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AQUATIC ECOSYSTEM SERVICES

Review Paper

Ecosystem services provided by freshwater and marine diatoms

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Abstract Diatoms, a unique group of algae colonising a wide range of aquatic habitats and contributing to human well-being in many ways. We list and summarise these services using the classification of the Millennium Ecosystem Assessment (MEA), i.e. supporting, regulating, provisioning and cultural services. The most relevant supporting services are photosynthesis and primary production, as well as sediment formation. They also play a key role in nutrient cycling and habitat provisioning and serve as food for many organisms. Regulating services as oxygen production, climate control or sediment stabilisation are difficult to discuss without diatoms. Many provisioning services, directly used by humans, can be obtained from diatoms. These are tangible products such as medicines and immunostimulants but direct

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technologies such as wastewater treatment, micro- and nanotechnologies were also developed using diatoms. Studying of the past, present, and future linked to diatoms as a tool for palaeolimnology, ecological status assessment of waters and climate modelling is essential. Finally, the impressive morphology and ornaments of diatom frustules make them one of the most spectacular microorganisms, inspiring artists or providing a number of educational opportunities. Therefore, protecting aquatic habitats they inhabit is not simply a nature conservation issue but the key for human well-being in the future.

Keywords Bacillariophyta · Primary production · Diatomite · Climate regulation · Micro- and nanotechnology · Forensic science · Inspiration value

Introduction

"Few objects are more beautiful than the minute siliceous cases of the diatomaceae: were these created that they might be examined and admired under the high powers of the microscope?" C. Darwin (Origin of Species, 1859, p. 239).

As Charles Darwin wrote, jewellery-like diatoms are one of the most beautiful microscopic creatures in the World. But what is the real value of these organisms for society and how can they serve human well-being? Since our society is driven by economics, there is a need to estimate the monetary value of ecosystem services. One attempt (Costanza et al., 1997) suggested a value that is equal to, or twice as high as the World's GDP. This paper attracted the interest of policy-makers, economists, ecologists and the public leading to the establishment of the Millennium Ecosystem Assessment in 2001 (MEA; web1) and the global initiative of The Economics of Ecosystems and Biodiversity in 2007 (TEEB; web2).

Despite the huge differences in the area of marine and freshwater ecosystems, species richness of planktic algae including cyanobacteria is very similar (Falkowski et al., 2004) in these environments (Reid et al., 2019). While there is a significant bias towards higher trophic levels in focusing on the decline and extinction of species, photosynthetic algae are largely neglected probably because of their small size and invisibility to naked eyes. Diatoms are one of the most diverse groups of freshwater algae (Falkowski et al., 2004). They occur in both planktic and benthic habitats where, among other groups of algae, they play pivotal roles in food web and energy transport, especially at certain times of year (e.g. spring in temperate lakes, spring and autumn/winter in biofilm). Since diatoms are an integral part of the community where they live, it is often difficult to separate their contribution to ecosystem functioning from the benefits of the mixed communities. However and historically, the role of diatoms as "indicators" has been emphasized because they respond sensitively to changes in environmental conditions and several species have wide geographical distribution and relatively well-known ecological demands. Diatoms are also significant test subjects for biotechnological studies and used more and more widely in water management e.g. in biocontrol, modification or wastewater treatment. Thus, it should reveal the benefits they serve separately from the mixed communities in which they live, or the benefits that are largely provided by them. Although diatoms are widely used in various fields of applied science contributing to the well-being of humanity has not been synthesised yet.

In this review, we summarise ecosystem services provided by diatoms using the four main ecosystem service groups suggested by MEA (2003, 2005): supporting, regulating, provisioning and cultural services. Many of these services are of a largely historic interest with high relevance for understanding the effects of contemporary policy interventions (e.g. primary production, photosynthesis, food sources, climate regulation, biological control, etc.). Other services are part of rapidly evolving fields of science for diatom research (e.g. medicines, nanotechnology, genetic resources, wastewater treatment technologies) or provide a direct link between people and diatoms (e.g. environmental education, inspiration). We do not neglect examples of the negative impacts of diatoms on ecosystems and finally reveal the importance of biodiversity of diatoms and their contribution to ecosystem services for the purpose of providing a link among scientist, catchment managers, policymakers and legislators. This synthesised knowledge can help us to recognize the value of diatoms in human well-being and services they provide (Fig. 1).

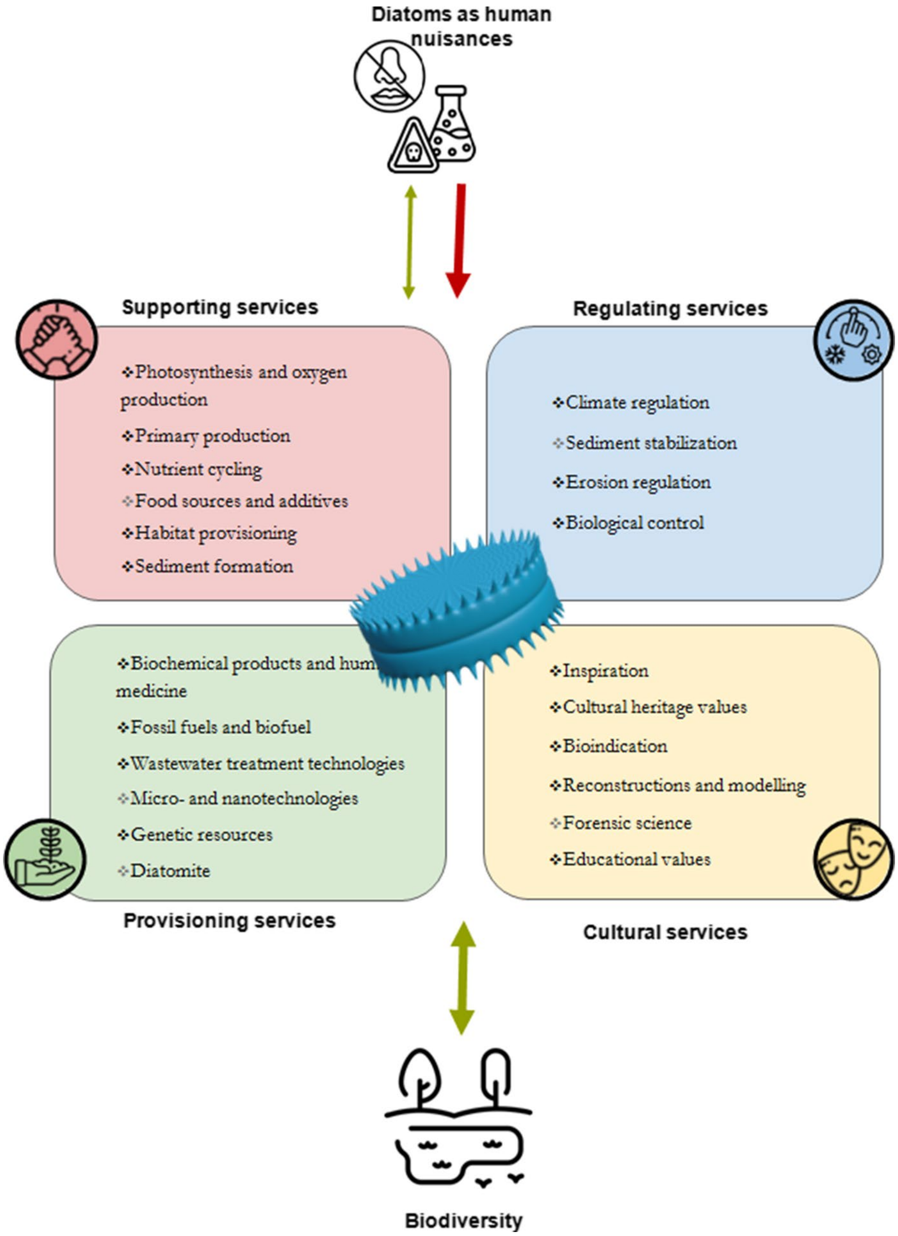

Fig. 1 Ecosystem services—biodiversity—human nuisances by diatoms: a relationship aspect. Red arrow: negative effect; green arrows: positive effect; the width of the arrows indicate the strength of the relationships; black drops: ecosystem services according to Millennium Assessment Report (MEA); grey drops: ecosystem services not mentioned by MEA but important for human life and well-being. The figure has been designed using icons from Flaticon.com

ESs provided by diatoms—a general overview: supporting-, regulating-, provisioning- and cultural services

As other aquatic microscopic organisms, diatoms are largely out of public interest simply because of their small cell sizes. While some services provided by diatoms can be easily perceived as benefits for humans such as oxygen production, medicinal benefits, fossil and biofuel production, others such as nutrient cycling, photosynthesis or sediment formation are often overlooked though are essential for maintaining life on Earth in its present form.

Ecosystem services are classified into four categories by the MEA (2003, 2005). Supporting services include all services, which are essential for the production and proper functioning of the other three categories. Any changes in these services affect the others and can jeopardise the global biogeochemical balance (MEA, 2005). Supporting services have either indirect impacts on human well-being, or the expression of their impact requires a long time. Thus, services such as photosynthesis, primary production, oxygen production, nutrient cycling and sediment formation belong to this group. Regulating services encompass the benefits that are obtained from the regulation of ecosystem processes. These include services as climate regulation, sediment stabilisation and biological top-down or bottom-up controls. These services already have a direct impact on humans, but they are strongly connected to supporting services. For example, the upheaval of the nutrient cycle can have a negative effect on climate regulation or biological control. Provisioning services are the most tangible and include all products obtained from ecosystems and used directly by humans. These services include e.g. foods, biochemicals, pharmaceutical industry, forensic science, biofuels and genetic resources. Last, but not least, cultural services are non-material benefits provided by ecosystems such as aesthetic values, inspiration, recreational and educational values.

Here, we identified 23 ESs provided by diatoms, revealing the major contribution of these organisms to ecosystem services and to human well-being.

Supporting ecosystem services

Diatoms as a taxonomic group of algae do not represent one particular ecological group (Stenger-Kovács et al., 2012; Salmaso et al., 2015) but contribute at different degrees to different kinds of assemblages like phytoplankton, phytobenthos, in both marine, brackish and freshwater habitats (Round et al., 1990). Additionally, they can inhabit soil (Pfister et al., 2017) even in harsh, cold environments (e.g. *Pinnularia borealis* Ehrenberg—Pinseel et al., 2020) as well as natural and artificial rock surfaces e.g. walls of metro stations (*inter alia Diadesmis contenta* (Grunow ex Van Heurck) D. G. Mann, *Grunowia sinuata* (Thwaites) Rabenhorst, *Nitzschia amphibia* Grunow or *Pinnularia appendiculata* (C. Arardh) Cleve—Ivarsson et al., 2013) and low-light subterranean environments (e.g. *Navicula mutica* var. *nivalis* (Ehrenberg) Hustedt, *Navicula contenta* f. *biceps* Arnott ex Hustedt, *Navicula contenta* Grunow—Komáromy et al., 1985; Buczkó & Rajczy, 1989; Falasco et al., 2014). Thus, their contribution to some functions provided by the ecological group they are part of (e.g. photosynthesis, primary production) depend simply on their presence and contribution to the biomass. However, other features specific to diatoms (e.g. the high density silica cell wall) equip them with well demarcated functions and services (Fig. 2).

Photosynthesis, oxygen production, primary production

Except for some cases where mixotrophy was detected (*inter alia*: *Cyclotella cryptica* Reimann, J. C. Lewin & Guillard, *Cylindrotheca fusiformis* Reimann & J. C. Lewin, *Fistulifera solaris* S. Mayama, M. Matsumoto, K. Nemoto & T. Tanaka, *Nitzschia brevirostris* Hustedt or *Skeletonema costatum* (Greville) Cleve—Marella et al., 2021; Villanova & Spetea, 2021), diatoms are primarily photosynthetic autotrophs with a huge contribution to all ecosystem services relying on photosynthesis. One of the main outcomes of their photosynthesis is oxygen production. Although cyanobacteria invented production of oxygen already around 3 billion years ago, the partial pressure in the atmosphere did not exceed but only a few percent the recent one (Benoiston et al., 2017). Widespread distribution of diatoms and coccolithophorids corresponds to the increase in O_2 in the Eocene and Oligocene (Falkowski et al., 2004; Naselli-Flores & Padisák, 2022) and contributed ultimately to the accelerating diversification of placental mammals and allowed the appearance and evolution of large sized biota (Falkowski et al., 2005; Bininda-Emonds et al., 2007).

Diatoms have a significant role in the global primary production, too. Marine environments are highly overrepresented in this aspect (Yool & Tyrrell, 2003; Ragueneau et al., 2006; Benoiston et al., 2017) as almost half (~ 54 Pg C year^{-1}) of the global primary production is produced by marine phytoplankton (Field et al., 1998; Naselli-Flores & Padisák, 2022). Some attempts have been made to identify class-specific primary production and estimated around 20–40% contribution of diatoms to total primary production (Uitz et al., 2010; Malviya et al., 2016), which is a huge contribution compared to their formerly estimated ~ 5–25% biomass contribution to total marine phytoplankton biomass defined with satellite colour identification of algal pigments (Alvain et al., 2008), or even to their 1% biomass

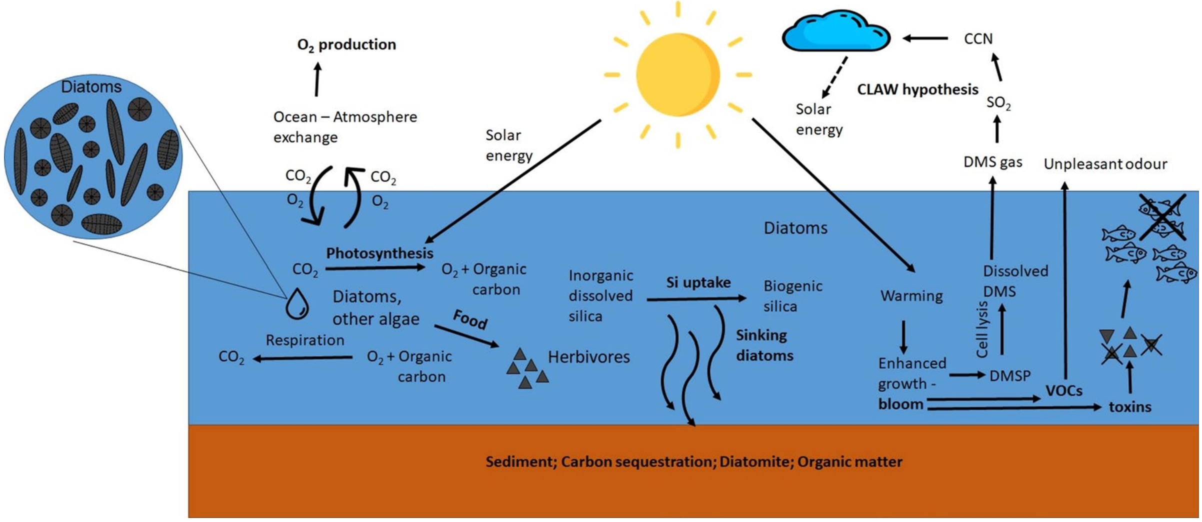

Fig. 2 Supporting and regulating services provided by marine diatoms and some of their negative impacts. Abbreviations: *CNN* cloud condensation nuclei; *DMS* dimethylsulphide; *DMSP* dimethylsulphoniopropinate; *VOCs* volatile organic compounds. Dashed arrow—negative effect; Solid arrow—positive effects. The figure has been designed using icons from Flaticon.com

contribution to Earth's photosynthetic organisms (Field et al., 1998). Diatoms are dominant members not only of planktic but also of the benthic microalgal communities. They can form massive algal mats on the sediments of the coastal zones, where the benthic primary production may account for ~ 70% of the pelagic production (Glud et al., 2002). In case of water level decrease as a consequence of consecutive dry years, benthic primary production largely provided by diatoms may exceed that of the planktic in closed-basin lakes (Padisák et al., 2006; Üveges et al., 2011). Regardless of their 1% area coverage on the Earth, inland waters have a comparable contribution in global primary production and carbon flux as marine and terrestrial habitats (Likens, 1975; Battin et al., 2009; Tranvik et al., 2009).

The proportion of diatoms in different ecosystems vary significantly depending on spatial, environmental, biological variables and seasonality (Soininen, 2007; Malviya et al., 2016). For example, during the vernal period in deep oligo- or mesotrophic lakes, the phytoplankton is characterised by centric diatoms, making up a major part of the community, thus contributing more to the primary production than during the stratified period (Reynolds, 2006). In such habitats, diatoms may reach an annual average contribution of 20–50% to the total phytoplankton biomass with a strong seasonality, reaching their maximum during the spring bloom when they almost exclusively dominate the community (Padisák et al., 2003). Though species other than diatoms become dominant later in the year, the composition and especially size of the dominant diatoms in spring has major consequences for the subsequent phases of seasonal succession. A good example in known from Lake Stechlin, Germany. During the onset of stratification, small-celled centric diatoms sink much slower than large-sized ones (Padisák et al., 2003). Moreover, small cells can serve as food for heterotrophic protists and phagocytic mixotrophs (like *Ochromonas*). Therefore, the nutrient content of small cells (e.g. *Cyclotella tripartita* Håkansson) largely remains in the epilimnion and that of the large sized diatoms as *Stephanodisus neoastraea* Håkansson et Hickel or *Aulacoseira islandica* (O. Müller) Simonsen sink very fast removing high amounts of nutrients within their protoplasms from the epilimnion. As a consequrnce, nutrient availability of the phytoplankton for the rest of the vegetation period depends largely on the species composition of the spring diatom bloom with consequences for upper trophic levels (Padisák et al., 2010; Selmeczy et al., 2019).

Diatoms form a major part of periphytic communities, thus contributing significantly to the primary production both in lakes and rivers. Their contribution is especially high in shallow, nutrient-poor condition and high transparency, even reaching ~ 75% of the periphytic biomass (Vadeboncoeur & Steinman, 2002; Sánchez et al., 2017). In littoral zones of lakes, primary production of epipsammic diatoms may override that of the planktic (Üveges et al., 2011). Periphyton and especially diatoms are the dominant biological component in rivers, especially in smaller streams, where conditions for development of phytoplankton is very limited or not possible at all. In such habitats, attached algae and especially diatoms contribute majorly to primary production and nutrient cycles (Hornick et al., 1981; Stevenson et al., 1996; Flipo et al., 2007).

Nutrient cycles

Being eaten, decomposed or sequestered and fossilised, diatoms play a crucial role in the nutrient cycles (Gordon & Seckbach, 2019). Although the amount of organic carbon produced by phytoplankton is similar to that of rainforests (Field et al., 1998), an important difference is that diatoms are consumed rapidly, fuelling the food web either still in the upper layers or in deep waters after sedimentation (Armbrust, 2009). A significant portion of this carbon is not consumed though, and it is estimated that diatoms alone are responsible for 40% (~1.5–2.8 Gton C yr^{-1}) of the total oceanic carbon sequestration (Benoiston et al., 2017). The relatively high specific mass and associated to the fast sinking of diatoms compared to other algae (Reynolds, 2006) make them highly efficient in exporting nutrients from the productive layers to the bottom not only in marine environments but in lakes as well (Ardiles et al., 2012).

A unique feature of diatoms is their cell wall (frustule), mainly made of silicon, therefore, they have a major impact in the global silicon cycle (Yool & Tyrrell, 2003; Basile-Doelsch et al., 2005). Diatoms extract silica from the water column as dissolved, reactive inorganic silica (DRSi; largely $Si(OH)_4$). The global biogenic silica, produced mainly by marine diatoms, is estimated as 200–280 Tmol Si yr^{-1} (Nelson et al., 1995; Struyf et al., 2009). By comparison, silica accumulated in terrestrial plants is estimated to be 60–200 Tmol Si yr^{-1}, the annual release by weathering of silicates is ~19–46 Tmol yr^{-1} and the global input of dissolved Si from rivers to the oceans is estimated to 5 Tmol Si yr^{-1} (Conley, 2002; Struyf et al., 2009). Important differences were observed in silica acquisition between freshwater and marine diatoms (Conley et al., 1989). Due to a set of physiological and environmental factors, cells of freshwater diatom walls contain around one order of magnitude more silica than that of marine species (Alverson, 2007). This is in good accordance with the observation that the concentration of silica in lakes and rivers is estimated at 100–150 µmol l^{-1} (Paasche, 1980; Tréguer et al., 1995); much higher than that in the oceans (< 10 µmol l^{-1} on the surface and not more than 160 µmol l^{-1} in deep layers; Martin-Jézéquel et al., 2000). Sedimented diatoms in lakes are more likely to be resuspended, thus silica may be reintroduced in the cycle, while diatoms in the seafloor are much less likely to reappear in the upper layers of the oceans (Tréguer et al., 1995). Still, lakes are the second largest pool of biogenic silica, with a rate of silica burial that can reach up to 1.30 Tmol yr^{-1} (Frings et al., 2014).

Food source and food additives

Diatoms develop a high quantity of biomass through primary production. Although it is definitely a provisioning service for organisms feeding on diatoms, it does not provide direct resources to humans and thus, categorised as supporting service by the MEA. Diatoms are high-quality food sources for grazers and scrapers, being the most important primary producers from headwater streams to midsize rivers (Vadeboncoeur & Power, 2017). Since diatoms are rich in polyunsaturated fatty acids (PUFAs), docosanhexaenoic acid (DHA) as well as long-chain eiscosapentaenoic acid (EPA) synthesiser (Marella et al., 2020a), they are more nutritious and digestible than terrestrial plants. According to Cebrian (1999), consumption efficiency is approximately 40 times higher from attached algal communities to grazers than from terrestrial forest organic materials to shredders. Thus, diatoms are a fundamental and efficient food source for snails, larvae of a number of mayflies and caddisfly species or other macroinvertebrates (Frost & Elser, 2002). Beside macroinvertebrates, numerous omnivorous and herbivorous fish species feed on the periphyton, consuming diatoms (Reinthal, 1990). Diatoms living in the pelagic zone provide palatable and nutritious food for the zooplankton community because they contain PUFAs as well, while cyanobacteria and green algae are PUFA and sterol-deficient primary producers (Sommer et al., 2012). Planktic diatoms have important interspecific relationships, for example, *Asterionella formosa* Hassall is a typical host for parasitic chytrids and infections by cytrid zoospores make this large diatom edible for the zooplankton. Such relationships are important to maintain genetic polymorphism and biodiversity (Kagami et al., 2014; Van den Wyngaert et al., 2022).

As diatoms contain high concentrations of important essential nutrients, they are used as food additives for vertebrates and invertebrates in aquacultures (Gatenby et al., 1997, 2003; Spolaore et al., 2006; Peltomaa et al., 2019). In the early larval stage, marine finfish species consume live prey such as microalgae including planktic diatoms as *Chaetoceros*, *Skeletonema*, and *Thalassiosira* (Coutteau, 1996; Kumaran et al., 2017). In addition, shrimps and lobsters are fed mostly by planktic algae including diatoms, while gastropod molluscs consume benthic species when they settle out from the plankton (Kaparapu, 2018).

Habitat provisioning, endosymbiotic relationships

Planktic diatoms may provide surface for microorganisms (i.e. bacteria, fungi) to grow but habitat provisioning by the periphyton/phytobenthos dominated by diatoms is more important. This complex habitat growing on any kind of submerged substrates, provides habitat not only for microorganisms (Fig. 3a, b) but also for the meiofauna (Peters, 2005). Similarly to terrestrial plant communities, microphytobenthos serves as microforests in aquatic environments (Fig. 3c), providing essential functions for the ecosystem and maintaining biodiversity (Stevenson et al., 1996).

A very special type of habitat provisioning when diatom cells harbour other photoautotroph organisms as nitrogen-fixing cyanobacteria. Nitrogen-fixing endosymbiotic relationships are usually observed in oligotrophic tropical and subtropical regions where they play pivotal roles in the N-cycle (Stancheva & Lowe, 2019). In freshwater ecosystems, members of the order Rhopalodiales host coccoid N-fixing cyanobacteria (Drum & Pankratz, 1965; Lowe et al., 1984; Nakayama et al., 2011). The number and ecological significance of this relationship is definitely higher

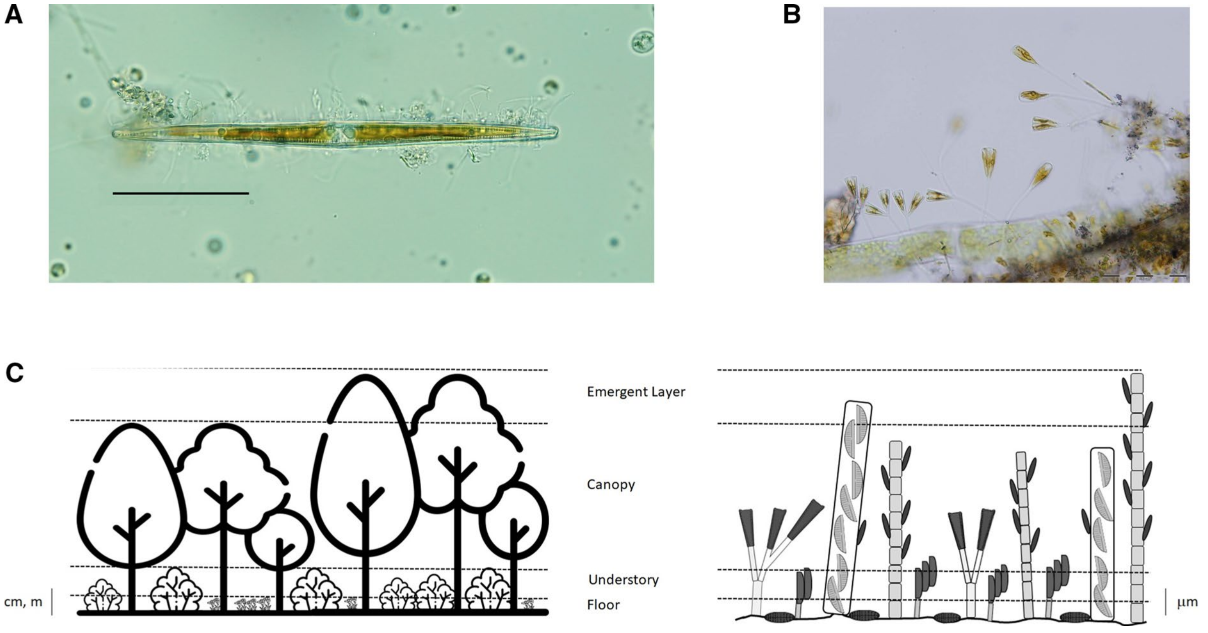

Fig. 3 Supporting and regulating services provided by diatoms: habitats for microorganisms as bacteria (**a, b**) or even other diatoms (**b**). Photos by Enikő Török-Krasznai (**a**) and Kálmán Tapolczai (**b**); schematic representation of basic structure (layers) in periphyton and forest (**c**). The Fig. 3c has been designed using icons from Flaticon.com

in environments with low inorganic nitrogen concentrations and low N/P ratio, where N-fixation significantly contributes to N-supply (DeYoe et al., 1992; Stancheva et al., 2013). In addition, the endosymbiontic relationship affects higher trophic levels such as aquatic insects, whose abundance may multiply in habitats with high biomass of endosymbiotic *Epithemia* cells (Stancheva & Lowe, 2019).

Sediment formation

One of the supporting services defined by the MEA is soil formation as a fertile soil positively influences other supporting services, thus indirectly contributing to human well-being. In case of diatoms, this term is less interpretable but a slight modification to sediment formation is appropriate (Naselli-Flores & Padisák, 2022; Thomaz, 2022). A quantity of silica, not dissolved and recycled, sinks to the bottom, forming a diatomaceous sediment in the oceans and lakes. Further dissolution of the diatom frustules occurs and an estimated ratio of 0.05–0.15% silica produced by diatoms is preserved (Blatt et al., 1972). The siliceous sedimentary rock formed by diatoms, called diatomaceous earth or diatomite may appear as several hundred meters thick vast diatomaceous deposits (Sims et al., 2006).

Regulating services

Climate regulation, dimethylsulphide

Since O_2 production and carbon fixation are always coupled with O_2 consumption by e.g. respiration, the extraction of carbon from the carbon cycle via sequestration is critical for climate regulation (Benoiston et al., 2017). Anthropogenic climate change imposes, however, negative effects on diatoms and consequently on their regulatory mechanisms. A global model showed that climate change makes surface oceans more nutrient-depleted that favours the development of small phytoplankton species instead of the bigger diatoms (Bopp et al., 2005). But even within diatoms, small species are hypothesised to replace bigger ones which has a further effect on the silicification of these organisms (Kuefner et al., 2020).

Dimethylsulphide (DMS), one of the derivatives of dimethylsulphoniopropinate (DMSP), is produced in high amounts by marine planktic algae including diatoms and is one of the most relevant compounds in climate control (CLAW hypothesis; Charlson et al., 1987). The emitted marine DMS accounts for nearly half of the global sulphur emission, ranging from 15 and 33 TgS per year (Kettle & Andreae, 2000; Lana et al., 2011). Although dinoflagellates and haptophytes are the main DMSP producers in oceans (Keller et al., 1989; Dani & Loreto, 2017), diatoms produce significant amounts as well (Keller et al., 1989). Recent studies suggest that polar oceans are the hotspots of DMS emission (Dani & Loreto, 2017) and diatoms often dominate there. However, the synthesis of DMSP by diatoms is strongly up-regulated by seasonality or environmental factors, e.g. nutrient limitation, salinization or light availability (Bucciarelli & Sunda, 2003; Gypens et al., 2014; Kettles et al., 2014).

In large rivers, large centric diatoms may be dominant members of phytoplankton (Abonyi et al., 2018a), but nutrient-deficient environments resulted by the enhanced water retention (Abonyi et al., 2020) can lead to a shift towards small-sized, mainly filamentous diatoms increasing the chance of the more frequent occurrence of clear-water state upsetting nutrient cycling and changing physical and chemical parameters of the water. In addition, increase in the dominance of benthic diatoms can be expected due to the more frequent occurrence of extremely high water levels and flow conditions (Abonyi et al., 2020). These two phenomena can significantly decrease the ecosystem functioning of phytoplankton in large rivers. In small streams, contribution of benthic diatoms to primary production is substantially more pronounced than that of planktic assemblages. Extreme traits as small or large sizes, halophilic, pioneer or even aerophilic characteristics can become frequent or dominant in benthic assemblages during drought and drying up of streams (Sabater et al., 2016; Novais et al., 2020; Lukács et al., 2021). Depending on the duration of unpleasant conditions, significant loss in diversity and functioning can be predicted (Crabot et al., 2021; Tornés et al., 2021), which negatively affect higher trophic levels. Loss in periphytic algal biomass is also a common phenomenon during drying up (Sabater et al., 2016), which can finally lead to loss of microclimate regulation.

Sediment stabilisation, erosion regulation

Benthic diatoms play a crucial role in sediment stabilisation (Arlinghaus et al., 2021). They form biofilm mainly to be able to settle down (Tong & Derek, 2021), but biofilm also protects organisms from hostile environments, predation, pollutants and serves as carbon storage (Arlinghaus et al., 2021). Within the biofilm, the single cells, colonies and filaments themselves can directly cover the sediment and prevent its destabilisation. In addition, diatoms produce and release large amounts of extracellular organic compounds (EPS) as polysaccharides and proteins (Bruckner et al., 2011), which help to glue together the sediment particles.

Obviously, erosion regulation, a further service provided by benthic diatoms, is strongly and negatively related to sediment stabilisation. As EPS is not only distributed horizontally but also vertically; its stabilising effect is not limited to the sediment surface. In addition, diatoms that spend some time in the upper layer, also prevent the sediment from erosion. But it is a vice versa situation because the fine sediment grains provide a relatively stable surface for diatoms (Arlinghaus et al., 2021).

Biological control, wastewater treatment

Diatoms have a number of characteristics such as the silica cell wall, high reproduction rate (Nalley et al., 2018; Naselli-Flores & Padisák, 2022), ornithine-urea cycle (Allen et al., 2011), etc., which allow them to effectively remove macro- and micronutrients as well as trace elements from waters. These characteristics can be successfully involved in biological control and wastewater treatment. While freshwaters are overburdened with surplus nutrient supply mainly by human activities, wastewaters contain a number of elements that can lead to intense growth of algae (Justić et al., 1995; Reynolds, 2006). These conditions favour bloom-forming, potentially toxic cyanobacteria (Marella et al., 2020a). Diatoms, however, prevent the development of harmful algal blooms as they store nitrogen (McCarthy et al., 2017) and, in contrast to green algae and plants, are characterised by ornithine-urea cycle, allowing them to re-assimilate nitrogen through catabolic processes (Allen et al., 2011).

Wastewaters often have low transparency, due to the high total suspended solids concentration or to deep dark color. Diatoms tolerate low-light conditions due to their fucoxanthin content, which needs less light to become light-saturated (Marella et al., 2020a). In addition, wastewater may contain a wide variety of heavy metals even in very high concentrations. Diatoms can effectively remove heavy metals by biosorption, bioaccumulation, biomineralization or biotransportation (Marella et al., 2020b).

Provisioning services

Biochemical products and human medicine

Unlike a set of other algae species, diatoms are not used in human nutrition directly, though they would be suitable. During their metabolisms, they synthesise PUFAs, vitamins, carotenoids, amino acids in amounts (Marella et al., 2020a) comparable to production efficiency of conventional vegetables and crops (Bozarth et al., 2009). However, other products, e.g. biochemicals, genetic resources, silica cell wall based technological developments can be directly obtained from diatoms.

As it was recently explored, several diatom taxa produce high amounts of bioactive compounds such as polyphenols, carotenoids, chlorophylls or β-glucans, sulphated polysaccharides, etc. that have been identified as immunostimulants (Boukhris et al., 2017; Saleh et al., 2020; Sharma et al., 2021). These molecules have been shown to have strong antibacterial activity, thus, diatoms can be effectively used as food additives in fish diets (Saleh et al., 2020). In human medicine, bioactive molecules and compounds produced by diatoms are used to reduce the risks of hyperglycemia, coronary heart disease and to lower blood cholesterol levels. Aqueous or organic extracts of marine planktic species have been proved to be effective against HIV and some types of cancer (Mishra et al. 2017).

Fossil fuels

Diatoms are found throughout the world's oceans but the Southern Ocean is typically characterised by diatom communities. The highly favourable environment for them is generated by the Antarctic Circumpolar Current, which exists since around the Eocene (Benoiston et al., 2017). The proliferation of marine diatoms is coeval with enormous deposits of hydrocarbon-rich source rocks in this area. These diatomaceous deposits are important sources of oil and gas mostly in the Southern Ocean, but in the Caspian- and North Sea region as well (Krebs et al., 2010; Cermeño, 2016). These, together, accounts for over 10% of the world's conventional oil and gas stock (Klemme & Ulmishek, 1991), which is the latest generation of marine fossil fuels.

Biofuel production

The lipid content of diatoms reaches the threshold ideal for biofuel production under suitable nutrient supply. While an up-to-date laboratory study highlighted that silicate and trace metals are crucial in lipid production of freshwater diatoms in addition to P, N and C (Marella et al., 2018), use of algal flow way technology may be effective in biofuel precursor production by diatoms (Marella et al., 2019).

Wastewater treatment technologies

Wastewater treatment technologies such as high-rate algae ponds (HRAPs) or algal turf scrubber (ATS), based on the removal of nutrients during cell metabolisms, are multi-algal systems in which diatoms may also be dominant at least in some periods in addition mainly to green algae and cyanobacteria (Craggs et al., 1996; Adey et al., 2011; Park et al., 2011; Marella et al., 2019). These technologies have been already used in practice (web3; web4). As spin-off benefits, high algal biomass, formed in ATS and HRAPs systems, usually contains valuable bioactive compounds such as lipids (Marella et al., 2019) that can be used in biofuel production or feeding.

Micro- and nanotechnology, space science

The silica cell wall is a unique physiological feature of diatoms, into which living diatom cells can insert different kinds of trace- or microelements. This property provides a potential use of diatoms in micro- and nanotechnology. A *Pinnularia* sp., for example, is able to insert germanium in their cell wall, which can then potentially be used as semiconductor (Jeffryes et al., 2008). Frustules of *Coscinodiscus lineatus* (Tempère & Peragallo) Hustedt coated by ZnS nanoparticles is widely used in photonic or optical technologies (Ragni et al., 2018). Diatoms are involved in the development of Lab-on-chip techniques and in biosensor design. Due to the special structure of their silica wall, diatoms are increasingly used as drug delivery vehicles (Mishra et al., 2017; Marella et al., 2020b). NASA uses diatoms, for example, in wastewater treatment to support space travels in its space programs (Gordon & Parkinson, 2005), thus we can definitely state that this algal group is of a great importance not only in recent biotechnological trends but also in the future (Mishra et al., 2017; Marella et al., 2020b).

Genetic resources

Diatoms are important genetic resources because they are directly involved in genetic engineering studies increasing their photosynthetic efficiency, their capacity to produce bioactive compounds or their applicability in nanotechnology. The marine *Phaeodactlyum tricornutum* Bohlin is one of the seven diatom species whose genome has been already sequenced (Basu et al., 2017). This species is a widely used model organism of evolutionary (Rastogi et al., 2018), physiological (Domergue et al., 2002; Singh et al., 2015; Watanabe et al., 2018) and even applied biological (Mayer et al., 2019) experiments. Genetic engineering studies of *P. tricornutum* usually focusses on increasing the content of bioactive molecules as PUFAs (Peng et al., 2014) including mostly EPA (Domergue et al., 2002; Peng et al., 2014) and terpenoids (Fabris et al., 2020) using modern molecular techniques. The first centric diatom whose genome has been sequenced, was *Thalassiosira pseudonana* Hasle & Heimdal (Armbrust et al., 2004) and it has become a widely used model organism to study the formation of the silica cell wall. Tesson et al. (2017) was the first who altered the silica structure and frustule size of *T. pseudonana* by genetic modification and proved that knocking down a single gene is effective enough to change the phenotypic appearance of the species. *T. pseudonana* cell walls are also a desirable matrix for drug delivery applications and developments as demonstrated by Delalat et al. (2015). Enzyme immobilisation is another way to apply genetically engineered cell walls in practice (Poulsen et al., 2007; Sheppard et al., 2012). It seems, the in vivo immobilisation of enzymes used by diatom cells has multiple advantages compared to conventional methods thus there is a huge potential of using genetically engineered diatoms in enzymology (Sheppard et al., 2012).

Diatomite: dynamite, building material, floating bricks, other industrial use

Diatomite, or diatomaceous earth is a soft, porous, fine-grained, lightweight, siliceous sedimentary rock with a great economical potential. The origin, development and taphonomy of diatomite are regularly reviewed (Bakr, 2010; Harwood, 2010; Flower, 2013; Ghobara & Mohamed, 2019; Sriram et al., 2020; Zaharská et al., 2020). Nothing shows its economic significance better than the fact that the production of diatomite was estimated at 770,000 tons/year with an estimated processed value of $260 million in 2020 (web5). However, diatomite is a finite resource, thus in this review we mention only three snapshots about its use. The first commercial application, and perhaps the most notable early use of diatomite, was the production of dynamite, as discovered in 1867 by Alfred Nobel. Expansion of railroads and construction of canals for shipping, construction of tunnels, dams and highways, and the extraction of the coal and raw materials would not have occurred at the same pace without the convenient explosive power of diatomite-encased nitroglycerine (Harwood, 2010). Before the paramount contribution of dynamite to the technical development of humankind the use of diatomaceous earth has a history of use by humans, spanning nearly two millennia. The “floating bricks” of antiquity and vases made of diatomite are known from the Greeks (Ehrenberg, 1842). The Greeks were also the first to use diatomite as a mild abrasive. Reconstruction of the dome of Hagia Sofia Church in Constantinople used diatomite as a building material as early as AD 432 (Harwood, 2010). Recently, the main uses of diatomite include filtration aid, mild abrasive, mechanical insecticide, absorbent for liquids, matting agent for coatings, reinforcing filler in plastics and rubber, porous support for chemical catalysts, activator in blood clotting studies, pet litter, a thermal insulator, soil for potted plants, dry cleaning, recreation, sewage treatment (Cummins, 1975; Ghobara & Mohamed, 2019; web6). In addition, solar-driven interface evaporation is a sustainable and green method for seawater desalination and wastewater purification, which has attracted great attention due to the expectation to solve the global freshwater crisis (Li et al., 2021). Thus, diatomite could be an important matter of sustainable and green methods.

Cultural services

Inspiration value and cultural heritage

“*Diatoms have been the most commonly portrayed microalgae—their shape, symmetry, beauty, and ecological importance are hard to compete with*” (Spaulding et al., 2022).

The beauty of diatoms has been noted since the beginning of the use of microscopes. Many diatom monographs begin with the story that already in 1703, a fellow of the Royal Society of London observed the first diatom colonies (Round et al., 1990). It cannot be stressed enough, that despite the long history of diatom research, the general public is not very familiar with diatoms, although they are in a number of ways closely related to our existence and wellbeing.

In the artistic aspect of diatoms, the first to mention is due to Ernst Haeckel (web7), the author of the famous multivolume series “*Kunstformen der Natur*” (Haeckel 1899–1904). The implementation of photo documentation of diatoms revolutionised the connection of science and art. The first diatom photomicrographs were probably taken by the apothecary Mayer in Frankfurt/Main in 1860, but it is not clear whether they showed diatoms (Sterrenburg pers. com.). It has still remained unclear who published the first diatom microphotograph, but some examples were found for the early printed diatom microphotographs (Jahn, 2002). Early diatomists made several experiments to find the best ways of documentation, as suggested by unpublished microphotographs in historical collections (e.g. Johannes Kinker’s collection—Sterrenburg & de Wolf, 2004; Pantocsek’ collection—Buczkó, 2012; Fig. 4a). Diatom assortments represent a special kind of art in the use of diatoms and it has a long history. Making “Typenplatten” and ″ Salonpreparat” was very popular in the 19th century (Burba et al., 2009; Kranz, 2009). These days, Klaus Kemp is often mentioned as “the last practitioner of the Victorian art of diatom arrangement” (web8). As the beauty of diatoms has always been in the focus of artists, scientists, and everybody who once had a chance to meet diatoms, the summaries and reviews are also presented regularly (Pappas, 2014; Tiffany and Nagy, 2019).

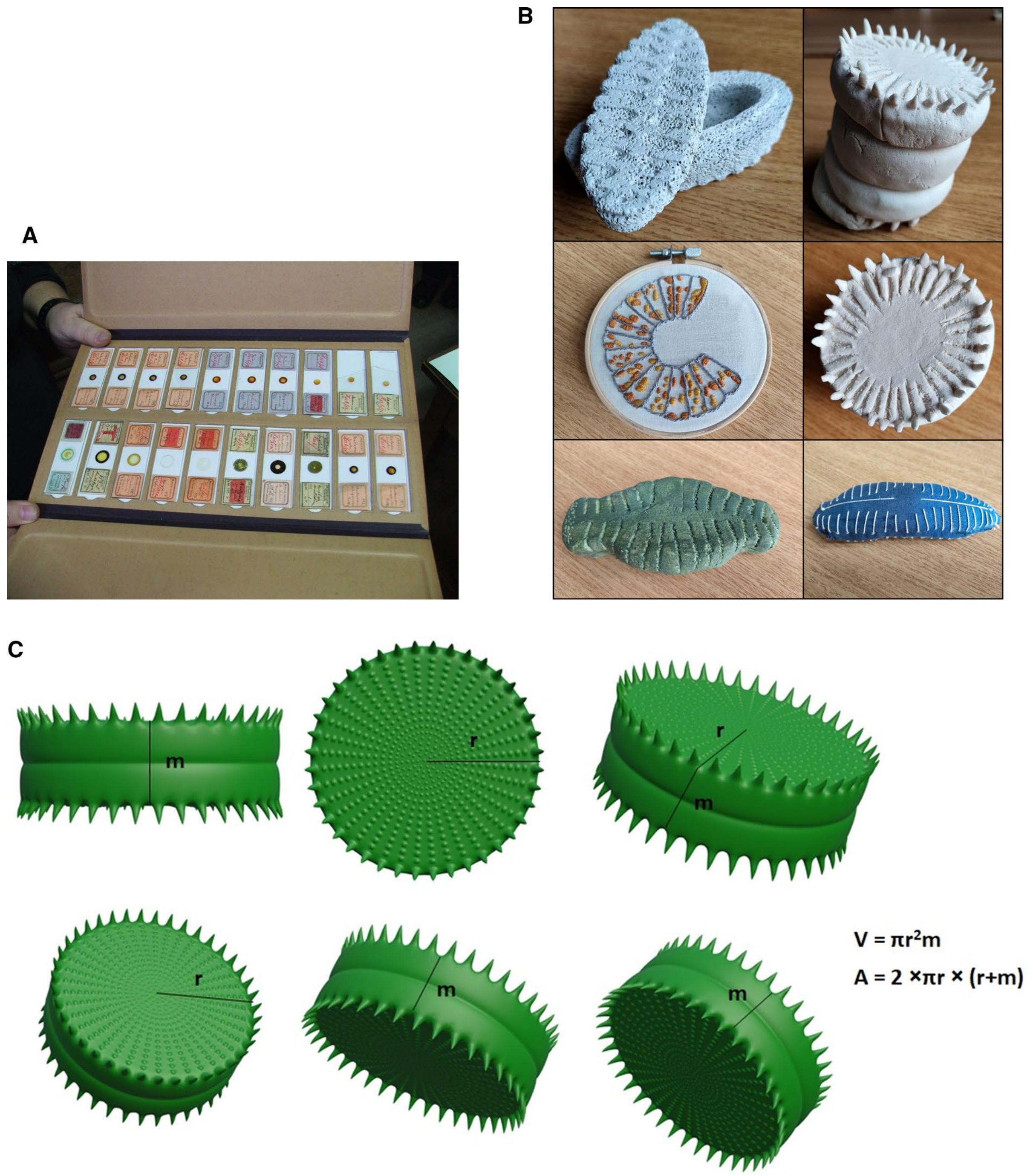

Fig. 4 Cultural services provided by diatoms: A small piece from the Pantocsek' collection (**a**). The photo was taken by Gábor Kiss in 2012 during a visit to the Botanical Department of the Hungarian Natural History Museum organised by the Algology Forum; Diatom models made for the algology course by undergraduate students at University of Pannonia, Hungary (**b**). Photo by Kálmán Tapolczai; The 3D model of *Stephanodiscus* sp. in different views to illustrate the dimensions of diatom frustule and calculation of cell volume (V) and surface area (A) using the model; r: radius; m: thickness (**c**). 3D algae images by Verona Lerf

A lesser-known appearance of cultural services provided by diatoms is "the diatoms on stamps" (Wynne & Edlund, 2019; web9). The enlargement of microscopic creatures including diatoms also impacted art (e.g. *Urban Hydrology*—web10). Moreover, the exhibitions can play a special role in presenting diatoms to the public. Galleries themselves are outstanding in their own right, and exhibitions about diatoms are an easy way to spread information (Mayama, 2005; web11).

Diatoms as a tool for reconstruction, prediction, ecological status assessment and forensic science

The finely ornamented solid valves of diatoms preserve well in the sediments or even in or on human bodies. Moreover, diatoms are abundant and widely distributed biota with well defined autecology for many species (Round et al., 1990; van Dam et al., 1994; Lecointe et al., 2008). Thus, they are good indicators of salinity, pH changes, trophic condition of both freshwater and marine environments (Wilson et al., 1994). These properties make diatoms not only ideal organisms for reconstructing the past climate (paleoecological proxy) but also for predicting it in the future. In addition, they are widely used in ecological status assessment as bioindicators and serve as evidence in criminal investigations.

It has been recently recognized that climate is a dominant force in aquatic ecosystem processes (web7) and understanding its consequences has a crucial importance in the recent climate crisis. The lack of long-term monitoring data is a significant limit for the evaluation of the recent trends and shifts. At this point, the diatom-based reconstruction has pivotal importance in the freshwater and marine environment, including the transience between them (Denys & de Wolf, 2001). Moreover, diatoms alone or as a functional group, are frequently used model organisms in the prediction and modelling of the ecological causes and consequences of global climate and anthropogenic changes (such as HAB blooms, primary production, eutrophication), for which purpose a variety of approaches were applied from the simple laboratory experiments (e.g. Sun et al., 2011; Lengyel et al., 2020), through micro- and mesocosms studies (e.g. Domis et al. 2007; da Silva et al., 2019) to complex ecosystem models from regional to global scales. The results of projections are quite contradictory due to several reasons (e.g. Blenckner, 2005; Litchman et al., 2006) but most of the models predict reduction in biomass and abundance of diatoms (Bopp et al., 2005; Markensten et al., 2010; Trolle et al., 2011; Chen et al., 2014; Laufkötter et al., 2015; Krause & Lomas, 2020), shifts in their distribution (Barton et al., 2016; Busseni et al., 2020) and composition (Pound et al., 2021), changes in timing of blooms (Mooij et al., 2007; He et al., 2011) as a consequence of changes in temperature or duration of ice-cover (Yang et al., 2016). These are important results regarding the maintenance of ecosystem services (e.g. increasing frequency of blooms, reduced biogeochemical role and productivity, changing ecosystem structures, etc.) and for water management.

Diatoms are one of the five biological quality elements in the assessment of the ecological status of waters (WFD; EC, 2000). Currently, diatom-based biomonitoring has three pillars: in addition to the morphological species based analyses, diatom traits (Larras et al., 2017; Stenger-Kovács et al., 2018) and environmental DNA (eDNA)-based molecular methods are also involved in assessment (Kahlert et al., 2021; Riato et al., 2021). Especially the metabarcoding analysis of eDNA samples has become a very promising tool to assess biodiversity of several group of organisms, and the currently developed methodology is more advanced in case of diatoms than for e.g. other groups of phytoplankton (Bruce et al., 2021; Cordier et al., 2021). Beside recalculating conventional indices with species lists obtained via metabarcoding, alternative approaches have emerged to exploit the potentials of metabarcoding for a fine-tuned quality assessment using a phylogenetic signal (Keck et al., 2018), "taxonomy-free" approach (Apothéloz-Perret-Gentil et al., 2017; Tapolczai et al., 2019; Feio et al., 2020) or detecting cryptic diversity (Kahlert et al., 2021; Pérez-Burillo et al., 2021; Tapolczai et al., 2021).

Despite the rarity of cases when diatoms can provide clincher in forensic science, their use is quite well-known from crime stories. Numerous studies have demonstrated that diatoms provide valuable, supportive evidence for the cause of death when a body is found in water (Peabody & Cameron, 2010; Levkov et al., 2017). To differentiate ante-mortem and post-mortem drowning no better method is known than the diatom test, either based on morpho-species identification (Pollanen, 1998) or on molecular methods (Vinayak & Gautam, 2019); often independently from the date of death that could happen even some thousand years ago (Andrade et al., 2022). Diatoms have also been used to study crime scenes e.g. detecting evidence on clothes, hairs or other materials (Peabody & Cameron, 2010; Vinayak & Gautam, 2019).

Environmental education, citizen science

Educating the public is essential to discover diatoms and to recognise the importance of these tiny microorganisms in human life. The STEAM project is a good example for bringing closer marine life to the students (Boyle, 2021). In this project diatoms can be used in the kaleidoscope to help for understanding the hyperbolic geometry (Boyle, 2021).

As an example, how to make students more involved in biological courses, undergraduate students at the Limnology Department of University of Pannonia (Hungary) are asked to make diatom models for the algology course. Besides the artistic value, the exercise helps them to better understand the morphological structure of these organisms (Fig. 4b). In Ireland, McGlynn et al. (2019) have outlined a marine science and art project involving papier-mâché activities based around the theme of hydrothermal vents, this was aimed at primary children and showcased how links can be made between pupils' understanding from biology. A brand-new project is the establishment of the Pandorina website (web12), which is still in its infancy but the founders' aim is to provide useful tools and information for scientists and practitioners to get their work done faster, smoother and easier. Their future aim is to create an open repository of real-like microalgae including diatom images using 3-dimensional models (Fig. 4c). Borics et al (2021) 3D printed algal shapes not only visualise algae, diatoms among them, for the public but serve scientific purposes as calculating surface/volume ratios, studying behaviour of different forms in fluid media applying realistic specific gravity ratios.

Doubtlessly, the most important recent forum of diatom research including all issues and all related fields, is the diatoms.org webpage (web13). According to their definition the "Diatoms of North America is a collaborative work in progress, growing and changing as science advances". The biweekly webinar series, hosted by "diatoms.org", is an outstanding education platform (web14).

Diatomists are also very active in popular scientific actions. There are several posts and webpages where the interesting/exciting facts and information are available for diatom experts, voluntaries, amateur diatomists, undergraduate students as well as the broad range of those interested in this group of siliceous algae (web15; web16). Articles and features appeal to a broad audience, including people who do not know what diatoms might be (e.g. "*Diatoms of the Month*" and "*Diatoms of the Year*" projects—Abonyi et al., 2018b; web15; web16).

The beauty of diatoms has permanently inspired artists and designers since they became visible for humans. A wide collection of pictures, wallpapers, clothes, artworks are available on the market and the choice is very easy on-line (web17).

Negative impacts of diatoms

Invasive species

Diatoms can contribute to human well-being in a number of ways as demonstrated in the previous sections of this review. However, the negative impacts and nuisances caused by them are also important to mention. Spread of invasive species, massive algal blooms and toxicity may be some of the most important inconveniences that may result in economic and ecological damages and can be more memorable and frequently mentioned topics in everyday life. Many of these negative impacts can be traced back to the decrease in biodiversity, not only in diatoms but at entire ecosystem level (see chapter below "*Biodiversity of diatoms and ecosystem services—options in the shadow of threats*"). But even in these negative events, the positive ones can be found and turned to the advantage of humanity (see paragraph below "*positive characteristics of invasive species*" or above *"CLAW hypothesis"*).

Diatoms are traditionally considered as cosmopolitan, however, it has been already questioned by some studies (e.g. Kociolek & Spaulding, 2000; Naselli-Flores & Padisák, 2016). Due to their very fast proliferation in several aquatic ecosystems, an increasing number of species can be considered invaders (e.g. Coste & Ector, 2000). They gain their foothold, change the structure of the food chain and exclude native species (Silkin et al., 2016). Generally, the hotspots of these alien diatom species are the anthropogenically impacted environments (Wilk-Woźniak & Najberek, 2013; Vidaković et al., 2016; Buczkó et al., 2022). Beside the natural, potential vectors (water current, wind, animals and humans; Kristiansen, 1996; Padisák et al., 2016) the introduction of fish species, the ship ballast waters and aquaculture practises (Edwards et al., 2001; Saber et al., 2022) can explain diatom-invasions.

Invasive species can cause huge economic (in aquacultures, fisheries, tourism) and environmental problems; they threaten human and ecosystems health (Saccà, 2015). Their massive biomass can lead to the disruption of the food web in the area, reducing the habitats of several groups of organisms (e.g. aquatic macroinvertebrates, fishes) and endangering the biodiversity of the communities living there (Bray, 2014). It results in significant and even drastic changes in ecosystems leading to changes in ecosystem functioning, trophic interaction and habitats (Chapin et al., 2000; Sala et al., 2000; Bray, 2014). The bloom of invasive diatoms and their produced mucilage (*Didymosphenia geminata* (Lyngbye) Mart. Schmidt, *Lindavia intermedia* (Manguin ex Kociolek & Reviers) Nakov, Guillory, Julius, Theriot & Alverson ex W. C. Daniels, Novis & Edlund, *Cymbella janischii* (A. W. F. Schmidt) De Toni, *Coscinodiscus wailesii* Gran & Angst) called „lake snow", block municipal and domestic water intakes, clog filters in irrigation, boat cooling systems and domestic water filters, adhere to power plant infrastructures, foul fishing nets and cages and degrade the aesthetic and recreational values of aquatic ecosystems (Laing and Gollasch, 2002; Bothwell et al., 2014; Novis et al., 2017; Rodríguez et al, 2017; Ahmmed et al., 2021; Kilroy et al., 2021; Kato-Unoki et al., 2022). Microalgae cultures used for biofuel production, carbondioxide capture and for the production of high value products are also threatened by invasive diatom species (e.g. *Phaeodactylum tricornutum* Bohlin), which survives in extreme conditions and have competitive advantages against species to be cultured (Goldman et al., 1982).

However, positive characteristics of invasive species can be found, which should be used for the benefit of the society. For example, invasive diatom species can provide a source of bioactive (chemical and nutritional) compounds in industrial applications, in this way we can reduce their populations avoiding environmental and ecological problems (Pereira et al., 2021).

Blooms, toxicity, taste- and odour compounds

In freshwaters, diatoms often form dense blooms during low-temperature periods when nutrient supply including trace elements and flow/stratification conditions are favourable (Moorhouse et al., 2018; Xia et al., 2019; Nwankwegu et al., 2020; Shen et al., 2021). Massive blooms can change the structure and functioning of the ecosystem and thus, they can have a negative impact on the entire food web and energy transport (Dodds et al., 2009). Tourism and catering industries can have serious financial losses caused by algal blooms. In addition, blooms these blooms can jeopardise water quality and drinking water supply e.g. by blocking filters of water filtration equipment (Moorhouse et al., 2018). Under-ice diatom blooms represent a natural, specialised life strategy relying on convection currents in the upper, thin, still illuminated layer of the water column (e.g. *Stephanocostis chantaica* Genkal et Kuzmina—Scheffler & Padisák, 2000; *Aulacoseira baicalensis* (K. I. Meyer) Simonsen and *A. skwortzowii* (O. Müller) Haworthe—Popovskaya et al., 2006).

Another emerging issue of water blooms is their epidemiological/toxicological significance because bloom forming algae can produce a number of compounds that have toxic effects to aquatic organisms, livestock or even humans (Bates et al., 2018; Violi et al., 2019). *Pseudo-nitzschia multiseries* (Hasle) Hasle, a marine species, was the first diatom identified as toxin producer in 1987 and caused amnesic shellfish poisoning (ASP) (Bates & Trainer, 2006; Pullido, 2008). The toxin that was responsible for the diseases and deaths that time was the domoic acids (DA). Recently, altogether 26 DA-producing diatoms are known worldwide. They are marine species, members of the genus *Pseudo-nitzschia*, usually with wide distribution (Bates et al., 2018). Although no further deaths have been reported since 1987, harmful algal blooms (HABs) of *Pseudo-nitzschia* spp. have often caused severe ecological and economic damages (Ritzman et al., 2018). Fisheries closures have resulted in direct harvest losses of fishes and shellfish and dismissal of fishermen. In addition, losses and expenses have been increased by decline in tourism, decline in sales volume of seafood industries, costs of monitoring and management, etc., and the final annual cost could reach or even exceed $83 million (Ritzman et al., 2018).

Recent studies highlighted that marine diatoms are able to produce β-methylamino-L-alanine (BMAA) and/or its isomers 2,4-diaminobutyric acid (2,4-DAB), and N-(2-aminoethyl)glycine (AEG) (Jiang et al., 2014; Révellion et al., 2015; Lage et al., 2016). Both centric and pennate diatoms identified as BMAA and/or its isomers producers were originated from algal collections all over the world (Jiang et al., 2014; Révellion et al., 2015; Lage et al., 2016) or field samples (France) (Révellion et al., 2015). These compounds are non-protein amino acids and can cause amyotrophic lateral sclerosis (ALS) in humans. Because they are able to bioaccumulate through food webs and to be aerosolized, they pose a high risk to aquatic and terrestrial organisms (Violi et al., 2019).

Until 2019, freshwater diatoms were not considered toxin producers. Violi et al. (2019), however, detected BMAA and/or its isomers in four diatom taxa isolated from Australian freshwater habitats. To the best of our knowledge, so far, this is the only study that reported toxin production by freshwater diatoms.

In addition to toxins, diatoms can also produce bioactive compounds that, at present, are not considered harmful to humans but have unpleasant taste and odour (Watson, 2003). These unpleasant odours may cause tangible costs to water, aquaculture or even food industries (Watson, 2003), while some of them have positive impacts (see paragraph above "*CLAW hypothesis*"). They may have significant interspecific interactive roles and may act as intraspecific chemical signals (Watson, 2003). Periphytic diatoms, for example, can synthesise eicosanoic fatty acid in high content, which has an allelopathic effect against the freshwater grazer, *Thamnocephalus platyurus* Packard 1867 (Jüttner, 2001). Alicyclic alkenes, which are known as pheromones in marine brown algal assemblages, are produced and released seasonally by *Halamphora veneta* (Kützing) Levkov and *Gomphonema parvulum* (Kützing) Kützing. In addition, these compounds may have toxic effects on protozoans (Watson, 2003). Some marine diatoms are able to synthesise dimethylsulphoniopropinate (DMSP), which is considered an osmolyte and/or cryoprotectant agent. The cabbage-smelling dimethylsulphide (DMS) and acrylate as the two important derivatives of DMPS, produced during cell damage (Watson, 2003). While DMS plays an important role in climate control (paragraph "*CLAW hypothesis*"), acrylate is bactericidal and toxic to micrograzers (Watson, 2003).

Many of the above-mentioned negative impacts of diatoms are the consequences of anthropogenic activities such as eutrophication, globalisation and the intensification of climate change. Dangers and nuisances caused by diatoms could be significantly reduced by living a responsible, environmentally conscious life.

Biodiversity of diatoms and ecosystem services—options in the shadow of threats

Human society, as well as human well-being and ecosystem services provided by organisms including aquatic ones strongly depends on biodiversity (Díaz et al., 2006; Naselli-Flores & Padisák, 2022; Thomaz, 2022). The present knowledge about biodiversity has been strongly biased towards large terrestrial, easily observable animals or organisms used in human activities (MEA, 2003). The knowledge of biodiversity of aquatic and subterranean biota, invertebrates or microorganisms including algae is underrepresented (MEA, 2003). Most processes, whether human-induced or of natural origin that contribute to the biodiversity loss in terrestrial areas or in macroscopic communities also affect microorganisms with diatoms among them (MEA, 2005; Bray, 2014; Reid et al., 2019). Their assemblages are directly impacted by many of the threats listed by Reid et al. (2019) including changing climate (Novais et al., 2020; Várbíró et al., 2020; Tornés et al., 2021; B-Béres et al., 2019, 2022), biological invasions (Kato-Unoki et al., 2022; Kilroy et al., 2021), harmful algal blooms (Taylor & Bothwell, 2014), emerging contaminants (Smucker & Vis, 2009), microplastic pollution (Harrison et al., 2012), freshwater salinization (Potapova & Charles, 2003) and cumulative stressors. These effects can irreversibly change composition and biodiversity of diatoms influencing ecosystem services. While it is the scientists' responsibility to provide reliable background for legislation, concrete actions to slow down biodiversity loss can be developed by policy makers or the civil society (Díaz et al., 2006). It is quite a challenge: while many global and local acts exist to protect macroscopic life (e.g. Ramsar Convention, 1971; Act of Nature Conservation, 1996; Ministerial Order, 2001), for aquatic microscopic organisms as diatoms, the Water Framework Directive (WFD; EC, 2000) is perhaps the closest to these recommendations in Europe. Although the WFD focuses more on the global ecological health of water bodies rather than directly and exclusively on the protection of biodiversity and the endangered or rare microscopic species, its objectives can provide a set of clear policy drivers to protect many of the functions that diatoms provide.

In the microscopic world it is difficult to clearly define what a rare, protected, or even invasive species is (Cantonati et al., 2022). Recognizing this difficulty, algologists made available "red lists" (Németh, 2005; Hofmann et al., 2018), which are of great help to detect the direction of floral changes. In case of microbiota, including diatoms, protection of individual specimens is impossible: only habitat protection may preserve them. Additionally, as most of the recent evaluation criteria of scientists neglect local papers describing flora of particular ecosystems such papers are increasingly rare. A refreshing exception is e.g. the one published by T-Krasznai and B-Béres (2021). In the shadow of threats to biodiversity defined by Reid et al. (2019), there is an urgent need to protect biodiversity of diatoms and maintain ecosystem services provided by these microorganisms.

Concluding remarks

In this review, we collected a number of examples how diatoms contribute to ESs defined by MEA (2003, 2005). In addition, we revealed further services not mentioned by MEA but important for human life and well-being. These services are mainly related to technological developments or indirect solutions for food demand from the population explosion. We also summarised the inconveniences caused by diatoms, but we drew attention to the possibilities of transforming these unpleasant situations to potential useful services. There is a very close, positive relationship between ecosystem services and biodiversity, therefore we briefly pointed out the threats to diatom diversity. These often interrelated and often human-induced events can trigger even irreversible processes in diatom assemblages that can upset the balance of entire ecosystems. However, the current legislations are not, or only partially suitable for protecting microscopic organisms and conserving their habitats. Habitat and diatom diversity loss may lead to a situation where certain services cannot be provided anymore. The responsibility of scientists is to draw the attention of legislators to these shortcomings and offer alternatives for appropriate acts. An additional, and perhaps the most difficult responsibility of science and scientists is to arouse public interest in diatoms and introduce them to these beautiful creatures and their "home". Maybe naively but hopefully, the education, community organisation and arts will increase people's responsibility for nature, for diatoms.

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Data availability N.A.

Declarations

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References

Abonyi, A., É. Ács, A. Hidas, I. Grigorszky, G. Várbíró, G. Borics & K. T. Kiss, 2018a. Functional diversity of phytoplankton highlights long-term gradual regime shift in the middle section of the Danube River due to global warming, human impacts and oligotrophication. Freshwater Biology 63: 456–472.

Abonyi, A., V. B-Béres & K. Buczkó, 2018b. Az Év Algája, a *Staurosirella grunowii*. Honismeret 46: 100–101.

Abonyi, A., K. T. Kiss, A. Hidas, G. Borics, G. Várbíró & É. Ács, 2020. Cell size decrease and altered size structure of phytoplankton constrain ecosystem functioning in the middle Danube River over multiple decades. Ecosystems 23: 1254–1264.

Act of Nature Conservation, 1996. Act No. LIII. of 1996 on Nature Conservation in Hungary.

Adey, W., P. Kangas & W. Mulbry, 2011. Algal Turf Scrubbing: cleaning surface waters with solar energy while producing a biofuel. Bioscience 61: 434–441.

Ahmmed, F., S. J. Fraser-Miller, P. S. Garagoda Arachchige, M. Schallenberg, P. Novis & K. C. Gordon, 2021. Lake snow caused by the invasive diatom *Lindavia intermedia* can be discriminated from different sites and from other algae using vibrational spectroscopy. Journal of Raman Spectroscopy 52: 2597.

Allen, A. E., C. L. Dupont, M. Oborník, A. Horák, A. Nunes-Nesi, J. P. McCrow, H. Zheng, D. A. Johnson, H. Hu, A. R. Fernie & C. Bowler, 2011. Evolution and metabolic significance of the urea cycle in photosynthetic diatoms. Nature 473: 203–207.

Alvain, S., C. Moulin, Y. Dandonneau & H. Loisel, 2008. Seasonal distribution and succession of dominant phytoplankton groups in the global ocean: a satellite view. Global Biogeochemical Cycles 22: GB3001.

Alverson, A. J., 2007. Strong purifying selection in the silicon transporters of marine and freshwater diatoms. Limnology and Oceanography 52: 1420–1429.

Andrade, P., J. Goff, R. Pearce, A. Cundy, D. Sear & V. Castro, 2022. Evidence for a mid-Holocene drowning from the Atacama Desert coast of Chile. Journal of Archaeological Science 140: 105565.

Apothéloz-Perret-Gentil, L., A. Cordonier, F. Straub, J. Iseli, P. Esling & J. Pawlowski, 2017. Taxonomy-free molecular diatom index for high-throughput eDNA biomonitoring. Molecular Ecology Resources 17: 1231–1242.

Ardiles, V., J. Alcocer, G. Vilaclara, L. A. Oseguera & L. Velasco, 2012. Diatom fluxes in a tropical, oligotrophic lake dominated by large-sized phytoplankton. Hydrobiologia 679: 77–90.

Arlinghaus, P., W. Zhang, A. Wrede, C. Schrum & A. Neumann, 2021. Impact of benthos on morphodynamics from a modeling perspective. Earth-Science Reviews 2021: 103803.

Armbrust, E. V., 2009. The life of diatoms in the world's oceans. Nature 459: 185–192.

Armbrust, E. V., J. A. Berges, C. Bowler, B. R. Green, D. Martinez, N. H. Putnam, S. Zhou, A. E. Allen, K. E. Apt, M. Bechner, M. A. Brzezinski, B. K. Chaal, A. Chiovitti, A. K. Davis, M. S. Demarest, J. C. Detter, T. Glavina, D. Goodstein, M. Z. Hadi, U. Hellsten, M. Hildebrand, B. D. Jenkins, J. Jurka, V. V. Kapitonov, N. Kröger, W. W. Lau, T. W. Lane, F. W. Larimer, J. C. Lippmeier, S. Lucas, M. Medina, A. Montsant, M. Obornik, M. S. Parker, B. Palenik, G. J. Pazour, P. M. Richardson, T. A. Rynearson, M. A. Saito, D. C. Schwartz, K. Thamatrakoln, K. Valentin, A. Vardi, F. P. Wilkerson & D. S. Rokhsar, 2004. The genome of the diatom *Thalassiosira pseudonana*: ecology, evolution, and metabolism. Science 306: 79–86.

B-Béres, V., B. Tóthmérész, I. Bácsi, G. Borics, A. Abonyi, K. Tapolczai, F. Rimet, A. Bouchez, G. Várbíró & P. Török, 2019. Autumn drought drives functional diversity of benthic diatom assemblages of continental intermittent streams. Advances in Water Resources 126: 129–136.

B-Béres, V., Zs. Kókai, G. Várbíró, G. Mustazhapova, Z. Csabai, B. Pernecker, G. Borics, I. Bácsi & P. Boda, 2022. Flow intermittence drives the benthic algal composition, biodiversity and diatom-based quality of small hilly streams in the Pannonian Ecoregion. Frontiers in Ecology and Evolution 127: 107782.

Bakr, H. E. G. M. M., 2010. Diatomite: its characterization, modifications and applications. Asian Journal of Materials Science 2: 121–136.

Barton, A. D., A. J. Irwin, Z. V. Finkel & C. A. Stock, 2016. Anthropogenic climate change drives shift and shuffle in North Atlantic phytoplankton communities. Proceedings of the National Academy of Sciences 113: 2964–2969.

Basile-Doelsch, I., J. D. Meunier & C. Parron, 2005. Another continental pool in the terrestrial silicon cycle. Nature 433: 399–402.

Basu, S., S. Patil, D. Mapleson, M. T. Russo, L. Vitale, C. Fevola, F. Maumus, R. Casotti, T. Mock, M. Caccamo, M. Montresor, R. Sanges & M. I. Ferrante, 2017. Finding a partner in the ocean: molecular and evolutionary bases of the response to sexual cues in a planktonic diatom. New Phytologyst 215: 140–156.

Bates, S. S. & V. L. Trainer, 2006. The ecology of harmful diatoms. In Granéli, E. & J. T. Turner (eds), Ecology of harmful algae: ecological studies (analysis and synthesis) Springer, Berlin, Heidelberg: 81–93.

Bates, S. S., K. A. Hubbard, N. Lundholm, M. Montresor & C. P. Leaw, 2018. *Pseudo-nitzschia*, *Nitzschia*, and domoic acid: new research since 2011. Harmful Algae 79: 3–43.

Battin, T. J., S. Luyssaert, L. A. Kaplan, A. K. Aufdenkampe, A. Richter & L. J. Tranvik, 2009. The boundless carbon cycle. Nature Geoscience 2: 598–600.

Benoiston, A.-S., F. M. Ibarbalz, L. Bittner, L. Guidi, O. Jahn, S. Dutkiewicz & C. Bowler, 2017. The evolution of diatoms and their biogeochemical functions. Philosophical

Transactions of the Royal Society b: Biological Sciences the Royal Society 372: 20160397.

Bininda-Emonds, O. R. P., M. Cardillo, K. E. Jones, R. D. E. MacPhee, R. M. D. Beck, R. Grenyer, S. A. Price, R. A. Vos, J. L. Gittleman & A. Purvis, 2007. The delayed rise of present-day mammals. Nature 446: 507–512.

Blatt, H., G. Middleton & R. Murray, 1972. Origin of sedimentary rocks, Prentice-Hall, Englewood Cliffs, NJ:

Blenckner, T., 2005. A conceptual model of climate-related effects on lake ecosystems. Hydrobiologia 533: 1–14.

Bopp, L., O. Aumont, P. Cadule, S. Alvain & M. Gehlen, 2005. Response of diatoms distribution to global warming and potential implications: a global model study. Geophysical Research Letters 32: L19606.

Borics, G., V. Lerf, E. T. Krasznai, I. Stanković, L. Pickó & V. B-Béres & G. Várbíró, 2021. Biovolume and surface area calculations for microalgae, using realistic 3D models. Science of the Total Environment 773: 145538.

Bothwell, M. L., B. W. Taylor & C. Kilroy, 2014. The Didymo story: the role of low dissolved phosphorus in the formation of *Didymosphenia geminata* blooms. Diatom Research 29: 229–236.

Boukhris, S., K. Athmouni, I. Hamza-Mnif, R. Siala-Elleuch, H. Ayadi, M. Nasri & A. Sellami-Kamoun, 2017. The Potential of a brown microalga cultivated in high salt medium for the production of high-value compounds. BioMed Research International 2017: 4018562.

Boyle, J., 2021. Oceans of inspiration: a marine based STEAM project. European Journal of STEM Education 6: 15.

Bozarth, A., U. G. Maier & S. Zauner, 2009. Diatoms in biotechnology: modern tools and applications. Applied Microbiology and Biotechnology 82: 195–201.

Bray, J. P. 2014. The invasion ecology of *Didymosphenia geminata*. PhD thesis, University of Canterbury.

Bruce, K., R. Blackman, S. J. Bourlat, A. M. Hellström, J. Bakker, I. Bista, K. Bohmann, A. Bouchez, R. Brys, K. Clark, V. Elbrecht, S. Fazi, V. Fonseca, B. Hänfling, F. Leese, E. Mächler, A. R. Mahon, K. Meissner, K. Panksep, J. Pawlowski, P. S. Yáñez, M. Seymour, B. Thalinger, A. Valentini, P. Woodcock, M. Traugott, V. Vasselon & K. Deiner, 2021. A practical guide to DNA-based methods for biodiversity assessment. Advanced Books Pensoft Publishers 1: e68634.

Bruckner, C. G., C. Rehm, H. P. Grossart & P. G. Kroth, 2011. Growth and release of extracellular organic compounds by benthic diatoms depend on interactions with bacteria. Environmental Microbiology 13: 1052–1063.

Bucciarelli, E. & W. G. Sunda, 2003. Influence of CO_2, nitrate, phosphate, and silicate limitation on intracellular dimethylsulfoniopropionate in batch cultures of the coastal diatom *Thalassiosira pseudonana*. Limnology and Oceanography 48: 2256–2265.

Buczkó, K., 2012. The Pantocsek diatom and photomicrograph collection from 19th to the 21st century. Beihefte zur Nova Hedwigia 141: 535–546.

Buczkó, K. & M. Rajczy, 1989. Contributions to the flora of the Hungarian caves. II. Flora of three caves near Beremend. Hungary. Studia Botanica Hungarica 21: 13–25.

Buczkó, K., Zs. Trábert, Cs. Stenger-Kovács, K. Tapolczai, T. Bíró, M. Duleba, A. Földi, J. Korponai, E. Vadkerti, Zs. Végvári & É. Ács, 2022. Rapid expansion of an aquatic invasive species (AIS) in Central-European surface waters; a case study of *Achnanthidium delmontii*. Ecological Indicators 135: 108547.

Burba, M., W.-H. Kusber & R. Jahn, 2009. Das Universum im Mikroskop—Biodiversität und Ästhetik der Diatomeen. Museums Journal 23: 82–83.

Busseni, G., L. Caputi, R. Piredda, P. Fremont, B. Hay Mele, L. Campese, E. Scalco, C. de Vargas, C. Bowler & F. d'Ovidio, 2020. Large scale patterns of marine diatom richness: drivers and trends in a changing ocean. Global Ecology and Biogeography 29: 1915–1928.

Cantonati, M., G. Hofmann, D. Spitale, M. Werum & H. Lange-Bertalot, 2022. Diatom red lists: important tools to assess and preserve biodiversity and habitats in the face of direct impacts and environmental change. Biodiversity and Conservation. https://doi.org/10.1007/s10531-021-02339-9 accessed on 23 August 2022.

Cebrian, J., 1999. Patterns in the fate of production in plant communities. The American Naturalist 154: 449–468.

Cermeño, P., 2016. The geological story of marine diatoms and the last generation of fossil fuels. Perspectives in Phycology 3: 53–60.

Chapin, F. S., III., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack & S. Diaz, 2000. Consequences of changing biodiversity. Nature 405(6783): 234–242.

Charlson, R. J., J. E. Lovelock, M. O. Andreae & S. G. Warren, 1987. Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. Nature 326: 655.

Chen, Q., C. Zhang, F. Recknagel, J. Guo & K. Blanckaert, 2014. Adaptation and multiple parameter optimization of the simulation model SALMO as prerequisite for scenario analysis on a shallow eutrophic Lake. Ecological Modelling 273: 109–116.

Conley, D. J., 2002. Terrestrial ecosystems and the global biogeochemical silica cycle. Global Biogeochemical Cycles 16: 1121.

Conley, D. J., S. S. Kilham & E. Theriot, 1989. Differences in silica content between marine and freshwater diatoms. Limnology and Oceanography 34: 205–212.

Cordier, T., L. Alonso-Sáez, L. Apothéloz-Perret-Gentil, E. Aylagas, D. A. Bohan, A. Bouchez, A. Chariton, S. Creer, L. Frühe, F. Keck, N. Keeley, O. Laroche, F. Leese, X. Pochon, T. Stoeck, J. Pawlowski & A. Lanzén, 2021. Ecosystems monitoring powered by environmental genomics: a review of current strategies with an implementation roadmap. Molecular Ecology 30: 2937–2958.

Costanza, R., R. d'Arge, R. De Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O'Neill, J. Paruelo, R. G. Raskin, P. Sutton & M. van den Belt, 1997. The value of the world's ecosystem services and natural capital. Nature 387: 253–260.

Coste, M. & L. Ector, 2000. Invasive, exotic or rare diatoms in France: main observations during the last decade. Systematics and Geography of Plants 70: 373–400.

Coutteau, P., 1996. Micro-algae. In Lavens, P. & P. Sorgeloos (eds), Manual on the production and use of live food for aquaculture FAO Fisheries, Technical Paper, Rome: 7–48.

Crabot, J., C. P. Mondy, P. Usseglio-Polatera, K. M. Fritz, P. J. Wood, M. J. Greenwood, M. T. Bogan, E. I. Meyer & T. Datry, 2021. A global perspective on the functional responses of stream communities to flow intermittence. Ecography 44: 1511–1523.

Craggs, R. J., H. W. Adey, B. K. Jessup & W. J. Oswald, 1996. A controlled stream mesocosm for tertiary treatment of sewage. Ecological Engineering 6: 149–169.

Cummins, A. B., 1975. Terra Diatomacea, Johns-Manville, Denver:

da Silva, C. F. M., L. C. Torgan & F. Schneck, 2019. Temperature and surface runoff affect the community of periphytic diatoms and have distinct effects on functional groups: evidence of a mesocosms experiment. Hydrobiologia 839: 37–50.

Dani, K. G. S. & F. Loreto, 2017. Trade-off between dimethyl sulfide and isoprene emissions from marine phytoplankton. Trends in Plants Science 22: 361–372.

Darwin, C. R., 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. London: John Murray.

Delalat, B., V. Sheppard, S. Rasi Ghaemi, S. Rao, C. A. Prestidge, G. McPhee, M.-L. Rogers, J. F. Donoghue, V. Pillay, T. G. Johns, N. Kröger & N. H. Voelcker, 2015. Targeted drug delivery using genetically engineered diatom biosilica. Nature Communication 6: 8791.

Denys, L. & H. E. I. N. de Wolf, 2001. Diatoms as indicators of coastal paleo-environments and relative sea-level change. In Smol, J. P. & E. F. Stoermer (eds), The diatoms: applications for the environmental and earth sciences Cambridge University Press, Cambridge: 277–297.

DeYoe, H. R., R. L. Lowe & J. C. Marks, 1992. Effects of nitrogen and phosphorus on the endosymbiont load of *Rhopalodia gibba* and *Epithemia turgida* (Bacillariophyceae). Journal of Phycology 28: 773–777.

Díaz, S., J. Fargione, F. S. Chapin III. & D. Tilman, 2006. Biodiversity loss threatens human well-being. PloS Biology 4: e277.

Dodds, W. K., W. W. Bouska, J. L. Eitzmann, T. J. Pilger, K. L. Pitts, A. J. Riley, J. T. Schloesser & D. J. Thornbrugh, 2009. Eutrophication of US freshwaters: analysis of potential economic damages. Environmental Science and Technology 43: 12–19.

Domergue, F., J. Lerchl, U. Zähringer & E. Heinz, 2002. Cloning and functional characterization of *Phaeodactylum tricornutum* front-end desaturases involved in eicosapentaenoic acid biosynthesis. European Journal of Biochemistry 269: 4105–4113.

Domis, L. N. D. S., W. M. Mooij & J. Huisman, 2007. Climate-induced shifts in an experimental phytoplankton community: a mechanistic approach. Hydrobiologia 584: 403–413.

Drum, R. W. & S. Pankratz, 1965. Fine structure of an unusual cytoplasmic inclusion in the diatom genus, *Rhopalodia*. Protoplasma 60: 141–149.

EC, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23rd October 2000 establishing a framework for Community action in the field of water policy. Official Journal of the European Communities, 22 December, L 327/1. European Commission, Brussels.

Edwards, M., A. W. G. John, D. G. Johns & P. Reid, 2001. Case history and persistence of the nonindigenous diatom *Coscinodiscus wailesii* in the north-east Atlantic. Journal of the Marine Biological Association of the UK 81: 207–211.

Ehrenberg, C. G., 1842. Uber die wie Kork auf Wasser schwimmenden Mauersteine der Alten Griechen und Roemer. Berichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin. 8: 132–137.

Fabris, M., J. George, U. Kuzhiumparambil, C. A. Lawson, A. C. Jaramillo-Madrid, R. M. Abbriano, C. E. Vickers & P. Ralph, 2020. Extrachromosomal genetic engineering of the marine diatom *Phaeodactylum tricornutum* enables the heterologous production of monoterpenoids. ACS Synthetic Biology 9: 598–612.

Falasco, E., L. Ector, M. Isaia, C. E. Wetzel, L. Hoffmann & F. Bona, 2014. Diatom flora in subterranean ecosystems: a review. International Journal of Speleology 43: 231–251.

Falkowski, P. G., M. E. Katz, A. H. Knoll, A. Quigg, J. A. Raven, O. Schofield & F. J. R. Taylor, 2004. The evolution of modern eukaryotic phytoplankton. Science 305: 354–360.

Falkowski, P. G., M. E. Katz, A. J. Milligan, K. Fennel, B. S. Cramer, M. P. Aubry, R. A. Berner, M. J. Novacek & W. M. Zapol, 2005. The rise of oxygen over the past 205 million years and the evolution of large placental mammals. Science American Association for the Advancement of Science 309: 2202–2204.

Feio, M. J., S. R. Q. Serra, A. Mortágua, A. Bouchez, F. Rimet, V. Vasselon & S. F. P. Almeida, 2020. A taxonomy-free approach based on machine learning to assess the quality of rivers with diatoms. Science of the Total Environment 722: 137900.

Field, C. B., M. J. Behrenfeld, J. T. Randerson & P. Falkowski, 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. Science American Association for the Advancement of Science 281: 237–240.

Flipo, N., C. Rabouille, M. Poulin, S. Even, M.-H. Tusseau-Vuillemin & M. Lalande, 2007. Primary production in headwater streams of the Seine basin: the grand Morin river case study. Science of the Total Environment 375: 98–109.

Flower, R. J., 2013. Diatom methods diatomites: their formation, distribution, and uses. In Elias, S. A. & C. J. Mork (eds), Encyclopedia of quaternary science Elsevier, Amsterdam: 501–506.

Frings, P. J., W. Clymans, E. Jeppesen, T. L. Lauridsen, E. Struyf & D. J. Conley, 2014. Lack of steady-state in the global biogeochemical Si cycle: emerging evidence from lake Si sequestration. Biogeochemistry 117: 255–277.

Frost, P. C. & J. J. Elser, 2002. Growth responses of littoral mayflies to the phosphorus content of their food. Ecology Letters 5: 232–240.

Gatenby, C. M., B. C. Parker & R. J. Neves, 1997. Growth and survival of juvenile rainbow mussels, *Villosa iris* (Bivalvia: Unionidae), reared on algal diets and sediment. American Malacological Bulletin 14: 57–66.

Gatenby, C. M., D. M. Orcutt, D. A. Kreeger, B. C. Parker, V. A. Jones & R. J. Neves, 2003. Biochemical composition of three algal species proposed as food for captive freshwater mussels. Journal of Applied Phycology 15: 1–11.

Ghobara, M. M. & A. Mohamed, 2019. Diatomite in use: occurrence, characterization, modification, and prospective trends. In Seckbach, J. & R. Gordon (eds), Diatoms—fundamentals and applications Wiley, Beverly MA: 471–510.

Glud, R. N., M. Kühl, F. Wenzhöfer & S. Rysgaard, 2002. Benthic diatoms of a high Arctic fjord (Young Sound, NE Greenland): importance for ecosystem primary production. Marine Ecology Progress Series 238: 15–29.

Goldman, J. C., J. Azov, C. B. Riley & M. R. Denett, 1982. The effect of pH in intensive microalgal cultures. I. Biomass regulation. Journal of Experimental Marine Biology and Ecology 27: 1–13.

Gordon, R. & J. Parkinson, 2005. Potential roles for diatomists in nanotechnology. Journal of Nanoscience and Nanotechnology 5: 35–40.

Gordon, R. & J. Seckbach, 2019. Diatoms: fundamentals and applications, Wiley-Scrivener, Salem, MA, Hoboken, NJ:

Gypens, N., A. V. Borges, G. Speeckaert & C. Lancelot, 2014. The dimethylsulfide cycle in the eutrophied southern North Sea: a model study integrating phytoplankton and bacterial processes. PLOS ONE 9: e85862.

Haeckel, E., 1899–1904. Kunstformen der Natur. 51 pp. + 100 Tables. Bibliographisches Institut, Leipzig.

Harrison, J. P., T. J. Hoellein, M. Sapp, A. S. Tagg, Y. Ju-Nam & J. J. Ojeda, 2012. Microplastic-associated biofilms: a comparison of freshwater and marine environments. In Wagner, M. & S. Lambert (eds), Freshwater microplastics—emerging environmental contaminants? Springer Open, Cham: 181–201.

Harwood, D. M., 2010. Diatomite. In Stoermer, E. F. & J. P. Smol (eds), The diatoms: applications for the environmental and Earth sciences Cambridge University Press: 570–574.

He, G., H. Fang, S. Bai, X. Liu, M. Chen & J. Bai, 2011. Application of a three-dimensional eutrophication model for the Beijing Guanting Reservoir, China. Ecological Modelling 222: 1491–1501.

Hofmann, G., H. Lange-Bertalot, M. Werum & R. Klee, 2018. Rote Liste und Gesamtartenliste der limnischen Kieselalgen (Bacillariophyta) Deutschlands. In Metzing, D., N. Hofbauer, G. Ludwig & G. Matzke-Hajek (eds), Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands, Band 7: Pflanzen—Naturschutz und Biologische Vielfalt, Vol. 70. Landwirtschaftsverlag, Münster: 601–708.

Hornick, L. E., J. R. Webster & E. F. Benfield, 1981. Periphyton production in an appalachian mountain trout stream. The American Midland Naturalist University of Notre Dame 106: 22–36.

Ivarsson, L. N., M. Ivarsson, J. Lundberg, T. Sallstedt & C. Rydin, 2013. Epilithic and aerophilic diatoms in the artificial environment of Kungsträdgården metro station, Stockholm, Sweden. International Journal of Speleology 42: 289–297.

Jahn, R., 2002. Otto Müller's names of diatoms (Bacillariophyceae) and extant original material at the Botanical Museum Berlin-Dahlem (B). Willdenowia 32: 155–173.

Jeffryes, C., T. Gutu, J. Jiao & G. L. Rorrer, 2008. Two-stage photobioreactor process for the metabolic insertion of nanostructured germanium into the silica microstructure of the diatom *Pinnularia* sp. Materials Science and Engineering: C 28: 107–118.

Jiang, L., J. Eriksson, S. Lage, S. Jonasson, S. Shams, M. Mehine, L. L. Ilag & U. Rasmussen, 2014. Diatoms: a novel source for the neurotoxin BMAA in aquatic environments. PLOS ONE. 9: e84578.

Justić, D., N. N. Rabalais, R. E. Turner & Q. Dortch, 1995. Changes in nutrient structure of river-dominated coastal waters: stoichiometric nutrient balance and its consequences. Estuarine, Coastal and Shelf Science 40: 339–356.

Jüttner, F., 2001. Liberation of 5,8,11,14,17-eicosapentaenoic acid and other polyunsaturated fatty acids from lipids as a grazer defense reaction in epilithic diatom biofilms. Journal of Phycology 37: 744–755.

Kagami, M., T. Miki & G. Takimoto, 2014. Mycoloop: chytrids in aquatic food webs. Frontiers in Microbiology 5: 166.

Kahlert, M., B. Bailet, T. Chonova, S. M. Karjalainen, S. C. Schneider & K. Tapolczai, 2021. Same same, but different: the response of diatoms to environmental gradients in Fennoscandian streams and lakes—barcodes, traits and microscope data compared. Ecological Indicators 130: 108088.

Komáromy, Z. s., Padisák, J. & Rajczy, M, 1985. Flora in the lamp-lit areas of the cave "Anna-barlang" near Lillafüred (Hungary). Annales Historico-Naturales Musei Nationalis Hungarici 77: 103–112.

Kaparapu, J., 2018. Application of microalgae in aquaculture. Phykos 48: 21–26.

Kato-Unoki, Y., A. Kurihara, T. Kuge, Y. Shimasaki, Y. Suzawa & S. Mayama, 2022. Genetic evidence for the invasion of *Cymbella janischii* (A. Schmidt) De Toni in Japan. BioInvasions Records. https://www.reabic.net/journals/bir/2022/2/BIR_2022_Kato-Unoki_etal.pdf accessed on 23 August 2022.

Keck, F., V. Vasselon, F. Rimet, A. Bouchez & M. Kahlert, 2018. Boosting DNA metabarcoding for biomonitoring with phylogenetic estimation of operational taxonomic units' ecological profiles. Molecular Ecology Resources 18: 1299–1309.

Keller, M. D., W. K. Bellows & R. R. L. Guillard, 1989. Dimethyl sulfide production in marine phytoplankton. In Saltzman, E. S. & W. J. Cooper (eds), Biogenic sulfur in the environment American Chemical Society, Washington DC: 167–182.

Kettle, A. J. & M. O. Andreae, 2000. Flux of dimethylsulfide from the oceans: a comparison of updated data sets and flux models. Journal of Geophysical Research: Atmospheres 105: 26793–26808.

Kettles, N. L., S. Kopriva & G. Malin, 2014. Insights into the regulation of DMSP synthesis in the diatom *Thalassiosira pseudonana* through APR activity, proteomics and gene expression analyses on cells acclimating to changes in salinity, light and nitrogen. PLOS ONE 9: e94795.

Kilroy, C., A. L. Whitehead, S. A. Wood, M. J. Vandergoes, P. Lambert & P. M. Novis, 2021. Predicting the potential distribution of the invasive freshwater diatom *Lindavia intermedia* in New Zealand lakes. Aquatic Invasions 16: 415–442.

Klemme, H. D. & G. F. Ulmishek, 1991. Effective petroleum source rocks of the world: stratigraphic distribution and controlling depositional factors1. AAPG Bulletin 75: 1809–1851.

Kociolek, J. P. & S. A. Spaulding, 2000. Freshwater diatom biogeography. Nova Hedwigia 71: 223–241.

Kranz, H., 2009. Diatomeen im 19. Jahrhundert. Typenplatten und Salonpräparate von Johann Diedrich Möller. Abhandlungen herausgegeben vom Naturwissenschaftlichen Verein zu Bremen 112: 109.

Krause, J. W. & M. W. Lomas, 2020. Understanding diatoms' past and future biogeochemical role in high-latitude seas. Geophysical Research Letters 47: e2019GL085602.

Krebs, W. N., A. Y. Gladenkov & G. D. Jones, 2010. Diatoms in oil and gas exploration. In Stoermer, E. F. & J. P. Smol (eds), The diatoms: applications for the environmental and Earth sciences Cambridge University Press, Cambridge: 523–533.

Kristiansen, J., 1996. Dispersal of freshwater algae—a review. Hydrobiologia 336: 151–157.

Kuefner, W., S. Ossyssek, J. Geist & U. Raeder, 2020. The silicification value: a novel diatom-based indicator to assess climate change in freshwater habitats. Diatom Research 35: 1–16.

Kumaran, J., B. Jose, V. Joseph & I. S. Bright Singh, 2017. Optimization of growth requirements of marine diatom *Chaetoceros muelleri* using response surface methodology. Aquaculture Research 48: 1513–1524.

Lage, S., A. Burian, U. Rasmussen, P. R. Costa, H. Annadotter, A. Godhe & S. Rydberg, 2016. BMAA extraction of cyanobacteria samples: which method to choose? Environmental Science and Pollution Research International 23: 338–350.

Laing, I. & S. Gollasch, 2002. *Coscinodiscus wailesii*—a nuisance diatom in European waters. In Leppäkoski, E., S. Gollasch & S. Olenin (eds), Invasive aquatic species of Europe: distribution, impacts and management Springer, Dordrecht: 53–55.

Lana, A., T. G. Bell, R. Simó, S. M. Vallina, J. Ballabrera-Poy, A. J. Kettle, J. Dachs, L. Bopp, E. S. Saltzman, J. Stefels, J. E. Johnson & P. S. Liss, 2011. An updated climatology of surface dimethlysulfide concentrations and emission fluxes in the global ocean. Global Biogeochemichal Cycles 25: GB1004.

Larras, F., R. Coulaud, E. Gautreau, E. Billoir, J. Rosebery & P. Usseglio-Polatera, 2017. Assessing anthropogenic pressures on streams: a random forest approach based on benthic diatom communities. Science of the Total Environment 586: 1101–1112.

Laufkötter, C., M. Vogt, N. Gruber, M. Aita-Noguchi, O. Aumont, L. Bopp, E. Buitenhuis, S. C. Doney, J. Dunne & T. Hashioka, 2015. Drivers and uncertainties of future global marine primary production in marine ecosystem models. Biogeosciences 12: 6955–6984.

Lecointe C., M. Coste & J. Prygiel, 2008. OMNIDIA version 5.2 software for diatom-based water quality assessment. CDROM.

Lengyel, E., D. Lázár, A. J. Trájer & C. Stenger-Kovács, 2020. Climate change projections for Carpathian soda pans on the basis of photosynthesis evidence from typical diatom species. Science of the Total Environment 710: 136241.

Levkov, Z., D. M. Williams, D. Nikolovska & S. Tofilovska, 2017. The use of diatoms in forensic science: advantages and limitations of the diatom test in cases of drowning. In Williams, M., T. Hill, I. Boomer & I. P. Wilkinson (eds), The archaeological and forensic applications of microfossils: a deeper understanding of human history The Micropalaeontological Society, Special Publication, Geological Society, London: 261–277.

Li, J., F. Yu, Y. Yu, L. Jiang, X. Wang, X. Yang, W. . Lü. Li & X. Sun, 2021. Photothermal diatomite/CNT combined aerogel for high-efficiency solar steam generation and wastewater purification. Solar RRL. https://doi.org/10.1002/solr.202101011 accessed on 8 March 2022.

Likens, G. E., 1975. Primary production of inland aquatic ecosystems. In Lieth, H. & R. H. Whittaker (eds), Primary productivity of the biosphere Springer, Berlin, Heidelberg: 185–202.

Litchman, E., C. Klausmeier, J. Miller, O. Schofield & P. Falkowski, 2006. Multi-nutrient, multi-group model of present and future oceanic phytoplankton communities. Biogeosciences 3: 585–606.

Lowe, R. L., B. H. Rosen & G. W. Fairchild, 1984. Endosymbiotic blue-green algae in freshwater diatoms: an advantage in nitrogen poor habitats. Journal of Phycology 20: 24.

Lukács, Á., I. Bácsi, Zs. Nemes-Kókai, G. Borics, G. Várbíró, E. T-Krasznai & V. B-Béres, 2021. Strong influence of climatic extremes on diversity of benthic algae and cyanobacteria in a lowland intermittent stream. Ecohydrology 14: e2286.

Malviya, S., E. Scalco, S. Audic, F. Vincent, A. Veluchamy, J. Poulain, P. Wincker, D. Iudicone, C. de Vargas, L. Bittner, A. Zingone & C. Bowler, 2016. Insights into global diatom distribution and diversity in the world's ocean. Proceedings of the National Academy of Sciences National Academy of Sciences 113: E1516–E1525.

Marella, T. K., N. R. Parine & A. Tiwari, 2018. Potential of diatom consortium developed by nutrient enrichment for biodiesel production and simultaneous nutrient removal from waste water. Saudi Journal of Biological Sciences 25: 704–709.

Marella, T. K., A. Datta, M. D. Patil, S. Dixit & A. Tiwari, 2019. Biodiesel production through algal cultivation in urban wastewater using algal floway. Bioresource Technology 280: 222–228.

Marella, T. K., A. Saxena & A. Tiwari, 2020a. Diatom mediated heavy metal remediation: a review. Bioresource Technology 305: 123068.

Marella, T. K., I. Y. Lopez-Pacheco, R. Parra-Saldívar, S. Dixit & A. Tiwari, 2020b. Wealth from waste: diatoms as tools for phycoremediation of wastewater and for obtaining value from the biomass. Science of the Total Environment 724: 137960.

Marella, T. K., R. Bhattacharjya & A. Tiwari, 2021. Impact of organic carbon acquisition on growth and functional biomolecule production in diatoms. Microbial Cell Factories 20: 135.

Markensten, H., K. Moore & I. Persson, 2010. Simulated lake phytoplankton composition shifts toward cyanobacteria dominance in a future warmer climate. Ecological Applications 20: 752–767.

Martin-Jézéquel, V., M. Hildebrand & M. A. Brzezinski, 2000. Silicon metabolism in diatoms: implications for growth. Journal of Phycology 36: 821–840.

Mayama, S., 2005. A novel approach to the popularization of diatomology: an exhibition of diatoms, presented as a fusion of science and art (4). Diatom 21: 61–70.

Mayer, C., M. Come, L. Ulmann, G. C. Zitelli, C. Faraloni, H. Nazih, K. Ouguerram, B. Chénias & V. Mimouni, 2019. Preventive effects of the marine microalga *Phaeodactylum tricornutum*, used as a food supplement, on risk factors associated with metabolic syndrome in wistar rats. Nutrients 11: 1069.

McCarthy, J. K., S. R. Smith, J. P. McCrow, M. Tan, H. Zheng, K. Beeri, R. Roth, C. Lichtle, U. Goodenough, C. P. Bowler, C. L. Dupont & A. E. Allen, 2017. Nitrate reductase knockout uncouples nitrate transport from nitrate assimilation and drives repartitioning of carbon flux in a model pennate diatom. Plant Cell 29: 2047–2070.

McGlynn, J., C. Dromgool-Regan & N. Burke, 2019. A hydrothermal AdVENTure—build your own unknown art and science project. Explorers planning guide for primary school teachers. Marine Institute and Tulca. https://oar.marine.ie/handle/10793/1391 accessed on 8 March 2022.

MEA 2003 Millennium Ecosystem Assessment, 2003. Ecosystems and human well-being: a framework for assessment, Island Press, Washington DC:

MEA 2005 Millennium Ecosystem Assessment, 2005. Ecosystems and human well-being: biodiversity synthesis, World Resources Institute, Washington, DC:

Mishra, M., A. P. Arukha, T. Bashir, D. Yadav & G. B. K. Prasad, 2017. All new faces of diatoms: potential source of nanomaterials and beyond. Frontiers in Microbiology 8: 1239.

Mooij, W. M., J. H. Janse, L. N. De Senerpont Domis, S. Hülsmann & B. W. Ibelings, 2007. Predicting the effect of climate change on temperate shallow lakes with the ecosystem model PC Lake. Hydrobiologia 584: 443–454.

Moorhouse, H. L., D. S. Read, S. McGowan, M. Wagner, C. Roberts, L. K. Armstrong, D. J. E. Nicholls, H. D. Wickham, M. G. Hutchins & M. J. Bowes, 2018. Characterisation of a major phytoplankton bloom in the River Thames (UK) using flow cytometry and high performance liquid chromatography. Science of the Total Environment 624: 366–376.

Morrisseau, S. & C. Voyer, 2014. Tackling invasive species using citizen science. The Green Teach 102: 15–17.

Nakayama, T., Y. Ikegami, T. Nakayama, K. Ishida, Y. Inagaki & I. Inouye, 2011. Spheroid bodies in Rhopalodiacean diatoms were derived from a single endosymbiotic cyanobacterium. Journal of Plant Research 124: 93–97.

Nalley, J. O., D. R. O'Donnell & E. Litchman, 2018. Temperature effects on growth rates and fatty acid content in freshwater algae and cyanobacteria. Algal Research 35: 500–507.

Naselli-Flores, L. & J. Padisák, 2016. Blowing in the wind: how many roads can a phytoplanktont walk down? A synthesis on phytoplankton biogeography and spatial processes. Hydrobiologia 764: 303–313.

Naselli-Flores, L. & J. Padisák, 2022. Ecosystem services provided by marine and freshwater phytoplankton. Hydrobiologia. https://doi.org/10.1007/s10750-022-04795-y accessed on 8 March 2022.

Nelson, D. M., P. Tréguer, M. A. Brzezinski, A. Leynaert & B. Quéguiner, 1995. Production and dissolution of biogenic silica in the ocean: revised global estimates, comparison with regional data and relationship to biogenic sedimentation. Global Biogeochemical Cycles 9: 359–372.

Németh, J., 2005. Red list of algae in Hungary. Acta Botanica Hungarica 47: 379–417.

Novais, M. H., E. A. Morales, A. M. Penha, A. Bouchez, A. Barthès, M. J. Costa, R. Salgado, J. Santos & M. Morais, 2020. Benthic diatom community dynamics in Mediterranean intermittent streams: effects of water availability and their potential as indicators of dry-phase ecological status. Science of the Total Environment 719: 137462.

Novis, P., C. Mitchell & A. Podolyan, 2017. *Lindavia intermedia*, the causative organism of New Zealand lake snow: relationships between New Zealand, North American and European populations according to molecular and morphological data. Landcare Research Contract Report LC2991, prepared for Otago Regional Council, Dunedin.

Nwankwegu, A. S., Y. Li, Y. Huang, J. Wei, E. Norgbey, D. Ji, Y. Pu, L. A. Nuamah, Z. Yang, Y. Jiang & H. W. Paerl, 2020. Nitrate repletion during spring bloom intensifies phytoplankton iron demand in Yangtze River tributary, China. Environmental Pollution 264: 114626.

Ministerial Order, 2001. Ministry of Environment and Water: Departmental Order 13/2001 (V.9.) on the Protected Species in Hungary.

Paasche, E., 1980. Silicon. In Morris, I. (ed), The physiological ecology of phytoplankton Blackwell, Oxford: 259–284.

Padisák, J., W. Scheffler, C. Sípos, P. Kasprzak, R. Koschel & L. Krienitz, 2003. Spatial and temporal pattern of development and decline of the spring diatom populations in Lake Stechlin in 1999. Archiv für Hydrobiologie Beiheft Advances in Limnology 58: 135–155.

Padisák, J., G. Molnár, É. Soróczki-Pintér, É. Hajnal & D. G. George, 2006. Four consecutive dry years in Lake Balaton (Hungary): consequences for phytoplankton biomass and composition. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 29: 1153–1159.

Padisák, J., É. Hajnal, L. Krienitz, J. Lakner & V. Üveges, 2010. Rarity, ecological memory, rate of floral change in phytoplankton—and the mystery of the Red Cock. Hydrobiologia 653: 45–67.

Padisák, J., G. Vasas & G. Borics, 2016. Phycogeography of freshwater phytoplankton—traditional knowledge and new molecular tools. Hydrobiologia 764: 3–27.

Pappas, J., 2014. Collecting microfossils: Diatoms as science and art. https://deepblue.lib.umich.edu/bitstream/handle/2027.42/106589/JLP-Friends%20Apr%202014%20talk%205-8-14-Annotated.pdf?sequence=1 accessed on 3 January 2022.

Park, J. B., R. J. Craggs & A. N. Shilton, 2011. Recycling algae to improve species control and harvest efficiency from a high rate algal pond. Water Research 45: 6637–6649.

Peabody, A. J. & N. G. Cameron, 2010. Forensic science and diatoms. In Smol, J. P. & E. F. Stoermer (eds), The diatoms: applications for the environmental and earth sciences Cambridge University Press, Cambridge: 534–539.

Peltomaa, E., H. Hällfors & S. J. Taipale, 2019. Comparison of diatoms and dinoflagellates from different habitats as sources of PUFAs. Marine Drugs 17: 233.

Peng, K. T., C. N. Zheng, J. Xue, X. Y. Chen, W. D. Yang, J. S. Liu, W. Bai & H. Y. Li, 2014. Delta 5 fatty acid desaturase upregulates the synthesis of polyunsaturated fatty acids in the marine diatom *Phaeodactylum tricornutum*. Journal of Agricultural and Food Chemistry 62: 8773–8776.

Pereira, A. G., M. Fraga-Corral, P. Garcia-Oliveira, C. Lourenço-Lopes, M. Carpena, M. A. Prieto & J. Simal-Gandara, 2021. The use of invasive algae species as a source of secondary metabolites and biological activities: Spain as case-study. Marine Drugs 19: 178.

Pérez-Burillo, J., R. Trobajo, M. Leira, F. Keck, F. Rimet, J. Sigró & D. G. Mann, 2021. DNA metabarcoding reveals differences in distribution patterns and ecological preferences among genetic variants within some key freshwater diatom species. Science of the Total Environment Elsevier 798: 149029.

Peters, L., 2005. Periphyton as a habitat for meiofauna : a case of a neglected community. Doctoral dissertation.

Pfister, L., C. E. Wetzel, J. Klaus, N. Martínez-Carreras, M. Antonelli, A. J. Teuling & J. J. McDonnell, 2017. Terrestrial diatoms as tracers in catchment hydrology: a review: terrestrial diatoms as tracers. Wiley Interdisciplinary Reviews: Water 4: e1241.

Pinseel, E., S. B. Janssens, E. Verleyen, P. Vanormelingen, T. J. Kohler, E. M. Biersma, K. Sabbe, B. Van de Vijver & W. Vyverman, 2020. Global radiation in a rare biosphere soil diatom. Nature Communications 11: 2382.

Pollanen, M. S., 1998. Forensic diatomology and drowning, Elsevier, Amsterdam:

Popovskaya, G. I., Y. V. Likhoshway, S. I. Genkal & A. D. Firsova, 2006. The role of endemic diatom algae in the phytoplankton of Lake Baikal. Hydrobiologia 568: 87–94.

Potapova, M. & D. F. Charles, 2003. Distribution of benthic diatoms in U.S. rivers in relation to conductivity and ionic composition. Freshwater Biology 48: 1311–1328.

Poulsen, N., C. Berne, J. Spain & N. Kröger, 2007. Silica immobilization of an enzyme via genetic engineering of the diatom *Thalassiosira pseudonana*. Angewandte Chemie International Edition 46: 1843–1846.

Pound, K. L., C. A. Larson & S. I. Passy, 2021. Current distributions and future climate-driven changes in diatoms, insects and fish in US streams. Global Ecology and Biogeography 30: 63–78.

Pullido, O. M., 2008. Domoic acid toxicologic pathology: a review. Marine Drugs 6: 180–219.

Ragni, R., S. R. Cicco, D. Vona & G. M. Farinola, 2018. Multiple routes to smart nanostructured materials from diatom microalgae: a chemical perspective. Advanced Materials 30: e1704289.

Ragueneau, O., S. Schultes, K. Bidle, P. Claquin & B. Moriceau, 2006. Si and C interactions in the world ocean: importance of ecological processes and implications for the role of diatoms in the biological pump. Global Biogeochemical Cycles 20: GB4S02.

Ramsar Convention, 1971. Convention on wetlands of international importance especially as waterfowl habitat, Ramsar.

Rastogi, A., U. Maheswari, R. G. Dorrell, F. R. J. Vieira, F. Maumus, A. Kustka, J. McCarthy, A. E. Allen, P. Kersey, C. Bowler & L. Tirichine, 2018. Integrative analysis of large scale transcriptome data draws a comprehensive landscape of *Phaeodactylum tricornutum* genome and evolutionary origin of diatoms. Scientific Reports 8: 4834.

Reid, A. J., A. K. Carlson, I. F. Creed, E. J. Eliason, P. A. Gell, P. T. J. Johnson, K. A. Kidd, T. J. MacCormack, J. D. Olden, S. J. Ormerod, J. P. Smol, W. W. Taylor, K. Tockner, J. C. Vermaire, D. Dudgeon & S. J. Cooke, 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological Reviews 94: 849–873.

Reinthal, P. N., 1990. The feeding habits of a group of herbivorous rock-dwelling cichlid fishes (Cichlidae: Perciformes) from Lake Malawi, Africa. Environmental Biology of Fishes 27: 215–233.

Réveillon, D., E. Abadie, V. Séchet, E. Masseret, P. Hess & Z. Amzil, 2015. β-N-methylamino-l-alanine (BMAA) and isomers: Distribution in different food web compartments of Thau lagoon, French Mediterranean Sea. Marine Environmental Research 110: 8–18.

Reynolds, C. S., 2006. The ecology of phytoplankton, Cambridge University Press, Cambridge:

Riato, L., J. Stoddard, P. Kaufmann, D. Peck, R. A. Hill, A. Herlihy & S. Paulsen, 2021. Genus-level, trait-based multimetric indices for diatom assessment of rivers and streams across the conterminous U.S. To be presented at Diatom Web Academy Seminar Series, N/A, Virtual, October 26, 2021.

Ritzman, J., A. Brodbeck, S. Brostrom, S. McGrew, S. Dreyer, T. Klinger & S. K. Moore, 2018. Economic and sociocultural impacts of fisheries closures in two fishing-dependent communities following the massive 2015 U.S. West Coast harmful algal bloom. Harmful Algae 80: 35–45.

Rodríguez, D., J. Morales, F. Flechoso, J. A. Sánchez, A. Negro & M. Lizana, 2017. On the distribution and general abundance of non-native species associated with the Ebro River (Castejón, Navarra, NE Spain). Russian Journal of Biological Invasions 8: 189–196.

Round, F. E., R. M. Crawford & D. G. Mann, 1990. The diatoms: biology & morphology of the genera, Cambridge University Press, New York:

Sabater, S., X. Timoner, C. Borrego & V. Acuña, 2016. Stream biofilm responses to flow intermittency: from cells to ecosystems. Frontiers in Environmental Sciences 4: 14.

Saber, A. A., A. Borrini, H. Saber, M. El-Sheekh, A. A. Gontcharov & M. Cantonati, 2022. A marine invasive benthic diatom species [*Licmophora normaniana* (Greville) Wahrer, 1985] in an inland oasis mineral spring in Egypt. BioInvasions Records 11: 13–22.

Saccà, A., 2015. Invasive aquatic microorganisms: patterns of introduction and impacts. In Waterman, R. (ed), Biological invasions Nova Science Publishers Inc: 1–37.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge,

H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Syke, B. H. Walker, M. Walker & D. H. Wall, 2000. Global biodiversity scenarios for the year 2100. Science 287: 1770–1774.

Saleh, N. E., R. F. Ismail, A.E.-D.H. Sayed, E. H. Zaghloul & H. Saleh, 2020. Comprehensive assessment of benthic diatom (*Amphora coffeaeformis*) as a feed additive in Nile tilapia (*Oreochromis niloticus*) diet. Aquaculture Research 51: 3506–3519.

Salmaso, N., L. Naselli-Flores & J. Padisák, 2015. Functional classifications and their application in phytoplankton ecology. Freshwater Biology 60: 603–619.

Sánchez, M. L., P. Rodríguez, A. M. Torremorell, I. Izaguirre & H. Pizarro, 2017. Phytoplankton and periphyton primary production in clear and turbid shallow lakes: influence of the light environment on the interactions between these communities. Wetlands 37: 67–77.

Scheffler, W. & J. Padisák, 2000. *Stephanocostis chantaicus* (Bacillariophyceae): morphology and population dynamics of a rare centric diatom growing in winter under ice in the oligotrophic Lake Stechlin, Germany. Algological Studies 133: 49–69.

Selmeczy, G. B., A. Abonyi, L. Krienitz, P. Kasprzak, P. Casper, A. Telcs, Z. Somogyvári & J. Padisák, 2019. Old sins have long shadows: climate change weakens efficiency of trophic coupling of phyto-and zooplankton in a deep oligo-mesotrophic lowland lake (Stechlin, Germany)—a causality analysis. Hydrobiologia 831: 101–117.

Sharma, N., D. P. Simon, A. M. Diaz-Garza, E. Fantino, A. Messaabi, F. Meddeb-Mouelhi, H. Germain & I. Desgagné-Penix, 2021. Diatoms biotechnology: various industrial applications for a greener tomorrow. Frontiers in Marine Science 8: 636613.

Shen, L., M. Dou, R. Xia, G. Li & B. Yang, 2021. Effects of hydrological change on the risk of riverine algal blooms: case study in the mid-downstream of the Han River. China Environmental Science and Pollution Research 28: 19851–19865.

Sheppard, V. C., A. Scheffel, N. Poulsen & N. Kröger, 2012. Live diatom silica immobilization of multimeric and redox-active enzymes. Applied and Environmental Microbiology 78: 211–218.

Silkin, V. A., A. I. Abakumov, L. A. Pautova, S. V. Pakhomova & A. V. Lifanchuk, 2016. Mechanisms of regulation of invasive processes in phytoplankton on the example of the north-eastern part of the Black Sea. Aquatic Ecology 50: 221–234.

Sims, P. A., D. G. Mann & L. K. Medlin, 2006. Evolution of the diatoms: insights from fossil, biological and molecular data. Phycologia 45: 361–402.

Singh, D., R. Carlson, D. Fell & M. Poolman, 2015. Modelling metabolism of the diatom *Phaeodactylum tricornutum*. Biochemical Society Transactions 43: 1182–1186.

Smucker, N. J. & M. L. Vis, 2009. Use of diatoms to assess agricultural and coal mining impacts on streams and a multiassemblage case study. Journal of the North American Benthological Society 28: 659–675.

Soininen, J., 2007. Environmental and spatial control of freshwater diatoms—a review. Diatom Research 22: 473–490.

Sommer, U., R. Adrian, L. De Senerpont Domis, J. J. Elser, U. Gaedke, B. Ibelings, E. Jeppesen, M. Lürling, J. C. Molinero, W. M. Mooij, E. van Donk & M. Winder, 2012. Beyond the plankton ecology group (PEG) model: mechanisms driving plankton succession. Annual Review of Ecology, Evolution, and Systematics 43: 429–448.

Spaulding, S. A., I. W. Bishop, M. B. Edlund, S. Lee, P. Furey, E. Jovanovska & M. Potapova, 2022. Diatoms of North America. Retrieved 3rd January 2022, from https://diatoms.org. accessed on 3 January 2022.

Spolaore, P., C. Joannis-Cassan, E. Duran & A. Isambert, 2006. Commercial applications of microalgae. Journal of Bioscience and Bioengineering 101: 87–96.

Sriram, G., M. Kigga, U. T. Uthappa, R. M. Rego, V. Thendral, T. Kumeria, J. Ho-Young & M. D. Kurkuri, 2020. Naturally available diatomite and their surface modification for the removal of hazardous dye and metal ions: a review. Advances in Colloid and Interface Science 282: 102198.

Stancheva, R. & R. Lowe, 2019. Diatom symbioses with other photoautotroph. In Seckbach, J. & R. Gordon (eds), Diatoms—fundamentals and applications Wiley, Beverly MA: 225–244.

Stancheva, R., R. G. Sheath, B. A. Read, K. D. McArthur, C. Schroepfer, J. P. Kociolek & A. E. Fetscher, 2013. Nitrogen-fixing cyanobacteria (free-living and diatom endosymbionts): their use in southern California stream bioassessment. Hydrobiologia 720: 111–127.

Stenger-Kovács, C., E. Lengyel, L. O. Crossetti & V: Üveges, J. Padisák, 2012. Diatom ecological guilds as indicators of temporally changing stressors and disturbances in the small Torna-stream, Hungary. Ecological Indicators 24: 138–147.

Stenger-Kovács, C., K. Körmendi, E. Lengyel, A. Abonyi, É. Hajnal, B. Szabó, K. Buczkó & J. Padisák, 2018. Expanding the trait-based concept of benthic diatoms: development of trait- and species-based indices for conductivity as the master variable of ecological status in continental saline lakes. Ecological Indicators 95: 63–74.

Sterrenburg, F. A. S. & H. De Wolf, 2004. The Kinker diatom collection: discovery—exploration—exploitation. In Winkler Prins, C. F. & S. K. Donovan (eds), VII International Symposium Cultural Heritage in Geosciences, Mining and Metallurgy: Libraries—Archives—Museums: Museums and their collections, Leiden (The Netherlands). Scripta Geologica Special Issue 4: 253–260.

Stevenson, R. J., M. L. Bothwell, R. L. Lowe & J. H. Thorp, 1996. Algal ecology: freshwater benthic ecosystem, Academic Press:

Struyf, E., A. Smis, S. Van Damme, P. Meire & D. J. Conley, 2009. The global biogeochemical silicon cycle. Silicon 1: 207–213.

Sun, J., D. A. Hutchins, Y. Feng, E. L. Seubert, D. A. Caron & F.-X. Fu, 2011. Effects of changing pCO_2 and phosphate availability on domoic acid production and physiology of the marine harmful bloom diatom *Pseudo-nitzschia multiseries*. Limnology and Oceanography 56: 829–840.

Tapolczai, K., F. Keck, A. Bouchez, F. Rimet, M. Kahlert & V. Vasselon, 2019. Diatom DNA metabarcoding for biomonitoring: Strategies to avoid major taxonomical and bioinformatical biases limiting molecular indices capacities. Frontiers in Ecology and Evolution 7: 409.

Tapolczai, K., G. B. Selmeczy, B. Szabó, V. Béres, F. Keck, A. Bouchez, F. Rimet & J. Padisák, 2021. The potential of exact sequence variants (ESVs) to interpret and assess the impact of agricultural pressure on stream diatom assemblages revealed by DNA metabarcoding. Ecological Indicators 122: 107322.

Taylor, B. W. & M. L. Bothwell, 2014. The origin of invasive microorganisms matters for science, policy, and management: the case of *Didymosphenia geminata*. Bioscience 64: 531–537.

Tesson, B., S. J. L. Lerch & M. Hildebrand, 2017. Characterization of a new protein family associated with the silica deposition vesicle membrane enables genetic manipulation of diatom silica. Scientific Reports 7: 13457.

Thomaz, S. M., 2022. Ecosystem services provided by freshwater macrophytes. Hydrobiologia. https://doi.org/10.1007/s10750-021-04739-y accessed on 3 January 2022.

Tiffany, M. A. & S. S. Nagy, 2019. The beauty of diatoms. In Seckbach, J. & R. Gordon (eds), Diatoms—fundamentals and applications Wiley, Beverly MA: 33–42.

T-Krasznai, E. & V. B-Béres, 2021. Rarely mentioned species in Hungary: can we step into the same lake? Biologia 76: 1661–1673.

Tong, C. Y. & C. J. C. Derek, 2021. Biofilm formation of benthic diatoms on commercial polyvinylidene fluoride membrane. Algal Research 55: 102260.

Tornés, E., M. Colls, V. Acuña & S. Sabater, 2021. Duration of water flow interruption drives the structure and functional diversity of stream benthic diatoms. Science of the Total Environment 770: 144675.

Tranvik, L. J., J. A. Downing, J. B. Cotner, S. A. Loiselle, R. G. Striegl, T. J. Ballatore, P. Dillon, K. Finlay, K. Fortino, L. B. Knoll, P. L. Kortelainen, T. Kutser, S. Larsen, I. Laurion, D. M. Leech, S. L. McCallister, D. M. McKnight, J. M. Melack, E. Overholt, J. A. Porter, Y. Prairie, W. H. Renwick, F. Roland, B. S. Sherman, D. W. Schindler, S. Sobek, A. Tremblay, M. J. Vanni, A. M. Verschoor, E. von Wachenfeldt & G. A. Weyhenmeyer, 2009. Lakes and reservoirs as regulators of carbon cycling and climate. Limnology and Oceanography 54: 2298–2314.

Tréguer, P., D. M. Nelson, A. J. Van Bennekom, D. J. DeMaster, A. Leynaert & B. Quéguiner, 1995. The silica balance in the world ocean: a reestimate. Science American Association for the Advancement of Science 268: 375–379.

Trolle, D., D. P. Hamilton, C. A. Pilditch, I. C. Duggan & E. Jeppesen, 2011. Predicting the effects of climate change on trophic status of three morphologically varying lakes: implications for lake restoration and management. Environmental Modelling & Software 26: 354–370.

Uitz, J., H. Claustre, B. Gentili & D. Stramski, 2010. Phytoplankton class-specific primary production in the world's oceans: seasonal and interannual variability from satellite observations. Global Biogeochemical Cycles 24: GB3016.

Üveges, V., J. Padisák, L. Vörös & A. W. Kovács, 2011. Primary production of epipsammic algal communities in Lake Balaton (Hungary). Hydrobiologia 660: 17–27.

Vadeboncoeur, Y. & M. E. Power, 2017. Attached algae: the cryptic base of inverted trophic pyramids in freshwaters. Annual Review of Ecology, Evolution, and Systematics 48: 255–279.

Vadeboncoeur, Y. & A. D. Steinman, 2002. Periphyton function in lake ecosystems. The Scientific World Journal 2: 1449–1468.

Vaish, A., T. Grossmann & A. Woodward, 2008. Not all emotions are created equal: The negativity bias in social-emotional development. Psychological Bulletin 134: 383–403.

van Dam, H., A. Mertens & J. Sinkeldam, 1994. A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. Netherland Journal of Aquatic Ecology 28: 117–133.

Van den Wyngaert, S., L. Ganzert, K. Seto, K. Rojas-Jimenez, R. Agha, S. A. Berger, J. Woodhouse, J. Padisák, C. Wurzbacher, M. Kagami & H.-P. Grossart, 2022. Seasonality of parasitic and saprotrophic zoosporic fungi: linking sequence data to ecological traits. ISME Journal. https://doi.org/10.1038/s41396-022-01267-y accessed on 9 June 2022.

Várbíró, G., G. Borics, M. H. Novais, M. M. Morais, F. Rimet, A. Bouchez, K. Tapolczai, I. Bácsi, P. Usseglio-Polatera & V. B-Béres, 2020. Environmental filtering and limiting similarity as main forces driving diatom community structure in Mediterranean and continental temporary and perennial streams. Science of the Total Environment 741: 140459.

Vidaković, D., J. Krizmanić, G. Subakov-Simić & V. Karadžić, 2016. Distribution of invasive species *Actinocyclus normanii* (Hemidiscaceae, Bacillariophyta) in Serbia. Studia Botanica Hungarica 47: 201–212.

Villanova, V. & C. Spetea, 2021. Mixotrophy in diatoms: molecular mechanism and industrial potential. Physiologia Plantarum 173: 603–611.

Vinayak, V. & S. Gautam, 2019. Diatoms in forensics: a molecular approach to diatom testing in forensic science. In Seckbach, J. & R. Gordon (eds), Diatoms: fundamentals and applications Wiley, Beverly, MA: 435–470.

Violi, J. P., J. A. Facey, S. M. Mitrovic, A. Colville & K. J. Rodgers, 2019. Production of β-methylamino-L-alanine (BMAA) and its isomers by freshwater diatoms. Toxins 11: 512.

Watanabe, Y., T. Kadono, N. Kira, K. Suzuki, O. Iwata, K. Ohnishi, H. Yamaguchi & M. Adachi, 2018. Development of endogenous promoters that drive high-level expression of introduced genes in the model diatom *Phaeodactylum tricornutum*. Marine Genomics 42: 41–48.

Watson, S., 2003. Cyanobacterial and eukaryotic algal odour compounds: signals or by-products? A review of their biological activity. Phycologia 42: 335–350.

web1 https://www.millenniumassessment.org/en/History.html accessed on 8 March 2022.

web2 http://teebweb.org/about/approach/ accessed on 8 March 2022.

web3 https://www.lga.sa.gov.au/about-lga/what-we-do/community-wastewater-management-systems/high-rate-algal-ponds-hrap accessed on 8 March 2022.

web4 https://hydromentia.com/ accessed on 8 March 2022.

web5 https://pubs.usgs.gov/periodicals/mcs2021/mcs2021-diatomite.pdf accessed on 8 March 2022.

web6 https://en.wikipedia.org/wiki/Diatomaceous_earth accessed on 8 March 2022.

web7 https://en.wikipedia.org/wiki/Ernst_Haeckel accessed on 8 March 2022.

web8 https://www.youtube.com/watch?v=qxkbSk--EUY accessed on 8 March 2022.

web9 https://diatoms.org/news/whoa-there-are-diatoms-on-postage-stamps accessed on 8 March 2022.

web10 https://en.wikipedia.org/wiki/Urban_Hydrology accessed on 8 March 2022.

web11 https://www.maartenvandeneynde.com/?rd_news=1153&lang=en accessed on 8 March 2022.

web12 https://pandorina.org/ accessed on 8 March 2022.

web13 https://diatoms.org/ accessed on 8 March 2022.

web14 https://diatoms.org/news/diatom-web-academy-22 accessed on 8 March 2022.

web15 https://isdr.org/about-dom/ accessed on 8 March 2022.

web16 https://www.dbg-phykologie.de/en/alga-of-the-year accessed on 8 March 2022.

web17 https://www.mediastorehouse.com/dmcs-search.html?find=diatom accessed on 8 March 2022.

Wilk-Woźniak, E. & K. Najberek, 2013. Towards clarifying the presence of alien algae in inland waters—can we predict places of their occurrence? Biologia 68: 838–844.

Wilson, S. E., B. F. Cumming & J. P. Smol, 1994. Diatom-salinity relationships in 111 lakes from the Interior Plateau of British Columbia, Canada: the development of diatom-based models for paleosalinity reconstructions. Journal of Paleolimnology 12: 197–221.

Wynne, M. J. & M. B. Edlund, 2019. Micro-algae on postage stamps. Phycological Newsletter 55: 19–22.

Xia, R., Y. Zhang, G. Wang, Y. Zhang, M. Dou, X. Hou, Y. Qiao, Q. Wang & Z. Yang, 2019. Multi-factor identification and modelling analyses for managing large river algal blooms. Environmental Pollution 254: 113056.

Yang, Y., C. Stenger-Kovács, J. Padisák & K. Pettersson, 2016. Effects of winter severity on spring phytoplankton development in a temperate lake (Lake Erken, Sweden). Hydrobiologia 780: 47–57.

Yool, A. & T. Tyrrell, 2003. Role of diatoms in regulating the ocean's silicon cycle. Global Biogeochemical Cycles 17: 1103.

Zahajská, P., S. Opfergelt, S. Fritz, J. Stadmark & D. Conley, 2020. What is diatomite? Quaternary Research 96: 48–52.