



Review Paper

Diatom community response to inland water salinization: a review

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Abstract Both natural and anthropogenic processes can lead to the increasing salinity of surface waters. The knowledge about the ecological consequences of salinization on the biota is limited especially in case of microbiota, like diatoms. We collected the existing knowledge about the relationship between salinity and diatoms in fresh and saline waters. Based on the

available papers, conductivity and ion composition are the most important variables shaping diatom communities. Secondary salinization can mask regional differences in diatom assemblages. Trait-based analyses highlight the competitive advantages of motile guild and the extreme trait categories in these environments. The increasing conductivity along a wide conductivity scale decreases the alpha-diversity. Salinization induces the spread and invasion of marine and brackish species into inland freshwaters as well as that of freshwater species tolerating elevated conductivity and/or need specific ions. Concerning food

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webs, salinity can directly change diatom communities and the subsequent upper trophic levels but most likely this effect manifests as a top-down regulation. Applicable diatom indices are available to assess the level of salinization. Furthermore, diatom-inferred salinity reconstructions are widely applied to assess the past changes of salinity. However, future models predicting ecological consequences of salinization are scarce and sometimes contradictory.

Keywords Salinity · Diatom composition · Diversity · Ecological status · Invasion · Predictions

An overview of salinization

Salinity is one of the main factors controlling Earth's life (Bradley, 2008). In contrast to the open sea, a permanent environment, salinity of inland waters changes six orders of magnitude from almost distilled to hypersaline water (Hammer, 1986). The ion content of surface waters and the composition of the major ions are determined by natural factors such as bedrock of the watershed, rainfalls and aerosol deposits (Williams, 2002; Millán et al., 2011) (Fig. 1.). Freshwaters are dominated mainly by Ca^{2+} and HCO_3^- , athalassic, saline lakes by Na^+ (and Mg^{2+}) and Cl^- , while soda lakes by Na^+ and $\text{HCO}_3^- / \text{CO}_3^{2-} / \text{Cl}^-$ or SO_4^{2-} (Grant et al., 1998) showing a high variability in salt composition (Schagerl, 2021).

Permanent and ephemeral saline lakes may develop in endorheic basins (10% of the global land area), where, on average, the evaporation is higher than the annual average rainfall (Schagerl, 2021). This process is the *natural (primary) salinization*, which is controlled by the glacial and interglacial cycles occurring during the Earth's history (Herbert et al., 2015). Tidal influences, seasonal cycles, windy and rainy events can also influence this process (Rengasamy, 2006).

Human activities interfere with the global hydrological- and salt cycles leading to man-made increases in salinity of inland waters, sometimes even modifying the salt composition, which is known as *secondary salinization*. Vegetation clearing on the catchment areas, water extractions (agricultural irrigation from surface waters, lowering the groundwater table by pumping), fertilizers, agricultural and industrial wastewaters (Liu et al., 2020), rising of the saline groundwater (Wagner et al., 2013), mining activities (Bağ et al., 2020), road (especially at high latitudes or altitudes) and airplane salting (Kaushal et al., 2005), accelerated weathering of rocks by acid rains, erosion of impervious surfaces and hydromorphological modifications can significantly increase the dissolved salt content of the surface waters (Kaushal et al., 2021) (Fig. 1.). These activities not only increase the salinity of waters but also change pH and alkalinity (Haq et al., 2018; Kaushal et al., 2018, 2019), and mobilize toxic heavy metals (Schuler & Relyea, 2018; Kaushal et al., 2019). Finally, in these altered and salinized

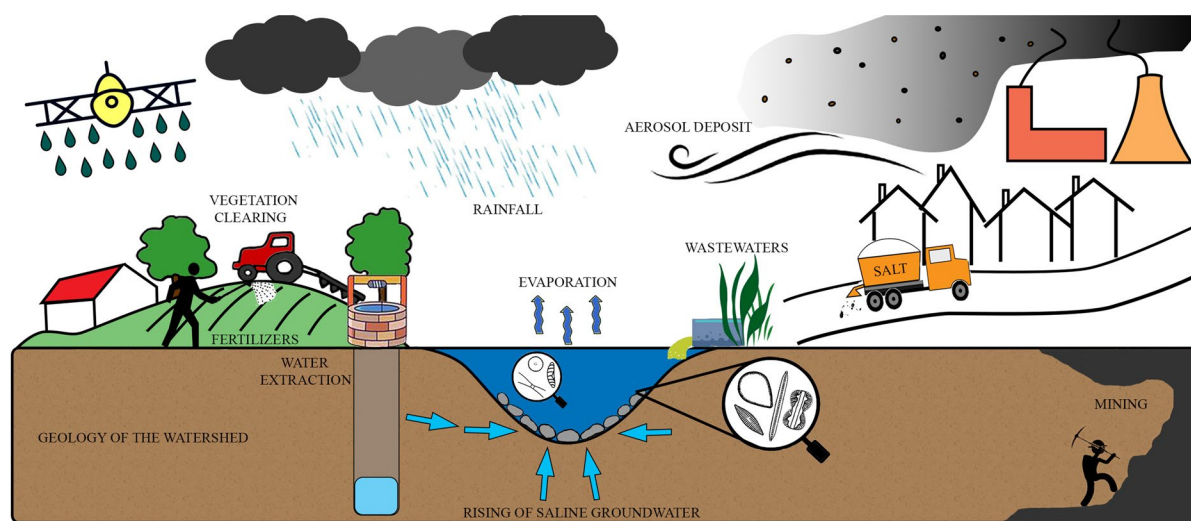


Fig. 1 Schematic figure of surface water salinization

environments biota will be characterized by more intense metal uptake due to their modified osmoregulation (Grosell et al., 2007). Salt can also stimulate eutrophication (it mobilizes the N and P forms; Duan et al., 2012) and reduce carbon storage (Herbert et al., 2015), which has serious consequences for the water quality (van Dijk et al., 2019).

Mediterranean climate regions characterised by low net rainfalls, warm, dry conditions; (Ondrasek and Rengel, 2021) are especially impacted by salinization (Benson et al., 2019). Runoff events, prolonged droughts and seasonal low river flows support this process (Prat & Munné, 2000), and even large rivers turn to saline or brackish conditions in these regions (Beatty et al., 2011). The climate change induced increased global temperature, changes in the distribution and intensity of precipitation, enhanced evaporation, evapotranspiration, frequent and severe droughts, accelerated run-offs and altered cloud formation result in further changes of hydrological cycle of waters, which have already intensified and globally extended salinization for humid regions and several types of aquatic ecosystems (saline lakes, freshwater lakes, reservoirs, wetlands and running waters; Cañedo-Argüelles, 2020). The drought-induced salinization (Chamberlain et al., 2020) combined with other environmental constraints (e.g., pollution, acidity) alters aquatic ecosystems (Cañedo-Argüelles, 2020) and threatens the general ecosystem resilience (Ondrasek & Rengel, 2021).

Freshwater secondary salinization was experienced already by the ancient civilizations (Mesopotamians; Jacobsen & Adams, 1958) and has led to major environmental, economic and social tensions (drinking water supply, economic development; Guo et al., 2015) of the Anthropocene (Kaushal et al., 2021). This phenomenon is defined as *Freshwater Salinization Syndrome* (FSS) by Kaushal et al. (2019). Nevertheless, the increasing salinization was neglected over a long time compared to other water quality problems such as the acid rain or the eutrophication (Kaushal et al., 2021). Recently, one third of the global freshwater bodies could be affected by salinization (Cañedo-Argüelles, 2020).

The residence time of salt ions in waters is considerably longer than was expected previously (Cooper et al., 2014). Even if we reduce or eliminate them, e.g., the usage of road salt, the salt ions will remain in waters for decades (Kelly et al.,

2019). Salinity of waters is easily measured and monitored, however, knowing how it alters ecosystems is more crucial than simply detecting the ion content. Namely, the effects of salinization on waters are mostly irreversible: the natural features of the water bodies are altered which induce a cascade of biological and ecological changes (e.g., biodiversity loss, taxonomic replacement, toxic effects; Williams, 2001) at population, community and ecosystem levels (Cañedo-Argüelles et al., 2019). Freshwaters are very sensitive to even a small rise of salt concentration because their biota are adapted to relatively constant ion concentrations and ratios (Cañedo-Argüelles, 2020). However, our knowledge about impacts of salinization is limited from ecological and evolutionary perspectives (Cunillera-Montcusí et al., 2022).

Diatoms are excellent indicators of environmental changes. Their response through compositional alteration was already applied in the understanding and management of surface water eutrophication and acidity (e.g., Stroemer and Smol, 2010). Nevertheless, primarily macroinvertebrate and zooplankton communities are in the centre of recent salinization studies. Microorganisms like diatoms are a neglected part of these researches despite their key role in ecosystem functioning as primary producers (Cunillera-Montcusí et al., 2022) and as indicators of salinity (e.g., Pan et al., 1996). This is the first study, which reviews the effects of salinization on diatoms (Fig. 1.) covering the whole salinity gradient from oligohaline to highly saline waters by collecting knowledge to reveal and handle the global challenge of salinization. In this review, first, we focus on the halobion systems in the diatom research history, then, we reveal the salinization induced community level changes from a taxonomical and functional point of view in fresh and saline ecosystems. We highlight the dispersal and invasion of diatom species as well as the changes in the food webs driven by increased ion content. Moreover, the salinity-related diatom indices in ecological status assessment were also collected. Finally, we focus on the past salinity reconstructions and future modelling of salinity using diatoms.

Conductivity is generally used as a proxy for salinity (total ion content of the water), which is easily measurable in the field and widely applied in most of the diatom studies revealing the effect of salinity on diatoms. In order to compare the results across

studies we uniformly used the conductivity and its unit for indicating the salinity level of different ecosystems by applying approximate conversions of Herbert et al. (2015). Species names of diatoms was used as was mentioned originally in the cited literature, but we provide the new names and the authors in the supplement (Supplement 1).

Diatom species along the salinity gradient – classification systems

Perhaps the first pioneer study mentioning the relation of diatom communities and salinity is the one by Ehrenberg's (1836), which classified species as marine or freshwater. During the twentieth century, several classification systems were developed, which differ in calculation of the salinity spectra in terms of numbers of individuals (Hustedt, 1957) or species (e.g., van der Werff & Huls, 1957–1974), or the system was based on the salinity optima (Kolbe, 1927), or the salinity tolerances of species (Simonsen, 1962) (Table 1). Many of the early studies were conducted in and around the Baltic area (e.g., Heiden, 1914), which then were difficult to adapt in other localities different from the Baltic area (e.g., Proshkina-Lavrenko, 1953; Carpelan, 1978). Therefore, these systems were modified from time to time resulting in the emergence of new systems (Table 1). Halobion systems were refined by (i) modification (new subdivisions and boundaries) of the categories (e.g., Ehrlich et al., 2016); Hustedt, 1957; Hustedt, 1957; Välikangas, 1926; or (ii) by adapting them for specific regions (e.g., Hustedt, 1957, Van der Werff & Huls, 1957–1974). Furthermore, Dahl (1956) recognized (iii) the importance of the fluctuation of salinity, which was appeared in Carpelan's systems (1978), similarly to den Hartog (1974), who (iv) took the importance of continuity or discontinuity of the transition between fresh and sea water in consideration and established nine main brackish habitats. Moreover, it has been clear all over the time that the salinity is not the only factor determining the distribution of the species and (v) there was a need for a classification recognizing and reflecting the effect of more than one factor (e.g., pH, temperature; Proshinka-Lavrenko, 1953; Carpelan, 1978). Another

problem of the classification systems was that they contained relatively few taxa (e.g., Kolbe used 308 species, of which 60 are precarious) thus, over time, many researchers (vi) supplemented the existing systems with further taxa (e.g., Klock, 1930; Petersen, 1943; Proshinka-Lavrenko, 1953; Cholnoky, 1968; Pankow, 1990).

Diatom species occur in the whole range of salinity, however, most of them have distributional limits near the overlap of the subsaline and hyposaline ranges (Fritz et al., 2010; Fritz, 2013). It is clearly seen from classification systems that at least two important salinity thresholds exist (0.2 and 5–7 g l⁻¹ [370 and 7900–11,000 μS cm⁻¹]) limiting their distribution. These breaks represent discontinuities in the diatom composition (Juggins, 1992), as well as marked decrease in species diversity (Remane & Schlieper, 1971).

Anyway, Kolbe's (1927), Hustedt's (1957) and Simonsen's (1962) halobion classifications are the commonly and widely applied ones (having 356, 632 and 283 citations up to date according to the Google Scholar on January 2023), which provided a good basis for applications and developments of new systems, in paleolimnology as well (e.g., Gasse et al., 1987; Denys, 1991; Haila et al., 2006). Despite the abundance of classification systems, many schemes still have problems such as allochthoneity and imprecision in quantitative interpretation, which reduce their accuracy and resolution (Juggins, 1992). Moreover, several taxa have remained unclassified and sometimes the classifications are inadequate/dubious, or the species can belong to different categories depending on the halobion systems selected or due to the lack of sufficient distributional information. Furthermore, the consideration of long-term changes in salinity level seems to be also necessary to reveal the real verification of the species' requirements and tolerances, which can lead to a need for changes in the halobion classification (e.g., *Fragilaria famelica* and *Halamphora sydowii*; Żelazna-Wieczorek et al., 2015). As a summary, the halobion category of the species should be taken into account only with a very due care and it is clear that these classification systems should be revised because of their aforementioned shortcomings.

Table 1 Diatom classification systems along the salinity gradient

	Heiden (1914)		Brockmann (1914)		Redeke (1922)		Välikangas (1926, 1933)		Venice (1959)			
	Baltic sea	Salinity [‰]	Eustaries around Baltic Sea	Salinity [‰]	Dutch brackish waters	Cl ⁻ [g l ⁻¹]	Baltic Sea, Gulf of Finland	Salinity [‰]	waters in northern and southern Europe, South Africa	Cl ⁻ [‰]	Salinity [‰]	
Freshwater	Freshwater	<0.1	Freshwater	<0.1	Oligohaline	0.1–1	Oligohaline	(0.2)0.5–(2)3	Limnetic (freshwater)	<0.3	<0.5	
Marine	Fresh-brackish	0.1–6	Upper brackish water	0.1–6	Mesohaline	1–10	Mesohaline Beta Alpha	3–16.5 (2)3–8(10) 8–16.5 (10–20)	Mixohaline Oligohaline Mesohaline Polyhaline Mixoeuthaline	0.3–16.5 (22); 0.3–3 3–10 10–16.5	0.5–30(40) 0.5–5 5–18 18–30 >30 < adjacent euthaline sea	
	Brackish	6–18	Lower brackish water	6–18	Polyhaline	10 <	Polyhaline	16.5 <	Euthaline	16.5–22	30–40	
	Brackish-marine	18–30	Brackish-marine coastal fringe	18–30					Hyperhaline	22 <	40 <	
	Desalinated bays of the Baltic Sea	~2.5	High sea	30 <								
	Baltic Sea	7.9–12.5										
	Northern Sea	30 <										
	Kolbe (1927)				Budde (1932)		Hustedt (1957)		Simonsen (1962)		Van der Werff & Huils (1957–1974)	
	Sperenberg region, Germany	Cl ⁻ [g l ⁻¹]	Salinity [g l ⁻¹]	Westphalia, Germany	Cl ⁻ [g l ⁻¹]	River Weser, Germany	Salinity [g l ⁻¹]	Baltic Sea	Salinity[‰]	The Netherlands	Cl ⁻ [g l ⁻¹]	Salinity [g l ⁻¹]
	Oligohalobous	<2	<5	Oligohalobien (halophil)	<2	Halophobian	Exclusively freshwater	Euryhaline oligohalobien Meio Meso Pleio Halo	0–3/5 0–8/10 0–17/20 0–35	Fresh	<0.1	<0.18

Table 1 (continued)

Kolbe (1927)		Budde (1932)		Hustedt (1957)		Simonsen (1962)		Van der Werff & Huils (1957–1974)		
Sperenberg region, Germany	Salinity [g l ⁻¹]	Westphalia, Germany	Cl ⁻ [g l ⁻¹]	River Weser, Germany	Salinity [g l ⁻¹]	Baltic Sea	Salinity [%]	The Netherlands	Cl ⁻ [g l ⁻¹]	Salinity [g l ⁻¹]
Mesohalobous	2–15	Mesohalobien Beta Alpha	2–6 7–20	Oligohalobian Halophilous Indifferent	<0.2	Mesohalobien Euryhaline Holoeuryhaline	0–30 0–35	Fresh-brackish	0.1–0.5	0.18–0.9
Euhalobous	17–20	Euhalobien	30–50	Mesohalobian Beta Alpha Euryhaline	0.2–10 10< 0.2–30	Euryhaline polyhalobien Oligo Meio Meso Pleio	35–30 35–20/17 35–8/10 35–3/5	Brackish-fresh	0.5–1	0.9–1.8
Polyhalobous	20<	Polyhalobien	60–80	Polyhalobian	30<			Brackish Brackish-marine Marine brackish Marine	1–5 5–10 10–17 17<	1.8–9 9–18 18–30 30<
Lowe (1974)		Ehrlich et al., (2016)		Carpelan (1978)		Juggins (1992)		Van Dam et al. (1994)		
Data were collected from 48 literatures worldwide	Salinity [g l ⁻¹]	Bardawil Lagoon, Northern Sinai	Salinity [%]	Californian coastal lagoons	Salinity [%]	River Thames, England	Salinity [g l ⁻¹]	The Netherlands	Cl ⁻ [g l ⁻¹]	Salinity [%]
Oligohalobous Halophilous Indifferent Halophobous Mesohalobous Beta Alpha Euhalobous	<0.5 0.5–10 10–30 30–40	Freshwater	0–20	Freshwater	0–5	Freshwater	<0.2 (optima <1)	Fresh	<0.1	<0.2
		Holoeyryhaline	2–150	Oligohaline	5–15	Brackish	0.2–20 (optima 1–15)	Fresh brackish	<0.5	<0.9
		Marine steno-haline	30–40	Mesohaline	15–40	Marine	20< (optima 15<)	Brackish fresh	0.5–1	0.9–1.8

Table 1 (continued)

Lowe (1974)	Ehrlich et al., (2016)	Carpelan (1978)	Juggins (1992)	Van Dam et al. (1994)
Data were collected from 48 literatures worldwide	Bardawil Lagoon, Northern Sinai	Californian coastal lagoons	River Thames, England	The Netherlands
Salinity [g l^{-1}]	Salinity [%]	Salinity [%]	Salinity [g l^{-1}]	Salinity [%]
40 <	5–70	0–100	1–5	1.8–9
Polyhalobous	Marine euryhaline	Holeuryhaline	Brackish	
Euryhalobous (euryhalinuous)		Polyhaline		
Over broad ranges, often encompassing 2 or more large spectral designations		10–15 to 40–100		
		Marine		
		10–15 to 40		

Changes in species composition

Freshwaters

Natural, geological background

Beside the fact that marine, brackish and freshwater environments host different species, significant compositional changes can be identified within narrower (e.g., freshwater conditions) scales, too. The type of bedrock of the catchment area is the main natural driver determining the water's ionic composition, conductivity, pH and thus, the diatom composition (Ziemann, 1997). In order to study this effect, large spatial scale studies have been conducted covering both calcareous and siliceous watersheds and supported their significant role in diatom distribution (Patrick & Reimer, 1966; Sabater & Roca, 1990, 1992; Potapova & Charles, 2003; Urrea & Sabater, 2009; Mirzahasanlou et al., 2021). Urrea & Sabater (2009) showed that river sites in the two watershed types differed remarkably in terms of species: *Cymbella affinis*, *Diatoma moniliformis*, *Diploneis oblongella*, *Encyonopsis microcephala* and *Gomphonema olivaceum* in calcareous waters and *Melosira varians*, *Navicula capitatoradiata* and *Staurosirella pinnata* in the siliceous waters. It is important to emphasize that the community shaping effect of conductivity was much stronger for the silicious subcatchment (Urrea & Sabater, 2009).

Ion preference

Conductivity and ion composition as the most important variables shaping diatom communities was highlighted quite early (Cholnoky, 1968), and then have been repeatedly shown in several studies (Pan et al., 1996; Carpenter & Waite, 2000; Winter & Duthie, 2000; Almeida, 2001; Trobajo, 2004; Soininen, 2007; Soininen & Weckström, 2009; Bere & Tundisi, 2011b; Potapova, 2011; Virtanen & Soininen, 2012, Srivastava et al., 2017, Ali et al., 2018). Even at low salinity level, the effect of salinity on diatom communities is well documented (Soininen, 2002; Virtanen & Soininen, 2012; Heikkinen et al., 2022) and already a 0.5 mg l^{-1} additional salt content can change the community structure of diatoms (Dixit et al., 1999). However, understanding the exact effect of salinity on species composition and ecosystem functioning

in freshwaters have remained a big challenge (Castillo et al., 2018) including the need (i) to separate the effects of the different components of salinity and thus, (i-a) to distinguish the natural components from anthropogenic ones and (i-b) to separate the effects of salinity related pollution from, e.g., eutrophication or organic pollution.

The most comprehensive attempt to disentangle these mixed effects and to get a detailed insight of the importance of ionic composition, is a study covering > 1100 river sites in the United States with a conductivity range from 10 to 14,500 $\mu\text{S cm}^{-1}$ (Potapova & Charles, 2003). First, a general conductivity gradient, regardless the ionic composition was identified in accordance with other studies (e.g., Negro & De Hoyos, 2005; Soinenen, 2007; Bere & Tundisi, 2009). Species associated with high conductivity in Potapova & Charles (2003) were, e.g., *Biremis circumtexta*, *Denticula kuetzingii*, *Nitzschia bita*, *N. umbonata*, *Tabularia fasciculata*. The next most important observation was a specific gradient of monovalent-to-divalent cation ratio, namely Ca^{2+} , Mg^{2+} to Na^{+} and K^{+} (e.g., Bere & Tundisi, 2011b; Bere, 2014; Riato et al., 2017; Vanhoutte et al., 2006). Diverse communities were associated both with high levels of Mg^{2+} and Ca^{2+} (e.g., *Nitzschia palea*, *Gomphonema parvulum*, *Planothidium lanceolatum*, *Caloneis hyaline*) and low concentrations of these ions (*Eunotia* spp., *Pinnularia* spp. and *Aulacoseira* spp.) (Potapova & Charles, 2003; Bere & Tundisi, 2011b). However, those taxa with preference to high Mg^{2+} proportion (e.g., *Biremis circumtexta*, *Nitzschia umbonata*, *Cymatopleura apiculata*, *Sellaphora pupula* var. *elliptica*, *Navicula exilis*, *Simonsenia delognei*) were also found at high conductivity values (Potapova & Charles, 2003). Moreover, $\text{K}^{+}:\text{Ca}^{2+}$ ratio determines the distribution of euryhaline diatom species like *Amphiprora alata*, *Achnanthes brevipes*, *Bacillaria paradoxa*, *Melosira nummuloides* and *Nitzschia sigma*. In the study of Potapova & Charles (2003) the proportion of Cl^{-} correlated well with that of Na^{+} and K^{+} and it is worth to emphasise since several studies found this ion as one of the most important ones in affecting diatom compositions, favouring some characteristic species like *Diatoma vulgare*, *D. moniliformis* and *D. mesodon* (Bere & Tundisi, 2011b; Stenger-Kovács et al., 2013; Kókai et al., 2015; Tapolczai et al., 2021). Cl^{-} may originate not only from anthropogenic sources, but also

from natural ones like from terrestrial biotopes due to enhanced chemical weathering (Kamenik et al., 2001; Heikkinen et al., 2022), which was favoured by several diatom species (*Cavinula jaernefeltii*, *Staurosira pseudoconstruens*, *Pseudostaurosira subsalina*) in Arctic ponds (Heikkinen et al., 2022). An interesting finding of Potapova & Charles (2003) is that taxa with high Na^{+} and Cl^{-} proportion preference can have either very low (e.g., *Psammothidium helveticum* or several acidophilus *Eunotia* spp. from coastal soft-waters), or high (*Navicula salinicola* from saline rivers from the arid region) conductivity optima. Another gradient from SO_4^{2-} to $\text{HCO}_3^{-} + \text{CO}_3^{2-}$ can further influence diatom community (e.g., Hancock, 1973; Sabater & Roca, 1990; Verb & Vis, 2000; Vanhoutte et al., 2006; Urrea & Sabater, 2009). This gradient was found to correlate with mining discharge contamination and species like *Diatoma moniliformis*, *Biremis circumtexta*, *Ctenophora pulchella*, *Brachysira microcephala*, *Eunotia exigua* and *Stenopterobia delicatissima* (Potapova & Charles, 2003).

Effect of trophic status

Beside the salinity constraint, the other major environmental factor controlling benthic diatom assemblages is the trophic level independently from region or habitat type (e.g., Dixit et al., 1999; King et al., 2000; DeNicola et al., 2004; Urrea & Sabater, 2009; Bere & Tundisi, 2011b; Srivastava et al., 2017) and their interacting effect cannot be neglected. For instance, under low ion content, elevated nutrient concentrations do not promote the dominance of the otherwise eutrophic *Nitzschia* or *Navicula* species (Soinenen & Niemelä, 2002). In lakes, the selection of the dominant diatom species during the spring bloom largely depends on morphometric properties of the given lakes and their trophic state. In oligotrophic lakes typically small-sized *Cyclotella* spp. provide the spring bloom (Reynolds et al. 2002; see species-specific examples in Padišák et al., 2009), but species selection depends on whether the lake is base-poor and alkaline, Ca-rich lakes. For example, *Cyclotella tripartita* is an uncommon species occurring only in alkaline, oligotrophic, northern circumpolar lakes (Scheffler & Padišák, 1997). In mesotrophic-eutrophic lakes, some species of mostly *Aulacoseira* and *Stephanodiscus* are typical with no clear preference to salt quality and content. In shallow, eutrophic,

turbid habitats the spring bloom is characterized by small-sized, elongated diatoms, mostly representatives of the genera *Fragilaria/Synedra* and *Nitzschia* spp., which are also typical in, e.g., shallow soda ponds in the Carpathian basin (Stenger-Kovács et al., 2014).

Effect of landuse

Secondary salinization overwrites and masks regional differences and homogenize impacted sites (Urrea & Sabater, 2009) with pollution tolerant taxa (e.g., *Navicula lanceolata*, *N. cryptotenella*, *N. gregaria*, *N. veneta*, *Nitzschia frustulum*, *N. palea*, *N. amphibia*, *Surirella angusta*) regardless of geochemistry (Carpenter & Waite, 2000; Toman et al., 2014). In ponds highly impacted by agricultural land-use *Fragilaria* spp. were found to dominate and their abundance showed the strongest, positive correlation with conductivity (Della Bella & Mancini, 2009). The effect of elevated conductivity by land-use and the selection of conductivity-tolerant taxa (*Nitzschia palea*, *Gomphonema acuminatum*, *G. parvulum*, *Sellaphora pupula*, *Nupela praecipua*, *Planothidium lanceolatum*, *Fallacia monoculata*, *Pinnularia subcapitata*, *Rhoicosphenia abbreviata*, *Cyclotella meneghiniana*, *Conticribra weissflogii*) was shown by several authors (e.g., Michels et al., 2006; Walker & Pan, 2006; Chessman & Townsend, 2010; Bere & Tundisi, 2011a; Mangadze et al., 2015; Stenger-Kovács et al., 2020; Tapolczai et al., 2021). Diatom assemblages characteristic of different salinity regimes caused by land use can be also identified: e.g., *Amphora coffeaeformis*, *Hantzschia baltica* and *Navicula salinicola* were commonly associated with hypersaline conditions (Taukulis & John, 2006).

Effect of mining

Coal mining can extremely increase the salinity of waters (Smucker & Vis, 2009), sometimes to the level of marine environments (Bağ et al., 2020). At this high salinity level, occurrence of brackish-marine or invasive species, like *Pleurosira laevis*, *Ctenophora pulchella*, *Achnanthes brevipes* var. *intermedia*, *Pleurosigma salinarum*, *Halamphora coffeaeformis* (Bağ et al., 2020) and *Navicula flandriae* are reported (Halabowski et al., 2021). Schröder et al. (2015) defined a threshold around 1200 $\mu\text{S cm}^{-1}$ as

a clear change in the diatom community composition, with some species favouring higher conductivity like *Amphora libyca*, *Bacillaria paxillifera*, *Navicula subhamulata*, *Nitzschia inconspicua*, *Rhoicosphenia abbreviata*. Potapova & Charles (2003) found that high values on the defined $\text{SO}_4^{2-}/(\text{HCO}_3^- + \text{CO}_3^{2-})$ gradient were represented by typically halophilous and acidophilus taxa (*Diatoma moniliformis*, *Biremis circumtexta*, *Ctenophora pulchella*, *Brachysira microcephala*, *Eunotia exigua*, *Stenopterobia delicatissima*) indicating the coal mining discharge pollution in US streams. Gold mining can also significantly increase the ion content of the otherwise low-conductivity streams favouring the occurrence of, e.g., *Navicula capitatoradiata*, *Luticola mutica* and *Surirella* spp. (Potapova, 1996). Even 10 years after the termination of the mining activities, the extreme saline conditions still influenced the diatom assemblages with presence of halophilic diatom taxa (*Achnanthes thermalis*, *Navicula incertata*) and it reduced the chrysophyte cyst/diatom valve ratio (Perrett et al. 2021). Salt mine operations also modify the diatom assemblage resulting in high abundance of *Nitzschia frustulum*, *Surirella ovata* and *Navicula atomus* (Sabater et al., 1987). Post ore mining reservoirs are impacted with high pH, conductivity, SO_4^{2-} , Na^+ and K^+ levels favoured several centric species (e.g., *Thalassiosira duostira*, *Stephanodiscus binatus*, *Discostella woltereckii*, *Aulacoseira pseudomuzzanensis*) (Olszyński & Żelazna-Wieczorek, 2018). Wunsam et al. (2002) demonstrated that the elevated Cl^- concentrations delivered from the industrial tailings from soda and salt mining industries since 1883 resulted in a higher portion of an *Achnanthes minutissima* morphotype in a deep alpine lake, compared to the reference lakes in Austria. In that case, the impact on the epilithic diatom flora was subtle and indicated seasonally restricted effects of the industrial emissions. In other cases, however, the effect can be strong and sudden. The high Cl^- concentration derived from potash mines generated a *Thalassiosira* bloom in German rivers causing more than 200% oxygen saturation (Buhse, 1989). Moreover, with the combination of high nutrient concentration and salinity, further diatom blooms (*Thalassiosira fluviatilis*, *Cyclotella meneghiniana* and *Cyclotella nana*) were reported (Ziemann, 1967).

Effect of climate change

At high latitudes, water bodies are particularly sensitive to climate change induced warming, where shortened ice-periods and eventually increasing evapotranspiration that can enhance the originally low conductivity values (Griffiths et al., 2017). In impacted Arctic lakes, therefore, characteristic taxa like *Diatoma* spp. increased their dominance (Griffiths et al., 2017). In Siberia, there are some lakes with naturally high ion-content but warming is expected to further increase their salinity as indicated by the species such as *Cyclotella meneghiniana*, *Anomoeoneis* spp., and *Epithemia adnata* (Pestryakova et al., 2018). Streams and lakes in the ice-free zones of the Antarctic/subantarctic region are often considered poorly inhabited possess a very diverse diatom flora, where conductivity and nutrients are also the most important driving factors of the communities (Kopalová & van de Vijver, 2013; Kopalová et al., 2013, 2019; Saunders et al., 2015). In this region, some characteristic species, e.g., *Denticula jamesrossensis*, *Amphora veneta* and *Craticula* cf. *molesta* are reported showing the elevated conductivity (Sabbe et al., 2004; Kopalová et al., 2019). In South Shetland Islands *Navicula gregaria*, *Hippodonta hungarica* correlated well with the enhanced salinity, which species known to prefer such conditions in other regions (Kopalová & van de Vijver, 2013). Global warming has an important influence on high altitude water bodies fed by melting rock glaciers which is the source of a set of different ions and thus elevating water conductivity (Thies et al., 2013). A study conducted in the Tyrolean Alps (Thies et al.,

2013) showed that impacted streams possessed more homogenous communities, while reference sites with their low conductivity and slightly acidic pH due to the siliceous bedrock hosted characteristically different but heterogeneous communities with, e.g., *Psammothidium* spp. Some special habitats, such as subtropical peatlands are also exposed to climate change and enrichment of inorganic elements (Chen et al., 2021). Here, a shift from *Pinnularia* species to taxa preferring less-acidic habitats was observed since the last century in relation to the increase of, e.g., Na^+ and Ca^{2+} ions.

Intermittent watercourses are as common as perennial waters (Tooth, 2000; Datry et al., 2014; Messenger et al., 2021) and their number will globally increase in the coming decades (Pumo et al., 2016). One of the most important properties that allows some diatom groups to survive in intermittent waters is their ability to tolerate increasing concentration of nutrients (Piano et al., 2017; Novais et al., 2020) and other ions (see more in Magand et al., 2020) during drying up. Thus, not only diatom species indicating high-nutrient content appear within these assemblages, but also halophilic species (*Caloneis amphisbaena* var. *subsalina*, *Craticula halophila*, *Nitzschia tryblionella*). However, the proportion of halophilic species is typically the highest not in the dry phase, but when the water flow slows down and an almost stagnant aquatic environment develops (Kókai et al., 2015) or later, when disconnected pools are formed (Novais et al., 2020). Survival in the dry phase requires a quite different adaptation strategy from algae, including tolerance of desiccation, osmotic changes, increased light intensity and UV radiation (Timoner et al., 2014; Sabater et al., 2016, 2017). One such

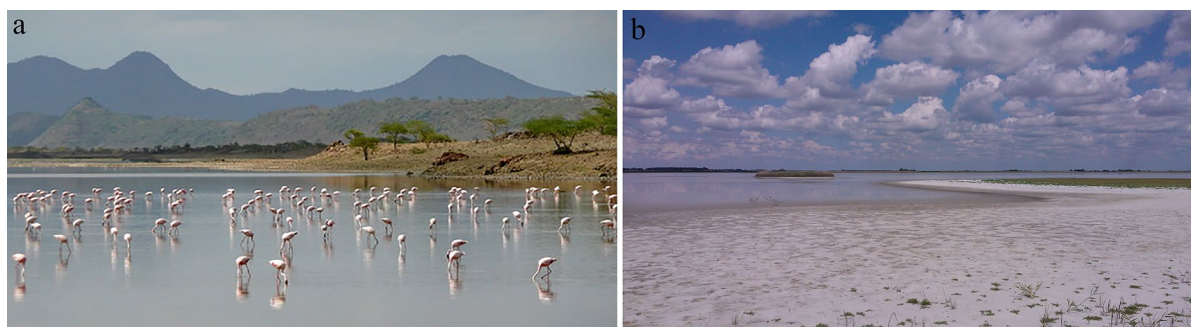


Fig. 2 Saline lakes: **a** Lake Magadi, Kenya (February, 2009, Photo: Lothar Krienitz – with permission); **b** Zab-szék, Hungary (May, 2014)

important property is the ability of mucilage production, which protects diatoms from desiccation and osmotic changes during desiccation (McKew et al., 2011; Sabater et al., 2017). Periodicity of dry and wet phases often exhibit different patterns in individual lakes that complicates to raise a general view on associated diatom assemblages (Lengyel et al., 2019).

Saline waters

In alkaline saline lakes (Fig. 2.) diatoms are also widespread and they are present in considerable quantities both in benthic and planktic communities (Tuite, 1981; Afonina & Tashlykova, 2020). Sometimes diatoms appear in diverse taxonomic composition (Fritz et al., 1993; Gasse et al., 1995; Reed, 1998b) in these types of lakes, but in other cases, only two or three species contribute to more than 70% relative abundance (Servant-Vildary & Roux, 1990) of the community. Diatom taxa living here have definitely broad tolerance ranges, consequently, they are able to withstand even the major fluctuations in salinity (Gasse, 1987). This applies to the most abundant taxa at this end of the salinity spectrum, such as *Amphora acutiuscula*, *Navicula salinicola*, *N. phyllepta* (Fig. 3.d), *Navicula crucicula* var. *cruciculoides* (Reed, 1998b).

Species specificity and regional differences in saline lakes

Several diatom taxa are exclusive for extremely low-oxygen levels (e.g., *Halamphora borealis*, *H. tenerrima*, *H. acutiuscula*, *Navicula phylleptosoma*, *N. salinicola* or *Stauraphora lanceolata*), which is related to their ability to inhabit highly saline inland waters (Želazna-Wieczorek et al., 2015). Species such as *Navicula cincta*, *Navicymbula pusilla* (Fig. 3.e), *Nitzschia hungarica* (Fig. 3.h) and *N. pusilla* are widely distributed in waters rich in dissolved minerals (Wojtal, 2013; Želazna-Wieczorek et al., 2015) including those rich even in metal ions.

Though there are regional and habitat differences in African lakes, *Anomoeoneis sphaerophora* (Fig. 3.a), *Rhopalodia gibberula*, *Craticula elkab* (Fig. 3.c), *Nitzschia communis* (Fig. 3.f) and *Thalassiosira faurii* are common diatom species among others (Tuite, 1981; Gasse et al., 1995; Verschuren et al., 1999; Samylina et al., 2014; Ogato & Kifle, 2017). In Europe, Spanish saline lakes are characterised by *Cyclotella quillensis*, *Chaetoceros muelleri*, *Synedra pulchella* (Fig. 3.g), *Amphora coffeaeformis* and *Nitzschia inconspicua* at elevated salt concentrations (Reed, 1998b). Polish saline spring water (Wojtal, 2013) and salt water outflows and marshes (Želazna-Wieczorek et al., 2015) are dominated by *Nitzschia pusilla* and some *Halamphora* species (*H. borealis*,

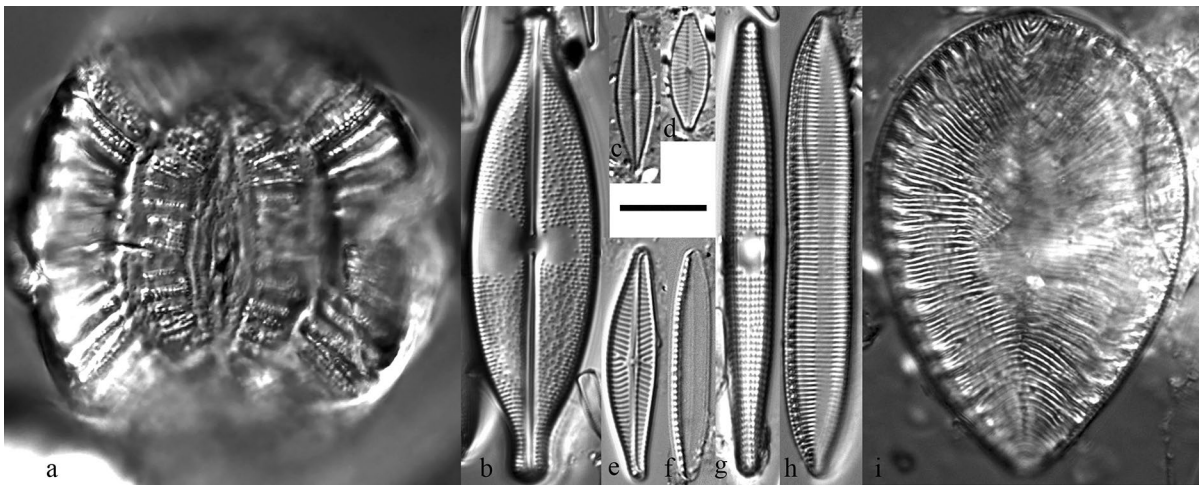


Fig. 3 Some of the most typical diatom taxa found in saline lakes: **a** *Campylodiscus clypeus* var. *bicostatus*, **b** *Anomoeoneis sphaerophora*, **c** *Craticula elkab*, **d** *Navicula phyllepta*,

e *Navicymbula pusilla*, **f** *Nitzschia communis*, **g** *Synedra pulchella*, **h** *Nitzschia hungarica*, **i** *Surirella peisonis* (scale bar = 10 μ m)

H. tenerrima, *H. acutiuscula*). In degraded saline lakes, basically, freshwater diatoms prevail due to the lack of natural hydrological cycle, insufficient conservation management, nutrient and pesticide pollution (Lengyel et al., 2016; Ćirić et al., 2021).

Planktic diatoms in saline lakes

In lakes with very high-salinity planktic diatoms are typically outcompeted by cyanobacteria and chlorophytes and their presence is negligible or restricted to some halophilic non-planktic species (e.g., Afonina & Tashlykova, 2018). In African saline lakes (Fig. 2.a) planktic diatom (e.g., *Thalassiosira* species (Ogato & Kifle, 2017) dominated only at moderate salinity range (Hecky & Kilham, 1973). However, some evidence showed that the anionic composition of these lakes may be selective for some of the benthic species (Hecky & Kilham, 1973). In an oligotrophic alkaline soda lake (Turkey) *Epithemia* and *Rhopalodia* are the dominant elements of the plankton (Kocer & Şen, 2012).

In the lack of long-term studies on saline lakes with fluctuating conductivity, it is difficult to find examples on its effect of planktic diatom population dynamics. An example is Neusiedlersee (Austria, Hungary), a large, shallow lake with seasonal and decadal conductivity fluctuations between 2000 and 3500 $\mu\text{S cm}^{-1}$. In the open water of this lake, phytoplankton is permanently (except the ice-covered period) dominated by large diatoms (long chains of *Fragilaria construens*, additionally *Campylodiscus clypeus* (Fig. 3.a) and *Surirella peisonis* (Fig. 3.i). These species show decadal fluctuations that accord to high- or low conductivity pattern (Padisák & Dokulil, 1994). One of them is *Chaetoceros muellerii*, the only freshwater member of the marine genus, *Chaetoceros*. The species appears in considerable amounts in the open waters of the lake in high conductivity (over about 3000 $\mu\text{S cm}^{-1}$) periods and survives in the humic lakes enclosed in the reed-belts during the low-conductivity years (Padisák, 1998). Other studies also support that the 3000 $\mu\text{S cm}^{-1}$ conductivity threshold is crucial for the appearance of *C. muellerii* (Calvo et al., 1993; Barone et al., 2010).

Ion preference in saline lakes

In turbid, soda pans of the Carpathian basin (Europe) (Fig. 2b) where *Nitzschia* and *Navicula* species are the most frequent species, primarily the conductivity and the anions determine the diatom compositions (Stenger-Kovács et al., 2014; Földi et al., 2018; Vidaković et al., 2019; Ćirić et al., 2021), which are also characteristic at generic level in other saline lakes (e.g., Gasse, 1986; Blanco et al., 2013). However, in hypersaline environments diatom response is more pronounced to the ion composition than to the salinity alone (Servant-Vildary & Roux, 1990), especially to major anions (Reed, 1998b): e.g., *Anomoeoneis sphaerophora* (Fig. 3.b) connected to higher HCO_3^- concentration, *Mastogloia* spp. to Cl^- rich waters, while *Synedra pulchella* to SO_4^{2-} dominance (Blinn, 1993). However, there is a counterexample, when the anion preference proved invalid: *Campylodiscus clypeus* (Fig. 3.a) is an iconic species frequently recorded from inland saline lakes, where the dominant anions are often CO_3^{2-} and SO_4^{2-} , rather than Cl^- (Miller, 1982). A detailed study using a combined dataset from North America and Africa could not provide evidence to this anion liking: it revealed that *Campylodiscus clypeus* does not show a clear ion type preference (Carvalho et al., 1996). However, characteristic diatom species can be distinguished along the salinity levels: (i) halophobe or oligohalob species are, e.g., *Achnanthes linearis*, *Cymbella affinis*, *Rhopalodia gibba*, (ii) typical mesohalob species is *Achnanthes chilensis* and (iii) *Mastogloia smithii* var. *ampicephala* was restricted to hypersaline environment (Servant-Vildary & Roux, 1990) (See in detail in chapter of “Diatom species along salinity gradient – classification systems”).

Changes in guild and trait composition in fresh and saline ecosystems

Passy (2007) classified diatom taxa into guilds and her concept has been supplemented with a number of other traits such as cell size, length and width ratio, life forms, mobility (e.g., Berthon et al., 2011; Lukács et al., 2021). In the last decade, these studies have become widespread in diatom research (Tapolczai et al., 2016). Therefore, more and more research has revealed a strong impact of elevated ion content and

conductivity on the proportion of morphological and functional characteristics of diatoms (Kókai et al., 2015; Stenger-Kovács et al., 2018, 2020; Heine-Fuster et al., 2021; Vendrell-Puigmitja et al., 2021).

Traits

One of the most easily measurable trait with ecological significance is the cell size (see more Rimet & Bouchez, 2012). Though the number of case studies has been few, they show that high salinity and conductivity push assemblages to a higher proportion of trait extremes such as small size or large size categories. Similar to naturally saline lakes (Ács et al., 2019b), the hypersaline effluent of an abandoned potash mine (max. conductivity 13,200 $\mu\text{S cm}^{-1}$; Cl^{-} 117,000 mg l^{-1}) in a microcosmos experiment resulted in proportional changes in cell size distribution of diatom assemblages inducing an increase in ratio of small-sized taxa (Vendrell-Puigmitja et al., 2021). Prolonged drought causing an increase in conductivity as well as in Cl^{-} , HCO_3^{-} , PO_4^{3-} and NO_3^{-} concentrations (max. conductivity 3530 $\mu\text{S cm}^{-1}$; Cl^{-} 557 mg l^{-1}) can also alter the cell size composition in streams (Kókai et al., 2015). In this study, extreme size categories correlated positively either with elevated nutrient content (small size category), or with enhanced Cl^{-} concentration (large size category). Ecological conditions of continental soda pans (max. conductivity 15,000 $\mu\text{S cm}^{-1}$) can be also revealed by proportional differences and changes in cell size composition. Small diatoms ($<300 \mu\text{m}^3$) indicated the high conductivity, consequently pristine conditions while larger sized species indicated the worse ecological condition of these soda lakes (Stenger-Kovács et al., 2018).

Guilds

Diatom guilds are characteristic for high conductivity and salt content. Land-use and urbanisation studies by Hlúbiková et al. (2014) and Stenger-Kovács et al. (2020) confirmed that the motile diatom ecological guild is a strong indicator for salinization in stream ecosystems. However, Zhao et al. (2021) also found a strong significant, positive relationship between anthropogenic salinization and elevated proportion of the high profile guild in Chinese streams. In soda lakes (Fig. 2.b), mostly motile diatom species

dominate (Samylina et al., 2014; Stenger-Kovács et al., 2014). These stress tolerant species can survive and adapt to this special environment characterised by high salinity and turbidity, strong daily temperature fluctuation and ephemeral features (Stenger-Kovács et al., 2014). In addition, Heine-Fuster et al. (2021) investigated biofilms originating from very high-altitude salt flats where independently of the ion composition, high salt content was indicated by both motile- and low profile guild taxa. In extreme environments as closed-basin temporary streams in Gauteng Province of South Africa, similarly, low profile guild taxa, mostly pioneer and/or adnate ones were found as indicative for drought induced elevation in Na^{+} content and alkalinity (Riati et al., 2017).

These studies highlight that salinization significantly transforms trait composition of diatom assemblages. It should be emphasised, however, that although some conclusions can already be drawn about the directions of compositional change (size extremes – high conductivity' relationship), further analyses are needed to define salt tolerant traits.

Effect of salinization on diatom diversity

Environmental extremities (pH, conductivity, temperature, light etc.) substantially determine biodiversity and compositional diversity at least for two reasons (Padisák & Naselli-Flores, 2021). First is that extreme conditions qualify as stress factors that select for one or only some species that are able to survive in such environments. Secondly, in typically very permanent aquatic habitats with special stress factors the stochasticity of, e.g., weather-generated disturbance events cannot act at a way than in lakes with "average properties" (Borics et al., 2013).

Diatom diversity in freshwater springs and rivers

Elevated salinity induced by land use

Conductivity is or among the most important variables which determine alpha- (species richness) and beta-diversity in springs and rivers from different regions (e.g., tropical, boreal, subarctic, high latitude and altitude), where the conductivity is characteristically low and its enhancement induces an increase of diatom species richness (Teittinen & Soininen, 2015

[67–1015 $\mu\text{S cm}^{-1}$]; Teittinen et al., 2016 [17–154 $\mu\text{S cm}^{-1}$]; Jyrkänkallio-Mikkola et al., 2018; Taxböck et al., 2020). Anthropogenic activities like catchment land use can increase the nutrient content, turbidity and conductivity of streams (Naymik et al., 2005). In these environments species richness (Naymik et al., 2005; Urrea & Sabater, 2009 [39–3610 $\mu\text{S cm}^{-1}$]; Teittinen et al., 2015), Shannon diversity (Naymik et al., 2005 [46–90 $\mu\text{S cm}^{-1}$]), beta-diversity (Pajunen et al., 2017), as well as functional (guild) diversity (Stenger-Kovács et al., 2013 [956–1886 $\mu\text{S cm}^{-1}$]) show a highly significant positive relationship with conductivity because of the high number of emerged, unique species (Pajunen et al., 2017). However, in agriculturally affected sites having significantly higher conductivity, Ca^{2+} , Mg^{2+} , Na^+ , Cl^- , and P content, the species richness and diversity followed a hump-shaped distribution: moderately impacted sites had the highest richness and diversity (Smucker & Vis, 2009) [1550–9940 $\mu\text{S cm}^{-1}$]. This conductivity level and the dependent response of diatom diversity was also supported in lotic mesocosm experiments (Cohen, 2010). However, on a wider conductivity scale (from fresh [$\sim 5000 \mu\text{S cm}^{-1}$] to hypersaline [$\sim 72,500 \mu\text{S cm}^{-1}$]) an inverse trend was observed between species richness and salt loading in the wheatbelt region of Western Australia (Taukulis & John, 2006).

Elevated salinity induced by mining and industry

The other globally important anthropogenic activity, which can significantly or even drastically increase the mineral content of surface waters, is the mining (Schowe et al., 2013). Its very strong effect on diatom diversity was reported in a number of papers. A study of phylogenetic diversity (OTU richness) in Appalachian rivers (US) revealed large (41%) decline of algal diversity at even low levels of mining impact (Simonin et al., 2021). In reference streams, diatoms were the most abundant taxa among the algae and they were lost in mined streams and taxonomic composition shifted to the dominance of Cyanobacteria with the increased conductivity (Simonin et al., 2021 [37.5–1922 $\mu\text{S cm}^{-1}$]). Consequently, the elevated conductivity, Ca^{2+} , Mg^{2+} , pH, SO_4^{2-} and metal concentration on the watershed as complex effect significantly reduces the diatom richness and species diversity (Verb & Vis, 2000; Jüttner et al., 2003 [9–345

$\mu\text{S cm}^{-1}$]; Smucker & Vis, 2009, 2011 [185–1247 $\mu\text{S cm}^{-1}$]; Schowe et al., 2013 [22–1919 $\mu\text{S cm}^{-1}$]) as was also shown in a microcosmos experiment (Vendrell-Puigmitja et al., 2021 [$\sim 22,000 \mu\text{S cm}^{-1}$]). In Polish rivers salinized by mining, the diatom taxonomic richness was \sim two-fold lower (Bağ et al., 2020 [~ 300 – $52,000 \mu\text{S cm}^{-1}$]) than in not salinized waters. This diatom diversity reduction can be sometimes catastrophic because of the complexity of this environmental change (Luís et al., 2009, 2013 [39–17,140 $\mu\text{S cm}^{-1}$]). Industrial pollution with increased heavy metal, nitrogen and conductivity level can cause similar effects: the degraded condition is associated with low species richness and diversity (Pandey et al., 2018 [170–4007 $\mu\text{S cm}^{-1}$]). The remediation procedures proved to be effective as was documented by the increasing proportion of less tolerant taxa and diversity (Luís et al., 2009, 2013).

Climate change derived salinity

As a consequence of global climate change, the decreasing water flow conditions in dry months in temperate (Kókai et al., 2015), in semi-arid Mediterranean streams (Ros et al., 2009 [7000–17,500 $\mu\text{S cm}^{-1}$]), in dryland rivers (Vélez-Agudelo et al., 2021 [~ 100 – $2000 \mu\text{S cm}^{-1}$]), in permafrost thawings (Benito et al., 2018 [11–421,655 $\mu\text{S cm}^{-1}$]; Rotta et al., 2018 [some – 516 $\mu\text{S cm}^{-1}$]), in meltings of rock glaciers (Thies et al., 2013 [some – $\sim 510 \mu\text{S cm}^{-1}$]) increase the conductivity, a set of different ions (e.g., SO_4^{2-}), alkalinity, pH and trace elements lead to decreases of diatom diversity, loss of taxa, consequently, to more homogenous communities.

Diatom diversity pattern in freshwater lakes

Freshwater lakes with natural, low-conductivity level

In boreal, freshwater lakes the conductivity driven by HCO_3^- explained both the taxonomic and phylogenetic diversity of diatoms (Stoof-Leichsenring et al., 2020). Low salinity apparently does not limit the number of co-existing planktic diatom species in lakes, therefore, has no negative impact on compositional diversity as exemplified by the rich flora and high diversity of Lake Baikal, Russia (conductivity: 16–18 $\mu\text{S cm}^{-1}$; Yoshioka et al., 2002), among them 10% are considered endemic, especially diatoms

like *Aulacoseira baikalensis*, *Cyclotella baicalensis*, *Cyclotella minuta* and *Stephanodiscus meyerii* (Genkal & Bondarenko, 2006). Other examples exist all over the world, as, for example the Faxinal Reservoir, Brazil (conductivity: $27 \mu\text{S cm}^{-1}$; Becker et al., 2008). However, in Arctic lakes with low conductivity ($13\text{--}131 \mu\text{S cm}^{-1}$) the highest species richness was found in “more mineralised” lakes, and the rise of the conductivity induced the increase of the species richness (Barinova & Stenina, 2013) in benthic communities. A similar pattern was found in fens (Bojková, 2009), and peatlands (Mutinová et al., 2017): diatom species richness increased from mineral poor to mineral rich tufa forming fens ($31\text{--}599 \mu\text{S cm}^{-1}$; Bojková, 2009). In mountain regions, lakes diatom diversity was higher above $238 \mu\text{S cm}^{-1}$ (Nauomoski, 2012) than below, moreover, in dry seasons the atmospheric deposition of sea aerosoles enhanced their Na^+ and Cl^- concentration followed by appearance of halophilic species, which are rare in these area (Ognjanova-Rumenova et al., 2009).

Freshwater lakes with higher conductivity level

At elevated conductivity ranges species richness and diversity showed clear negative correlation with the conductivity as observed in wetlands ($138\text{--}2430 \mu\text{S cm}^{-1}$; Gell et al., 2002), in wetlands created by sand mining ($>3499 \mu\text{S cm}^{-1}$; John, 1993) and in subarctic lakes, affected by gold mining ($285\text{--}22,900 \mu\text{S cm}^{-1}$; Perrett et al., 2021). The reductions in the density, species richness and diversity of epiphytic diatoms in intermittent wetlands was also supported by a field experiment applying high-salt ($8500 \mu\text{S cm}^{-1}$) and the low-salt ($3000 \mu\text{S cm}^{-1}$) treatments (James et al., 2009). However, some studies proved the opposite or no response in diversity and functional diversity indices to the increasing conductivity (Singh et al., 2011; Teittinen et al., 2018 [$2.6\text{--}77.4 \mu\text{S cm}^{-1}$]; Aykut et al., 2021 [$312\text{--}1322 \mu\text{S cm}^{-1}$]).

Diversity changes in freshwater metacommunities

Diatom metacommunity studies of lakes revealed that the conductivity had a significant positive effect on the overall species beta-diversity (Rodríguez-Alcalá et al., 2020 [conductivity: $9\text{--}1010 \mu\text{S cm}^{-1}$]; Wang et al., 2020) and significant negative effect on the species nestedness (Wang et al., 2020). Opposite result

was shown in lakes (USA) with very low conductivity ($<18 \mu\text{S cm}^{-1}$) where higher local contribution to beta diversity (LCBD) was recognised, but above this conductivity level the LCBD decreased (Winegardner et al., 2017). Similarly, to high elevation, naturally salty tropical lakes (South America) where conductivity also negatively correlated with the richness component of the LCBD, but the replacement component increased with increasing conductivity (Benito et al., 2020). However, metacommunity studies of diatoms have just started, and these seemingly contradictory results can be clarified with time and continuously increasing knowledge on this area.

In summary, conductivity and ion composition are the main factors determining the diversity variations in both hemispheres (Vyverman et al., 2007). The above-mentioned studies revealed the conductivity level and anthropogenic activity type dependent response of diatom diversity in streams and lakes. Generally, in salt poor environments a small enhancement of conductivity can generate an increase of diatom diversity similar to mild catchment land use. But the more intensive land use (agricultural and/or urban) and the industrial pollution (minings) with the further rising of conductivity and with the extension of conductivity scale initiates a clear opposite trend as observed and supported by the global pattern (Soininen et al., 2016 [$0\text{--}6000 \mu\text{S cm}^{-1}$]) (Fig. 4.).

Saline lakes

It is a general phenomenon that diatom species number and diversity of saline lakes (Fig. 2.) are lower than in freshwater ones (Servant-Vildary & Roux, 1990). In alkaline saline lakes of the Carpathian basin (Fig. 2.b) the high conductivity level allows only for reduced species richness, Shannon diversity, phylogenetic diversity (average taxonomic distance; Stenger-Kovács et al., 2016; Ćirić et al., 2021) and trait-diversity (Ács et al., 2019b) because only a few closely related taxa can survive in these highly stressed habitats (Stenger-Kovács et al., 2016). The increasing conductivity in saline lakes further reduces the naturally low species number and diversity (Blinn, 1993; Samylyna et al., 2014) even within the same year (Nagy et al., 2006). A mesocosm study highlighted that the highest loss rate of the diversity occurs between $79,000\text{--}118,000 \mu\text{S cm}^{-1}$ (Herbst & Blinn, 1998), which is in line with more field studies

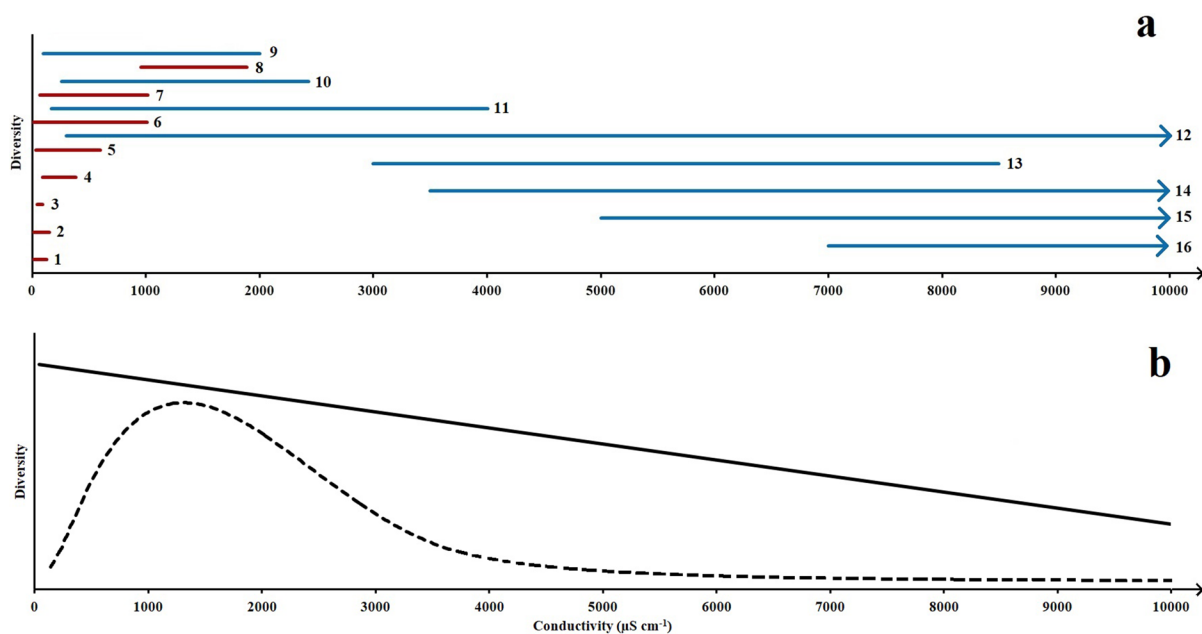


Fig. 4 Schematic figure of the correlations (red line: positive relationship, blue line: negative relationship) between diversity and conductivity (a) on the basis of some examples of literatures (1) Barinova & Stenina, 2013; (2) Teittinen et al., 2016; (3) Naymik et al., 2005; (4) Mutinová et al., 2017; (5) Bojková, 2009; (6) Rodríguez-Alcalá et al., 2020; (7) Teittinen et al.,

2015; (8) Stenger-Kovács et al., 2013; (9) Vélez-Agudelo et al., 2021; (10) Gell et al., 2002; (11) Pandey et al., 2018; (12) Bağ et al., 2020; (13) James et al., 2009; (14) John, 1993; (15) Taukulis & John, 2006; (16) Ros et al., 2009), and its general trend (b dashed line: in smaller resolution; line: global)

of saline lakes in Western-North-America $\sim 79,000 \mu\text{S cm}^{-1}$; Blinn, 1993; Wilson et al., 1996) and Australia (Blinn, 1995).

Closed lake basins can be characterised by naturally or anthropogenically (climate change and hydrological modifications) induced fluctuation of their salinity. The maintenance of their hydrological cycle and natural status is a key for their future preservation, their disturbance and degradation will result in desalination with enhancing diatom diversity and species number, which is not characteristic for the pristine status of saline lakes (Lengyel et al., 2016; Stenger-Kovács et al., 2016; Heine-Fuster et al., 2021). In this context, conductivity could be a variable to ensure conservation of diatom communities in naturally salty waters (Benito et al., 2020).

Diatom dispersal and invasions

Species dispersion from marine environment to inland waters

It is known from marine ecosystems that a small sized centric diatom (*Cyclotella marina*) can cause harmful algal bloom far from its type locality (Tokyo Bay, Japan and Korean waters) in a tropical region (Gulf of Mexico) (Aké-Castillo et al., 2012). Another marine diatom (*Synedropsis roundii*) characteristic for Arctic and Antarctic habitats, broadens its distribution into the Mediterranean lagoons (Blanco et al., 2019) where it can tolerate fluctuating salinities presumably due to its genetic adaptation (Prasad & Livingston, 2005). From the Indian and Pacific Oceans *Coscinodiscus wailesii* was introduced with ballast water to European waters. This species has a high tolerance to heavy metals, especially to copper, cadmium and zinc, and formed dense blooms with high amounts of mucilage (Laing & Gollasch, 2002). The marine invasive benthic diatom species (*Licmophora*

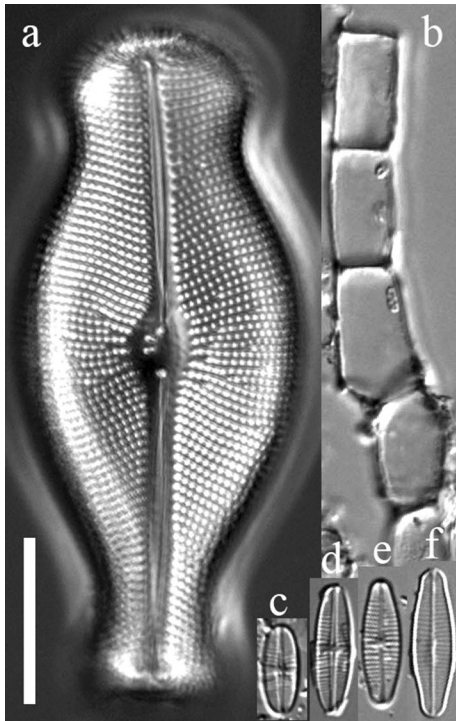


Fig. 5 Spreading diatom species due to the increase in salinity (scale bar = 10 μm): **a** *Didymosphenia geminata*, **b** *Skeletonema subsalsum*, **c, d** *Achnanthisidium delmontii*, **e, f** *Achnanthisidium druartii*

normaniana) appeared in an oasis mineral spring in Egypt (presumably because of fish farming activities), where the conductivity was very high ($>4000 \mu\text{S cm}^{-1}$) with notable concentrations of heavy metals (Saber et al., 2022). *Actinocyclus normanii* and *A. normanii* f. *subsalsus* are also considered as marine and brackish species. Their dispersal from brackish to freshwaters supported their invasive features (Kaštovský et al., 2010; Vidaković et al., 2016). Mine waters are the habitats, which simulate brackish and saline environments and open the way of the establishment of marine and brackish algal species (e.g., *Gyrosigma fasciola*, *Conticribra guillardii*; Wilk-Woźniak & Najberek, 2013).

Species dispersion through inland waters in connection to increased ion concentration

In the *Skeletonema* genus there are only two non-marine species; *S. subsalsum* (Fig. 5.b) and *S. potamos*, which occur in saline, brackish and in

freshwater habitats as well. The abundance of *S. potamos* increased and after 10 years it could become the dominant element of the planktic communities in rivers (Kiss et al., 1994; Duleba et al., 2014) where elevated salinity derived from agricultural discharge and higher than usual water temperature was characteristic (Kaeriyama et al., 2011).

Achnanthisidium delmontii (Fig. 5.c,d) and *A. druartii* (Fig. 5.e,f) inhabit freshwaters with high conductivity and calcium concentration. These species are typical invasive freshwater diatoms with rapid expansion and proliferation in Europe (Pérès et al., 2012; Ivanov, 2018; Cantonati et al., 2022) and *A. delmontii* even throughout the eastern US (Ciugulea & Potapova, 2020). It is worth to note that the first report of *A. delmontii* in North America exactly coincided with its first European occurrence; both in 2007. *A. delmontii* reorganises the benthic community composition and it spreads along the flow direction in the River Danube, which is an important invasion corridor of Europe (Buczko et al., 2022).

The original area of the distribution of *Didymosphenia geminata* (Fig. 5.a) is North America and Europe, but it spread and bloomed in the Southern Hemisphere representing a growing ecological and economic problem in the last decades (Kilroy et al., 2006; Blanco & Ector, 2009; Bray, 2014). Though both native and invasive bloom-forming genotypes of *D. geminata* prefer oligotrophic waters, the latter ecotype is positively correlated with secondary nutrients as Ca^+ and SO_4^{2-} ions (Lindstrøm & Skulberg 2008; Whitton et al., 2009; Rost et al., 2011). Although Ca^+ content decreases in freshwaters worldwide (Reid et al., 2019), its concentrations, however, can be locally high enough, which, simultaneously with other factors, may lead to bloom formation of *D. geminata* (Rost et al., 2011). In contrast to Ca^+ , freshwaters are strongly impacted by anthropogenic SO_4^{2-} pollution modifying the nitrogen-phosphorus-carbon cycles (Zak et al., 2021). The risk is low that SO_4^{2-} will increase up to such concentrations, which could induce further proliferation of *D. geminata*. Acid mine drainage, however, could significantly enhance the concentration of SO_4^{2-} in surface waters (Fernando et al., 2018), which can contribute the evolution towards heavy metal tolerant strains (Whitton et al., 2009).

River salinization can induce biological invasions (Piscart et al., 2011). The spread and the invasion process of the halophilic or salt-resistant species is clearly visible. They replace the native species of the original communities, consequently, threaten the characteristic species composition and biodiversity (Saber et al., 2022). The application of road salts and industrial sewage may further support the expansion of halophytic species (Kaštovský et al., 2010) in the future as well as the increased salt concentration induced by the extreme weather events (droughts; T-Krasznai et al., 2014).

Changes in food webs

Lotic habitats

Salinization can significantly alter the food web dynamics both in lacustrine and riverine ecosystems. The increasing salt concentration and the change of major ion composition in lotic environments show decadal trends (Dugan et al., 2017) altering the abundance and composition of diatoms (eg. Porter-Goff et al., 2013; see more details in chapter “Changes in species composition”). Species exchange in the benthic diatom community may significantly alter the algal food resources, which could affect the macroinvertebrate community, especially that of the grazers’ feeding trait (Hintz & Relyea, 2019). However, our knowledge of the real impacts of increasing salt concentration on the relationship of grazers and periphyton is deficient. We know that macroinvertebrate communities are sensitive to salt pulses (Cañedo-Argüelles et al., 2014) and grazers show different responses to salinization. On one side there is stronger grazing pressure on the periphyton if the dominance of the tadpole snail (*Physella acuta* [Draparnaud 1805]) is characteristic, since the abundance of this species increased up to $1000 \text{ mg l}^{-1} \text{ Cl}^{-1}$ ($\sim 2500 \mu\text{S cm}^{-1}$) (Kefford & Nugegoda, 2005). On the other hand, grazing pressure can decrease if sensitive species such as marsh-rams horn (*Helisoma trivolvis* [Say 1817]) dominate (Hintz & Relyea, 2019).

Lentic habitats

Responses to salinization in lacustrine ecosystems are quite complex because it generally parallels

eutrophication (Judd et al., 2005; Lind et al., 2018). Road salt effluents in a lentic ecosystem could result in a higher density layer at lower parts or at the bottom of the lake, which alter the stratification patterns, and could fasten oxygen depletion in the surface of the sediment leading to release high amounts of sedimentary, biological active phosphorus (Sibert et al., 2015; Ficker et al., 2018). As a consequence, phytoplankton biomass increases because of (i) the direct effect of nutrients cascading to zooplankton and, depending on the proliferating phytoplankton species may lead to uncoupling of the food web (Selmečzy et al., 2019) and (ii) the decline of the zooplankton community as a result of elevated salt concentration (Hintz et al., 2017; Sinclair & Arnott, 2018). However, Moffett et al. (2022) observed in a mesocosm experiment that in oligotrophic alpine lakes salinization can lead an initial increase of the zooplankton, which reduces the phytoplankton biomass. Moreover, two long-term experiments (Coldsnow et al., 2017; Hintz et al., 2019) revealed the potential of rapidly increasing tolerance of zooplankton to elevated salt concentration, which suggests decreasing phytoplankton biomass as well. But, the comparison of the salinity tolerance of typical diatom species in the spring community of temperate lakes and the tolerance of zooplankton shows that the decreasing grazing pressure and increasing biomass of diatoms are more likely to occur. Additionally, synergistic effects of eutrophication symptoms caused by salinization through available food for zooplankton and the increased concentration of salt sooner or later decreases the abundance and diversity of the zooplankton community (Lind et al., 2018; Hintz & Relyea, 2019). The increased nutrients and salinity favour the *Asterionella* (Judd et al., 2005), which occurs in even slightly brackish environment. The salinity tolerance of the cosmopolitan planktic species, *Cyclorella meneghiniana*, is also well documented, which is common in freshwaters and in brackish habitats as well (Roubeix & Lancelot, 2008). Because of sizes, grazeability of these two species is remarkably different.

In lakes, increased periphyton biomass was observed at elevated nutrients and salt concentrations in the experiments of Lind et al. (2018) probably because grazing pressure decreased as a consequence of the increased salt concentration was toxic for the most important grazer, the banded mystery snail *Viviparus georgianus* (Isaac Lea, 1834). In another experiment, periphyton and snails remained unaffected (Hintz et al., 2017) when only the salt concentration was increased.

Fish could structure the periphyton as well, especially, in case of omnivorous fish dominance because most of them include periphyton in their diet (Brucet et al., 2012). Since fish have relatively high salinity tolerances compared to zooplankton (Lind et al., 2018) or to other grazers, salinization most likely affects the periphytic diatom community through direct effects or via other trophic relationships.

In conclusion, the increased salt concentration can alter the abundance and diversity of different trophic levels and the interactions among them, additionally it can alter ecosystem functions, as well (Hintz & Relyea, 2019).

Capturing the salinity-related conditions by diatom indices

Special Halobien Indices for freshwaters

The increases in salinity, and thus conductivity can change water quality and ecological status of inland waters (James et al., 2009). From the 1960s, a Halobien index was developed and had been improved in Germany (Ziemann, 1967, 1968, 1971, 1999, 2010) to assess the level of salinization in rivers caused by minings. However, the application of this index remained regionally restricted (Ziemann et al., 2001; Ziemann, 2005; Szigyártó, 2014; Schulz, 2016) presumably because the halobic classes of diatom species applied by this index were published in several hard-to-find literature (Ziemann, 1975, 1982, 1999; Pankow, 1990; Strecker, 1997; Hofmann, 1998). Meanwhile, halobiontic (brackish water diatoms according to van Dam et al., 1994) diatoms were applied as a metric to indicate salinity, conductivity and Cl^- concentration in running waters (Porter et al., 2008). Within the frame of the NAWQUA Program (Geological Survey's National Water-Quality Assessment, US), a special diatom index was developed to detect especially the effect of the acid mine drainage (Zalack et al., 2010) in the US and recently in South Africa (Riati et al., 2018). Furthermore, Halobic index-Diatom based (HI-D) was developed in Italy (Dell'uomo & Torrisi, 2011) as a part of the EPI-D index to detect mineral pollution in rivers based mainly on systems developed by Kolbe (1927), Hustedt (1956), Ziemann (1982) and van Dam et al. (1994) providing the reliability of a given species as

an indicator (Dell'uomo & Torrisi, 2011). Moreover, in lakes the chrysophyte cyst/diatom valve ratio is also used as indicator of salinization (Smol, 1985; Zeeb & Smol, 2001): the decreasing ratio indicates enhanced salinity Perrett et al. (2021).

General indices for freshwaters applied in salinity indication

International/interstate water management legislations like the Water Framework Directive (WFD) (European Communities, 2000) in the EU, and the Clear Water Act (CWA) in the United States (US EPA 2009, 2013) initiated the application and development of several diatom indices (Charles et al., 2021) to assess the ecological status of surface waters, mostly in lotic environments. In Europe, most of the existing diatom indices were collected in the OMNIDIA software (Lecoite et al., 1993), therefore, they are easily reachable and applicable (Table 2). Different diatom indices use different species pools, therefore, their applicability depends on ecoregions. Most of the indices included in OMNIDIA cannot only indicate the saprobic, trophic or overall status of the rivers, but they clearly correlate with the conductivity of waters and are applicable to detect the salt pollution and define the level of the degradation even in other regions (Table 2). Although the possibility is given to use these indices to follow the processes of salinization in freshwaters, specific salinity indices are required to be developed and tested to detect salt pollution properly (Schulz & Cañedo-Argüelles, 2019). For example there are efforts to develop an index based on teratological forms using geometric morphometry (Cerisier et al., 2019) and percentage of deformities (Lavoie et al., 2017; Falasco et al., 2021).

Diatom Indices for saline lakes

Besides the applicability of the categorization of the species by the different systems (see chapter "Diatom species along salinity gradient – classification systems"), a more precise autecological index (SCI-specific conductance index) was developed for saline lakes to indicate the response of given diatom species along the salinity gradient (Blinn, 1993). However, the evaluation of the status of natural saline lakes requires inclusion of other considerations, where higher salinity values are associated with good status,

Table 2 Diatom indices and their correlation with conductivity (*), conductivity and different ions (***) or only with specific ions (without marks) applied in different habitats and regions

Index	Reference	Habitat	Region	Paper
APDI	Artois-Picardie Diatom Index, Prygiel et al. (1996)	Temperate river* River***	South Africa Poland	Dalu et al. (2016) Kwandrans et al. (1998)
BDI	Biological Diatom Index, Lenoir & Coste (1996)	Temperate rivers*	South Africa	Dalu et al. (2016) Mangadze et al. (2019)
BIWQ	Biological Index of Water Quality, Lobo et al. (2004)	Temperate rivers*	South Africa	Dalu et al. (2016) Mangadze et al. (2019)
CDI	Comprehensive Diatom Index, Yu et al. (2021)	Lakes*	China	Yu et al. (2021)
CEE	Commission of Economical Community, Descy & Coste (1991)	River*** Temperate rivers* Rivers*** Subtropical streams*	Poland South Africa France Australia	Kwandrans et al. (1998) Mangadze et al. (2019) Prygiel & Coste (1993) Tan et al. (2017)
DDI	Duero Diatom Index, Álvarez-Blanco et al. (2013)	Rivers*	Spain	Álvarez-Blanco et al. (2013)
Descy	Descy's pollution metric, Descy (1979)	River***	Poland	Kwandrans et al. (1998)
DI-CH	Swiss Diatom Index, BUWAL (2002); Lecoointe et al. (2003)	Subtropical river Subtropical streams***	China Australia	Tan et al. (2013, 2017)
DSIAR	Diatom Species Index for Australian Rivers, Chessman et al. (2007)	Tropical and temperate rivers*	Australia	Chessman & Townsend (2010)
EPI-D	Eutrophication Pollution Index, Dell'Uomo (1996)	Subtropical river Temperate rivers* Mediterranean river***	China South Africa Turkey	Tan et al. (2013) Mangadze et al. (2019) Çetin et al. (2021)
GDI	Generic Diatom index, Coste & Aypas-sorho (1991)	Floodplain system* Rivers***	South Africa France	Musa & Greenfield (2018) Prygiel & Coste (1993)
IBD	Biological Diatom Index, Prygiel & Coste (2000)	Subtropical river	China	Tan et al. (2013)
IDSE	Leclercq & Maquet (1987)	Temperate rivers* River***	South Africa Poland	Dalu et al. (2016) Kwandrans et al. (1998)
IPS	Specific pollution sensitivity Index, Cemargef (1982)	Subtropical streams* Rivers*** Temperate river system*	Poland South Africa Australia France	Dalu et al. (2016) Kwandrans et al. (1998) De la Rey et al. (2004) Tan et al. (2017) Prygiel & Coste (1993)
PDI	Pampean Diatom Index, Gómez & Licuirsí (2001)	Subtropical river*	China	Tan et al. (2013)
SADI	South African Diatom Index, Mangadze et al. (2019)	Temperate rivers*	South Africa	Mangadze et al. (2019)
SHE	Schiefele and Schreiner's Index, Schiefele & Schreiner (1991)	Subtropical river River*** Subtropical streams***	China Poland Australia	Tan et al. (2013, 2017) Kwandrans et al. (1998)
SI	Saprobic Index, Rott et al. (1997)	Subtropical streams*	Australia	Tan et al. (2017)
TDI	Trophic Diatom Index, Kelly & Whitton (1995)	Temperate rivers* High altitude river	South Africa Iran	Mangadze et al. (2019) Atazadeh et al. (2007)
TI	Specific Trophic Index, Rott et al. (1999)	Temperate rivers*	South Africa	Mangadze et al. (2019)
SLA	Sládeček's Index, Sládeček (1986)	Subtropical streams*	Australia	Tan et al. (2017)
WAT	Watanabe, Watanabe et al. (1986)	Subtropical river Temperate rivers* Subtropical streams*	China South Africa Australia	Tan et al. (2013, 2017) Mangadze et al. (2019)

since desalination and artificial freshwater inputs can threaten these ecosystems (Stenger-Kovács et al., 2018). From this point of view, the development of Conductivity Index for Lakes (SCIL; Ács, 2007) was moving forward since it assesses the status of shallow, large, slightly alkaline lakes at an appropriate way. Another step was the extension of the application of the Halobien index formula (Ziemann, 1971, 1999) with the well-known van Dam halobity categories (van Dam, 1994) for the assessment of the ecological status of soda ponds (Földi et al., 2018; Duleba et al., 2021). Contemporarily, trait- (TBI) and species-based (DISP) diatom indices were developed specifically for these continental saline lakes (Stenger-Kovács et al., 2018).

Diatom-based reconstruction of past salinity

Diatoms are important paleosalinity indicators and potential climate tracers in athalassic environments due to their abundance, diversity and sensitivity to salinity change (Gasse, 1983, 1987; Fritz et al., 1991; Reed, 1998a; Reed et al., 2012). Recent concern about global change and its impact on human societies has stimulated interest in paleolimnology using diatom records from arid/semi-arid regions (Mackay et al., 2014; Covert & Medeiros, 2021). Diatom assemblages from lacustrine deposits offer the possibility for quantitative reconstruction of shifts in hydrology and climate on broad time scales (Fritz, 1990; Fritz et al., 1991; Barker et al., 1994; Birks, 2010; Maslennikova, 2020). Although the relationships that link lake salinity with climate are very complex, salt concentration in lakes can be regarded as a proxy of climate change although it does not allow a direct estimate of paleoclimatic variables (Gasse et al., 1997).

There is a direct link between climate and surface water hydrology in arid and semi-arid regions as closed-basin lakes may fluctuate in both water level and water chemistry in response to seasonal, interannual or long-term climatic variability (Gasse et al., 1995). The chemistry of closed basins lakes responds to the hydrological budget through the concentration or dilution of dissolved salts.

Diatom-inferred salinity reconstruction of subsaline to hyposaline lakes in semiarid to arid climates can be the best independent method for climate reconstruction because variations in precipitation

and evaporation cause salinity changes that are sufficiently extensive to produce shifts in diatom species composition (Fritz, 2013). Closed lakes are found in the dry interiors of continents, in subtropical deserts and in dry polar regions. Thus, diatom-inferred salinity can be used to reconstruct effective moisture from lake deposits in many regions of the Globe (Fritz, 2013).

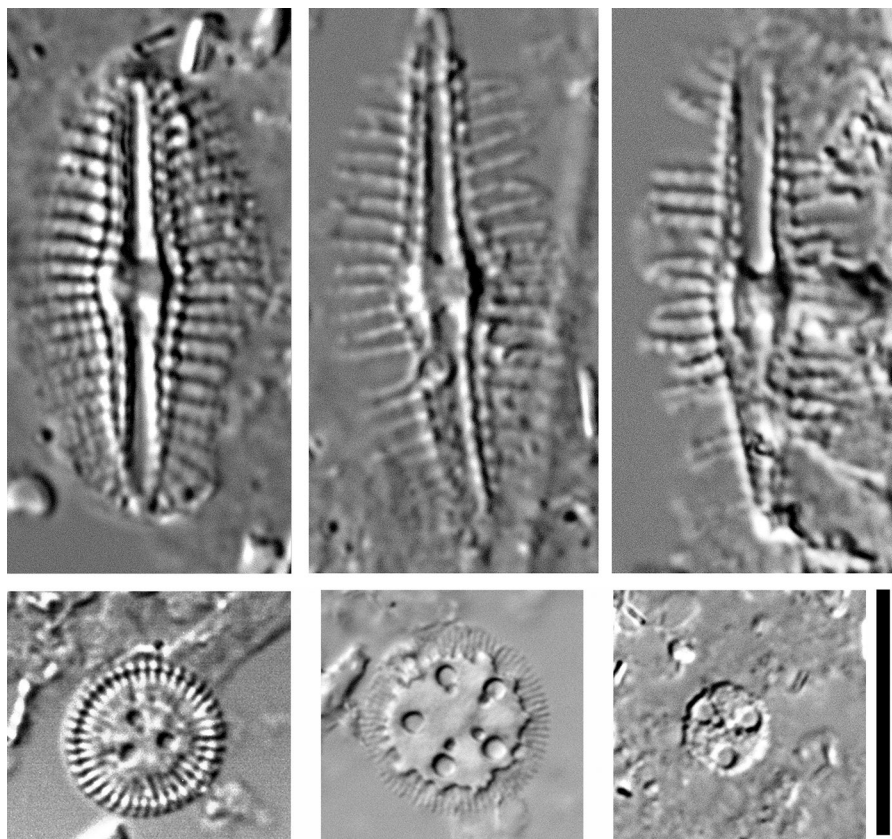
Starting from the mid-1980s, transfer functions applied to fossil diatom assemblages have increasingly been used in paleoenvironmental studies to quantitatively reconstruct salinity (Gasse, 2002; Fritz, 2013; Tolotti et al., 2021; Han et al., 2022). These transfer functions are based on modern calibration data sets, which sample a group of contemporary lakes that span a salinity gradient and use these lakes to characterise the salinity range of diatom species and the so-called salinity optimum, the salinity at which each diatom species is the most abundant. A variety of statistical techniques can be used to generate transfer functions for the reconstruction of salinity or other environmental variables (Birks, 2010; Fritz 2013). Maybe the most challenging task in this field is to tackle the explanatory variable of anions. However, diatom-based salinity transfer functions have so far been developed for different regions and datasets (collected by Vélez-Agudelo et al. 2021).

Shifts between freshwater and saline diatom taxa have been used effectively to infer moisture variation on orbital and millennial time scales in extant and former lake basins, like in the Owens Lake basin in North America (Bradbury, 1997), in Lake Titicaca (Bolivia-Peru) in the tropical Andes (Fritz et al., 2012), but probably the best-known example for drastic changes effective moisture variations. In Africa, diatom analysis has been instrumental in documenting massive precipitation changes during the late Quaternary, including the greening of the Sahara and Sahel in the early to middle Holocene (Gasse, 2002). Also in Africa, massive reduction in lake level is evident during the late Pleistocene from the diatom records in Lake Malawi (Stone et al., 2011).

Bias of reconstruction

However, application of the transfer functions should proceed with caution as several factors may affect the accuracy of hydrochemical reconstructions and their palaeoclimatic interpretation (Gasse et al., 1995).

Fig. 6 Dissolution process of diatom valves (cf. *Diploneis* and *Pantocsekia* spp.) in alkaline, saline waters (scale bar = 10 μm)



First, water bodies in arid and semi-arid zones commonly experience large fluctuations in water chemistry, which influence diatom productivity and community composition during a single hydrological cycle. The taphocenoses may thus contain a mixed assemblage of diatoms derived from different source communities, which reflect a range of water qualities. Second, taphonomic problems related to diatom dissolution are critical in saline waters. Dissolution of diatoms (Fig. 6.) can bias the assemblage by selective dissolution of weakly silicified forms. Diatom dissolution is highest in sodium carbonate solutions, where high pH (>9) enhances the dissociation of silicic acid, but dissolution also occurs in other salt solutions. The process depends on both ionic composition and concentration and thus is site specific (Barker et al., 1994; Reed, 1998a; Flower & Ryves, 2009; Fritz, 2013). Dissolution indices can be developed to correct for some of the bias imposed by taphonomic processes (Ryves et al., 2009).

Recently, the diatom-based salinity reconstructions are very popular and have been an often-used method

in paleolimnology. New and promising alternative approaches include the use of lipid biomarkers in sediments to produce high-resolution reconstructions of changes in lake water salinity and climate are being in progress (Han et al., 2022). Fritz (2013) discussed the pros and cons of using transfer function in salinity reconstructions and concluded that these methods are the most robust when they are corroborated by inferences from other proxies, such as ostracodes, chironomids, sedimentology, or sediment geochemistry (Gasse, 2002; Reed et al., 2012; Fritz, 2013).

Future models

As regard of inland waters, researches have already concluded from the early times that besides severe direct impacts (such as temperature, pH, etc.), climate change has also significant effects on the salinity level (Rawson & Moore, 1944; Hammer, 1990; Nielsen & Brock, 2009; Somura et al., 2009; Friedland et al., 2012; Jeppesen et al., 2015, 2020). Patterns

in precipitation, drought, runoff related to regulation of salinity level could be very different regionally (IPCC, 2021). Thus, not all habitats will be affected in the same way and individual lakes may exhibit high variability in their responses to climate change (Blenckner, 2005) similarly as reviewed by Selmečzy et al. (2017): we see or foresee the effect but directions are habitat specific and often opposite. Furthermore, IPCC projections do not consider the concurrent changes in water abstraction (such as increasing irrigation) which can further accelerate salinization processes (Jeppesen et al., 2020). Despite the fact, that a variety of possible approaches (such as laboratory culture experiments, mesocosm studies, models) exist in order to simulate climate change scenarios on diatoms, most of them focus mainly on the impacts of temperature, pH, eutrophication and water management (e.g., Mooij et al., 2007; Burger et al., 2008; Trolle et al., 2008; He et al., 2011; Chen et al., 2014; Bussi et al., 2016; Ladwig et al., 2018; da Silva et al., 2019; Groß et al., 2021). The simulation of the effects of salinity on diatoms has received less attention and were mainly restricted to marine/coastal ecosystems (e.g., Miller & Kamykowski, 1986; Peperzak, 2003; Doucette et al. 2008; Svensson et al., 2014; Ayache et al., 2019, 2020; Glaser & Karsten, 2020) even though significant and remarkable changes in this highly determinant environmental factor have already been predicted in inland ecosystems (e.g., Cunillera-Montcusí et al., 2022). Only some studies on saline lakes can be found, which revealed that standing crop and the photosynthetic oxygen production of benthic diatoms will be reduced with increased salinity (e.g., Herbst & Blinn, 1998). Although an enhanced primary production of the most typical *Nitzschia* species of soda pans (*N. aurariae*, *N. reskoi*, *N. supralitorea*) is expected, with the increasing average conductivity based on future projections, they will not be able to tolerate and survive the salinity extremities (Lengyel et al., 2015, 2020).

Final remarks

Salinization processes have accelerated with clear regional (Dugan et al., 2017; Le Trong et al., 2019) and global signals (Cunillera-Montcusí et al., 2022). Salinization is consequential upon ecosystem functions and services (Castillo et al., 2018) through

the loss of biodiversity, shifts in the composition of aquatic communities (dominance of salt-tolerant species, proliferation of invasive species [Schulz & Cañedo-Argüelles, 2019]), which has negative effect on the human health and well-being (Kaushal, 2016). Salinity has unequivocal effects on diatom community level with food-web consequences. However, in the absence of comprehensive experimental studies, which simultaneously focus on more than two trophic levels in case of increasing salt concentration we know very little about the interaction of the food web elements in aquatic environments. Salinity can cause several serious impacts on diatoms, which in turn, can easily lead to threat and loss of ecosystem services (B-Béres et al., 2022). Models are also missing though they would be very important and necessary to develop for adequate future management. Furthermore, we cannot forget that the dilution of naturally saline ecosystems (desalinization) because of artificial freshwater inputs/agricultural runoffs represents an equally important problem (Velasco et al., 2006) as salinization, which also threatens biodiversity (Gutiérrez-Cánovas et al., 2019).

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Data availability N.A.

Declarations

Conflict of interest The co-author Judit Padisák is an Associate Editor of *Hydrobiologia* and a guest editor of this volume, therefore, she cannot participate in processing of this paper.

Ethical approval We followed the ethical and professional principles.

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