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Inorganic mercury (Hg^{2+}) accumulation in autotrophic and mixotrophic planktonic protists: Implications for Hg trophodynamics in ultraoligotrophic Andean Patagonian lakes

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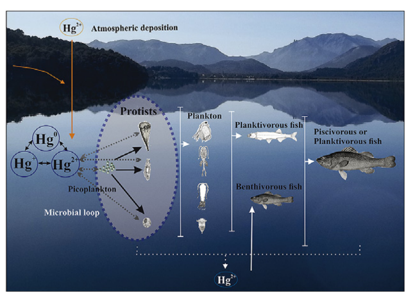
HIGHLIGHTS

- Picoplankton and protists are entry points of Hg^{2+} in Andean lakes.
- Pelagic microbiota mediates the Hg^{2+} flux among abiotic and biotic compartments.
- Picoplankton enhances Hg^{2+} incorporation in phytoflagellates and mixotrophic ciliates.
- Organisms' surface and surface:volume influence Hg^{2+} adsorption and internalization.
- Planktonic protists link pelagic-benthic Hg pathways in Andean Patagonian lakes.

GRAPHICAL ABSTRACT



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ABSTRACT

Microbial assemblages are typical of deep ultraoligotrophic Andean Patagonian lakes and comprise picoplankton and protists (phytoflagellates and mixotrophic ciliates), having a central role in the C cycle, primary production and in the incorporation of dissolved inorganic mercury (Hg^{2+}) into lake food webs. In this study we evaluated the mechanisms of Hg^{2+} incorporation in hetero- and autotrophic bacteria, in the autotrophic dinoflagellate (*Gymnodinium paradoxum*) and in two mixotrophic ciliates (*Stentor araucanus* and *Ophrydium naumanni*) dominating the planktonic microbial assemblage. The radioisotope ^{197}Hg was used to trace the Hg^{2+} incorporation in microbiota. Hg uptake was analyzed as a function of cell abundance (BCF: bioconcentration factor), cell surface (SCF: surface concentration factor) and cell volume (VCF: volume concentration factor). Overall, the results obtained showed that these organisms incorporate substantial amounts of dissolved Hg^{2+} passively (adsorption) and actively (bacteria consumption or attachment), displaying different Hg internalization and therefore, varying potential for Hg transfer. Surface area and quality, and surface:volume ratio (S:V) control the passive uptake in all the organisms. Active incorporation depends on bacteria consumption in the mixotrophic ciliates, or on bacteria association to surface in the autotrophic dinoflagellate. Hg bioaccumulated by pelagic protists can be transferred to higher trophic levels through plankton and fish feeding, regenerated to the dissolved phase by excretion, and/or transferred to the sediments by

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particle sinking. In ultraoligotrophic Andean Patagonian lakes, picoplankton and planktonic protists are key components of lake food webs, linking the pelagic and benthic Hg pathways, and thereby playing a central role in Hg trophodynamics.

1. Introduction

Mercury (Hg) is a ubiquitous pollutant of global concern due to its extreme toxicity and bioamplification of certain organic species occurring in aquatic systems and posing risks for wildlife and humans through fish consumption (Chen et al., 2008; Sunda, 2012). Elevated Hg enrichment has been often attributed to particular availability and accumulation efficiency at the base of the food webs (Driscoll et al., 2007; Stewart et al., 2008; Chasar et al., 2009). Bacteria and phytoplankton can take Hg and transfer it from the dissolved phase up to higher trophic levels, thus constituting a key entry point of this metal into food webs (Watras et al., 1998; Soto Cárdenas et al., 2014; Le Faucheur et al., 2014). Uptake of dissolved Hg is much higher in algae than those in subsequent trophic levels (Mason et al., 1994), nevertheless, the actual assimilation of Hg varies with water chemistry among other environmental factors (i.e. Hg concentration and fractionation between the particulate and dissolved phases and environmental occurrence of binding agents; Driscoll et al., 2007; Adams et al., 2009; Luenguen et al., 2012). Pelagic organisms process Hg through their metabolic activity and favor the burial of Hg in the sediments due to their senescence and sinking (Adams et al., 2009; Le Faucheur et al., 2014). Thus, understanding the factors influencing the incorporation of inorganic Hg (Hg^{2+}, the most abundant Hg species in solution) at the base of pelagic food webs, is essential to delineate Hg pathways in aquatic systems (Pickhardt et al., 2005; Carroll et al., 2011; Le Faucheur et al., 2014).

The main bioaccumulation pathways in planktonic organisms, including pico- and phytoplankton, are passive diffusion of neutral complexes across the cell membrane, and facilitated transport and predation (i.e. consumption of Hg-bearing organisms) (Twiss and Campbell, 1995; Mason et al., 1996; Wang, 2002; Gorski et al., 2006; Pickhardt and Fisher, 2007). The structure and trophic features of planktonic assemblages, such as the relative abundance of autotrophic, heterotrophic and/or mixotrophic species, may have an important part in determining the amount of Hg entering through this microbial loop (Soto Cárdenas et al., 2014). In addition, the abundance and size of organisms can affect the partitioning of Hg and its transference to higher levels in pelagic food webs. High abundance of organisms promotes lower Hg uptake (Chen and Folt, 2005; Luengen and Flegal, 2009; Chen et al., 2012), slowing down its transference to grazers (Adams et al., 2009). Small organisms accumulate trace metals more rapidly than larger ones due to their greater surface area to volume ratio (S:V) (Fisher et al., 1983; Soto Cárdenas et al., 2014). Biological surfaces like mucilage, cell walls and membranes have functional groups with differential affinities for Hg and thus, may control its partitioning. The extent to which Hg passes from basal organisms to grazers depends on the intracellular metal distribution (Reinfelder and Fisher, 1991; Twining and Fisher, 2004). Hg^{2+} bound to algal membranes is assimilated less efficiently than methylmercury (MeHg), which is incorporated into the cytoplasm and is more readily accumulated at higher trophic levels (Fisher et al., 1983; Rajamani et al., 2007).

Andean lakes of North Patagonia (Argentina) are remote and pristine systems devoid of local anthropogenic impact, however, moderate to high total Hg (THg) levels have been detected in different pelagic and benthic compartments (Arribére et al., 2010; Arcagni et al., 2013, 2018; Rizzo et al., 2014). In the region, inputs of Hg have been related to the intense volcanic activity (Ribeiro Guevara et al., 2010; Daga et al., 2014, 2016; Soto Cárdenas et al., 2018) of the Southern Volcanic Zone (Naranjo and Stern, 2004; Bertrand et al., 2014). Lake sediment records also exhibit signals of historical Hg deposition from long range atmospheric transport (Hermanns and Biester, 2013; Hermanns et al., 2013), forest fires and biomass burning (Ribeiro Guevara et al., 2010; Daga et al., 2008, 2014, 2016). In lakes of Nahuel Huapi National Park (NHNP), two main pathways of Hg trophic transfer have been recognized. On one hand, a pelagic pathway through which dissolved Hg^{2+} is accumulated by basal pelagic organisms and transferred to zooplankton and planktivorous fish. And, concomitantly, a benthic pathway in which MeHg is accumulated by macroinvertebrates (i.e. crayfish) from the sediments and transferred to benthic foraging fish (Arcagni et al., 2018; Soto Cárdenas et al., 2018).

Andean Patagonian lakes are ultra to oligotrophic systems that display extremely low nutrient levels, low dissolved organic carbon (DOC) concentrations and are exposed to high solar radiation levels (Morris et al., 1995). Picoplankton, nanoplankton and ciliates are the main constituents of microbial food webs of Andean Patagonian lakes, having a central role in the C cycle (Gerea et al., 2016), and in Hg^{2+} incorporation into pelagic food webs (Soto Cárdenas et al., 2014, 2018). These microbial assemblages are dominated by mixotrophic nanoflagellates adapted to low nutrient levels by alternating between autotrophic and heterotrophic nutrition, consuming bacteria and picocyanobacteria (Queimaliños et al., 2002; Woelfl and Geller, 2002; Gerea et al., 2016). Also, several common ciliate species are mixotrophic, using C fixed photosynthetically by endosymbiotic algae (Modenutti and Balseiro, 2002; Woelfl et al., 2010).

In these Andean lakes, the highest THg levels in different plankton size classes have been detected in organisms included in the microbial loop (Arribére et al., 2010; Rizzo et al., 2014). Picoplankton (bacteria and picocyanobacteria) internalizes more dissolved Hg^{2+} than larger plankton, constituting the most important entrance of Hg^{2+} to pelagic food webs. Whereas, two larger size fractions comprising dinoflagellates and mixotrophic ciliates scavenge dissolved Hg^{2+} transferring it to higher trophic levels, while regenerating a fraction to the environment (Soto Cárdenas et al., 2014, 2018), as has been shown for other microbial assemblages (Twiss and Campbell, 1995; Twining and Fisher, 2004).

The particular microbial communities of ultraoligotrophic Andean Patagonian lakes provide a unique opportunity to study the role of bacteria and mixotrophic protists linking abiotic and biotic compartments within the Hg cycle. In this investigation, we focused on the mechanisms of Hg^{2+} incorporation by organisms of the microbial assemblage including picoplankton (autotrophic and heterotrophic bacteria), phytoflagellates and mixotrophic ciliates. In this context, we assessed the specific Hg^{2+} uptake of three dominant protists considering their morphology and size, and discussed their potential to transfer Hg^{2+} to higher trophic levels. We analyzed experimentally the passive (adsorption) and active Hg^{2+} uptake (through interactions with picoplankton) in the