

Introduction



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Salt in freshwaters: causes, effects and prospects - introduction to the theme issue

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Humans are globally increasing the salt concentration of freshwaters (i.e. freshwater salinization), leading to significant effects at the population, community and ecosystem level. The present theme issue focuses on priority research questions and delivers results that contribute to shaping the future research agenda on freshwater salinization as well as fostering our capacity to manage salinization. The issue is structured along five topics: (i) the estimation of future salinity and evaluation of the relative contribution of the different drivers; (ii) the physiological responses of organisms to alterations in ion concentrations with a specific focus on the osmophysiology of freshwater insects and the responses of different organisms to seawater intrusion; (iii) the impact of salinization on ecosystem functioning, also considering the connections between riparian and stream ecosystems; (iv) the role of context in moderating the response to salinization. The contributions scrutinise the role of additional stressors, biotic interactions, the identify of the ions and their ratios, as well as of the biogeographic and evolutionary context; and (v) the public discourse on salinization and recommendations for management and regulation. In this paper we introduce the general background of salinization, outline research gaps and report key findings from the contributions to this theme issue.

This article is part of the theme issue 'Salt in freshwaters: causes, ecological consequences and future prospects'.

1. Salinization of freshwater ecosystems: state of the art and prospects

Freshwater ecosystems are essential for human societies, because they provide important services such as drinking and irrigation water, food, climate regulation and recreation. These services crucially depend on the integrity of populations and communities of freshwater organisms [1,2]. However, the extinction rates of freshwater species are among the highest worldwide [3–5]. This is owing to a multitude of anthropogenic stressors, including excess input of nutrients, hydromorphological alterations and continuous or repeated pollution [6,7], which cause ecological degradation. Although the exposure and effects of specific pollutants such as heavy metals or pesticides in freshwaters have received attention [8,9], other pollutants have been less studied. For example, although it has been known for a long time that human activities alter the total concentration of major ions (or salinity) and the composition of these ions in freshwater ecosystems [10], this issue has received relatively little attention [11]. Despite the documentation of salinity effects [12], it is often unknown how important salinity is in comparison to other stressors and how it may interact with these

stressors, how important the different drivers of salinization (i.e. an increase in the concentration of ions) are and how salinity might influence freshwater ecosystems in the future. Research that answers these questions is pivotal for a rational and efficient ecosystem management. The diagnosis of these gaps stimulated the organization and compilation of the present theme issue.

The ion content of inland surface waters is determined by several natural factors, including rainfall, rock weathering, seawater intrusion and aerosol deposits [13,14]. If these natural processes are the driver of salinization, this phenomenon is called primary salinization. However, given the strong influence of humans even on regional and global biogeochemical cycles, which have been captured in calling the current era the Anthropocene [15], human activities can accelerate these natural processes [16,17]. For example, construction activities, resource extraction and changes in land cover can bring bedrock materials to the surface that are subject to much more rapid chemical weathering, consequently increasing the transport of ions to surface waters [18–20]. Also, agriculture can produce highly saline irrigation return flows that enter freshwaters [21], and land clearing can bring naturally saline groundwaters to the surface [22]. In cold regions, salts are often applied to roads to prevent the build-up of ice and snow, which are washed into surrounding freshwaters during snowmelt and rain [23,24]. Overall, the salinization of freshwater ecosystems owing to human activities is called secondary salinization (hereafter termed freshwater salinization), and it has been documented in a wide variety of lakes [25,26], rivers [12] and wetlands [27]. At the same time, naturally saline ecosystems can be diluted owing to anthropogenic freshwater inputs [28], although this has received even less attention.

Freshwater animals need to maintain an osmotic balance between the ion concentration within their cells and their body fluids, which are strongly influenced by the salinity of the surrounding water owing to body permeability [29,30]. The maintenance of this balance is key to cellular stability (i.e. changes in osmotic pressure can cause cellular damage or death) and requires energy. Freshwater salinization, through an increase in osmotic pressure, can have drastic effects on the fitness and survival of freshwater organisms. In general, species richness declines along the salinity gradient in inland waters [31,32] and laboratory toxicity tests show that most freshwater species are extirpated once a certain threshold of salinity is exceeded [33–35]. However, this response largely depends on the identity of the ions, because the toxicity of ions to freshwater organisms varies [36–38]. Additionally, the interactions among ions can modify their toxicity [39–41]. Besides lethal effects, salinization can reduce organism and population fitness through sub-lethal effects; e.g. oxidative stress [42,43], delayed growth [44,45], reduced feeding efficiency [46,47], increased drift [38,48] and malformations [49,50]. Moreover, it can lead to important changes in the ecosystem structure and functioning by altering trophic interactions [51,52], biochemical cycles [27] and leaf decomposition [53,54]. However, as for other anthropogenic stressors, the implications of freshwater salinization at the ecosystem level are still poorly understood and our capacity for prediction is very limited.

2. The context and focus points of the theme issue

We have highlighted above that central research questions need to be addressed to be able to understand, predict, mitigate and remediate the impacts of salinization on individual organisms, populations, communities, ecosystems and human welfare. The present theme issue focuses on priority research questions and provides key findings, outlined below, that contribute to shaping the future research agenda on freshwater salinization as well as fostering our capacity to manage salinization.

(a) Which are (and will be) the main causes of freshwater salinization?

Early studies suggested that freshwater salinization was almost exclusively restricted to (semi-)arid and Mediterranean regions [55], but current knowledge suggests that it is also widely occurring in cold and temperate regions [12,17,25]. However, the relative contribution of different drivers (e.g. agriculture, mining, road de-icing) to freshwater salinization at large spatial scales remains unclear. In this issue, Estevez *et al.* [56] show that urbanization and agriculture are the main drivers of river and stream salinization in Spain, resulting in almost one-third of the entire river network salinized; though mining, which locally contributes to salinization in Spain [57,58], was not considered in this study.

The proportion of salinized freshwater ecosystems can be expected to increase in the future owing to a combination of anthropogenic pressure intensification and climate change. Le Trong *et al.* [59] predict an average increase in electrical conductivity (EC) between 10 and 15% owing to climate change in German surface waters towards the end of this century, with EC increases greater than 50% in approximately 10% of the sites. In a similar study covering most streams of the USA and including climate and land use change, Olson [60] forecasts EC increases greater than 50% in half of the streams and identifies land use change as the main driver of this increase. Olson identifies land use change as the main driver of this increase. Thus, both studies suggest that climate change largely leads to rather mild increases in Central European and US water bodies, though strong overall increases may occur owing to land use change. Overall, having robust estimates of future EC requires solid knowledge of changes in different drivers (e.g. hydrology, land use change).

(b) What are the physiological effects of freshwater salinization?

Although animal osmoregulation has been widely studied [29,30], the physiological responses of freshwater organisms to alterations in ion concentrations are still relatively poorly understood. In this issue, Kefford [61] challenges well-established biological principles by highlighting that mayfly species can suffer substantial mortality at an osmolality (i.e. osmotic concentration) lower than that of their internal fluid. This could be related with the increase in the uptake of ions, loss of pH regulation or Na poisoning, which requires testing in future studies. Also, Buchwalter *et al.* [62] show that elevated SO_4^{2-} , rather than causing a loss of SO_4^{2-} regulation in the mayfly *Neocloeon triangulifer*, imposes an energetic

demand associated with maintaining homeostasis that is manifested primarily in reduced growth rates and associated developmental delays. They also identify two genes related to SO_4^{2-} transport in this species, which may be a promising tool for investigating mechanisms of sulfate toxicity. Overall, these papers highlight large research gaps in the osmophysiology of freshwater insects in general and mayflies in particular, which is hampering our understanding of the mechanisms of salinity toxicity and how changes in ionic proportions alter toxicity.

Besides a lack of understanding of physiological mechanisms of salinity effects, we lack data on the sensitivity to salt, hampering the identification of particularly vulnerable parts of the ecosystem. For example, seawater intrusion will expose aquatic and terrestrial organisms to high NaCl concentrations in coastal areas, and their potential response remains largely unexplored. In this issue, Pereira *et al.* [63] and Venâncio *et al.* [64] show that increased salinity can considerably affect aquatic organisms (especially cyanobacteria and zooplankton), but may have little effect on soil organisms.

(c) What are the impacts of freshwater salinization on ecosystem functioning?

Given the links between biodiversity and ecosystem functioning [65,66], it is likely that the effects of freshwater salinization on the former can lead to alterations of the latter. Moreover, such changes in the aquatic system may propagate across ecosystems, e.g. affect riparian ecosystems [67]. Entrekin *et al.* [68] present a review and develop a conceptual framework of the impact of salinization on the connections between riparian and stream ecosystems. They suggest three main pathways: (i) changes in the organic matter processing (derived from riparian vegetation) by aquatic organisms; (ii) changes in the quality and quantity of the export of detritus from riparian vegetation into streams; and (iii) changes in microbial decomposer and detritivore growth in riparian areas, which may alter the quantity and quality of organic matter entering the streams. In another contribution, with a special focus on intermittent streams in drylands, Berger *et al.* [69] review the effects of salinization on ecosystem functioning and potential linkages to ecosystem services. Although only few studies have been conducted, they find a consistent negative effect on organic matter processing with a similar concentration–effect relationship across regions. They highlight research gaps regarding other ecosystem functions and their links to human well-being. Finally, in a study on the effect of salinization on organic matter processing by aquatic hyphomycetes, which is the dominant microbial group in streams [70], Gonçalves *et al.* [71] find minor impacts (i.e. the sporulation rates and conidia production were not affected by salt treatments). Overall, these studies highlight that salinization can alter ecosystem functioning, but that the magnitude of alteration probably varies with the organism group (e.g. microbial-driven ecosystem functions exhibit buffer capacity), and that the links to ecosystem services remain to be established.

(d) Which factors can modify salt toxicity?

Freshwater ecosystems are subjected to multiple simultaneous stressors, thus it is crucial to understand how their

effect on biodiversity is modified by potential interactions [72,73]. Kaushal *et al.* [74] describe a freshwater salinization syndrome (FSS), which is common in rivers and lakes primarily in North America and Europe. FSS results in a wide range of physico-chemical changes associated with increases in total salinity, pH, and concentrations of base cations, nutrients and metals. The combined ecological effects of FSS may involve complex and poorly understood interactions between these physico-chemical components. In a quantitative review of experimental studies on the combined effect of salinity and other abiotic factors on aquatic organisms, Velasco *et al.* [75] show that although around half of the changes were additive, antagonistic and synergistic interactions were also important, making it difficult to predict the effects of salinization when it co-occurs with other stressors. Also, they found a stronger negative individual effect of salinity on organismal performance traits than other stressors, suggesting that freshwater salinization should be prioritized in a multiple stressors context. An example of combined effects relevant within a context of global warming can be found in the study of Jackson & Funk [76], where NaCl toxicity to four mayfly species increased with water temperature (5–25°C).

One important issue that needs to be considered when assessing salt toxicity is ion concentration. Salinity is composed of multiple major ions that alter the sensitivity of freshwater species. Schulz & Cañedo-Argüelles [77] provide multiple examples for the variable sensitivity to different ions in a review of the German literature on freshwater salinization. Their study confirms that to fully understand the potential impact of salinity requires the consideration of the different ion mixtures. In this regard, Hills *et al.* [78] introduce a novel approach to assess the toxicity of untested ion mixtures that builds on previous knowledge of the sensitivity of aquatic fauna to other ion mixtures.

Finally, biotic interactions can moderate salinity stress. Bray *et al.* [79] show that biotic interactions (e.g. competition and predation) between salt sensitive and salt tolerant organisms can be as important as salt toxicity in determining the effect of salinity on stream macroinvertebrate communities. Also, Arribas *et al.* [80] suggest that saline species occupy saline habitats to avoid competition or parasitism, because, physiologically and in the absence of biotic interactions (i.e. according to laboratory toxicity tests), they can perform as well as freshwater species in freshwater habitats. In a related paper, Guitierrez-Cánovas *et al.* [81] analyse the response of invertebrates to changes in a salinity gradient in both directions: dilution (i.e. freshwater inputs) and salinization. Their results reveal that the regional pool of species and their dispersal and colonization capacities might play an important role in the response of aquatic communities to salinity changes. Finally, Hintz *et al.* [82] emphasize the role of the evolutionary context in their contribution. Salinity adapted *Daphnia* populations exerted a greater control on phytoplankton abundance, although this depended on the type of salt that they were exposed to.

Overall, these papers suggest that the impact which the modification of ion concentrations can have on freshwater organisms will depend on three main factors: (i) the identity of the ions and their ratios; (ii) co-occurring abiotic stressors and biotic interactions; and (iii) the biogeographic (e.g. source and sink population dynamics) and evolutionary (e.g. previous history of salt exposure) context.

(e) How can we control freshwater salinization?

At present freshwater salinization is poorly regulated and largely ignored in freshwater management. Salinity standards to protect freshwater biodiversity are lacking in most states or confederation of states and they are usually not legally enforced [83]. Gorostiza *et al.* [84] argue in this issue that this could be partly owing to the naturalization of salt pollution, i.e. given that salts occur naturally in freshwaters, people responsible for salt pollution have attributed high salinities in freshwaters to natural sources. Even when such attributions are incorrect, they can be difficult to counter in public debate. Regarding regulation, research has shown that ion-specific regulation is required to efficiently protect freshwater ecosystems. In this context, Bogart *et al.* [85] identify the Ca:Mg ratio as a major driver of toxic effects for freshwater species and suggest to establish guidelines based

on ion ratios and the natural background ion concentrations of Ca and Mg. Similarly, Schuler *et al.* [86] provide detailed recommendations for setting ion-specific regulations and suggest management solutions that include developing models to robustly estimate ion loadings from human activities and implementing technological solutions for remediating salt pollution after trade-off evaluation. Overall, the contributions stress the need for ion-specific regulations and provide guidance on how to implement them.

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