of metazooplankton that contributes to greater water clarity and is also much more likely to induce blooms of harmful algae.

Conclusion

From our review, metazooplankton may seem to have limited direct benefits for humans. However, it indirectly contributes to a plethora of important ecosystem services, such as provisioning of fish for human consumption, contributing to nutrient cycling and the natural filtration capacity of water, and playing a role in global climate regulation. Its value as a model organism for ecology, evolutionary, and molecular biology as well as ecotoxicology is widely recognized by the scientific community. Its link with water quality and food web structure makes metazooplankton a potentially powerful ecological indicator. Unfortunately, although recognized by some environmental assessment schemes (Yurista et al., 2005), this did not lead to its uptake as a biological quality criterion in the European Water Framework Directive (Jeppesen et al., 2011). As outlined by Keeler et al. (2012), water quality is not an ecosystem service as such but changes in water quality have a direct consequence for the provisioning of goods and services from aquatic ecosystems. Failure to recognize the important role metazooplankton has in maintaining good ecological water quality, leads to an under perception of metazooplankton through the lens of ecosystem service approaches.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article. The authors did not receive financial support from any external organization for the submitted work.

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