



Review Paper

Review of phenotypic response of diatoms to salinization with biotechnological relevance

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Abstract Salinization is one of the main global environmental issues of the Anthropocene with various consequences for aquatic ecosystems. To understand diatom ecology and evolution from this perspective without knowing the impact of salinity on their physiological and molecular mechanisms is unimaginable. For this reason, we collected the existing knowledge about the intracellular and morphological

changes of diatoms induced by salinity. The available studies revealed that salt stress can significantly affect, among others, their photosynthetic activities, pigment contents, growth rate, metabolism, and toxin synthesis. Acclimation capability of diatoms is apparent: they can adjust turgor pressure and ion homeostasis and produce compatible solutes for osmoprotection applying a number of biochemical pathways and complementary mechanisms. Morphological changes like shape resistance, post-auxospore formation, and several micro- and nano-sized sometimes species-specific variations can also be explained by the increasing salinity. Furthermore, abnormal forms indicate the extreme and complex effect of salinity and collateral stress factors. Their salinity tolerance threshold is species specific, which can be exploited by biotechnology. According to studies collected for

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this review, it is obvious that diatoms have various phenotypic responses to salinity; however, knowledge about their molecular background and long-term adaptation of the species are completely missing.

Keywords Diatoms · Acclimation · Physiological processes · Morphological variations · Industrial application

Introduction

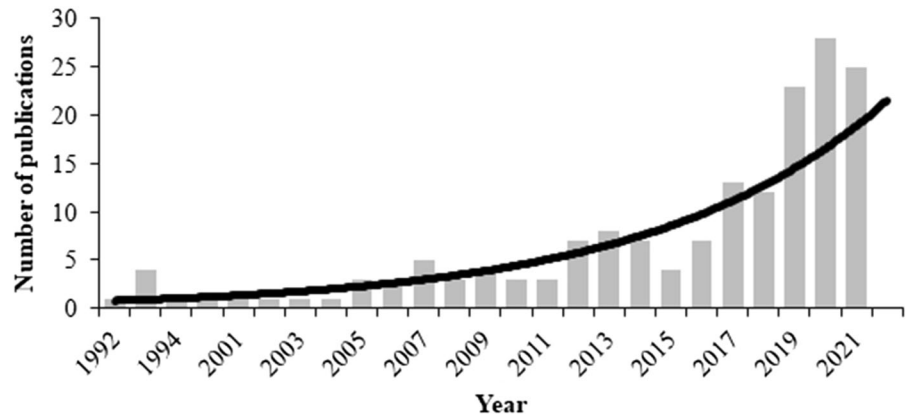
Though even the ancient civilizations experienced the phenomenon of salinization of aquatic ecosystems (Jacobsen & Adams, 1958), it had been considered as a local environmental problem up to the end of the twentieth century (e.g., Kirst, 1989). However, and quite recently, it has grown into a global problem. Natural processes can form saline inland surface waters (known as primary salinization, e.g., Rengasamy, 2006; Herbert et al., 2015), besides, anthropogenic activities such as mining, fertilizers, agricultural, and industrial wastewaters and climate change (Bağ et al., 2020; Liu et al., 2020) contribute considerably to enhancing the salinity of freshwaters (secondary salinization). Since many organisms are glycophytes (e.g., Sudhir & Murthy, 2004; Gupta & Huang, 2014), salinity became a strong evolutionary pressure (Latta et al., 2012) and, being one of the most important environmental constraints, it threatens aquatic biota and indirectly ecosystem services provided by them (Cunillera-Montcusí et al., 2022). Despite the recently increasing scientific interest in salinization (Fig. 1), a number of knowledge gaps exist (Cunillera-Montcusí et al., 2022), which would be keys for understanding and predicting its consequences for aquatic ecosystems, society, and economy.

Depending on qualitative and quantitative changes in salts, aquatic organisms can suffer from osmotic shock in different ways. Therefore, these substances can have different toxicities on the biota. Despite, in salinity regulation and legislation conductivity, thresholds are determined only for irrigation and drinking water, while thresholds which can be lethal for aquatic organisms are generally missing from these standards (Kunz et al., 2013; Cañedo-Argüelles et al., 2016; Schuler et al., 2019) or they are inadequate for their protection (Hintz et al., 2022).

In unfavorable circumstances organisms try to survive, regulate, and maintain their physiological integrity. Salt stress, both osmotic and ionic, influences several physiological processes (Sudhir & Murthy, 2004; Parida & Das, 2005; Gupta & Huang, 2014). Phenotypic alterations, which represent considerable costs for species (Coldsnow et al., 2017), are the basis of and stand behind the changes observed at community and higher levels. Biota are able to live within a certain degree of salinity changes, but different types of organisms can cope with salt stress in different ways (Erdmann & Hagemann, 2001; Ma et al., 2010). Physiological acclimation of aquatic organisms to salts has attracted considerable attention from the second half of the twentieth century, and some reviews were published in this topic over this time, including higher plants (Karsten, 2012; Kumar et al., 2014), animals (Kinne, 1966; Larsen et al., 2014; Pourmozaffar et al., 2020), bacteria (da Costa et al., 1998; Ma et al., 2010), algae (Kirst, 1989), and cyanobacteria (Erdmann & Hagemann, 2001). But none dealt specifically with diatoms, they were only mentioned marginally or in combination with other algae without specific details (in Kirst, 1989; Bisson & Kirst, 1995; Hagemann, 2016). However, this taxonomically separated algal group is among the most successful organisms from ecological and evolutionary point of view. Their silica cell wall and their cell functions are clearly different from other eukaryotic algae (Wilhelm et al., 2006), which assume their distinct phenotypic responses (intracellular and morphological changes) to salinization.

Studies of osmotic stress on diatoms date back to the 1970's (Schobert, 1974; Liu & Hellebust, 1976). These researches were sporadic and were focused only on few species. Detailed and comprehensive study about the physiological processes and acclimation strategies of diatoms as a main algal group of aquatic ecosystems have been lacking, despite their huge importance, for instance, in global primary production (Malviya et al., 2016) and nutrient and biogeochemical cycles (Struyf et al., 2009; Tréguer et al., 2018; Seckbach & Gordon, 2019). Furthermore, their salt acclimation properties can be also interesting for other reasons, since using their salt resistance strategy diatoms can open possibilities for their useful and efficient biotechnological applications (Seckbach & Gordon, 2019).

Fig. 1 Number of publications focusing on salinization of aquatic ecosystems on the basis of Web of Science database (searching for “salinization in aquatic ecosystems” at June 13, 2022) and its trend (black line)



Therefore, this review is conducted to collect and summarize present ecophysiological knowledge on diatoms, the possible effects of salinity on diatoms at cellular and intracellular level, their potential strategies against osmotic pressure, their tolerance to different ion concentrations, and their applicability in the field of biotechnology. (Diatom species mentioned in this review are collected in Supplement 1 with their authors and currently accepted names.)

Intracellular response

Changes in salinity can directly and indirectly affect photosynthetic organisms (Kirst, 1989; Hasegawa et al., 2000; Sudhir & Murthy, 2004; Parida & Das, 2005; Gupta & Huang, 2014; Hasanuzzaman & Tanveer, 2020), including diatoms by causing osmotic and salt stress. These effects can be expressed on physiological (e.g., photosynthesis, growth rate), biochemical (e.g., ion regulation, induction of enzymes), and molecular levels (e.g., gene expression) (Kirst, 1989; Munns, 2002; Parida & Das, 2005).

Depending on the salt concentration, the photosynthetic electron transport activities, respiration rate, and photosynthetic pigment content can change similarly to growth and reproduction rates (see examples in Brand, 1984). Salinity affects diatom protein synthesis, lipid, and fatty acid metabolism leading changes in membrane instability and permeability and furthermore can affect biosilification (detailed in the chapter of “[Morphological response of diatoms](#)”) and nutrient dynamics

reviewed by Saros & Fritz (2000a). Moreover, salinity can induce production of toxins (e.g., domoic acid; Lelong et al., 2012) and reactive oxygen species (ROS), of which the latter can lead to changes in various cellular components, such as proteins, lipids, and fatty acids (e.g., Mallick & Mohn, 2000). Moreover, it can alter the movement and the cell size of diatoms (Mitra et al., 2012). Table 1 summarizes the observed effects of salinity on diatoms.

Organisms can respond to increasing salinity by acclimation or adaptation (MacIntyre et al., 2002) to resist or survive salt stress (Hasegawa et al., 2000; Parida & Das, 2005; Gupta & Huang, 2014; Khan et al., 2020). During the adaptation irreversible change of genotype occurs among the generations leading evolutionary consequences (Orr, 2005), while acclimation means intra-generational quick changes, where cellular compartments and process change (Horowitz, 2001; MacIntyre et al., 2002). Osmoacclimation is a reversible biochemical, biophysical and physiological modification in cellular structure and function to osmotic stress (Reed, 1984). It is generally divided into three different main (restoration of the turgor and cell volume, restoration of ion homeostasis and osmotic adjustment) and several complementary processes (Kirst, 1989; Erdmann & Hegemann, 2001) (Fig. 2). Response to salinity changes is species- (McLachlan, 1961; Šolić et al., 1994; Clavero et al., 2000; Thessen et al., 2005; Petrou & Ralph, 2011) or even strain specific (Balzano et al., 2011; Glaser & Karsten, 2020). These differences contribute to their optimal fitness, influence competitive interactions, determine the potential magnitude and rate

Table 1 List of the experimentally studied diatom species in relation to salinity, the applied salinity range, their observed physiological responses, acclimation strategies, and their bibliographic references

Species name	Studied salinity ranges	Effects of salinity	Osmolytes	Further strategies	References
<i>Achnanthes delicatula</i> subsp. <i>hauckiana</i>	0.5–50 PSU	Maximum growth rate at 30 PSU	Glycine betaine; glycerol; homarine; proline	Proline accumulation via the ornithine pathway	Scholz and Liebezeit (2012)
<i>Amphora</i> sp.	7–12% (w/v) NaCl; 35–233 PSU	Maximal specific growth rate at 7%; able to grow from 35 to 129 ppt; maximal biomass, lipid, and carbohydrate productivity at ~80 ppt; decrease in cell volume after 90 ppt; low Fv/Fm values at salinities less than 45 ppt and more than 100 ppt			Ishika et al. (2018) and Indrayani et al. (2020)
<i>Chaetoceros muelleri</i>	10–233 PSU 0–800-mM NaCl,	Decrease in growth rate above 50 mM; able to grow between 35 and 55 ppt; maximal biomass production at 40 ppt; decrease in cell volume after 35 ppt; positive correlation with total lipid and carbohydrate content; decrease in sterol content (24-Methylenecholesta-5,24(24')-dien 3 β -ol)	Cyclohexanetetrol; glutamic acid	Active transport of Cl ⁻ and K ⁺	Fujii et al. (1995), Ishika et al. (2018) and Jaramillo-Madrid et al. (2020)
<i>Chaetoceros</i> cf. <i>wighamii</i>	20–35 PSU	Enhanced carbohydrate content; decrease in lipid and protein content; no effect on growth, cell density, biomass, and chlorophyll content		Increase in other constituent (mainly mineral fractions) referred to cellular osmotic adjustments	de Castro Araújo et al. (2005)
<i>Cyclotella cryptica</i>	50 to 1000 mol m ⁻³ NaCl; 0–36 PSU	Increasing growth rate and cell volume up to 400-mol m ⁻³ NaCl, then decreased; Able to grow across 0–36 PSU with different optimums	DMSP; glutamate; glycine betaine; homarine; proline; taurine	Uptake and accumulation of K ⁺ , Na ⁺ and Cl ⁻	Liu and Hellebust (1976), Dickson and Kirst (1987) and Nakov et al. (2020)

Table 1 (continued)

Species name	Studied salinity ranges	Effects of salinity	Osmolytes	Further strategies	References
<i>Cyclotella meneghiniana</i>	18–4000 mg Cl l ⁻¹ ; 50 to 1000-mol m ⁻³ NaCl; 0.1–0.6-M NaCl	Growth rate was lower and the cell size was higher at lower salinities; Growth rates were greater at higher Cl content; Increasing growth rate and cell volume up to 400 mol m ⁻³ NaCl and then decreased; Respiration and photosynthesis showed a constant decrease under increased osmotic stress	Proline, glycine betaine, homarine	Uptake and accumulation of K ⁺ , Na ⁺ , and Cl ⁻	Schobert (1974), Tuchman et al. (1984), Dickson and Kirst (1987), and Roubex and Lancelot (2008)
<i>Cylindrotheca fusiformis</i>	27–37 PSU	Decrease in grinding movement;	Mannose	Enhanced SOD activity;	Paul (1979)
<i>Cylindrotheca closterium</i>	5–140 PSU	negative effect on F/F_m and F_v/F_m ; production of ROS; protein and lipid damage; decreased cell division; slower growth rate; reduced chl-a, c and fucoxanthin content; negative correlation with cell length	DMSP; proline	production of EPS for maintaining physiological functions	Rijstenbil (2003), Van Bergeijk et al. (2003), De Miranda et al. (2005), Rijstenbil (2005), Apoya-Horton et al. (2006), Roncarati et al. (2008) and Steele et al. (2014)
<i>Cymbella pusilla</i>	5–11 PSU	Negative effects on growth rate			Saros and Fritz (2000b)
<i>Detonula confervacea</i>	5–35 PSU	Increase in cell division rate up to 20%, then decrease			Smayda (1969)
<i>Ditylum brightwellii</i>	0.5–13.5 PSU	Decline in grows and cell division rate at higher salinity; increased carbohydrate and protein contents at lowered salinity; increase in chlorophyll a content	Alanine; amino acids; glucose		Rijstenbil et al. (1989)

Table 1 (continued)

Species name	Studied salinity ranges	Effects of salinity	Osmolytes	Further strategies	References
<i>Fragilaritopsis cylindrus</i>	10–70 PSU	Loss of membrane integrity; enhanced ROS; increase in protein content; decrease in chlorophyll a content; changes in pigment composition; decrease in growth rate and photosynthetic efficiency (F_v/F_m); increase in α and ETR_{max}	DMSP; glycine betaine; proline	production of EPS; Cyclodiphilins against ROS; protein degradation for detoxifying ROS; ion homeostasis (Na^+ , K^+ , Ca^{2+}); three key genes involved in the proline synthesis pathway; preference of ornithine route over proline route	Krell (2006), Krell et al. (2007, 2008), Lyon et al. (2011), Petrou and Ralph (2011), Petrou et al. (2011), Aslam et al. (2012) and Lyon et al. (2016)
<i>Fragilaritopsis nana</i>	5–150 PSU	Maximum growth rates at a salinity of 33			Sjøgaard et al. (2011)
<i>Halamphora coffeaeformis</i>	0–95 PSU	Increase in growth rate up to 20% and then decrease; neutral lipid content was high at higher salinity; decrease in chlorophyll a content	Proline		Murugaraj and Jeyachandran (2007) and Navarro et al. (2021)
<i>Nitzschia americana</i>	8–32 PSU	Increase in α , P_{max} and growth rate			Miller and Kamykowski (1986)
<i>Nitzschia constricta</i>	0.5–50 PSU	Decreasing growth rate	DMSP; proline	Proline accumulation via the ornithine pathway	Scholz and Liebezeit (2012)
<i>Nitzschia frustulum</i> var. <i>frustulum</i>	artificial seawater medium			Production of rhamnose and xylose allowing thicker EPS gel	Allan et al. (1972)
<i>Nitzschia laevis</i>	5–30 mg L ⁻¹ NaCl	Growth rate and biomass were inhibited after NaCl of 10 mg L ⁻¹ ; decrease in neutral lipid, increase in polar lipid, sterols, and fatty acid content		Decrease in membrane permeability	Chen et al. (2008)
<i>Nitzschia ovalis</i>	5–120 PSU	Able to grow from 5 to 120 PSU, but normally at 90 PSU of salinity	1,4/2,5 cyclohexanetetrol; lysine; proline		Garza-Sánchez et al. (2009)

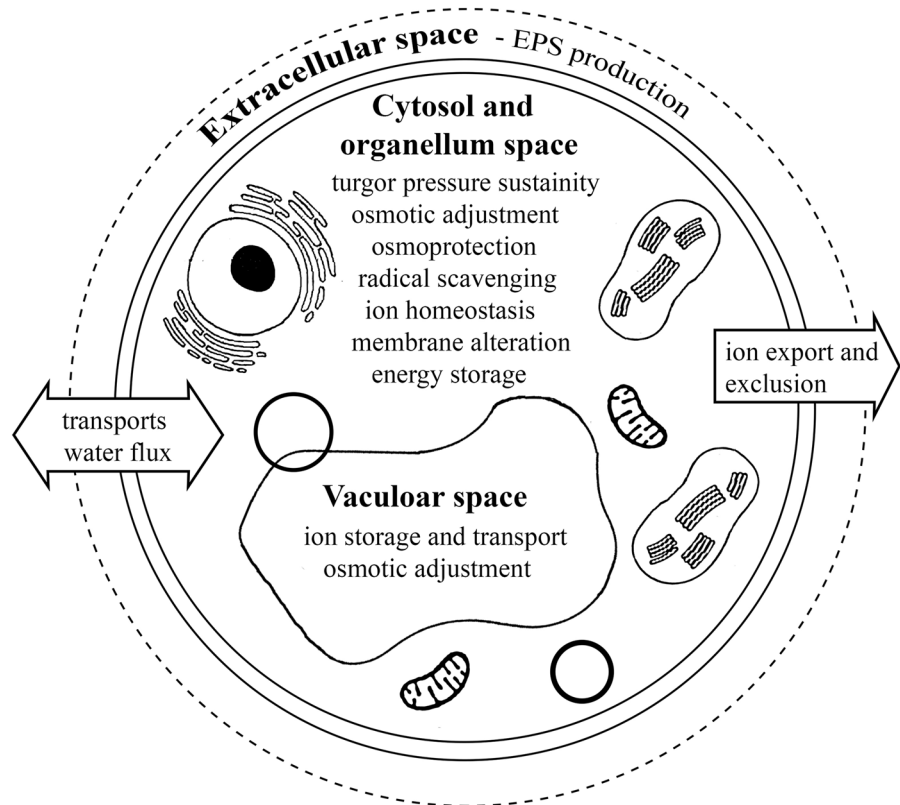
Table 1 (continued)

Species name	Studied salinity ranges	Effects of salinity	Osmolytes	Further strategies	References
<i>Nitzschia reskoi</i>	0–5250 mg L ⁻¹ Cl ⁻ ; 0–4800 mg L ⁻¹ SO ₄ ²⁻ ; 4100–11,670 μS cm ⁻¹	Increase in respiration rate; maximal photosynthetic rate was at 3253 mg L ⁻¹ Cl ⁻ and 3332 ± 120 mg L ⁻¹ SO ₄ ²⁻ (~ 8700 μS cm ⁻¹)	Arginine; proline	Cation homeostasis; glutathione serves as antioxidant; energy and carbon were stored in lipid form	Lengyel et al. (2015, 2020)
<i>Nitzschia</i> sp.	0–30 PSU	Turn down the carbon fixation process; increase in total lipid content	proline	Proline accumulation via glutamate pathway	Cheng et al. (2014)
<i>Navicula phyllepta</i>	0.5–50 PSU	No changes in growth rate	DMSP; glycerol; glycine betaine; proline	Proline accumulation via ornithine-urea cycle; uptake and accumulation of K ⁺ , Na ⁺ and Cl ⁻ ; breakdown of selective permeability in plasma membrane increase in adenosine level; production of EPS	Scholz and Liebezeit (2012)
<i>Phaeodactylum tricorutum</i>	50 to 1000 mol m ⁻³ NaCl; 10–233 PSU	Negative relationship with growth rate and cell volume; able to grow between 35 and 65 PSU; negative correlation with lipid and carbohydrate content; decrease in sterol content (Campesterol, Brassicasterol)	proline	Increase in zeaxanthin for avoid the ROS	Schobert, (1977, 1980), Dickson and Kirst (1987), Abduhali et al. (2006), Allen et al. (2011), Prestegard et al. (2014), Ishika et al. (2018) and Jaramillo-Madrid et al. (2020)
<i>Pseudo-nitzschia australis</i>	10–40 PSU	Maximal growth rate at 30–40 PSU; the highest cell biovolume at lower salinities; no effect on photosynthetic activity, F _v /F _m and pigment content; the highest DA content at higher salinity;	Taurine		Jackson et al. (1992) and Doucette et al. (2008)
<i>Pseudo-nitzschia multiseries</i>	6–48 PSU	increase in DA; high growth rate between 15 and 45 PSU			

Table 1 (continued)

Species name	Studied salinity ranges	Effects of salinity	Osmolytes	Further strategies	References
<i>Pseudo-nitzschia pseudodelicatissima</i>	5–35 PSU	Optimal growth rate at 25 PSU; Unable to grow at 5 and 10 PSU; Domoic acid was detected on a few occasions without significant correlation			Lundholm et al. (1997)
<i>Pseudo-nitzschia pungens</i>	5–35 PSU	Increasing DA; Maximal growth rate between 15 and 30 PSU	Proline	Proline accumulation via ornithine pathway	Armbrust et al. (2004) and Pedekar et al. (2018)
<i>Thalassiosira oceanica</i>	25–50 PSU	Hypersaline conditions decreased μ and F_v/F_m , while increased Chla; no growth was observed under hypersaline conditions	DMSP		McParland et al. (2020)
<i>Thalassiosira pseudonana</i>	0–60 PSU; 0.2–0.9 M NaCl	Increase in sterol content (Isofucosterol, Fucosterol); decrease in growth rate; decrease in cell length; optimum salinity above 15 PSU; no difference in F_v/F_m ; 24 protein change in their abundance	Betaine; DMSP; proline; sarcosine		Baek et al. (2011), Bromke et al. (2013), Kettles et al. (2014), Kageyama et al. (2018a, 2018b) and Jaramillo-Madrid et al. (2020)
<i>Thalassiosira rotula</i>	10–40 PSU	Maximal division rate and growth rate at 25–30 PSU			Krawiec (1982)
<i>Thalassiosira weissflogii</i>	5–55 PSU	Negative effect on growth rate, cell volume, and striking; decrease in lipid, protein and carbohydrate content; decrease in diadinoxanthin and increase in chlorophyll a concentration		Reduction in the cost of transcription; DMSP act as antioxidant; increase of the mineral fraction related to osmotic pressure adjustment; lost in membrane integrity	García et al. (2012), Radchenko and Il'Yash (2006), Bussard et al. (2017) and Thesiera et al. (2020)

Fig. 2 Schematic figure of intracellular processes in diatoms induced by salinity



of selection, therefore, influence the ecological success and evolutionary longevity (Godhe & Rynearson, 2016).

Restoration of the turgor and cell volume

Diatoms can sustain or adjust turgor pressure in only 5–10 s due to their perforated valves and the elastic girdle band. In contrast to the so-called soft algae, which can change their cell volume as a result of the entry or loss of water (Bisson & Kirst, 1995). Diatoms are capable to change the membrane permeability and fluidity (Erdmann & Hegemann, 2001; de Castro Araújo & Garcia, 2005; Parida & Das, 2005; Chen et al., 2008; Cheng et al., 2014; Indrayani et al., 2020; Jaramillo-Madrid et al., 2020) and regulate the water flux via alteration of lipid, protein, sterol, or fatty acid content of membranes (like *Nitzschia laevis*, Chen et al., 2008; *Thalassiosira pseudonana*, *Phaeodactylum tricornutum*, *Chaetoceros muelleri*, Jaramillo-Madrid et al., 2020; *Amphora* sp. Indrayani et al., 2020) (Table 1; Fig. 2). Water channels could facilitate water movement across the membranes, but

this kind of equipment has not been observed in diatoms unlike in some other algae (*Chara* sp., Henzler & Steudle, 1995; *Synechococcus* sp. Allakhverdiev et al., 2000) and in higher plants (Weig et al., 1997).

Restoration of ion homeostasis

In general, the unbalanced cellular ion homeostasis can be controlled by uptake/export of ions and changes in the permeability of the cell membrane (Erdmann & Hegemann, 2001). Diatoms are able to maintain their ion homeostasis by active transport of Cl^- , Na^+ , and K^+ ions out from the cell or into the vacuole through antiporter and transporter systems or by passive transport through membrane protein channels (Boyer, 1976; Fujii et al., 1995; Krell et al., 2008; Cheng et al., 2014; Nakov et al., 2020). Moreover, salt-induced alteration in membrane permeability and fluidity can regulate the restoration process of ion homeostasis, since a rigid membranes can lead to a moderately active Na^+/H^+ antiporter system (Allakhverdiev et al., 1999). However, accumulation of these ions in high amounts

(~ 100 mM) is disadvantageous for diatoms, since they may inhibit activities of many enzymatic processes (Kirst, 1989) (Fig. 2).

Osmotic adjustment

Osmotic adjustment is a slow process which lasts for 40–120 min in microalgae during which osmoprotection is induced by accumulation of compatible, osmotically active substances as low molecular weight organic molecules, and stress proteins occur until a new steady state is achieved (Kirst, 1989; Erdmann & Hegemann, 2001). Diatoms can produce compatible osmolytes; up-to-date 19 osmolytes are detected in them (Table 1). However, there might be other possible ones (e.g., dulcitol, trehalose), which have been already known in other algae and cyanobacteria (Erdmann & Hegemann, 2001). These compatible solutes can be arranged on the basis of the energetic budget necessary for the biosynthesis and by the degree of their solubility (Oren, 1999; Erdmann & Hegemann, 2001). Accordingly, the highest salt tolerance can be achieved by accumulation of glycerol. Its energetic cost is only 30 ATP equivalent per molecule and it is the most hydrophilic compound. The lowest tolerance level is represented by accumulating of disaccharides, for example, trehalose and sucrose, for which the energetic cost is 109 ATP equivalent per molecule. The most widely compatible solute used by diatoms is proline needing 62 ATP equivalent per molecule, which could be important in short-term acclimation, but might not be maintained in the long term (Nakov et al., 2020).

In order to expand their salinity tolerance, diatoms can produce compatible solutes having distinct protective properties (Kirst, 1996; Van Bergeijk et al., 2003; Scholz & Liebezeit, 2012) and can utilize different mechanisms with the same osmoregulators (Kauss, 1978; Krell et al., 2008; Cheng et al., 2014). For instance, the biochemical pathway seems to be more important than the accumulation of osmolytes themselves, which, in turn, could also explain the accumulation of different osmoprotectants (Garza-Sánchez et al., 2009; Scholz & Liebezeit, 2012). In proline accumulation, these differences can be achieved by the less energy-consuming ornithine pathway compared to glutamate route (like *Achnanthes delicatula*, *Fragilariopsis cylindrus*, *Nitzschia constricta*) or involving a new alternative pathway

such as the urea cycle as it was shown in case of *Thalassiosira pseudonana* and *Phaeodactylum tri-cornutum* (Armbrust et al., 2004; Krell et al., 2007, 2008; Allen et al., 2011; Scholz & Liebezeit, 2012). Furthermore, osmolytes are often insufficient alone for osmotic acclimation (Kauss, 1978; Hellebust, 1985) as they are coordinated and changed depending on the different ion species (Kirst, 1989).

Additionally, the synthesis of a single osmoprotectant such as dimethylsulfoniopropionate (DMSP) is too slow for short-term acclimation, but their uptake from the surrounding environment (e.g., after release from algal cells due to loss of membrane integrity; Lyon et al., 2016) is a relatively fast process to adjust osmotic pressure. This extracellular uptake is possible by use of their transport proteins, which is, otherwise, more typical for heterotrophic bacteria than phototrophic organisms (Erdmann & Hegemann, 2001). Moreover, they have a wide variety of transport systems, through which osmolytes may be facilitated by the adjustment process (Tuchman, 1996; Welsh, 2000) of DMSP (Van Bergeijk et al., 2003), proline (Schobert, 1980), glycine betaine (Keller et al., 1999), and amino acids (Admiraal et al., 1984; Nilsson & Sundbäck, 1996) (Fig. 2.).

Complementary mechanisms

Beside the main processes, diatoms have several secondary mechanisms that supplement their success in acclimation (Erdmann & Hegemann, 2001) (Fig. 2). Diatoms can produce extracellular polymeric substances and regulate their content and composition in order to reduce the negative impacts of osmotic and salt stress (Underwood & Aslam, 2015). Through this, they can, e.g., retain water, restrict the diffusion of anions, and modify their motility (Allan et al., 1972; Hoagland et al., 1993; Underwood & Paterson, 2003; Underwood et al., 2004; Abdullahi et al., 2006; Aslam et al., 2012; Steele et al., 2014). They can regulate their antioxidants via enhancing the production of carotenoids, xanthophylls, cyclophilins, and DMSP (Sunda et al., 2002; Theseira et al., 2020), in order to avoid ROS formation and prevent cell damage (Krell, 2006; Janknegt et al., 2008; Krell et al., 2008; Markina & Aizdaicher, 2016; Ayache et al., 2020). In addition, they can increase enzymatic activity of, e.g., superoxide dismutase, peroxiredoxin, and thioredoxin to detoxify ROS (Rijstenbil, 2003; Krell et al., 2008;

Roncarati et al., 2008). Since all of the mentioned acclimation strategies need extra energy, diatoms can vary the adenosine levels of the cells which support the cellular energy charge (Prestegard et al., 2014) or accumulate lipids in order to store energy and carbon (Cheng et al., 2014; Ishika et al., 2018; Navarro et al., 2021).

The process of salt response is related to the expression of various genes (e.g., Munns, 2002; Parida & Das, 2005), since genes are responsible for encoding salt stress proteins or for upregulation/downregulation of RNA (Parida & Das, 2005). Nevertheless, regarding diatoms, small amount of molecular-based approaches (mRNA sequencing, gene knockdown, and whole-genome shotgun) have been applied to explain their salt tolerance mechanisms (Ambrust et al., 2004; Krell, 2006; Krell et al., 2008, Allen et al., 2011; Bussard et al., 2017; Pinseel et al., 2022). These processes seem to be allied to generally multigenic traits and they are likely to act additively and synergistically as in higher plants (Parida & Das, 2005). Based on a genetic study, besides osmolyte production and ion homeostasis, other processes can also play important roles in the salt tolerance mechanisms of diatoms, such as ROS scavenging and protein degradation (Krell et al., 2008). Thus, the simultaneous metabolic processes seem to be also crucial in salt acclimation of diatoms like in higher plants (Parida & Das, 2005). During the acclimation, diatoms may reduce their transcription costs when they decrease the expressions of some genes and/or they change metabolic pathways to ensure the energy demand of their intracellular ion homeostasis (Haimovich-Dayana et al., 2013; Bussard et al., 2017). Furthermore, under high salt content clear intraspecific sequence differences (in *Cylindrotheca closterium*) can be observed and this differentiation can speed up the speciation processes (Balzano et al., 2011; Glaser & Karsten, 2020).

In summary, beyond the salinity limits, algal growth may be sacrificed to maintain osmotic adjustments for guaranteeing survival (Kirst, 1989). It is obvious that diatoms can apply many salt tolerance mechanisms. However, there are other possible strategies like role of stress hormones (Stirk et al., 2018), Ca^{2+} regulation (Bisson & Kirst, 1995), water channels (Allakhverdiev et al., 2000), and supplying extra energy by alternative pathways in photosynthesis (Sato et al., 1983, Erdmann & Hegemann, 2001),

which are known for other algae but still not for diatoms. Furthermore, since other physical and chemical parameters, such as nutrient enrichment (Saros & Fritz, 2000a), temperature (Lengyel et al., 2020), or different ionic compositions (Ziemann, 1967), may expand the tolerance range and their combined investigation has been an urgent need.

Morphological response of diatoms

Diatom species can adapt well to constraints, like salinity (Leterme et al., 2010), which induces several phenotypic changes of diatoms. This variation of morphological features explained by salinity was demonstrated already at the beginning of the twentieth century by Richter (1909) for *Nitzschia putrida*. The phenotypic changes of diatoms can be conspicuous in light microscopy or can be discovered only on nanoscales. In some cases, diatoms maintain their normal outline and in other cases they change it completely. This morphological plasticity is determined by the gene pool diversity (Cox, 2006) and can explain their ecological success in different, sometimes extreme environments (Leterme et al., 2013). *Vice versa*, these altered morphological features can indicate the changes of environmental drivers (Trobajo et al., 2004).

Shape resistance

Specific gravity of silica cell walls (2.4 g cm^{-3}) is more than twice as high as that of the protoplasm. Therefore, diatoms are too heavy to remain in suspension in waterbody without easily adjustable mechanisms. For minimizing sedimentary loss of species the following evolutionary mechanisms are available: to decrease size, to decrease specific gravity, and to increase form resistance (Naselli-Flores et al., 2021).

From the point of view of shape resistance, presence of *Chaetoceros*, a primarily marine genus, with only few species adapted to inhabit continental saline waters, is especially interesting. Its species exploit almost all evolutionary mechanisms to remain entrained in the euphotic layers. Cells are small, weakly silicified, and contain lipids as storage materials (Miller et al., 2014) (Fig. 3.) making the cells relatively light compared to other diatoms. Additionally, cells often form chains and/or long spines on the

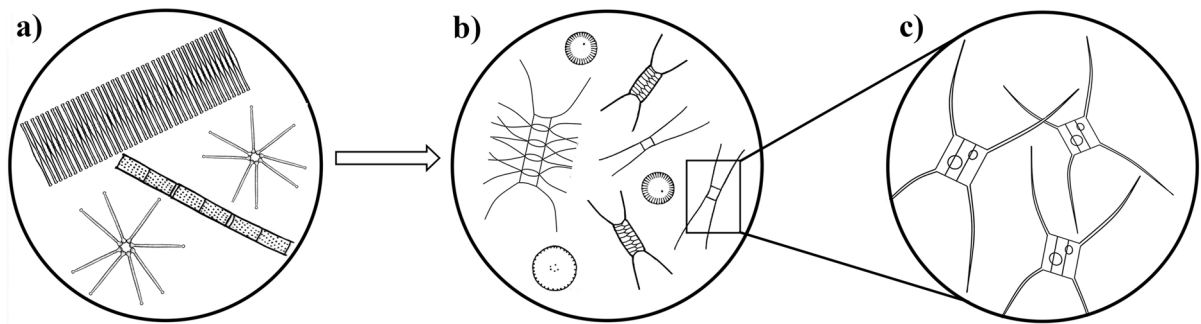


Fig. 3 Shape resistance of diatoms to changing salinity in the phytoplankton: **a** common forms of planktic diatoms in freshwaters. Diatom cells **b** with spines, chains, and **c** lipid materials in saline waters

valve, which increases form resistance (Padisák et al., 2003) (Fig. 3.). These features are largely shared with species of *Thalassiosira* and *Acanthoceras*. Because of their extended area and relatively stable environment, oceans represent diversity hot spots for diatoms (Potapova, 2011). Therefore, the above-mentioned diatoms are, presumably, did not adapted to increased salinization of freshwaters, but “backward.” They evolved under “average” marine conditions and progressively inhabited hyposaline regions, finally entering into inland waters. This required not only adaptation to relatively low salinity but also to the different ionic compositions of these habitats. Why do not we have more marine species in continental saline lakes? The answer is that waters with intermediate salt content are intermittent and isolated in space and time; therefore, they constitute migration barriers through both directions (Potapova, 2011). The separated evolution of freshwater and marine diatoms probably lay in their physiological thresholds (Potapova, 2011), which is a task to explore using laboratory experiments and ecophysiological tools.

Dimorphism

Salinity-dependent dimorphism is characteristic for some diatoms (*Cyclotella cryptica*, *C. meneghiniana*, *Anomoeoneis sphaerophora*, *Surirella peisonis*, *Navicula cuspidata*). The typical valve structure can be found at low salinities (Fig. 4a) and post-auxospores at high salinities (Schultz, 1971; Schmid, 1977, 1979). One common feature of dimorphism is the appearance of “craticula” and “heribaudii” (the normal vegetative cells produce four inner valves:

two craticulae and inside them two heribaudii; Round et al., 2000), which can develop during the resting spore formation as a protection from the elevated salt concentration or desiccation (Schmid, 1979, 2009; web1) as observed only in few members of the genus *Craticula* (Levkov et al., 2016) (Fig. 4b).

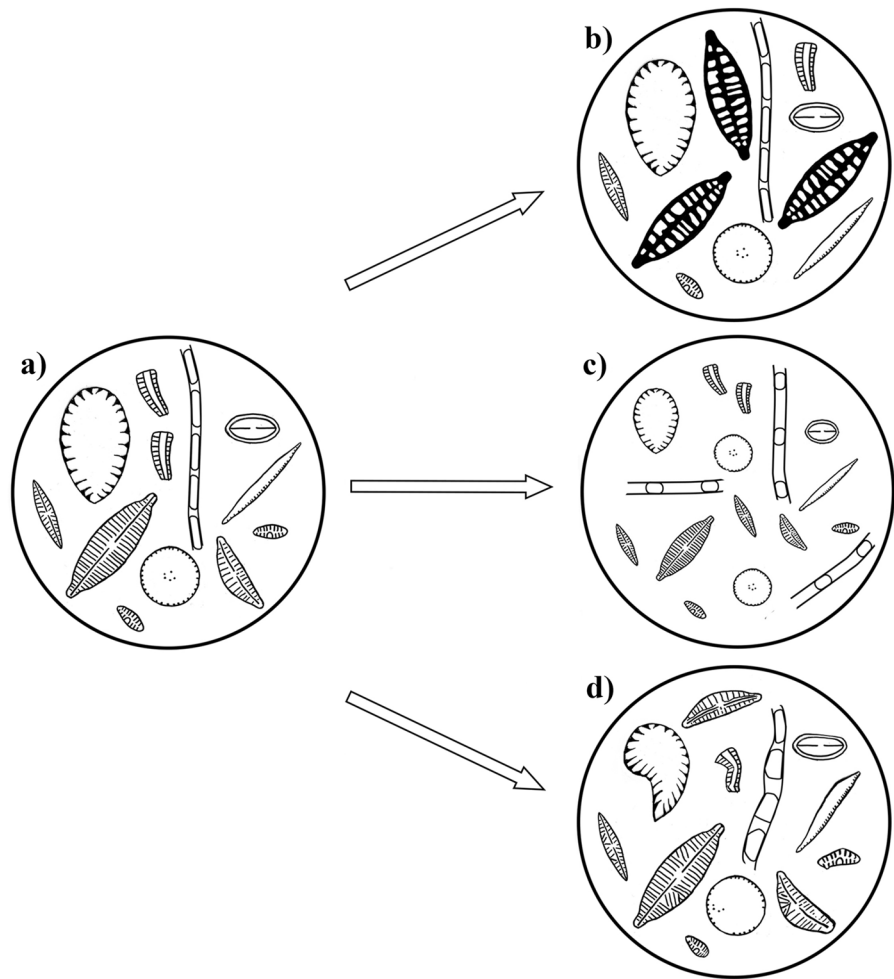
To cover the cell with organic casing (*Thalassiosira weissflogii*, *Achnantheidium minutissimum*, *Navicula minima*; Vrieling et al., 2007), serve a similar function, and save the cell against osmotic pressure (Gélabert et al., 2004).

Polymorphism

Salinity-caused osmotic pressure can also influence the chain morphology of diatoms. The distance between two adjacent cells of *Skeletonema subsalsum* and *S. potamos* Hasle (Fig. 4c) and the average cell number in a chain can increase with increasing salinity (*S. subsalsum*). At high salinity (35 psu) diatom species can enlarge their cell size resulting in shorter chains (Fig. 4c); moreover, the number of the chloroplasts in these cells can also increase (Hasle & Evenesen, 1975; Paasche et al., 1975; Sarno et al., 2007; Torgan et al., 2009; Balzano et al., 2011; Falasco et al., 2021).

Salinity may have a direct effect on cell morphogenesis (Roubeix & Lancelot, 2008) by affecting the thickness of the silica wall. Namely, the external ionic strength affect the uptake of silicic acid and other ions and their ratio determine the silica polymerization. Under high salinities the aggregation of small silica particles inside the silica deposition vesicle is less expressed, resulting in thicker but more hydrated biosilica (Vrieling et al., 2007). In case of, e.g.,

Fig. 4 Morphological response of diatoms to increasing salinity: **a** the initial, normal forms of diatom species at lower salt concentration. The appearance of **b** craticula” forms, **c** cell size reductions and altered chain morphologies, and **d** teratological forms with increasing salinity



Cyclotella meneghiniana and *Thalassiosira pseudonana* (Olsen & Paasche, 1986), these thin valves were observed with poorly developed spines and costae and sometimes missing silica granules along the valve mantle (*Cyclotella meneghiniana*) (Tuchman et al., 1984).

Complete cell size reduction (*Thalassiosira pseudonana* and *T. weissflogii*) (Fig. 4c) or only the height of the valve is demoted (*Cyclotella meneghiniana*) at higher salinity levels (Hildebrand et al. 2006; García et al., 2012). Height reduction is driven by turgor pressure during the interphase before the division. At high salinity, freshwater diatoms may not be able to produce so high intracellular osmolarity to reach the similar turgor pressure as at low salinity levels (Roubeix & Lancelot, 2008), which results in changes of size. Furthermore, smaller than average cell size of *Stephanodiscus minutulus*, *Brachysira*

vitrea, *Asterionella formosa*, *Achnanthes minutissima*, and *Tabellaria flocculosa* is also characteristic at enhanced heavy metal concentration (Lynn et al., 2000; Cattaneo et al., 2004; Su et al., 2018).

Specific surface area and the pore size of *Thalassiosira punctigera*, *Thalassiosira weissflogii*, *Cocconeis placentula*, and *Skeletonema subsalsum* increase with the increasing salinity (Paasche et al., 1975; Vrieling et al., 2007; Leterme et al., 2010, 2013). Through pores, as nanoscale features of the cell membrane, the nutrients and other chemicals are exchanged with size selective filtering of molecules and nanoparticles (Fritz et al., 2010; Su et al., 2018). With the pore size compensation the species can maintain a steady diffusive flux toward the cell (Leterme et al., 2010). But contradictory results exist. In case of *Cocconeis pinnata*, the elevated salinity induced bigger pore size, but smaller surface area (Leterme et al., 2013) than

average. There are further examples when salinity differently affects the valve morphology (changes in length, width, fibula, and stria density) both in pennate and centric diatoms (*Nitzschia pusilla*, *N. frustulum*, *N. palea*, *N. filiformis* var. *conferta*, *Craticula subminuscula*, *Eolimna subminuscula*, *Gomphonema augur*, *Nitzschia palea* var. *debilis* (Geissler, 1968, 1970a, 1970b; Schultz 1971; Schmid, 1977; Jahn, 1986; Wendker & Geissler, 1988; Wendker, 1990; Trobajo et al., 2011), and *Stephanodiscus hantzschii* (Geissler 1982, 1986). These contradictory results demonstrate that the morphological changes induced by salinity could be taxon or even clone specific (Trobajo et al., 2004).

Diatom teratological forms

Salinity can result in more pronounced, significant alterations in the valve structure leading to abnormal forms (Noune et al., 2023) (Fig. 4d). This significant modification and deformed outlines are referred to as teratological forms if they can potentially alter the physiological mechanisms and cell movement of diatoms (Falasco et al., 2009a). Significant changes in valve structure caused by salinity can be the number and place of the fultoportule (*Thalassiosira weissflogii*, Bussard et al., 2017; *Cyclotella meneghiniana*, Håkansson & Chepurnov, 1999) as well as the irregular or absent areolae (*Synedra acus*, Basharina et al., 2012; *Thalassiosira eccentrica*, Schmid, 1984). The osmotic stress may also result in displaced central nodules, fragmented raphae, altered stria pattern (*Anomoeoneis costata*, *Anomoeoneis sphaerophora* f. *costata*, *Cyclotella meneghiniana*, Håkansson & Chepurnov, 1999; *Cyclotella cryptica*, Noune et al., 2023), and abnormal valve outlines (*Navicula cryptocephala*, Aleem, 1950; *Navicula gregaria*, Cox, 1995; *Cyclotella cryptica*, Noune et al., 2023), which make the identification considerably difficult or impossible (Castillo et al., 1995) in highly saline environments.

In mining effluents, besides the high salinity, radioactive nuclides and high concentration of heavy metals further burden the aquatic ecosystems (Tipping et al., 2009), and besides the already mentioned teratological forms, further abnormal features can be detected as altered linear and central area in *Fragilaria capucina* var. *capitellata* (Falasco et al., 2009b), raphe modulations in *Cymbella excisa*, *Encyonema minutum* (Falasco et al., 2009b), *Eunotia*

subarcuatooides (Furey et al., 2009), *Cocconeis sawensis* (Al-Handal et al., 2014), and *Humidophila perpusilla* (Millan et al., 2020), raphe canal adjustments in *Nitzschia* genus (Adshead-Simonsen et al., 1981), unusual colony forms in *Tabellaria flocculosa* with cells attached as straight chain colonies instead of the common zigzag form (Adshead-Simonsen et al., 1981), and mixed, substantially uncommon outline of the valves in *Fragilaria vaucheriae*, *Synedra vaucheriae*, *Encyonema* sp., *Planothidium frequentissimum*, and *Navicula tripunctata* (Falasco et al., 2009b).

In a recently published review about the teratology of diatoms, salinity caused deformities are mainly mentioned as a part of “multiple” impact (Falasco et al., 2021) under extreme environmental conditions (Padisák & Naselli-Flores, 2021), like high concentration of sulfate and carbonate salts (*Cocconeis sawensis*, Al-Handal et al., 2014), natural radioactivity (*Crenotia angustior*, *Humidophila perpusilla*, *Planothidium frequentissimum*, Millan et al., 2020), low discharge and high temperature (*Achnanthes coarctata*, *Fragilaria crotonensis*, *Navicula tripunctata*, *Neidiomorpha binodis*, *Nitzschia* sp., *Ulnaria ulna*, *Sellaphora seminulum*, Lai et al., 2019), high UV radiation, geothermal flux, nutrient supply (*Cocconeis placentula*, *Nitzschia liebethruthii*, *Surirella chilensis*, Cabrol et al., 2007), and industrial contamination in the genus *Tabularia* is mentioned as an example as a collateral stress factor (Falasco et al., 2021) resulting in teratological forms of diatoms (Fig. 4d).

Although these external morphological changes presumably caused by intracellular changes in response to salinity, studies about the links between intracellular processes and cell wall morphogenesis are rare (as you can see above) just as there are minimal explanations of the gene-level regulation of the valve morphology (Bussard et al., 2016.). However, change in the morphology might be explained with the trouble in uptaking silica (Cattaneo et al., 2004; Vrieling et al., 2007), which is regulated by sulfhydryl (-SH) groups on the cell surface (Lewin, 1954) as they have a high affinity to heavy metals and other toxic compounds. The increasing -SH binders reduce the silica uptake and inhibit ATPs as active sites of the -SH groups (De La Rocha et al., 2000). An another explanation might be that at high salinity level cytoskeletal genes are down-regulated, which cause changes in the gene expressions resulting in

modification of the position of the silica deposition vesicle with the consequent modification of valve morphology (Bussard et al., 2016.) To understand these morphological changes in more detail, the extension of knowledge about molecular, physiological processes, and cell cycle regulation is necessary (Leterme et al., 2013). This knowledge would allow us to understand the plastic and genetic component of the salinity tolerance and the potential response on evolutionary time scale along increasing salinity (Castillo et al., 2018).

Salt tolerance of diatoms

Elevated salinity can cause sublethal or even lethal effects for a variety of organisms (e.g., Hart et al., 1991; Hintz & Relyea, 2019) depending on their tolerance ranges. The number of experimental studies analyzing the toxic effect of salinity or its different components on freshwater diatoms is limited. Most of the available studies are focusing on brackish and marine species; however, some of them are common in freshwaters with elevated ion content. The salt tolerance of *Nitzschia* species is often examined using different endpoints and units of salinity (Clavero et al., 2000; Trobajo et al., 2011; Lengyel et al., 2015, 2020; Bagmet et al., 2017).

Photosynthetic activity of *N. aurariae*, *N. reskoi*, and *N. supralitorea* along Cl^- and SO_4^{2-} gradients were measured, where the survival limit concentrations were 9, 8.5, and 11 g l^{-1} Cl^- and 12, 6.5, and 13.5 g l^{-1} SO_4^{2-} (Lengyel et al., 2020). However, 50% photosynthetic activity declines of *N. frustulum* (isolated from soda pans) were noticed at 5.25 g l^{-1} Cl^- and 4.8 g l^{-1} SO_4^{2-} concentrations (Lengyel et al., 2015, 2020). *N. frustulum* and *N. pusilla* isolated from brackish water showed a very broad salinity range (still well growing at 32 g l^{-1} ; Trobajo et al., 2011). In the study of Clavero et al. (2000), *N. frustulum*, *Navicula phyllepta*, and *Amphora angusta* still grew at about 75 g l^{-1} salinity. The freshwater clones of *Nitzschia palea* and *N. filiformis* var. *conferta* showed reduced growth above 16 g l^{-1} (Trobajo et al., 2011). A study highlighted that the reproductive rate of the isolated *N. palea* was not influenced by the original habitat where the species was isolated; this species survives at salinity of up to 22 g l^{-1} and dies at 37 g l^{-1} (Bagmet et al., 2017).

The hypothetical salinity threshold limits of diatoms are assumed from 0.2 to 18 g l^{-1} (Potapova, 2011); however, the above-mentioned studies revealed that this barrier is highly exceeded under natural conditions and is species specific. Further experiments and long-term mesocosm experiments would be needed to identify precisely these thresholds (Cañedo-Argüelles et al., 2016) and the examination of the impacts of complex chemical mixtures (“chemical cocktails”) is also urgent (Kaushal et al., 2021) to develop the recent water quality guidelines to protect aquatic ecosystems from secondary salinization (Hintz et al., 2022).

Biotechnology

Diatoms are a widely distributed group of microalgae with capabilities that make them ideal for multiple biotechnological applications. Although most of their biotechnological use is not specifically linked to their salt tolerance (B-Béres et al., 2022), there are some examples for those linked to salinity (Marella et al., 2020a, 2020b). One of them is to find a way using diatoms to obtain drinking water from unconventional water supplies as brackish groundwater or reclaimed water (Ikehata et al., 2018), although this ability of diatoms has only recently been used in water reuse and desalination (Ikehata et al., 2017, 2018; Alsar et al., 2020). It is well known that silica is essential for building the cell wall of diatoms, thus these algae efficiently extract dissolved silica from water. An up-to-date study pointed out that a diatom consortium dominated by *Nitzschia*, *Pseudostaurosira* and *Halamphora* species successfully removed more than 95% of reactive silica from brackish agricultural drainage water within 28 h (Ikehata et al., 2017). In addition, *Nitzschia* and *Pseudostaurosira* species were effectively applied in reverse osmosis methods, in which 95% of concentrate aqueous silica (78 mg l^{-1}) was removed under suboptimal conditions within 72 h (Ikehata et al., 2018). Not only diatom cells but also deionized diatomite (Diatomaceous Earth) can be used in desalination processes as the pretreated diatomite was able to remove even more than 50% of NaCl content of waters (Alsar et al., 2020).

It is also known that saline lakes host diatoms, like *Nitzschia palea*, which can produce

considerable amount of lipids for alternative fuel production (Abdel-Hamid et al., 2013). This production of diatoms are also characteristic during the removal of nutrients from natural and wastewater (Adey et al., 2011, 2013), when significant amount of biomass are produced with high percentage of various unsaturated or saturated fatty acids and lipids (20–30% of dry cell weight). These compounds are known to be widely used as raw material of cosmetics, medicines, biofuel precursors, and aquaculture food implementers (Mishra et al., 2017; Marella et al., 2020a, 2020b).

In the last decades, we witness the significant development of biotechnology. Diatoms seem to be a promising source (Seckbach & Gordon, 2019) as their special morphological features and intracellular processes may provide several unexplored potential for further industrial application especially in connection with salinization (Ishika et al., 2018; Navarro et al., 2021). However, there are many unanswered questions in this area. Research and a deeper understanding of the processes at both genotypic and phenotypic levels in diatoms would further accentuate its applicability in biotechnology (Mishra et al., 2017).

Conclusion

Diatoms have developed a number of salt tolerance mechanisms in order to ensure their success in continental salty environments. However, our knowledge has been limited concerning the intracellular changes and its consequences, similar to understanding the detailed process of biomineralization and the meaning of the morphological variations of these beautiful microscopic creatures. Although salinity tolerances are driven by genes and infraspecific genetic diversity, genomic, transcriptomic, proteomic, and metabolic studies and their combinations are almost completely missing; however, they would be crucial to discover the relevant processes and their energy costs. Salt-responsive genes, salt-sensible mutants, and the gene regulation of the morphological changes induced by salinity have been also sparsely explored. Besides short-term acclimation studies, further, long-term studies would be necessary to reveal the adaptation of diatoms to salinization. This knowledge would be an effective key for understanding the salinity induced processes also at higher (population, community, ecosystem, and above up to biogeochemistry) levels and

to manage the ecological and economic consequences of salinization. Furthermore, these results could open the way for more and more biotechnological applications as ecosystem services provided by diatoms.

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Data availability Ethical and professional principles were completely followed.

Declarations

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

Ethical approval Ethical and professional principles were completely followed.

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