



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).

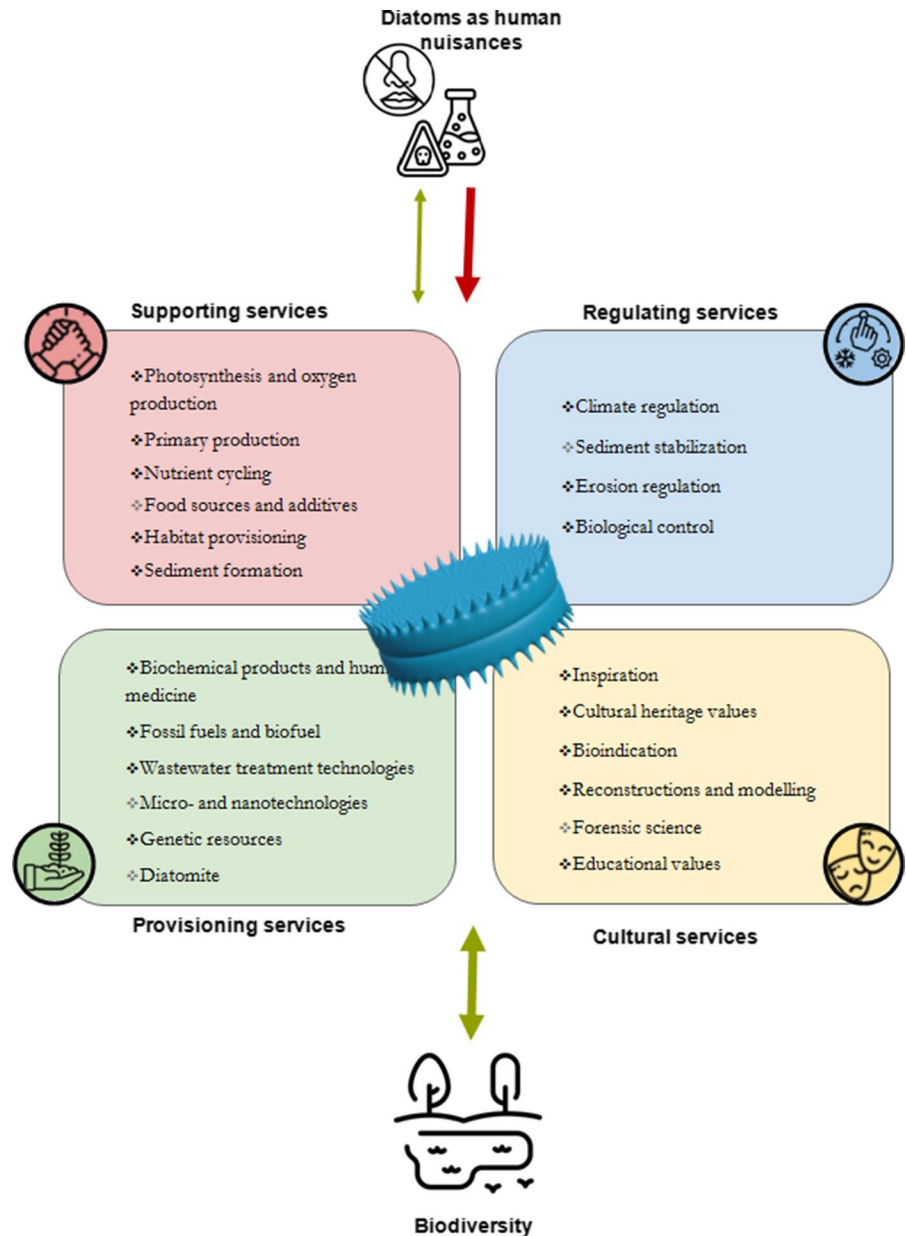
As Charles Darwin wrote, jewellery-like diatoms are one of the most beautiful microscopic creatures in the World. But what is the real value of these organisms for society and how can they serve human well-being? Since our society is driven by economics, there is a need to estimate the monetary value 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* *Diademsis 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 brevisrostris* 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 O₂ in the Eocene and Oligocene (Falkowski et al., 2004; Naselli-Flores & Padišák, 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 & Padišák, 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

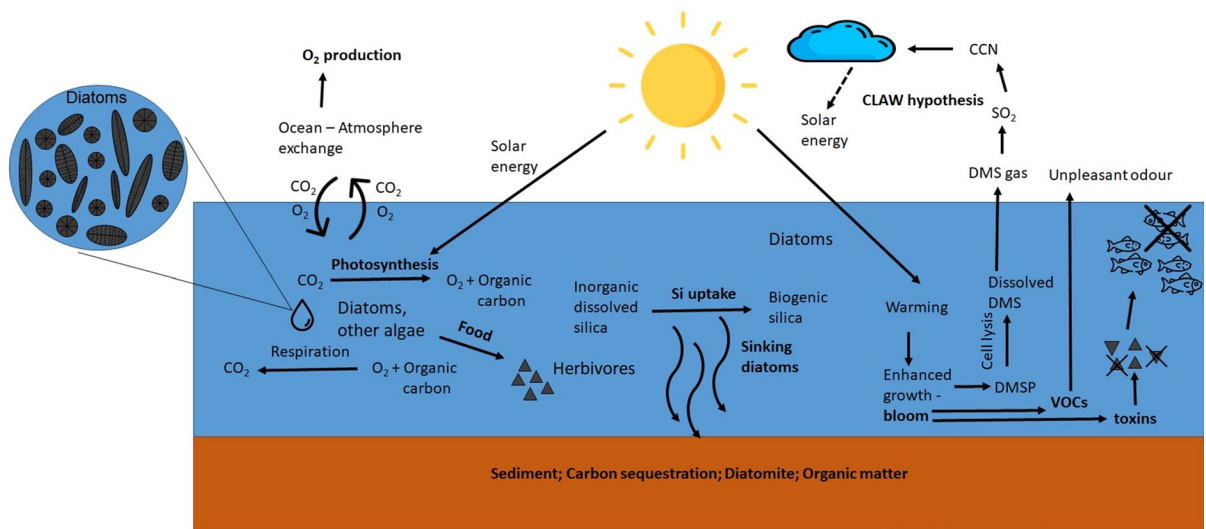


Fig. 2 Supporting and regulating services provided by marine diatoms and some of their negative impacts. Abbreviations: *CNN* cloud condensation nuclei; *DMS* dimethylsulphide; *DMSP* dimethylsulphoniopropionate; *VOCs* volatile organic

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 is 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 protoplasts from the epilimnion. As a consequence, 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; Selmečzy 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, fueling 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 mid-size rivers (Vadeboncoeur & Power, 2017). Since diatoms are rich in polyunsaturated fatty acids (PUFAs), docosahexaenoic acid (DHA) as well as long-chain eicosapentaenoic 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 chytrid 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

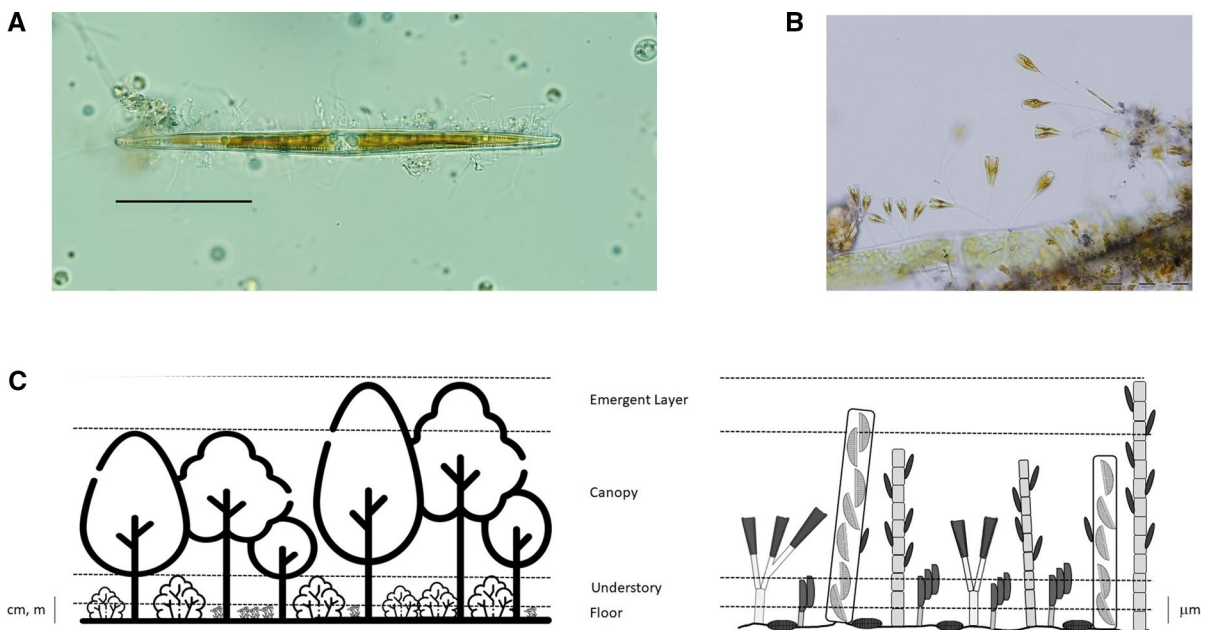


Fig. 3 Supporting and regulating services provided by diatoms: habitats for microorganisms as bacteria (**a**, **b**) or even other diatoms (**b**). Photos by Enikő Török-Krasznai (**a**) and

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 endosymbiotic relationship affects higher trophic levels such as aquatic insects, whose abundance may multiply in habitats with high biomass of endosymbiotic *Epi-themia* 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 O₂ production and carbon fixation are always coupled with O₂ 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 dimethylsulphoniopropionate (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 *Phaeodactylum tricorutum* 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. tricorutum* 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—Buczko, 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).

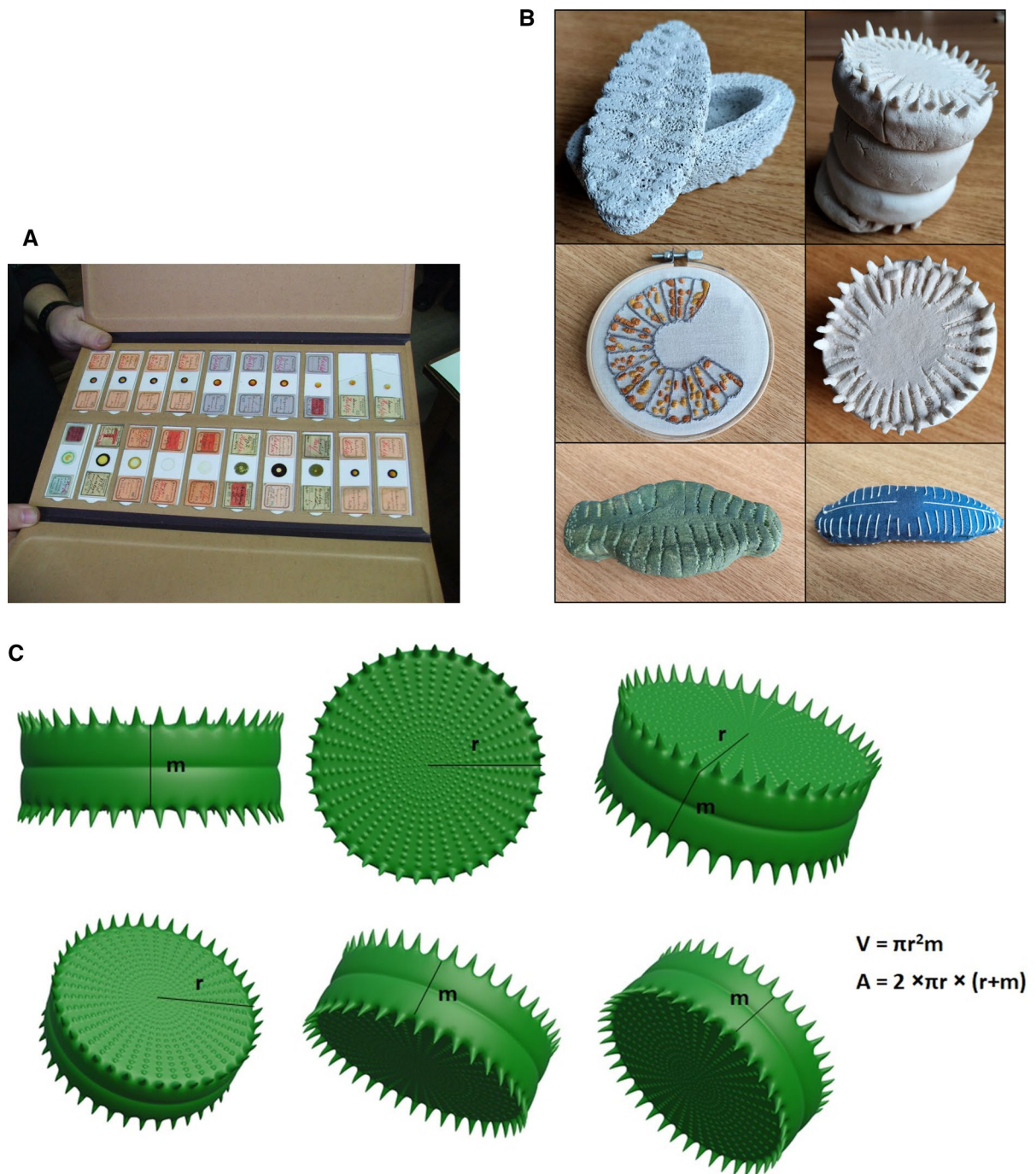


Fig. 4 Cultural services provided by diatoms: A small piece from the Pantocsek' collection (a). The photo was taken by Gábor Kiss in 2012 during a visit to the Botanical Department of the Hungarian Natural History Museum organised by the Algology Forum; Diatom models made for the algology course by undergraduate 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 micro-organisms 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 & Padišák, 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; Padišák 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 & Reviere) Nakov, Guillory, Julius, Theriot & Alverson ex W. C. Daniels, Novis & Edlund, *Cymbella janischii* (A. W. F. Schmidt) De Toni, *Coscinodiscus walesii* 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, carbon-dioxide 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 & Padišák, 2000; *Aulacoseira baicalensis* (K. I. Meyer) Simonsen and *A. skwortzowii* (O. Müller) Haworth—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 multiseriata* (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 dimethylsulphoniopropionate (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 & Padišák, 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 under-represented (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; Vár-bíró 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

Conflict of interest Judit Padisák is an associate editor of the *Hydrobiologia*, moreover guest editor for this (“Ecosystem services”) special volume. She most not access the process during proceeding this paper.

Ethical approval N.A.

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