REVIEW PAPER

Grazing impacts on phytoplankton in South American water ecosystems: a synthesis

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Abstract The role of grazing as a controlling factor of phytoplankton has an extensive debate in the literature. In this article, five mechanisms that have been explored as potential controlling factors of grazing influence on phytoplankton in South America are discussed and compared with other latitudinal works. The temperature impact on zooplankton is not conclusive, with planktivorous fish appearing as the main controlling factor of zooplankton size ranges. Fish grazing effects on phytoplankton look despicable, but the impact of exotic filter-feeding fish remains controversial. Microphagous rotifers and Copepoda nauplii affect phytoplankton by selective size grazing, while large Cladocera and Copepoda adults can control phytoplankton when they reach high densities in the absence of fish. Both groups mainly feed on small sizes, with microzooplankton having a higher impact on very small phytoplankton. Some contradictory evidence arises for large colonial and filamentous algae. Exotic invasive filter-feeding bivalves are selective grazers in experimental approximations. *Corbicula fluminea* feeds on smaller particles, does not have taxonomic preferences, and has lower densities in nature than *Limnoperna fortunei*. Their effect on nature is not fully documented. In sum, several aspects still need deep scrutiny to fully understand the role of grazing on phytoplankton in South America.

Keywords Inland water ecosystems · Zooplankton grazing · South America · Filter-feeding bivalves · Planktivorous fishes · Microalgae

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Introduction

One of the most critical issues for limnologists is understanding the biotic and abiotic factors that control the dynamics and structure of aquatic communities (Carpenter, 1987; McQueen et al., 1989). In the 80s, McQueen et al. (1989) introduced the top-down/bottom-up mechanism, predicting that top-down effects are more considerable at the top of the food web and weaker towards the bottom. Regarding phytoplankton, Benndorf et al. (2002) concluded that grazing impact would depend on the time scale, the lake depth, and the trophic state, with successful top-down control of phytoplankton being only expected in short-term experiments, shallow lakes, and in meso-trophic or slightly eutrophic deep lakes.

South America constitutes a vast continent with approximately 17.84 million km^2 of surface, most

parts included in the South Hemisphere. The continent is divided into thirteen countries. It compresses about 26% of the Earth's freshwater with the basins of the Amazon rivers (the largest on the planet), the Orinoco, and the Paraná as the most relevant rivers systems. However, studies stating the impact of grazing on phytoplankton structure are still dispersed. We have no conclusive information on the most important mechanisms that may control phytoplankton grazing in inland waters. We face rapid changes mediated by climatic change, global temperature rise, and increased anthropogenic disturbances, especially eutrophication. All of them become significant stressors of aquatic communities, affecting biological diversity and the ecological services that water ecosystems may provide (Brown et al., 2003; Bini et al., 2014; Magurran et al., 2014). In this changing world, the study of the controlling factors of natural communities should become a priority if we want to establish managing strategies to deal with and mitigate these effects to protect the aquatic biological diversity and the services that water ecosystems may provide.

Five mechanisms have been proposed and analyzed to explain the role of grazing on phytoplankton structure. First, to determine the role of grazing as a controlling factor of phytoplankton assemblages, and second to understand harmful algae proliferation and its mitigation in eutrophic ecosystems from all around the world. The first mechanism suggests that temperature may affect zooplankton capability to graze on phytoplankton (Levine et al., 1999; Sommer et al., 2003; Havens et al., 2007), a mechanism that certainly has been vigorously studied in Europe and North America but has been poorly documented in South America. The second mechanism emphasizes that small planktivorous fish exert a strong structuring effect on plankton communities through predation on large zooplankton (Drenner et al., 1986; Scasso et al., 2001; Boverí & Quirós, 2002; Iglesias et al., 2008, 2011); affecting by this way the phytoplankton structure because of cascading effects. A third mechanism suggests that differences in size and morphology of phytoplankton affect the degree of zooplankton grazing (Van Donk et al., 2011; Pančić & Kiørboe, 2018). A fourth mechanism proposes that widespread omnivorous-planktivorous fish can exploit mixed resources in several trophic levels, including phytoplankton (DeVries & Stein, 1992; Beveridge & Baird,

2000; Zhang et al., 2006; Ke et al., 2007; Okun et al., 2008; Attayde et al., 2010).

Exotic invasive bivalve species is a fifth mechanism that may have a critical role in phytoplankton from South America in the last thirty years. In this regard, *Limnoperna fortunei* Dunker, 1857 and *Corbicula fluminea* (Müller, 1774) are two exotic and invasive bivalves native to Asia. These species colonized South America in the seventies and the nineties, respectively (Ituarte, 1981; Pastorino et al., 1993). Both bivalves are filter-feeding, and studies performed in the past have demonstrated that these mollusks can reach high densities, with experimental and some field studies suggesting a high grazing impact on phytoplankton (Boltovskoy et al., 1995, 2015).

In this study, grazing impact as a controlling factor of phytoplankton is analyzed in works performed in South America, where all world climatic regions can be identified. Moreover, the revision of several water body types (from shallow to deep, lotic to lentic, and from natural to artificial ecosystems) gives an insight, through the analysis of the five mechanisms introduced above, on the role of grazing as a controlling factor of phytoplankton. This study attempts to recognize those aspects that still need more inquiry and give those researchers working in the exciting field of phytoplankton ecology a general framework to those factors that may govern phytoplankton structure in inland waters from South America. A study area still not deeply explored by limnologists and phycologists from all around the world.

Methods

This article is focalized on the grazing of nano and microphytoplankton ($> 2~\mu m$ of maximum linear dimension) in inland water ecosystems from South America. The studies analyzed here were published between 1988 and 2021 and covered eighty-three studies performed in the field or by using experiments or combining field plus experimental approximations (Fig. 1). Studies were found and selected using keywords related to the several mechanisms mentioned in SCOPUS, SCIELO and Google Scholar platforms. Other studies were reached by cross-reference, and several review articles were consulted (Fig. 2). The manuscript was organized first by explaining the mechanisms involved and then
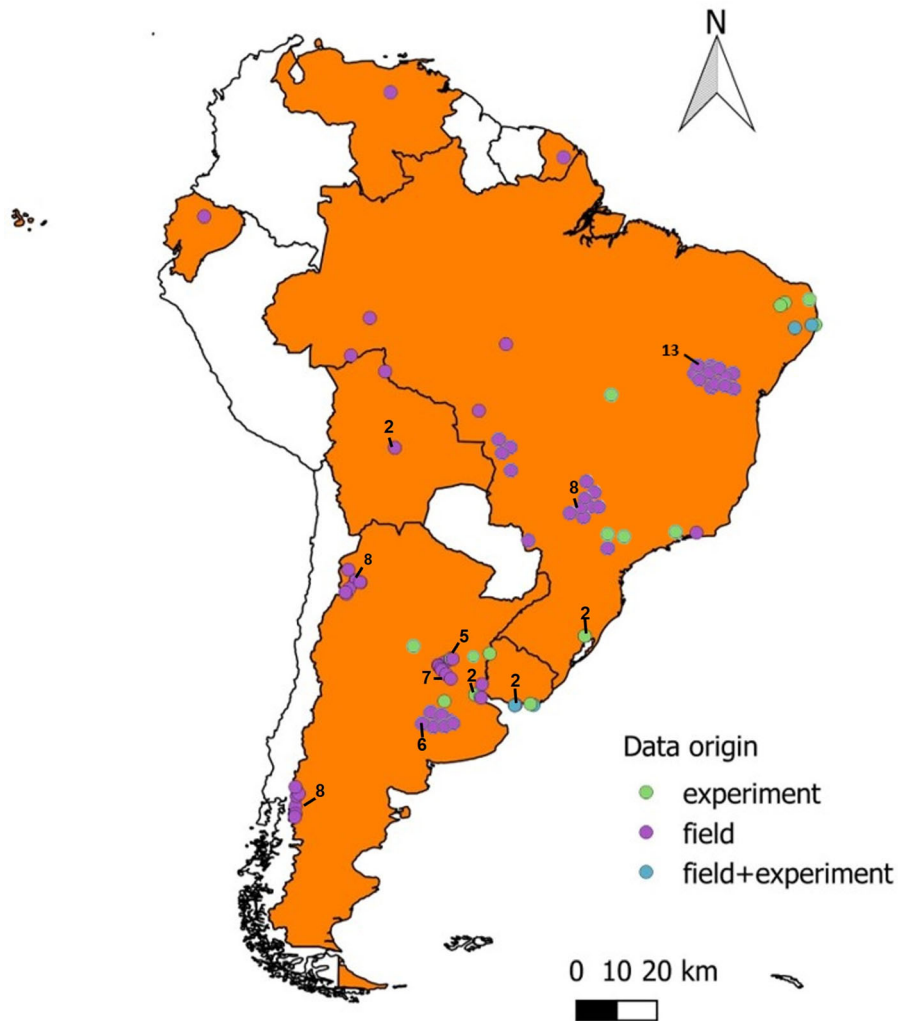
Fig. 1 South America map with those countries with applicable information regarding phytoplankton grazing impacts concerning zooplankton, planktivorous fish, or exotic invasive bivalves is available (in color). Color dots represent different kinds of studies (experimental, field, and experimental + field) performed and analyzed here. The position of the dots is georeferenced by considering the place where the experiment was done or the field study was conducted, respectively

analyzing the available information for South America. Some comparisons with similar information obtained from other regions and continents from the world were included and discussed. A conclusion summarizing all the information gathered is also presented to give an insight into the role of grazing as a controlling factor of phytoplankton structure in South American ecosystems. In this section, I also highlight some of the most critical aspects that I consider still require intensive study to improve our knowledge of the functioning of inland water ecosystems.

The first mechanism: temperature changes as drivers of zooplankton size and grazing capability on phytoplankton

Body size is one of the most critical parameters determining organism ecological and physiological characteristics (Peters, 1983). This first mechanism states that temperature affects body size, indirectly affecting the life-cycle timing of events and the resulting population age and size structure (Sebastian et al., 2012). Bergmann (1847) was the first who noted that endotherms organism size tended to increase with
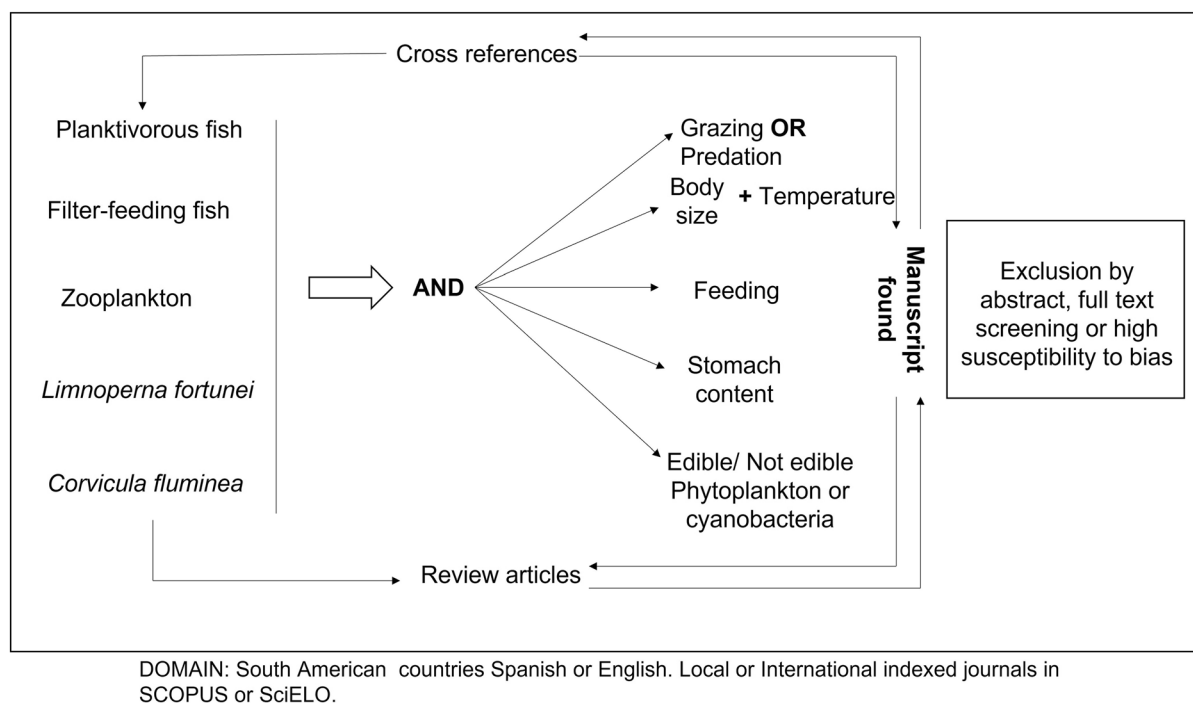
Fig. 2 This figure shows an overview of the mechanism used for article searching, screening, and quality assessment

latitude and lower temperatures, a pattern that was then also found in several groups of ectotherms, making it one of the most taxonomically widespread rules in biology (Atkinson et al., 1995). However, the mechanisms involved remain elusive and highly discussed (Angilletta & Dunham, 2003; Walters & Hassall, 2006; Karl & Fischer, 2008; Verberk et al., 2020).

Regarding zooplankton body size, Gillooly (2000), Gillooly & Doddson (2000), and after that, Havens et al. (2015) made extensive literature revisions by which they considered Cladoceran and Copepoda species. They concluded that the mean body length is smaller in tropical regions, increasing to maximum size in the temperate areas (50–60°) in both the Northern and Southern hemispheres. The authors also reported that mean body size declined from temperate to polar regions. However, the decline in size from temperate to polar areas is less conspicuous than in tropical regions. Havens et al. (2015) also suspected that for Cyclopoids, other variables such as fish predation might affect size, while for Calanoids body size was unrelated to temperature. No results for rotifers were informed. Contradictory results were reported by Weetman & Atkinson (2004), who found

that size at maturity increased with temperature in *Daphnia pulex* O.F.Müller, 1776 and *Daphnia curvirostris* Eylmann, 1887.

The most important of this analysis is that temperature in zooplankton body size may affect zooplankton grazing on phytoplankton. However, the answer could be complex. It is expected that the range of algae sizes grazed by zooplankton increases with increasing zooplankton body size. However, higher grazing impacts may result from high zooplankton biomass rather than the presence of large zooplankton (Cyr & Pace, 1992). For example, Cyr & Curtis (1999) compared several species of cladocerans and copepods. They found that communities dominated by small cladocerans, like *Bosmina* and *Ceriodaphnia,* grazed a narrower size range of algae above 16–36 μm of maximum linear dimension (MLD).

On the contrary, zooplankton communities dominated by larger cladocerans like *Daphnia* and *Diaphanosoma* graze over larger phytoplankton sizes (between 28 and 78 μm MLD). In the same sequence of experiments, calanoid copepods followed the same general relationship as small cladocerans (< 35 μm MLD). Despite it would be expected that copepods feed larger prey due to their greater size. In another

study, Cyr & Pace (1992) could not detect a general relationship between zooplankton size distribution and grazing rate over thirty zooplankton communities. The authors did not find that assemblages dominated by large zooplankton (mostly *Daphnia* and *Diaphanosoma*) have higher grazing rates than communities dominated by small size zooplankton.

Zooplankton grazing may also depend on the temperature in a contradictory way with the predictions of an inverse relationship between zooplankton body size and temperature. Several studies, like Burns (1969), Orcutt & Porter (1983), Stich & Lampert (1984), and Loiterton et al. (2004), have reported that the grazing rate of zooplankton increases with higher temperatures. This pattern is explained because aquatic poikilothermic organisms exhibit reduced metabolic rates with low water temperature, resulting in decreased locomotion and ingestion rates (Loiterton et al., 2004). In South America, we almost no have reports that document the effect of temperature on zooplankton body size or even studies comparing ingestion rates of several zooplankton groups under several climatic conditions. The exception that I could find is Iglesias et al. (2011). In a shallow lake of Uruguay with a low fish density, they found that the mean size of cladocerans represented almost exclusively by *Daphnia obtusa* Kurz, 1874 exceeded the mean size expected for the 35° latitude suggested by Gillooly & Dodson (2000).

Moreover, Sarma et al. (2005), by comparing cladocerans from temperate and warm latitudes, found that cladocerans have a larger body size in temperate ($\sim$ 5 mm) in comparison with warm (< 3 mm) areas. However, they assumed that cladoceran species diversity and size at maturity are probably more related to fish predation effects than temperature. They also considered that less edible phytoplankton species in the tropics, like cyanobacteria or large filamentous or colonial species might also affect the presence of large zooplankton (Fig. 3).

In sum, the effects of temperature on zooplankton body size and its cascading effects on phytoplankton remain elusive. For South America, we have no support to improve our understanding of the role of the temperature on zooplankton body size and grazing. A regional comparison under different temperature regimes would undoubtedly improve our understanding of the role of temperature on zooplankton body size, especially if we consider predictions of
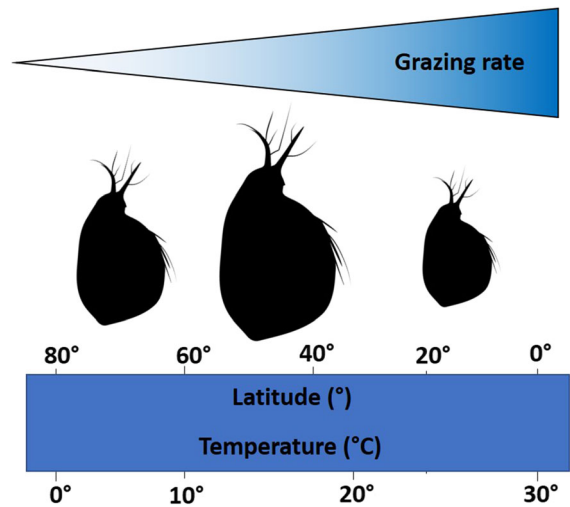
Fig. 3 Schematic illustration of the role of temperature as a controlling mechanism of zooplankton size (indicated by the cladoceran size figure) according to the references used in the manuscript. The grazing rate pressure expected on phytoplankton is also shown in the upper arrow

increasing global temperature rise shortly (IPCC inform, 2021. Available on https://www.ipcc.ch/2021/08/09/ar6-wg1-20210809-pr/).

The second mechanism: planktivorous fishes as a driver of phytoplankton through selective predation on large zooplankton

The size efficiency mechanism (Brooks & Dodson, 1965) predicts that the zooplankton community will be composed of small zooplankton species (between 200 up to $\sim$ 700 μm) in a system dominated by planktivorous fishes. With low planktivorous fishes abundance, large zooplankton species are expected to be dominant (> 700 up to $\sim$ 3000 μm) (Attkinson, 1995). Indeed, most planktivorous fishes are visual predators, and numerous contributions have been made in the past, predicting that these fishes select those larger zooplankton individuals. The implicit mechanism is based on the angle impinging on the fisheye, defined by the distance to the prey and the prey length (Brooks, 1968; Gardener, 1981; Wetterer, 1985, 1989). Other works have also highlighted the importance of lateral fish line sensory systems to detect their prey in low-light conditions or even during the night (e.g., Saunders & Montgomery, 1985; Mongomery and Milton, 1993).

Several authors, like Gliwicz & Pijanowska (1989), Horn (2003), and Hambright (2008), have already corroborated the Size Efficiency Mechanism indicating that the composition of a zooplankton community might become dominated by small-bodied species because planktivorous fish consume selectively large-bodied zooplankters. Furthermore, in this scenario, small, inconspicuous zooplankton taxa populations may benefit from size-selective fish predation because they become released from competition and grazing by larger zooplankton (Slusarczyk, 1997; Declerck et al., 2003; Havens et al., 2009). Gliwicz (1994) highlights some other critical indirect effects. These effects include reduced reproduction in the population because of the higher vulnerability of ovigerous females to predation, shifts in behavior (from foraging to predator avoidance), and physiological adjustments (from high to low feeding rate) in those species detecting danger from fish predators.

In South America, studies reporting high planktivorous fish stocks confirm this statement. It shows that zooplankton tends to be dominated by small-sized individuals, particularly rotifers and copepods nauplii (< 700 μm of MLD), throughout the year. Copepoda adults or large Cladocera has been reported during the winter or during the early spring when fish biomass is lower, or in those environments where was a low fish stock density (e.g., Scasso et al., 2001; José de Paggi & Paggi, 2007, 2008; Iglesias et al., 2008, 2011; Sosnovsky et al. 2010; Frau et al. 2013, 2019). In an insightful study performed by Costa Bonecker et al. (2012) in eight shallow lakes linked to the upper Paraná River (Brazil), they reported changes in zooplankton size structure regarding the presence of planktivorous fish in two seasons (rainy and dry seasons). *Lecane proiecta* Hauer, 1956, *Bosmina hagmanni* Stingelin, 1904, and *Notodiaptomus iheringi* (Wright S., 1935) were the most important species of each group (rotifer, cladoceran, and copepod) in abundance and biomass during the dry season (high fish density). In contrast, during the rainy season (low fish density), *Asplanchna* sp., *Diaphanosoma spinulosum* Herbst, 1975, and *Notodiaptomus amazonicus* (Wright S., 1935) were dominant. The percentage of individuals with small size (300–700 μm) was positively related to the fish density in biomass and density. In comparison, larger-sized individuals (> 700 μm), in both biomass and density, were negatively associated with the fish density, reflecting

a decrease of this size class with the increase of fish. Sosnovsky et al. (2010), in a large field study, including six Pampean lakes from Argentina, also reported that in turbid lakes, zooplankton biomass and size were relatively higher in the period of low fish abundance.

Experimental studies also support the previous statement, and some denote the cascading effect this may have on phytoplankton. In Argentina, Boveri & Quirós (2002) found, in an *ex-situ* experiment simulating Pampean shallow lake conditions, that *Odontesthes bonariensis* Valenciennes, 1835 positively selecting those larger cladocerans (*Daphnia* sp. > 700 μm of maximum linear dimension) and copepods (> 1000 μm). They also found that the fish stomach contents were composed of more than 95% cladocerans, and copepods represented more than 70% of total biomass. The authors also demonstrated an increment of 300% in Chlorophyll-*a* (Chl-*a*) concentration when fish were present. Similar results were obtained in Uruguay by Iglesias et al. (2008) in a field-experimental study performed in Blanca Lake with the planktivorous fish *Jenynsia multidentata* (Jenyns, 1842). The authors reported that *J. multidentata* predation plays an essential role in modulating zooplankton structure. In the field study, Copepoda nauplii and rotifers [*Keratella cochlearis* (Gosse, 1851), *Filinia longiseta* (Ehrenberg, 1834), and *Polyarthra* sp.] dominated zooplankton in the presence of fish. However, when fish density was the lowest during the winter, they reported an increment in cladoceran density [*Bosmina longirostris* (O.F.Müller, 1776) and *Diaphanosoma birgei* Kořínek, 1981]. The calanoid copepod *Notodiaptomus incompositus* (Brian, 1925) (up to 1500 μm of MLD) was also frequent and homogeneously distributed. A high decline of cladoceran in the presence of fish and an increment in microzooplankton density (< 700 μm) it was also reported. Compared with Cladocera, copepods have more swimming appendages, a more developed sensory system, and better neuromuscular coordination. These characteristics allow them to perform rapid evasive movements when they detect deformations in the flow field as hydrodynamic signals generated by the activity of predators (Caparroy et al., 2000; Dussart & Defaye, 2001). All of this could explain that some large copepods species, like *Notodiaptomus amazonicus* and *N. incompositus* may persist in the presence of planktivorous fish in some of the studies

previously reported. Moreover, vegetation, as a refuge for zooplankton, has been extensively discussed in the literature. However, vegetation effects may depend on the plant structure, fish predation habits, and the absence of other predators, like odonates larvae or shrimps among the roots (e.g., Meerhoff et al. 2003; Cazzanelli et al. 2008; Grutters et al. 2015; Gutierrez et al. 2021) (Fig. 4).

In another field-experimental approach, Iglesias et al. (2011) found that in Rivera Lake, with very low planktivorous fish density (< 1 kg ha^{-1}) and a fish assemblage dominated by *Cnesterodon decemmaculatus* (Jenyns, 1842), D*aphnia obtusa* (large individuals ~ 1000 μm) was the dominant species in abundance and biomass. In contrast, in Rodó Lake, with *C. decemmaculatus* dominating in high density (> 20 kg ha^{-1}), zooplankton was mainly represented by rotifers representing a biomass five-time lower than in Rivera Lake across the year. Contrasting Chl-*a* concentrations were obtained in both lakes with a negative correlation between cladoceran biomass and Chl-*a* concentration. In the in-situ experiments performed in the three other lakes (Diario, Blanca, and Nutrias), the authors found that large-sized cladocerans (*Daphnia*) became part, under free-fish conditions, of the zooplankton community in Nutrias Lake and occurred in high densities in Diario Lake. In Blanca Lake, large-sized *Simocephalus* sp. appeared for the first time in the water column. These changes were accompanied by low phytoplankton biomass. In Frau et al. (2019), we reported a high density (between 320 ind 100 m^{-2} in winter and 1018 ind 100 m^{-2} in summer species) of several planktivorous fish, such as *Jenynsia lineata* (Jenyns, 1842), *Hyphessobrycon wajat* Almirón & Casciotta, 1999, *Gambusia holbrooki* Girard, 1859 (introduced species), *C. decemmaculatus*, and *Ramnogaster melanostoma* (Eigenmann, 1907). We found that rotifers
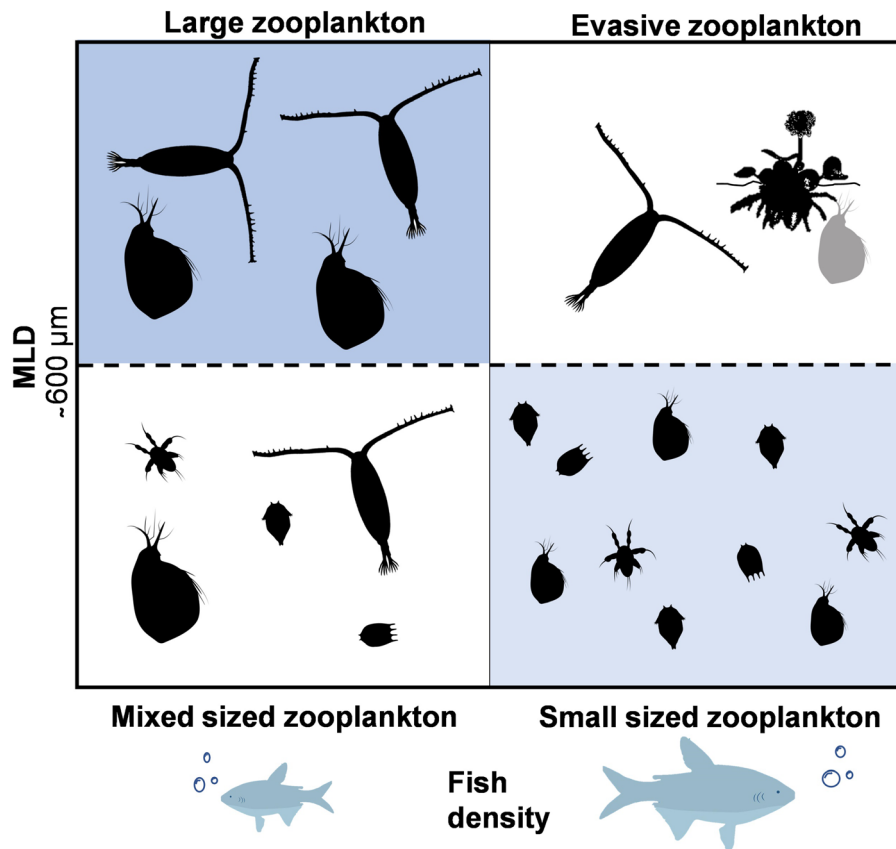
Fig. 4 A schematic illustration synthetizing the role of planktivorous fish as a controlling factor of zooplankton structure. Four possible scenarios are presented: high and low density of fishes, high density of fished plus evasive zooplankton, low fishes density, and a more diverse zooplankton structure

[*Brachionus caudatus* Barrois & Daday, 1894 and *Keratella tropica* (Apstein, 1907)] were dominant in the zooplankton assemblage year-round; appearing in very low-density individuals of Harpacticoidea Copepoda, *Bosmina* sp., *Alona* sp. and *Alonella* sp. Copepoda nauplii had a peak density during the early spring when lower fish density or activity was expected. In this study, we also analyzed zooplankton dormant eggs hatching. We found that more than 80% of total abundance were rotifers. The other 20% were represented by Copepoda nauplii and *Moina reticulata* (Daday, 1905) suggesting a high grazing impact on ovigerous Copepoda and Cladocera females as Gliwicz (1994) predicted. During the whole year, high phytoplankton densities were recorded with several Cyanobacteria blooms events identified. In an experimental study, Gutierrez et al. (2021) also reported profound changes in the zooplankton structure in the presence of fish. These changes consisted in a turnover from large cladocerans at the beginning of the experiment, like *Simocephalus vetulus* (O.F. Müller, 1776) and *Daphnia obtusa* to small cladocerans ($\sim$ 700 μm), like *Chydorus eurynotus* Sars, 1901, *Alona glabra* Sars, 1901, *Macrothrix elegans* Sars, 1901, *Coronatella monacantha* Sars, 1901, *Ceriodaphnia dubia* Richard, 1894, and rotifers at the end.

More evidence comes from Patagonian lakes in the southern part of South America. In this region, the climate tends to be temperate to cold and dominated by glacial origin deep lakes. In these lakes, when native planktivorous fishes like *Aplochiton zebra* Jenyns, 1842, *Galaxias maculatus* (Jenyns, 1842), and *Percichthys trucha* (Valenciennes, 1833) are abundant, the presence of large zooplankton is unusual (José de Paggi & Paggi, 1985; Pizzolón et al., 1995; Modenutti et al., 2003; Balseiro et al., 2004). Indeed, Balseiro et al. (2007) and Jönsson et al. (2011) indicate that the high abundance of planktivorous fishes in Patagonian Lakes prevents the cascading effect of zooplankton on phytoplankton. However, the salmonid introduction may alter the observed pattern (Macchi & Vigliano, 2014, for a complete revision). This is because salmonids predate on zooplanktivorous fish, which may have consequences on the zooplankton grazing activity still not well understood.

In other latitudes of the world, the information regarding this topic is abundant, and authors mainly recognize the role of planktivorous fish as one of the main drivers of zooplankton structure in natural water ecosystems. For example, Jeppesen et al. (1997) concluded that planktivorous fish played a crucial role in zooplankton structure more than food and temperature, as was previously stated. All of this by using an enclosure experiment in a New Zealand Lake plus a metanalysis and comparison of several Denmark and New Zealand studies. In North America, Post & McQueen (1987) concluded that planktivorous fish strongly negatively impact the zooplankton community biomass and size structure. Still, this effect is weaker on phytoplankton by manipulating yellow perch [*Perca flavescens* (Mitchill, 1814)] density. Schulze (2011) also analyzes the impact of planktivorous fishes predation on phytoplankton in twelve turbid reservoirs from North America and concludes that large cladocerans are highly affected. In a review article, Søndergaard et al. (2008) reported the positive effect of planktivorous fish removal in several Denmark lakes by favoring zooplankton development. More recently, in temperate, eutrophic lakes from North America and Europe, Bernes et al. (2015) analyzed the role of biomanipulation of planktivorous fishes stocks. They found that in several cases, planktivorous fishes' removal was traduced in a reduction of Chl-*a* concentration. The phenomenon was attributed to an increment in density and richness of zooplankton.

Summarizing, the role of planktivorous fishes as controlling factors of zooplankton communities seems to be a rule. This is for tropical to temperate and cold regions from South America, equal to other latitudes and environments. Indeed, this topic has been profoundly studied in the past, with strong supporting evidence.

The third mechanism: grazing effects of zooplankton on phytoplankton. A matter of size and palatability

Assessing zooplankton grazing on phytoplankton is crucial for understanding, modeling, and predicting the structure and dynamics of aquatic communities. The classical approach establishes phytoplankton palatability for zooplankton upon phytoplankton size is above 20–35 μm for palatable. Sizes > 35 μm is considered unpalatable (Lehman, 1989; Salmaso, 2002; Salmaso & Padisak, 2007). Besides, other morphological, physiological, and behavioral aspects, like external morphology, cell-wall characteristics, the

presence of defensive structures like horns, toxin production, timed migrations, or cyst hatching, may also affect the potential prey's palatability (Van Donk et al., 2011; Pančić & Kiørboe, 2018; Lürling, 2021).

In an extensive review, Colina et al. (2016) analyzed this topic by considering monospecific experiments of zooplankton clearance rate and grouping phytoplankton according to morphological characteristics stated by Kruk et al. (2010). They found that small organisms with high surface/volume and medium size, lacking specialized traits, have a high grazing rate. In contrast, unicellular flagellates of medium to large size have a medium grazing susceptibility. Rotifers have a significant ingestion rate on small unicellular algae (< 5 μm of MLD). In comparison, cladocerans may ingest medium unicellular size algae (21.8 μm) and medium–large flagellates (11.6 μm). On the contrary, copepods may consume medium-large flagellates and diatoms ($\sim$ 34 μm), all values fitting in the general description of MLD stated previously. The authors found insufficient evidence of grazing on small silica cell-wall flagellates (like *Chromulina* and some *Mallomonas* species) and large mucilaginous colonies. They also had no data for larval stages of copepods (nauplii and copepodites), abundant in freshwater bodies, and having contrasting feeding preferences than adults.

Notably, experiments with natural communities combining natural assemblages and times series analyses increase the validity of the conclusions arrived by Colina et al. (2016), who only focused on monospecific cultures. In Frau et al. (2017), we tested the ability of two macrozooplankton species [*Argyrodiaptomus* sp. (Copepoda) and *Daphnia obtusa* (Cladocera)] to graze on the phytoplankton of a shallow eutrophic lake in the absence of fish predation and at zooplankton densities higher than 100 ind l^{-1}. We considered phytoplankton maximum linear dimension and other aspects which may affect its palatability, such as cell envelopes and the presence of protuberances. Grazing of large zooplankton mainly affected small sizes algae (< 35 μm), such as small cyanobacteria colonies, small silica cell-wall algae, or large groups flexible enough to be handled (e.g., metabolic flagellates like *Euglena*) were the most affected. Consistent results were obtained by Eskinazi-Sant'Anna et al. (2002) and Rietzler et al. (2002). Eskinazi-Sant'Anna reported that 80% of the total ingested food by *Daphnia laevis* Birge, 1878 in the

Pampulha reservoir (Brazil) were colonial chlorophytes. These species included *Eutetramorus fottii* (Hindák) Komárek (now *Coenochloris fottii* (Hindák) Tsarenko), *Coelastrum pseudomicroporum* Korshikov, *Oocystis lacustris* Chodat, and two euglenophytes: *Trachelomonas volvocina* (Ehrenberg) Ehrenberg and *Euglena oxyuris* Schmarda [now *Lepocinclis oxyuris* (Schmarda) B.Marin & Melkonian]. Rietzler et al. (2002) found that *Argyrodiaptomus furcatus* Sars G.O., 1901 and *Notodiaptomus iheringi* preferred small size filamentous diatoms ($\sim$ 20 μm) and single-cell chlorophytes in Broa Reservoir (Brazil).

In other experimental studies performed in a shallow floodplain lake (Argentina), Sinistro et al. (2007, 2010) reported similar results with the cladocerans *Moina micrura* Kurz, 1875, *Diaphanosoma*, *Ceriodaphnia*, *Bosmina*, *Leydigia,* and calanoids copepods such as *Notodiaptomus incompositus* and *Notodiaptomus spiniger* (Brian, 1926). Their experiments showed an evident grazing effect, especially on nanophytoplankton species (< 30 μm) when zooplankton reached densities > 100 ind l^{-1}. Other experimental studies performed in Brazilian reservoirs have also informed a positive effect of zooplankton grazing on phytoplankton. Amorim et al. (2019) reported in the Ipojuca Reservoir (Brazil) an effective predation effect of *Macrothrix spinosa* King, 1853 on non-mucilaginous coenobial chlorophytes and small size cyanobacteria colonies. Dos Santos Severiano et al. (2017) found that *Thermocyclops decipiens* (Kiefer, 1929) effectively grazed on *Cyclotella meneghiniana* Kützing, *Merismopedia tenuissima* Lemmermann and *Desmodesmus protuberans* (F.E. Fritsch & M.F. Rich) E.Hegewald when these copepod species reached high densities (> 200 ind l^{-1}). In Dos Santos Severiano et al. (2018), the authors also found a negative effect of large zooplankton on *C. meneguiniana*, *Cryptomonas* sp., and *Aphanocapsa* sp. when the authors experimentally increased three and four times the natural densities of zooplankton registered in the Ipojuca reservoir.

On the contrary, some groups of phytoplankton may appear ellusive to zooplankton grazing effects. In Frau et al. (2017), we found that single-cell flagellates represented mainly by *Chlamydomonas* and *Phacotus* (unicellular flagellates) remained unaffected by all zooplankton fractions considered. Amorim et al. (2019) reported a similar result when they tested the

grazing effect of *M. spinosa* on unicellular flagellates. Indeed, all these small size algae may hinder zooplankton capture due to their small size and their high surface: volume ratio allowing them to quickly reverse the zooplankton grazing effect through an efficient uptake of nutrients and high growth rates (Reynolds, 1997; Sommer et al., 2003; Litchman et al., 2010; Kruk et al., 2010; Colina et al., 2016).

Contradictory data arises from several studies that reported no zooplankton grazing effect on phytoplankton from South American ecosystems. Lazzaro et al. (2003) reported in thirteen reservoirs from Brazil that phytoplankton was dominated by filamentous and large colonial cyanobacteria species, such as *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya & Subba Raju (now *Raphidiopsis raciborskii* (Woloszynska) Aguilera, Berrendero Gomez, Kastovsky, Echenique & Salerno), *Aphanizomenon gracile* Stearn, *Anabaena cylindrica* Lemmermann, *Microcystis flosaquae* (Wittrock) Kirchner, and *Oscillatoria* spp. At the same time, zooplankton was dominated by medium-large taxa (700 μm up to 3000 μm), such as *Notodiaptomus* spp., *Thermocyclops* spp., *Tropocyclops* spp. (all copepods), and cladocerans, like *Diaphanosoma excisum* Sars, 1885, *Ceriodaphnia cornuta* Sars, 1885), *M. micrura*, and *Daphnia guesneri* Herbst, 1967. The authors concluded that zooplankton grazing could be inefficient in these environments because of unpalatable cyanobacteria blooms. Similarly, Fonseca da Silva et al. (2019) reported in Garças Lake (Brazil), where rotifers were dominant, no effect on phytoplankton biovolume dominated by large Cyanobacteria mucilaginous colonies in an in-situ experiment.

Moreover, Von Rückert & Giani (2008) did not find conclusive evidence of zooplankton grazing control on natural phytoplankton from Pampulha reservoir (Brazil) using *Daphnia laevis*, *Moina micrura* and *Thermocyclops decipiens*. In this regard, they reported that in the presence of *Daphnia laevis* an evident reduction of *Merismopedia tenuissima* Lemmermann (Cyanobacteria) and in the presence of *T. decipiens* a decrease in density of *Trachelomonas volvocina* (Euglenophyta). The authors concluded that high food abundance was the most probable reason for the almost undetectable top-down effect.

Lacerot et al. (2013) concluded an inefficient grazing impact on *Aphanizomenon gracile* (filamentous cyanobacteria ~ 100 μm) as dominant species in

the presence of *Moina minuta* (~ 600 μm) as a top grazer. Rejas et al. (2005) reached similar conclusions as those of Lacerot et al. (*op. cit.*) in a set of two experimental studies performed in the Bufeos Lake (Bolivia), arguing that nutrients limitation was more critical than grazing. In this experiment, *Moina minuta* (~ 600 μm) and *Bosminopsis deitersi* Richard, 1895 (~ 800 μm) were the dominant phytoplankton grazers. Chl-*a* was used as a descriptor, so there is a lack of information about the phytoplankton structure. In the same lake, Ayala et al. (2003) found that large chlorophytes (> 35 μm), like *Gonium pectorale* O.F. Müller, *Dictyosphaerium pulchellum H.C. Wood* (now *Mucidosphaerium pulchellum* (H.C. Wood) C.Bock, Proschold & Krienitz), and large cyanobacteria, such as *Dolichospermum* sp., and *Microcystis* sp. were the dominant species. In this experiment again, Ayala et al. (*op. cit.*) found a lack of grazing effect in the presence of zooplankton.

The assumption that zooplankton species cannot feed on large colonies of filamentous algae is not necessarily conclusive. Nadin-Hurley & Duncan (1976) reported that large *Daphnia* species could ingest filamentous cyanobacteria into spaghetti-like bundles. In Brazil, Panosso et al. (2003) reported positive results when they studied the impact of *N. iheringi* (Copepoda) on filamentous and single cell-small colonies cyanobacteria in two experimental studies performed the Funil Reservoir but prefers other items. Bouvy et al. (2001) and Kâ et al. (2012) also reported the ability of tropical rotifers from Brazil (e.g., *Brachionus* spp. and *Keratella* spp.) and some copepod species like *Notodiaptomus cearensis* (Wright S., 1936) and *Thermocyclops decipiens* to cut large filamentous cyanobacteria into smaller pieces and consume them. Finally, dos Santos Severiano (2018) and Diniz et al. (2019) reported that calanoids Copepoda and cladocerans might effectively graze on colonial and filamentous cyanobacteria. In sum, the evidence suggests that some zooplankton species can ingest large cyanobacteria filaments or ingest small size no mucilaginous colonies. In this way, the lack of effect on large phytoplankton groups cannot be generalized to all zooplankton species.

In oligotrophic ecosystems from the Argentinian Patagonia, where calanoid copepods are abundant (Reissig et al., 2006; Hylander et al., 2012), similar grazing effects on small size phytoplankton could be

expected. This would be true if we generalize the results obtained by Modenutti et al. (1998), who revised the reported results from several previous studies performed in this region. They conclude that calanoids copepods have a crucial role as grazers on small mixotrophic algae (< 20 μm), like *Chrysochromulina parva* Lackey and *Rhodomonas lacustris* Pascher & Ruttner [now *Plagioselmis lacustris* (Pascher & Ruttner) Javornicky]. In similar Chilean ecosystems, de los Ríos Escalante & Kies (2017) demonstrate large zooplankton like calonoids copepods, such as *Tumeodiaptomus diabolicus* (Brehm, 1935), *Boeckella gracilipes* Daday, 1901, and *Boeckella michaelseni* Mrázek, 1901 are dominant in oligotrophic ecosystems. Daphnidae, Bosminidae, Sididae (cladocerans families) are better represented in mesotrophic and eutrophic lakes. However, no references to their cascading effect on phytoplankton structure could be found.

Shallow lakes situated at high elevations may constitute a particular study case. Although high altitude shallow lakes are rare globally, they are not uncommon in the Andes mountains of South America. In the inter-Andean valleys, alluvial deposits have created high-altitude plains on which shallow lakes have formed (Sarmiento et al., 2008). Van Colen et al. (2017) found inhibition of zooplankton grazing in a shallow lake from Ecuador. An effect attributed to the dominance of poeciliid planktivorous fish species, such as *Xiphophorus helleri* Heckel, 1848 and *Poecilia reticulata* Peters, 1859, actively feed on large zooplankton. The authors argued that despite *Daphnia pulex* increased its density during short periods, its small size and a phytoplankton assemblage dominated by *Cylindrospermopsis* (filamentous cyanobacteria) determined a null grazing effect. Similar results were reported by Saunders & Lewis (1988a) in Valencia Lake (Venezuela). They found that *Chaoborus* (Diptera larvae) predated intensively on zooplankton; however, when *Chaoborus* density decreased, zooplankton could not control phytoplankton biomass. In Frau et al. (2015), by studying a set of high-altitude shallow lakes from northwestern Argentina, we found that zooplankton is poorly represented in abundance and species richness. Rotifers, mainly *Brachionus* spp. and *Lecane* spp., are the most frequent. Occasionally, *Boeckella poopoensis* Marsh, 1906 reached high densities. In these environments, phytoplankton is dominated by large tychoplanktonic diatoms (like

Navicula, *Nitzschia*, and *Surirella* species), which may prevent adequate grazing and digestion, as previous authors have already suggested (Van Donk et al., 1997; DeMott, 2010). We did not find conclusive evidence that zooplankton from these lakes can control phytoplankton, even in the absence of fish. A generalization for high altitude lakes could not be made. Several factors with potential cascading effects not well understood include a high abundance of filter-feeding birds (like flamingos), a variable presence of planktivorous fishes, and a changing plankton composition among lakes and across the year.

Water residence time in lowland streams and rivers can be enough for phytoplankton and zooplankton development (Allan & Castillo, 2007; Bolgovics et al., 2017). However, the patterns observed for lowland streams seem to be like those for high-altitude lakes (Reynolds & Descy, 1996). Compared to lakes, lotic ecosystems typically support zooplankton biomass less than would be expected based on the density of phytoplankton (Pace et al., 1992). For example, studies performed in the Danube (Bothar, 1987), the Hudson (Pace, 1992), the Hawkesbury-Nepean (Kobayashi et al., 1996), the Rideau (Basu & Pick, 1997) or the Meuse (Servais et al., 2000) rivers have demonstrated that zooplankton grazing has little impact on phytoplankton structure. The evidence from lotic ecosystems from South America is not abundant. In the Apure (a tributary of the Orinoco), Saunders & Lewis (1988b) found no effect of zooplankton on phytoplankton structure. Also, some evidence gathered in a set of seven lowland streams from the central region of Argentina (Frau et al., 2020b) suggests that zooplankton is not a controlling factor of phytoplankton either. However, if we consider the previous evidence reported for other kind of environments, we still need more evidence to determine the grazing impact of zooplankton on nanophytoplankton (< 20 μm) and how this size selection may impact the phytoplankton structure in lowland streams.

Regarding microzooplankton (rotifers and copepods nauplii), Obertegger et al. (2011) classified them according to their feeding strategies. Raptorial catches single prey like ciliates and small algae; while microphagous obtains energy from tiny particles (e.g., bacteria, picoplankton, and small algae or protozoans, < 12 μm) (Baer, 2008; Devetter, 2009; Naselli-Flores & Barone, 2011). In Frau et al. (2019), we performed a field study in a eutrophic shallow lake

dominated by microphagous Rotifera, and we found evidence that the dominant rotifer species (*Brachionus* spp. and *Lecane* spp.) may efficiently control small Chlorophyceae (< 10 μm) by grazing. Besides, exogenous nauplii (> 150 μm) may also graze effectively in nanoplankton (between 2 and 20 μm) (Roff et al., 1995; Bruno et al., 2012). In Frau et al. (2020a), we reported that Copepoda nauplii might effectively graze on Cryptophyceae species. Other studies performed in Brazilian water ecosystems reached similar conclusions. Dos Santos Severiano (2017, 2018) and Diniz et al. (2019) reported that microzooplankton assemblages constituted by *Brachionus rubens* Ehrenberg, 1838 and Copepoda nauplii could effectively graze and control diatoms, chlorophytes, and small cyanobacteria. While Soares et al. (2010) also reported, in an experimental study, that *Brachionus calicyflorus* Pallas, 1776 can effectively feed on single-cell *Microcystis aeruginosa* (Kützing) Kützing (∼ 6 μm) and *Cylindrospermopsis* sp. (∼ 93 μm), with a deleterious effect of *Microcystis*.

In sum, the zooplankton grazing effect on phytoplankton may depend on a trade-off among morphological and ontogenetic characteristics of zooplankton (species traits and size) plus phytoplankton morphology (size and shape) and physiology (mainly reproduction capability and scape skills). However, in general terms, we can make a distinction of the potential sizes that could be ingested by several zooplankton groups. This classification will have several exceptions influenced by morphological and physiological characteristics of phytoplankton which may prevent their effective control even if they reach the edible size for zooplankton grazing (Fig. 5).

For other latitudes of the world, the role of zooplankton as a controlling factor of phytoplankton has been largely recognized. The size-efficiency hypothesis (Brooks and Dodson, 1965) showed that the planktonic community structure of temperate lentic environments could be strongly affected by selective zooplankton grazing, especially small fractions (< 15 μm; < 30 μm) (e.g., Bogdan & Gilbert, 1982; Sommer et al., 2001; Kagami et al., 2002; Agasild et al., 2007). Moreover, the role of zooplankton as a controlling factor of phytoplankton structure has also been shown to be an essential element for restoration in biomanipulation studies (Mehner et al., 2002; Jeppesen et al., 2007).

Remarkably, the zooplankton grazing effect on Cyanobacteria has been extensible debated in the literature. They represent a hazardous bloom-forming group and resist herbivory because of their low nutritional value, the potential of toxins production, and aggregation into colonies or filaments that prevent grazing (e.g., Rondel et al., 2008; Ger et al., 2014, 2016). However, in South America, as the reader can see, several references to the effective grazing effect of zooplankton on small colonies or some filamentous species were reported. However, some other studies have mentioned the contrary. The information available from other latitudes is more consistent. Moriarty et al. (1973) reported that *Thermocyclops hyalinus* (Rehberg, 1880) (Copepoda) effectively grazed on large *Microcystis* colonies while Vareschi & Jacobs (1984) reported a high grazing capacity of *Lovenula africana* (Daday, 1910) (Copepoda) and *Brachionus plicatilis* Müller, 1786 (Rotifera) feeding on *Spirulina* sp. Both dominant cyanobacteria species of Lake Nakuro (Africa). Gliwicz & Lampert (1990) and DeMott et al. (2001) concluded that large-bodied grazers, such as *Daphnia,* have a high clearance rate on large cyanobacteria filaments. Fulton (1988) showed that *Daphnia pulex* and *Daphnia parvula* Fordyce, 1901 consumed *Anabaena flosaquae* Brébisson ex Bornet & Flahault (now *Dolichospermum flosaquae* (Brébisson ex Bornet & Flahault) P. Wacklin, L. Hoffmann & J. Komárek) filaments with a length of 111 (± 18) μm. Larger filaments of *Aphanizomenon flosaquae* Ralfs ex Bornet & Flahault (210 ± 24 μm) and other *Dolichospermum* species (233 to 423 μm) were not consumed at all. Similarly, *Planktothrix rubescens* (De Candolle ex Gomont) Anagnostidis & Komárek measuring (< 100 μm MLD) were preferably ingested by adult of *Daphnia pulicaria* Forbes, 1893 over longer filaments (up to 984 μm) (Oberhaus et al., 2007). Urrutia-Cordero et al. (2015) reported that cyclopoid copepods and small cladocerans suppressed several species of *Anabaena* (now *Dolichospermum* species), *Microcystis,* and *Planktothrix* species under bloom conditions in late summer in a eutrophic lake from southern Sweden.

Additionally, it has been suggested that zooplankton might indirectly facilitate rather than control cyanobacterial dominance. Ger et al. (2018) found the copepod *Eudiaptomus gracilis* Sars G.O., 1863 promotes the dominance of a toxic strain of *Microcystis*
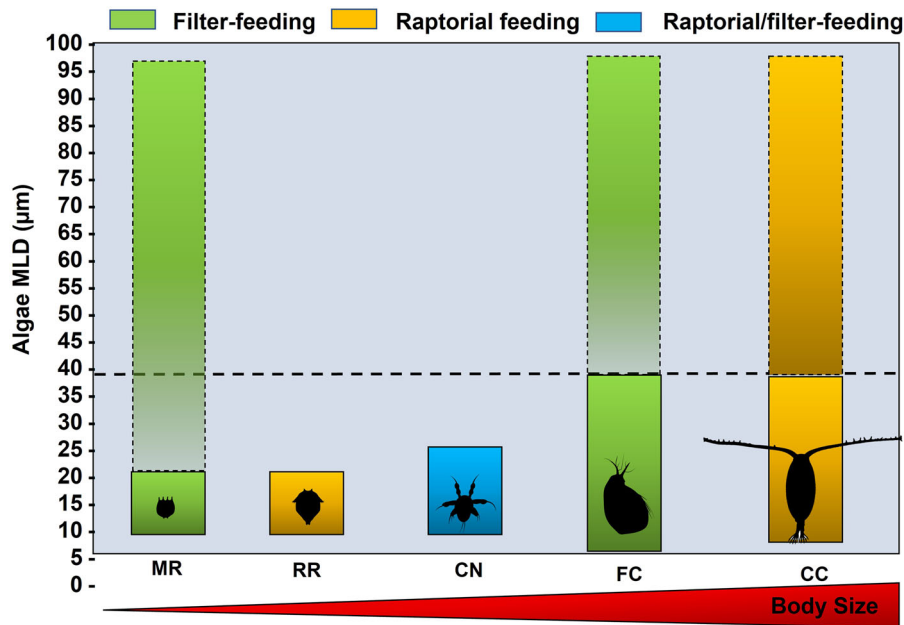
Fig. 5 Zooplankton grazing range size (according to maximum linear dimension) on phytoplankton according to available references described in the text. *MR* microphagous rotifera, *RR* raptorial rotifera, *CN* copepoda nauplii, *FC* filter-feeding Cladocerans, *CC* herbivorous calanoids copepoda. Dotted line bars indicate evidence found for some species but not a generalization for all the zooplankton groups

aeruginosa by grazing on *Cryptomonas pyrenoidifera* Geitler. At the same time, *Daphnia magna* Straus, 1820 does not affect cyanobacteria dominance. In another experiment, Ger et al. (2011) proved the same by using two strains of *Microcystis aeruginosa* (toxic and non-toxic) and a volvacean species (*Chlamydomona*s sp.). A mountain of evidence arises showing that zooplankton may adapt to toxic cyanobacteria strains after several generations (e.g., Pantel et al., 2015; Schaffner et al., 2019). In this respect, copepods, considered more selective grazers, would be more susceptible than generalist grazers. Generalists, like cladocerans, are more exposed but are also more tolerant to the toxins. Some zooplankton may be selective feeders and have a relatively high tolerance of ingested toxins [for a complete revision, consult Ger et al. (2014)]. The evidence reported seems highly related to the ontogeny characteristics of the zooplankton and cyanobacteria species tested. In South America, these kinds of experiments are not abundant. Leitão et al. (2018) is the exception. They found in an experimental study that the calanoid copepods *Notodiaptomus iheringi,* abundant in shallow lakes from Brazil, has a high grazing effect on *Cryptomonas,* facilitating *Microcystis* blooms; however, we have a lack of evidence in South America regarding zooplankton tolerance to toxic cyanobacteria.

So, the evidence reported and summarized in this work indicates that zooplankton may effectively graze on phytoplankton in the absence of fish. This effect would be more critical for small and very small size algae. However, some effective grazing could be expected depending on the species analyzed, especially for large filamentous cyanobacteria. This effect is not restricted to large zooplankton species, becoming rotifers and Copepoda nauplii, another relevant component. However, the effective grazing of zooplankton on phytoplankton would depend on zooplankton ontogenetic characteristics, density, morphological characteristics, size, and morpho-functional characteristics of phytoplankton. At this point, deepening the mechanisms of grazing and the species that could effectively feed on several phytoplankton groups would give us insight into the real functioning of several types of environments. Especially important to improve our understanding of the role of the zooplankton as controller of harmful algae in eutrophic ecosystems from South America.

The fourth mechanism: planktivorous fishes as drivers of phytoplankton structure

In South American water ecosystems, planktivorous fish may be dominant groups in fish assemblages (Agostinho et al., 2001; Scarabotti et al., 2011), with plenty of evidence of the effect of this kind of fish on zooplankton and its cascading effects on phytoplankton already discussed. However, their direct grazing impact on phytoplankton is still not well understood. In Table 1, I have summarized information for forty-one planktivorous-herbivorous fish species from South America that may feed directly on phytoplankton. I found that most fish species considered as phytoplankton feeders are omnivorous, iliophagous, or herbivorous. So, algae in their diet should be regarded as of a periphytic origin. Indeed, many periphytic algae species (especially diatoms, chlorophytes, and cyanobacteria) develop in the sediments or are attached to the roots and stalks of plants (Moss, 1981). So, no active feeding of planktivorous fish on algae should be expected.

Seventeen from forty-one fishes species remain as potential predators of phytoplankton because they were classified as 'Omnivore–algaeivore' species. These authors do not give enough supporting information on which phytoplankton species were found in the stomach-gut content. Nonetheless, considering that all these fish species are presumably visual predators, and most planktonic algae have < 300 μm, we cannot expect active feeding on free-living phytoplankton species. The exception would be those large periphytic mats of Oedogoniales, Zygnematales, or Chladophorales (all of them Chlorophyta) that may occasionally reach the water column as 'metaphyton' and be visually detected by fish. Some Cyanobacteria and Bacillariophyceae species may also form visually detectable 'mats' that could be potentially ingested by fish, so more studies are necessary regarding this topic.

Another relevant feeding strategy among planktivorous fish is filter-feeding, which has evolved and is widespread mainly in Cichlidae. Cichlidae counts with more than 1300 species distributed in Africa and South and Middle America (400 valid species) (Chakrabarty, 2004). Within the cichlid family, carnivores, herbivores, omnivores, planktivores, and detritivores species are known. Filter-feeding fish come equipped with protractile premaxillaries that allow them to 'gape' (extend out their mouths to create a vacuum tube). The vacuum created is used to draw water through their mouths and over their gills (oral pumping). Then, particles suspended in the water are strained and retained as food by filtering it through their exceptionally long and numerous, thin gill rakers (Lazzaro, 1987).

In South America, evidence for filter-feeding species comes mainly from Brazil, where introduced filter-feeding fish species, like tilapias and carps have been studied. Lazzaro (1991) compared a South American cichlid *Geophagus brasiliensis* (Quoy & Gaimard, 1824) and the African cichlid *Tilapia rendalli* (Boulenger, 1897). They found, in an experimental study, that both species exhibited similar selectivity patterns on zooplankton. For both species, feeding behavior depended on fish size. Fish < 30 mm were visual feeders, fish among 30–50 mm were either visually feeders or pump-filter feeders depending on zooplankton size (visual feeding on large evasive copepods to filter-feeding on small cladocerans and rotifers). In contrast, fish > 70 mm were pump-filter feeders. No direct effects on phytoplankton were reported in this study. Still, years after, Sampaio da Silva et al. (2014) studied the impact of *T. rendalli* on phytoplankton structure in a mesocosms approximation. They concluded that no beneficial grazing effect on phytoplankton biomass should be expected through direct grazing, even when phytoplankton is the main food item.

In the same line, Lazzaro et al. (2003) studied the cascading effect of several exotic introduced omnivorous pump-filter feeding species in thirteen Brazilian Reservoirs. In their study, they identified several fish species like *Oreochromis niloticus* (Linnaeus, 1758), *T. rendalli*, *Colossoma macropomum* (Cuvier, 1816), *Triportheus angulatus* (Spix & Agassiz, 1829), *Cyprinus carpio* Linnaeus, 1758, *Aristichthys nobilis* (Richardson, 1845), *Hypophthalmichthys molitrix* (Valenciennes, 1844), and *Ctenopharyngodon idella* (Valenciennes, 1844). They found that only the biomasses of facultative piscivores and omnivores were correlated with phytoplankton biomass. The dominant zooplankton group was Rotifera and were considered as inefficient grazers of Cyanobacteria (dominant phytoplankton group).

Attayde & Menezes (2008), Figeredo & Gianni (2005), and Okun et al. (2008) studied the impact of an exotic introduced planktivorous fish (*Oreochromis niloticus,* tilapia) in Brazil. In Attayde & Menezes (*op.*

Table 1 Planktivorous fish from South America reporting algae in their stomach and gut content

Trophic group	Fish Species	Country	Distribution	References
AI	*Rhytiodus microlepis* Kner, 1858*	BOLIVIA	Restricted	Pouilly et al. (2004)
AI	*Curimatella dorsalis* (Eigenmann & Eigenmann, 1889)*	BOLIVIA	Cosmopolitan	Pouilly et al. (2004)
AI	*Psectrogaster amazonica* Eigenmann & Eigenmann, 1889*	BOLIVIA	Restricted	Pouilly et al. (2004)
AI	*Engraulidae* sp.*	BOLIVIA	Restricted	Pouilly et al. (2004)
AI	*Steindachnerina* sp.*	BOLIVIA	Cosmopolitan	Pouilly et al. (2004)
AI	*Sturisoma nigrirostrum* Fowler, 1940*	BOLIVIA	Restricted	Pouilly et al. (2004)
AI	*Hypoptopoma joberti* (Vaillant, 1880)*	BOLIVIA	Restricted	Pouilly et al. (2004)
AI	*Psectrogaster rutiloides* (Kner, 1858)*	BOLIVIA	Restricted	Pouilly et al. (2004)
AI	*Loricariichthys maculatus* (Bloch, 1794)*	BOLIVIA	Restricted	Pouilly et al. (2004)
AI	*Anodus elongatus* Agassiz, 1829*	BOLIVIA	Cosmopolitan	Pouilly et al. (2004)
AI	*Potamorhina altamazonica* (Cope, 1878)*	BOLIVIA	Restricted	Pouilly et al. (2004)
AI	*Pseudohemiodon laticeps* (Regan, 1904)*	BOLIVIA	Cosmopolitan	Pouilly et al. (2004)
AI	*Curimatella immaculata* (Fernádez-Yepes, 1948)*	BOLIVIA	Cosmopolitan	Pouilly et al. (2004)
AI	*Curimatella alburna* (J.P. Müller & Troschel, 1844)*	BOLIVIA	Restricted	Pouilly et al. (2004)
AI	*Prochilodus nigricans* Spix & Agassiz, 1829*	BOLIVIA	Cosmopolitan	Pouilly et al. (2004)
AI	*Curimatella meyeri* (Steindachner, 1882)*	BOLIVIA	Restricted	Pouilly et al. (2004)
AI	*Psectrogaster curviventris* Eigenmann & Kennedy, 1903*	BOLIVIA	Restricted	Pouilly et al. (2004)
AI	*Potamorhina latior* (Spix & Agassiz, 1829)*	BOLIVIA	Restricted	Pouilly et al. (2004)
HO	*Hemiodus quadrimaculatus* Pellegrin, 1909	FRENCH GUIANA	?	de Mérona & Vigouroux (2006)
HO	*Leporinus fasciatus* (Bloch, 1794)	FRENCH GUIANA	Cosmopolitan	de Mérona & Vigouroux (2006)
HO	*Leporinus friderici* (Bloch, 1794)	FRENCH GUIANA	Restricted	de Mérona & Vigouroux (2006)
HO	*Leporinus granti* Eigenmann, 1912	FRENCH GUIANA	?	de Mérona & Vigouroux (2006)
HO	*Myleus rhomboidalis* (Cuvier, 1818)	FRENCH GUIANA	Restricted	de Mérona & Vigouroux (2006)
HO	*Myleus ternetzi* (Norman, 1929)	FRENCH GUIANA	Restricted	de Mérona & Vigouroux (2006)
HO	*Apareiodon affinis* (Steindachner, 1879)	BRAZIL	Cosmopolitan	Novakowski et al. (2008)
HO	*Hypostomus boulengeri* (Eigenmann and Kennedy, 1903) *	BRAZIL	cosmopolitan	Novakowski et al. (2008)
AI	*Loricaria* sp.*	BRAZIL*	Cosmopolitan	Novakowski et al. (2008)
AI	*Pterygoplichthys ambrosetti* (Holmberg, 1893)*	BRAZIL	cosmopolitan	Novakowski et al. (2008)
OA	*Psectrogaster curviventris* Eigenmann & Kennedy, 1903	BRAZIL	Restricted	Novakowski et al. (2008)
OA	*Trachydoras paraguayensis* (Eigenmann & Ward, 1907)	BRAZIL	Cosmopolitan	Novakowski et al. (2008)
H	*Astyanax minor* Garavello & Sampaio, 2010	BRAZIL	Cosmopolitan	Delariva et al. (2013)
H	*Apareiodon vittatus* Garavello, 1977	BRAZIL	Cosmopolitan	Delariva et al. (2013)
H	*Hypostomus myersi* (Gosline, 1948)	BRAZIL	Restricted	Delariva et al. (2013)

Table 1 continued

Trophic group	Fish Species	Country	Distribution	References
HO	*Mylossoma aureum (*Agassiz, 1829)*	BRAZIL	Restricted	da Silveira Suçuarana et al. (2016)
H	*Hemiodus semitaeniatus* Kner, 1858	BRAZIL	Restricted	Dary et al. (2017)
H	*Hemiodus unimaculatus* (Bloch, 1794)	BRAZIL	Restricted	Dary et al. (2017)
H	*Myleus setiger* Müller & Troschel, 1844 *	BRAZIL	Restricted	Dary et al. (2017)
H	*Myloplus schomburgkii* Jardine, 1841 *	BRAZIL	Restricted	Dary et al. (2017)
H	*Myloplus torquatus* (Kner, 1858)*	BRAZIL	Restricted	Dary et al. (2017)
OA	*Platanichthys platana* (Regan, 1917)	URUGUAY	Cosmopolitan	López Rodríguez et al. (2019)
OA	*Parapimelodus valenciennes* (Lütken, 1874)	URUGUAY	Cosmopolitan	López Rodríguez et al. (2019)
OA	*Astyanax lacustris* (Lütken, 1875)	URUGUAY	Cosmopolitan	López Rodríguez et al. (2019)

AI alagerivore–iliophage, *HO* herbivore–omnivore, *OA* omnivore–algaeivore, *H* herbivore

Asterisk (*) indicates that algae reported in these fishes' stomach content most probably comes from the periphyton considering the taxa described in the corresponding reference

cit.), the authors compared the effect of juvenile (zooplanktivorous visual predators) and adults (filter-feeding) on an experimental study performed in Itans Reservoir. They found higher densities of rotifers and lower densities of cladocerans in tilapias juveniles' treatments. However, there were no significant differences between the treatments with different stocking biomass of juveniles or several stocking biomasses of adults. Likewise, Okun et al. (2008) reported similar results with no differences among treatments with and without tilapias addition in large zooplankton abundance. In this experiment, *Ceriodaphnia cornuta* and *Bosmina longirostris* show a small pick in their abundance without fish. At the same time, dominant calanoid species (mainly *Notodiaptomus* spp.) and rotifers (*Keratella*, *Polyarthra*, *Trichocerca,* and *Brachionus*) nearly disappeared in all treatments (with the absence and presence of fish). No cascading effects on phytoplankton were reported.

In contrast, Figeredo & Gianni (2005) reported that this tilapia species consumes *Cylindrospermopsis raciborskii* (mean length 85 μm) (now *Raphidiopsis raciborskii*) in experimental conditions, producing a change in the phytoplankton structure from an assemblage dominated by cyanobacteria at the beginning to chlorophyceae at the end. Additional positive evidence of filter-feeding fish effects on phytoplankton comes from Starling (1993) in Brazil, who worked in experimental conditions with the introduced silver carp *Hypophthalmichthys molitrix*. He demonstrated an effective feeding impact on phytoplankton > 20 μm of MLD.

Novakowski et al. (2016) in a more recent study performed with four native Cichlidae species from the Cuiabá River (Brazil), found that these fishes have an omnivorous diet, including plants, macrocrustaceans larval insects, and detritus. They did not report algae in their diet. López Fernández et al. (2012) analyzed twenty-one stomach content from tribe Geophagini, one of the most diverse Neotropical cichlids. They found that the main food items were benthic invertebrates and small fish.

In comparison, there are abundant references with filter-feeding species from other continents, like Africa and North America, like *Sarotherodon*, *Dorosoma*, *Haplochromis,* and *Hypophthalmichthys*. All these genera have been shown an effective feeding one phytoplankton, including cyanobacteria species, as equal as zooplankton (Moriarty et al., 1973; Vareschi & Jacobs, 1984; DeVries & Stein, 1992; Beveridge &

Baird, 2000; Turker, 2003; Zhang et al., 2006; Ke et al., 2007).

For this fourth mechanism intending to determine the role of fishes (visual and filter-feeding species) as grazers of phytoplankton, the evidence available mainly supports the idea that visual planktivorous predators do not feed on algae, at least intentionally. For filter-feeding species, especially those introduced in South America, results reported are less conclusive, and the real phytoplankton effects remain elusive. It is essential to highlight that the impact of filter-feeding fish on phytoplankton can also occur indirectly by feeding on large zooplankton species (as several authors have proved in Brazil) or more directly size-selective ingestion of some algae species. Moreover, filter-feeder fishes do not visually select food; however, the ability of some algae to avoid ingestion or digestion can lead to changes in community structure. Indeed, species able to escape grazing (e.g., small size) can grow better when they are released from the competition of resources with more vulnerable species (consult Figeredo & Gianni (2005) for full references).

The fifth mechanism: filter-feeding exotic bivalves as drivers of phytoplankton structure

The introduction of non-native species, one of the most significant threats to the world's current biodiversity, has been poorly studied or even considered a priority among South American governments (Speziale et al., 2012); and particularly on non-native mollusk (Darrigran et al., 2020). Aquatic invasive bivalve species are an increasing concern due to their potential to affect the aquatic systems, especially native biodiversity from those environments where they are introduced and become established (Sousa et al., 2014; Gallardo et al., 2016).

Limnoperna fortunei and *C. fluminea*, both Asiatic origin species, appear as effective filter-feeders, demonstrating several ecological differences summarized in Table 2. The exotic bivalve *Limnoperna fortunei* has been proved to be a capable grazer of phytoplankton, reaching high filtration rates in experimental conditions. Sylvester et al. (2005) registered, using a monoculture, a filtration rate of 350 ml ind^{-1} h^{-1} at 25 °C, and we obtained a filtration rate in Frau et al. (2013) of 357 ml ind^{-1} h^{-1} at 28 °C by using a natural phytoplankton assemblage. In the same study, we found a decrease in phytoplankton density > 60%

and a change in the phytoplankton assemblage from single-cell organisms to single-cell flagellates in the presence of the mollusk. Moreover, Rojas Molina et al. (2010), by analyzing the stomach and gut content of individuals collected in natural environments linked to the Paraná River, showed that *L. fortunei* has preferences by large euglenophytes (74% of the phytoplankton stomach content, mainly *Trachelomonas volvocina*). Cataldo et al. (2012a), in an experiment performed in Río Tercero Reservoir (Argentina), showed that filtration of this mollusk on phytoplankton was not dependent on phytoplankton size. In Frau et al. (2016), we analyzed *L. fortunei* feeding selectivity on phytoplankton, and we found a positive selection of Chlorococcales, Desmidiales, Euglenophyceae (with some exceptions), and Chrysophyceae. Selectivity on large euglenophyceae was diminished in the presence of rotifers as a secondary feeding item. In contrast, Volvocales, Cryptophyceae, and loricate Euglenophyceae like *Trachelomonas* were rejected. This negative grazing effect was attributed to the rapid reproduction rate of volvaceans and cryptophytes, and *Trachelomonas* due to its inorganic protection shell (the lorica). Note, however, that this genus was reported as the most abundant in the stomach content analysis made by Rojas Molina et al. (2010) in natural conditions. This contradiction may suggest a rapid reproduction rate of *Trachelomonas* in the water column during the experimental condition that should be deepened. Besides, Cataldo et al. (2012b) found in Salto Grande reservoir (Argentina) that this bivalve boosts *Microcystis* growth. This is done by increasing the nutrients re-mineralization, by reducing the competence, and promoting *Microcystis* agglomerations through predation of small single-cell individuals, rejecting large mucilaginous colonies.

Most studies performed with this mussel species do not differentiate between particles ingested and those rejected as pseudofeces, leading to contrasting findings (Boltovskoy et al., 2015). Gazulha et al. (2012a) differentiated between particles ingested and particles expelled as pseudofeces in Brazil. They concluded that filtration rates of single-cell, colonial, and filamentous cyanobacteria are similar. In this study, *L. fortunei* ingested single cells and rejected filamentous and colonial forms. Gazulha et al. (2012b) obtained a similar result when they fed *L. fortunei* with a mixture of cyanobacteria and diatoms. The diatom *Nitzschia palea* (Kützing) W.Smith disappeared from the water

Table 2 Comparison of some ecologically relevant parameters from *Limnoperna fortunei* and *Corbicula fluminea* reported in South America (in bold) and some other parts of the world

	Adult size (maximum valve length)	Maximum density	Size range selectivity	Taxonomic selectivity	Maximum filtration rate	References
Limnoperna fortunei	**14–35 mm/** 20–40 mm	**10,000 ind m²/** 10,000 ind m²	**20–110 µm/** no data	Positive: Chlorophyceae, Euglenophyceae and Chrysophyceae. Negative: filamentous and colonial Cyanobacteria; Bacillariophyceae	**102 ml g DW h⁻¹/** no data	Morton (1973), Magara et al. (2001), Cataldo et al. (2012a, b), Gazulha et al. (2012a, b), Frau et al. (2013, 2016)
Corbicula fluminea	**15–33 mm/** 50–70 mm	**4500 ind m²/** 20,000 ind m²	**No data/** 0.3–16 µm	Not reported	**106.8 ml g DW h⁻¹/** 24 ml g DW h⁻¹	McMahon (1983), Boltovskoy et al. (1995), Cohen et al. (1984), Way (1990), Atkinson (2011), Marroni et al. (2016)

faster than *Microcystis aeruginosa*, but while *M. aeruginosa* was ingested, *N. palea* was rejected as pseudofeces by this bivalve.

In comparison, studies performed in South America with *C. fluminea* regarding its impact on phytoplankton are rare. Boltovskoy et al. (1995) first examined taxonomic prey selection by *C. fluminea* in South America by analyzing the gut content from individuals obtained from the Paraná River System (Argentina). In this study, Boltovskoy et al. (*op. cit.*) demonstrated that *C. fluminea* showed no taxonomic preferences for phytoplankton in an assemblage composed by diatoms, chlorophytes, and cryptophytes. More recently, Marroni et al. (2016), in an experiment performed in Uruguay, reported a filtration rate for this bivalve of 106.8 ml g DW h⁻¹ in a phytoplankton assemblage dominated by Euglenophyceae, Chlorophyceae, and filamentous cyanobacteria. However, no effective selection of phytoplankton was reported. Other studies performed out of South America have reported that *C. fluminea* selects its preys by size. It is suggested that this bivalve can sort particles up to 20 µm (Way et al., 1989) and select those up to 16 µm (Way et al., 1990). Finally, Atkinson et al. (2011) showed that *C. fluminea* selected phytoplankton prey by size-between 0.3 and 10 µm, yet without showing any taxonomic preference.

Another species highly invasive of the North Hemisphere (including European countries) is *Dreissena polymorpha* Pallas, 1771. In a very detailed comparison, Karatayev et al. (2007) found that *D. polymorpha* has many similar characteristics with *L. fortunei*. Both species are sessile, byssate bivalves with a planktonic larval stage and high reproductive capacity. Both species are highly active suspension feeders and can create substrate complexity otherwise not found in freshwater systems, acting as influential ecosystem engineers. For *D. polimorpha*, several studies performed in the field have proven the impact of this bivalve in those lakes and rivers invaded. Some studies demonstrated that *D. polimorpha* is a selective feeder with a high grazing rate and highly adapted to the invaded environments. This mussel has selective grazing showing a consistent preference for algae between 7 and 100 µm, particularly cryptophytes, and avoidance of large chlorophytes and cyanobacteria (Winkel & Davids, 1982; Caraco et al., 1997; Smith et al., 1998; Dionisio Pires, et al. 2002, 2004; Naddafi et al., 2007; Dölle & Kurzmann, 2020).

For *Corbicula*, which has also invaded North America and Europe (Araujo et al. 1992), international evidence regarding its impact on phytoplankton is less developed. Pioneer studies of Cohen et al. (1984) show a high reduction in Chl-*a* in the Potomac River, confirmed in experimental studies. Beaver et al. (1991), in an experimental study performed in Florida (USA) informed a pronounced effect on Chl-*a* concentration in a phytoplankton assemblage dominated by two filamentous cyanobacteria [*Lyngbya contorta* Lemmermann, now *Planktolyngbya contorta*

(Lemmermann) Anagnostidis & Komárek] and *Aphanocapsa delicatissima* West & G.S.West). More recently, Hwang et al. (2004) studied the effect of *Corbicula leana* Prime, 1864 on phytoplankton structure from two Korean lakes and found that a few phytoplankton species were removed by mussel grazing during the 24-h incubation period. These algae were *Chlamydomonas*, *Kirchneriella*, and *Tetraedron* (Chlorophytes), *Synechocystis*, and *Phormidium* (Cyanobacteria), *Dinobryon* (Chrysophyte), and some diatoms. Considering the large size of many of these algae and the restricted size that *C. fluminea* may ingest (above 20 μm), the most probably is that they were rejected as pseudofeces after filtration.

The effect of these two bivalves (*L. fortunei* and *C. fluminea*) in natural conditions could be somewhat different. Indeed, most parts of the studies reported here were made in experimental conditions, but several factors may influence the impact of these two bivalves in a natural environment. For *L. fortunei*, several authors have reported that this mollusk is a food item for numerous fish species and other organisms, like crabs and otters (García & Protogino, 2005; Paolucci et al., 2007; Sylvester et al., 2007). Moreover, despite previous reports that have informed high densities for *L. fortunei* in reservoirs (occasionally > 20,000 ind m^{-2}) (Boltovskoy et al., 2015), the evidence from natural ecosystems indicates that *L. fortunei* survival and growth are highly variable and the abundances reached much lower. This is because the flooding pulse in floodplain ecosystems affects the planktonic larval transport and settlement. The bivalve settlement also depends on the presence of macrophytes which function as nursery beds, or the presence of rigid substrates to develop until adult stages. Other factors like turbidity, food availability, and quality may also affect the survival of this species in natural conditions (Oliveira et al. 2011; Musin et al. 2015; Saigo et al. 2016; Ernandes-Silva et al., 2016). For *C. fluminea* its ecology is much less known in South America.

In sum, higher efforts should still be made to clarify the real impact of these two invasive bivalves in natural ecosystems. Changes across seasons related to environmental conditions and phytoplankton structure could influence the filtration rate and selectivity over phytoplankton, but we still lack enough supporting evidence.

Conclusions

In this review, I attempted to synthesize the available information regarding grazing impacts on the phytoplankton structure from South America by analyzing and classifying the available information under five explicative mechanisms. I also identified some existing gaps and needed research. At this point, several aspects should be highlighted, but remarkably, some of them regarding the origin and distribution of available studies become evident. First, we still lack reports from Paraguay, Chile, Perú, Colombia, Guayana, and Suriname. Moreover, a low number of studies regarding this topic have been reported in international specialized journals for countries like Ecuador, Bolivia, and Venezuela. Altitude, the climatic region, and the type of environment may influence the diversity of organisms, their size, the aquatic trophic state, and the relative abundance of the several plankton groups. So, we still need more studies to support or give new insights into the grazing impacts on phytoplankton from those countries mentioned. Moreover, reports for lotic environments, particularly lowland streams, are still scarce compared with lakes and reservoirs. We also have a poor understanding of trophic interactions in high-altitude shallow lakes (> 3000 m above sea level). Indeed, most of the information gathered here comes from warm and temperate climatic regions, reservoirs from Brazil, and field-experimental studies performed in Argentina and Uruguay with poor representation of other geographic and climatic regions in South America.

Notably, we lack the knowledge to determine the fundamental role of temperature as a driver of zooplankton size and its capability to graze on phytoplankton (the first mechanism). This is especially true for Rotifera. We have clear that large zooplankton tends to have lower maximum linear dimensions, especially cladocerans, than reported for other latitudes. Still, we have no conclusive evidence of how temperature may affect zooplankton capability graze on phytoplankton or if this smaller size could be directly linked to temperature. Climate change projections indicate a rise in global temperature, a general picture of an increase in cyanobacteria dominance, and a tendency of zooplankton smaller-bodied size (De Senerpont Domis et al., 2013). Nonetheless, we still cannot conclude if these changes may affect the

Table 3 Comparative table of the information regarding the five mechanisms analyzed in South American studies and some other world continents

Mechanism involved	South America	Other water ecosystems from the world
Temperature changes as drivers of zooplankton size and grazing capability on phytoplankton	Poorly understood mechanism	The evidence is not conclusive; however, most part of the studies suggest that despite temperature may affect size, the grazing rate of zooplankton and its effects on phytoplankton may depend from several other factors and be variable among species and zooplankton groups
Planktivorous fishes as driver of phytoplankton through selective predation on large zooplankton	**Zooplankton community might become dominated by small-bodied species because planktivorous fish consume large-bodied zooplankters**	**Zooplankton community might become dominated by small-bodied species because planktivorous fish consume large-bodied zooplankters**
Grazing effects of zooplankton on phytoplankton. A matter of size and palatability	**Maximum linear dimension of microalgae seems to be the main fact, being this accompanied morphophysiological characteristics that also become relevant**	**Maximum linear dimension of microalgae seems to be the main fact, being this accompanied morpho-physiological characteristics that also become relevant**
Planktivorous fishes as drivers of phytoplankton structure	No direct effects of phytoplankton have been reported	Abundant references with native filter-feeding species from north hemisphere ecosystems like *Dorosma* spp., *Oreochromis* spp., and *Hypophthalmichthys molitrix*. All these species have shown to effectively graze and control phytoplankton, as equal as zooplankton
Filter-feeding exotic bivalves as drivers of phytoplankton structure	*L. fortunei* show a selective feeding by composition and size in experimental studies while scarce information regarding *C. fluminea* is available	*D. polimorpha* is a selective filter-feeder that alters its feeding behavior in relation to phytoplankton composition to capture and ingest high quality phytoplankton, especially when phytoplankton occur in preferred size ranges. Its impact in natural conditions have been deeply studied

In bold are highlighted those mechanisms consistent between studies reported in South America and those reported in other parts of the world

planktonic trophic structure of South American inland waters and how these changes may impact the water ecosystem services provided.

The evidence summarized here supports the idea that grazing impacts on phytoplankton may depend on the nature of grazers (size and species) and the morpho-physiological features of phytoplankton (the second and third mechanism). This effect would be more apparent among macrozooplankton (Cladocera and Copepoda) above 700 μm and only when they reach high densities (> 100 ind l^{-1}). Moreover, the results obtained indicate a significant grazing impact on small (< 35 μm) and very small size phytoplankton (< 10 μm).

Microzooplankton (rotifers and nauplii) may have a similar grazing effect on phytoplankton structure, especially over lower size algae (< 20 μm) when they reach high densities. No effect should be expected in flagellates with high reproduction capability, like small chlorophytes and some cryptophytes. Macrozooplankton effects on larger algae should be expected in non-toxic filamentous cyanobacteria rather than large mucilaginous colonies. This is a tendency that should be solved with more studies on this topic. Cyanobacteria blooms are expected to rise (Paerl, 2017), so we still need to understand planktonic trophic interactions and their impact on cyanobacteria blooms, especially in eutrophic artificial environments, like reservoirs and urban lakes frequently impacted with cyanobacteria blooms.

Planktivorous or native filter-feeding fishes grazing effect on phytoplankton (the fourth mechanism) is not

decisive. These groups of fishes mainly affect phytoplankton throughout cascading effects on large zooplankton. However, some experimental inquiries are necessary to clarify the real impact of some fishes, like T. *paraguayensis* and *A. minor* classified as "algaeivore." Moreover, new studies seem to be required with some introduced filter-feeders fishes species considering some contradictory results and a poor understanding of the cascading effects that these filter-feeding species may have on phytoplankton.

About the impact of invasive exotic filter-feeding bivalves reported in South America (the fifth mechanism), we have much experimental data concerning *L. fortunei*. However, we do not have many field studies where other factors and conditions may affect the real impact of this bivalve on phytoplankton. For instance, this mussel has several interactions with different trophic levels, like predatory fish that feed on it. Besides, *L. fortunei* feeding impact strongly depends on its density, which depends on the availability of rigid substrates, floating vegetation, and the flooding pulse. So, its real effect on natural ecosystems is still not fully understood. For *C. fluminea*, the evidence is further truncated for South America, and a great effort should be made to test the real effect of these bivalve on natural phytoplankton assemblages. We know both mussels feed on small size phytoplankton. *L. fortunei* rejects diatoms and large cyanobacteria. In contrast, *C. fluminea* has a limited size selection (< 20 μm) and no other taxonomic selection criterion.

Compared with several studies performed for other latitudes, mainly North America and Europe, the studies summarized here support some general grazing mechanisms, especially the role of planktivorous fishes on zooplankton and their cascades effects on phytoplankton. Moreover, the importance of phytoplankton morpho-functional characteristics and ontogenetic characteristics of zooplankton appears to be very defined and relevant. However, the other mechanisms mentioned above seem contradictory or incomplete, requiring more specific studies (Table 3). Going back to Benndorf et al. (2002) revision performed eighteen years ago, the evidence reported here supports the authors' predictions of effective grazing effects in experiments, shallow lakes, and deep eutrophic lakes (mainly reservoirs). In addition, other critical aspects appear relevant. These aspects are invasive bivalves, the absence of planktivorous

fish in some environments, the localization of the water ecosystems (latitudinal and attitudinal), the composition and biomass of zooplankton, and the phytoplankton structure (size and palatability). In sum, several aspects are still poorly studied or contradictory in South American ecosystems. So, exciting new avenues of work in plankton ecology are expecting to be followed and deepened shortly.

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