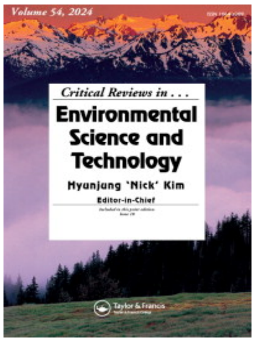

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Harnessing the power of tidal flat diatoms to combat climate change

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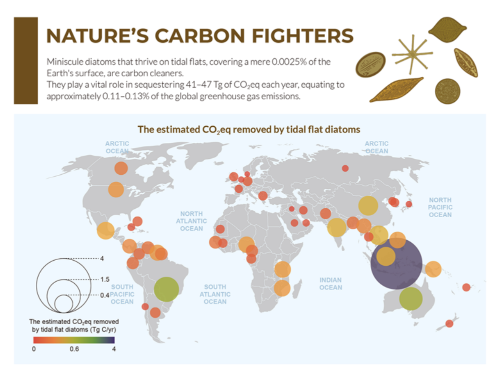
ABSTRACT

In approximately one decade, global temperatures will likely exceed a warming level that a United Nations Intergovernmental Panel on Climate Change report considers a “red alert for humanity”. We propose exploring tidal flat diatoms to address climate change challenges. Tidal flats are extensive coastal ecosystems crucial to the provisioning and regulation of aquatic environments. Diatoms contribute to tidal flat biomass production and account for 20% of global primary productivity and 40% of annual marine biomass production, making them crucial for nutrient cycling and sediment stabilization. Potential CO_2 removal from Korean tidal flats by diatoms is estimated to be 598,457–683,171 t CO_2 equivalents (CO_2e) annually, with the economic value of blue carbon (BC) resulting from diatom activity being approximately US$ 17.95–20.50 million. Dissemination of this potential could incentivize coastal wetland protection and climate change mitigation measures. The global estimated CO_2e removal potential of tidal flat diatoms is 40,957,346–46,754,961 t CO_2e, representing 0.11–0.13% of the annual global greenhouse gas emissions, even though tidal flats cover 0.0025% of the Earth’s surface and diatoms represent less than 0.5% (by weight) of all photosynthetic plants. Researchers should combine ecology and economics to develop standardized approaches for carbon input monitoring and quantification. Further, spatiotemporal analyses of environmental threats to tidal flat diatoms are necessary for conserving their biodiversity and function as a critical BC source. Land-based cultivation for large-scale biomass production and biorefinery processes can contribute to a greener, more prosperous future for humanity and the marine ecosystems upon which we rely.



NATURE’S CARBON FIGHTERS

Miniscule diatoms that thrive on tidal flats, covering a mere 0.0025% of the Earth's surface, are carbon cleaners.
They play a vital role in sequestering 41–47 Tg of CO_2eq each year, equating to approximately 0.11–0.13% of the global greenhouse gas emissions.

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KEYWORDS Blue carbon; carbon capture; climate change; conservation; diatoms; tidal flats

HANDLING EDITORS Hongbo Li and Scott Bradford

1. Introduction

The continued acceleration in hydrocarbon consumption, on which the global economy depends, has led to annual emissions of approximately 40 Gt CO_2 into the atmosphere, contributing to climate change (Friedlingstein et al., 2019). To address this issue, the 2018 Intergovernmental Panel on Climate Change (IPCC) Special Report stated that CO_2 emissions must fall to 0 between 2045 and 2080 to limit the global temperature increase to 1.5–2 °C, which was agreed upon at the Paris Climate Summit of 2015 (IPCC, 2018). However, global temperatures have risen by 1.2 °C, close to the 1.5 °C threshold, leading to more frequent and intense extreme weather events and climate disasters resulting in economic losses. For instance, over the past 30 years, temperatures in Europe have risen faster than on any other continent (World Meteorological Organization), and the European Union (EU) has lost approximately €145 billion within a decade owing to climate change-related events (Eurostat). Furthermore, despite the unprecedented reduction in human activity in 2020 because of the COVID-19 pandemic, CO_2 emissions decreased only slightly (Le Quéré et al., 2020). Therefore, the global average temperature is projected to increase by 1.4–5.8 °C by 2100, highlighting the urgent need to address climate change.

Oceans and seas offer many resources, such as food, energy, and minerals, whose use in various sectors has recently increased (Barbiet, 2023; OECD, 2016). As such, the Organization for Economic Co-operation and Development (OECD) has identified the oceans as the next great economic frontier, given that they offer opportunities for economic growth, employment, and innovation (OECD, 2016). Over the past two decades, several emerging marine economy sectors have gained prominence for their potential to address climate change, including blue carbon (BC) sequestration, marine energy, and biotechnology (Feng et al., 2023). These sectors offer training and employment opportunities and provide a tool for mitigating climate change issues, making their use vital (Feng et al., 2023; Macreadie et al., 2019).

Diatoms, prominent eukaryotic phototrophs inhabiting the global oceans, manifest as exceptionally successful and diverse taxa of paramount ecological importance. Serving as integral constituents of the marine trophic hierarchy and exhibiting a substantial role in oceanic carbon sequestration, diatoms epitomize crucial biogeochemical contributors. Their commendable photosynthetic capacity, enabling the fixation of an annual carbon quantum ranging between 10 and 20 gigatonnes (GtC), is facilitated by their intricate CO_2 concentration mechanisms (CCMs).

Operational within the confines of the euphotic layer, a consequential fraction of diatom-produced organic matter, ranging from 0.1% to 1%, undergoes particulate precipitation. This process instigates the efficacious translocation of surface-bound carbon to the depths of the ocean, thereby effectuating and enduring sequestration of atmospheric CO_2. This sequestration mechanism extends over protracted temporal scales, persisting for millennia. Residual organic matter not engaged in sequestration undergoes remineralization *via* respiratory processes.

Thus, diatoms, pivotal for the prolonged extrication of CO_2 from the carbon cycle, have emerged as substantive contributors to the perpetuation of the ecological equilibrium over extended periods of time, a phenomenon substantiated by the empirical findings articulated in Friedlingstein et al. (2020).

2. Potential value of diatoms

The role of photosynthetic organisms in mitigating CO_2 emissions has gained increasing attention, making them a potential sustainable tool to combat climate change. The Amazon rainforest is a prime example of the ecological services such organisms can provide by filtering and reprocessing harmful CO_2 emissions. Among photosynthetic organisms, microalgae have shown exceptional efficiency in CO_2 sequestration. Because of their energy-saving structures, they can fix CO_2 using solar energy 10–50 times more efficiently than terrestrial plants (Subashchandrabose et al., 2013). Furthermore, microalgae do not require arable land and can be cultivated on marginal lands, deserts, brackish water, or the open ocean, avoiding competition with agricultural land and food crop resources. They can also utilize CO_2 from flue gases containing pollutants from power plants and remediate nitrates, phosphates, and heavy metals in tertiary wastewater (Escapa et al., 2015). However, selecting suitable algae strains is crucial for successful CO_2 sequestration. The ideal strain should have a rapid productivity cycle, high photosynthetic efficiency, and elevated CO_2 tolerance. Further, it should be able to grow in a wide temperature range and have limited nutrient requirements while providing valuable byproducts.

Among microalgae, diatoms have particularly drawn interest owing to their ubiquitous presence in all aquatic environments and high growth rates in nutrient-rich environments. They are single-celled microalgae enclosed within silica walls and the most widely distributed organisms within tidal flat ecosystems. Diatoms are key contributors to primary production, nutrient cycling, and sediment stabilization, accounting for 20% of global carbon sequestration and 40% of marine biomass production, trapping substantial amounts of CO_2 (Smetacek, 1999). This may be related to diatom carbon-concentrating and -fixing systems that evolved when CO_2 levels were eight times higher than they are today. At the time, diatoms may have influenced environmental conditions by rapidly increasing their abundance, leading to a substantial reduction in atmospheric CO_2 and facilitating global cooling during the Eocene (Guidry et al., 2007; Rabosky & Sorhannus, 2009). Therefore, diatoms play a critical role in marine biological carbon pumps (Tréguer et al., 2018), with evidence suggesting that they can sequester more carbon than other algae owing to their C4 photosynthetic pathway (Sethi et al., 2020). This pathway actively increases the CO_2 concentration around the primary photosynthetic carboxylase, thus being at least 60 times more efficient than the more common C3 pathway (Giordano et al., 2005; Osborne & Sack, 2012; Roberts et al., 2007). However, despite these advantages over other algal groups, the CO_2 sequestration mechanisms of diatoms have not been widely investigated to date (Roberts et al., 2007; Sethi et al., 2020). Specifically, studies regarding the extent to which diatoms contribute to carbon export vary between diatom species, shell thickness, and life strategies; changes in diatom diversity and life cycle as well as their interactions with warmer and more acidic marine environments need to be fully understood to assess their contribution to biological pumps.

In addition to their CO_2 sequestration potential, diatoms have attracted increasing attention as a source of bioactive compounds and fine chemicals for industrial applications (Figure 1) (Hussein & Abdullah, 2020; Maher et al., 2018; Sardo et al., 2021; Vinayak et al., 2015). They are rich in minerals, fatty acids, proteins, flavonoids, and polysaccharides with anticancer, antioxidant, and antibacterial properties (Hussein & Abdullah, 2020; Kuppusamy et al., 2017), and their unique biology can be exploited to produce biopharmaceuticals, including recombinant proteins, antibodies, and vaccine antigens. Furthermore, diatom cells have silica walls with nano-pores and silica nano-spheres, which could produce absorbents, mineral filters, abrasives, and anticaking agents (Hussein & Abdullah, 2020; Kuppusamy et al., 2017). Despite their limitations concerning *in vivo* use, recent developments in diatom engineering have laid the foundation for their application in drug delivery (Phogat et al., 2021). Consequently, diatoms have been increasingly used in the pharmaceutical industry (e.g., immunotherapy, biosensing, and pharmaceutical production), and diatom feedstocks are promising renewable candidates for developing value-added bioproducts that form part of a sustainable bioeconomy.

3. Potential CO_2 constraint by South Korean tidal flat diatoms

The tidal flat system in South Korea accounts for 2,500 km^2 of the tidal wetlands of the Yellow Sea (~2,100 km^2 of its western coast and 400 km^2 of its southern coast). Moreover, along with

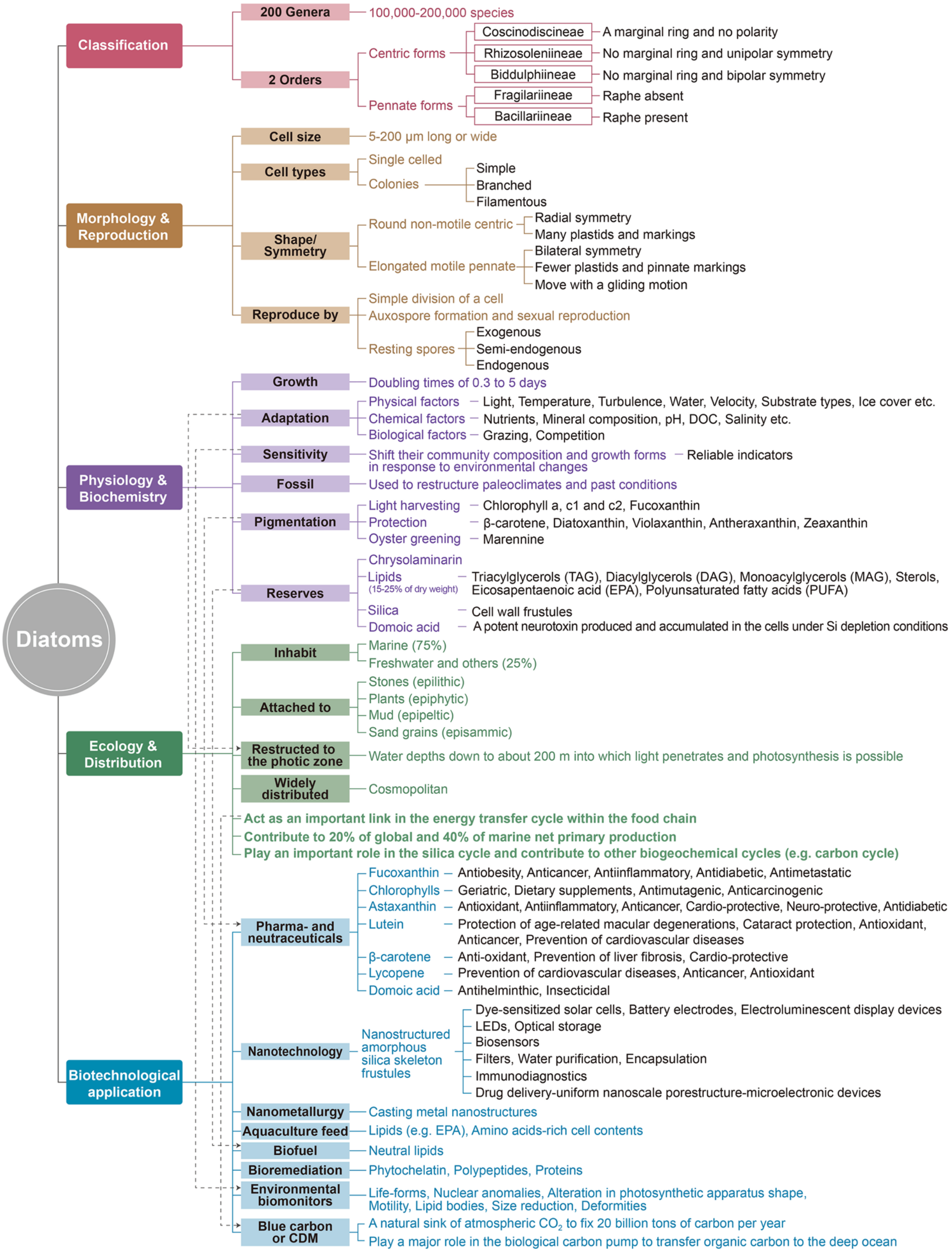
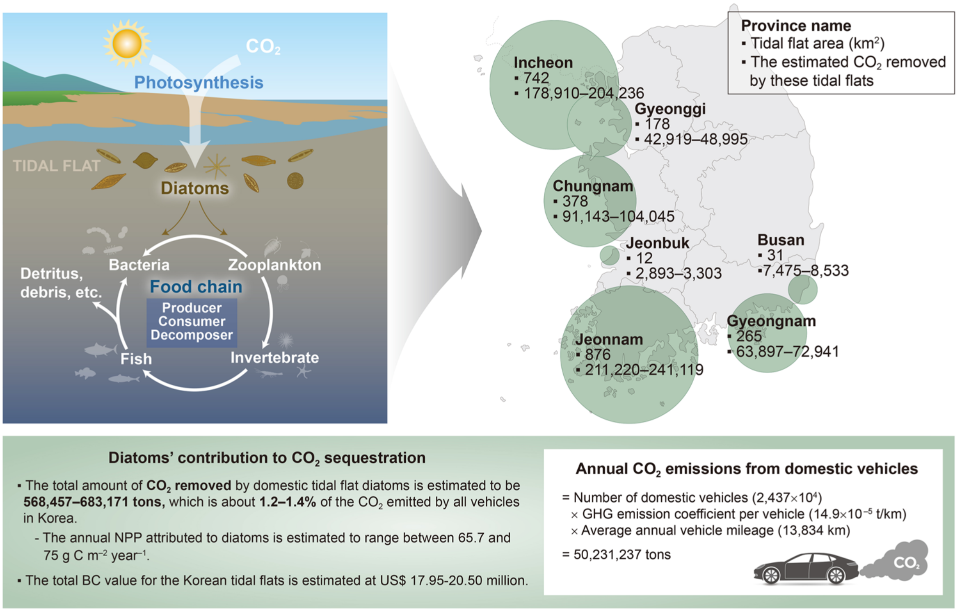


Figure 1. Mind map of diatoms for climate change mitigation. This overview highlights key characteristics of diatoms, including ecological diversity, biotechnology applications, taxonomy (morphology and reproduction), and physiology and biochemistry, to illustrate the overall characteristics of diatoms as our potential allies in climate change mitigation.

those on the eastern coast of the United States (5,918 km^2; Xu & Liu, 2023) and Canada (2,794 km^2; Rabinowitz & Andrews, 2022), the west coast of the North Sea (Wadden Sea, 11,500 km^2; Common Wadden Sea Secretariat, 2016), and the Amazon estuary (mangroves, 10,710 km^2; Kauffman et al., 2018), it is one of the most important tidal flat ecosystems globally.

Tidal flats are primarily dominated by microalgae, as highlighted by Chen and Lee in 2022. Additionally, diatoms play a significant role, constituting 40% of marine primary productivity and contributing 75% to coastal primary productivity, as indicated by Nelson et al. (1995). Lin



Diatoms' contribution to CO_2 sequestration

- The total amount of **CO_2 removed** by domestic tidal flat diatoms is estimated to be **568,457–683,171 tons,** which is about **1.2–1.4%** of the CO_2 emitted by all vehicles in Korea.
  - The annual NPP attributed to diatoms is estimated to range between 65.7 and 75 g C m^{-2} $year^{-1}$.
- The total BC value for the Korean tidal flats is estimated at US$ 17.95-20.50 million.

Annual CO_2 emissions from domestic vehicles

= Number of domestic vehicles ($2,437\times10^4$)
× GHG emission coefficient per vehicle (14.9×10^{-5} t/km)
× Average annual vehicle mileage (13,834 km)
= 50,231,237 tons

Figure 2. Sequestration and natural storage of CO_2 by diatoms based on theoretical calculations. The maximum daily NPP of tidal flat diatoms leads to two annual CO_2 equivalent (CO_2e) removal estimates for Korean tidal flats: 163,067 or 186,150 tons of carbon. Applying a global conversion, the prospective CO_2 sequestration potential of these diatoms ranges from 598,457 to 683,171 tons of CO_2e. In economic terms, based on a carbon market price of US$30 per ton in 2023, the estimated cumulative economic value of the biological carbon is between US$17.95 million and US$20.50 million.

et al. (2020) reported an average maximum daily net primary productivity (NPP) of 87.6 g C $m^{-2}yr^{-1}$ in tidal flats across a latitudinal gradient. Moreover, Charpy-Roubaud and Sournia (1990) measured the total diatom primary production in shallow ocean waters globally to be approximately 100 g C $m^{-2}yr^{-1}$.

In this context, the computed maximum daily NPP for tidal flat diatoms is either 65.7 (87.6×0.75) or 75 (100×0.75) g C $m^{-2}yr^{-1}$. To determine the annual estimated CO_2e removal potential of diatoms in Korean tidal flats, their NPP was multiplied by each tidal flat area, as illustrated in Figure 2. The total annual estimated CO_2e removal potential of diatoms in Korean tidal flats was then calculated to be either 163,067 tons C yr^{-1} (assuming 65.7 g C $m^{-2}yr^{-1}$) or 186,150 tons C yr^{-1} (assuming 75 g C $m^{-2}yr^{-1}$).

Applying a molecular weight ratio of 3.67, reflecting the molecular weight ratio of CO_2 to C, the prospective global CO_2 sequestration potential of tidal flat diatoms was determined to be either 598,457 or 683,171 tons CO_2e. To translate this ecological potential into economic terms, the average carbon market price of US$ 30 per ton of CO_2e in 2023 was considered, and the cumulative economic value of biological carbon resulting from diatom activity in Korean tidal flats was estimated at US$ 17.95 million or US$ 20.50 million. This high economic potential can be disseminated to incentivize coastal wetland conservation and climate change mitigation efforts.

4. Carbon credits for CO_2 sequestration by tidal flat diatoms

The Paris climate agreement paved the way for the creation of a global carbon market where credits for reducing or avoiding greenhouse gas emissions can be bought and sold. Since then, carbon markets have become one of the most widely used tools in the fight against climate change, and by 2021, trading had increased by 164%, reaching EUR 760 billion (USD 897 billion). As such, although the Paris climate agreement is highly technical, it could be of great importance to developing countries that contribute little to global greenhouse gas emissions but bear the brunt of climate change. In this regard, developing countries with extensive tidal flats could be major beneficiaries; in return for protecting their environment, they could receive carbon credits that other governments and businesses, often in higher-income countries, can purchase. This way, developing countries could tap into the global carbon market and use the profits to transition to the use of renewable energy to further develop their growing economies while simultaneously funding efforts to adapt to the economic damage resulting from climate change.

Covering approximately 127,921 km^2 of the Earth's surface, extensive tidal flat ecosystems have been documented by Murray in 2019. Latitudinal variations in carbon accumulation within the top few meters of tidal flat sediments have been observed, with Chen and Lee (2022) reporting carbon accumulation rates of 3.29: 1.95: 1.00: 0.52: 0.57: 0.41 in the latitudinal bands of 0–10°, 10–20°, 20–30°, 30–40°, 40–50°, and 50–60°, respectively (Figure 3).

To calculate the annual estimated CO_2e removal potential of diatoms in global tidal flats, the NPP of tidal flat diatoms was multiplied by each tidal flat area within individual longitudinal ranges (10° increments), factoring in the corresponding carbon accumulation rates. Summed, this yielded the total annual global estimated CO_2e removal potential of diatoms in tidal flat sediments—11,160,040 tons C yr^{-1} (assuming the NPP = 65.7 g C $m^{-2} yr^{-1}$) or 12,739,772 tons C yr^{-1} (assuming the NPP = 75 g C $m^{-2} yr^{-1}$). This estimate represents 0.11–0.13% of the annual global greenhouse gas emissions (37 Gt). Thus, despite all tidal flats globally covering only 0.0025% of the Earth's surface and diatoms comprising less than 0.5% (by weight) of all photosynthetic plants worldwide, their impact on global carbon sequestration is noteworthy (Figure 3). Figure 4 shows the theoretical pathways for carbon sequestration by diatoms in the tidal flat and in the ocean, based on existing information on carbon fluxes from the global diatom NPP. Although diatoms clearly contribute to carbon sequestration, further studies are required to clarify the large carbon export fluxes, including carbon export from tidal flats to surrounding waters and then to the open ocean.

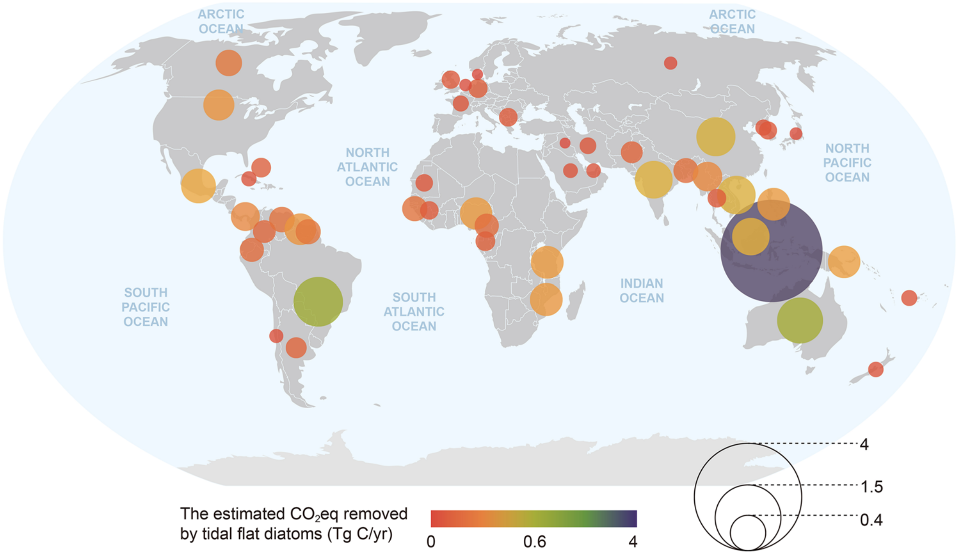


Figure 3. Theoretical estimation of CO_2 sequestration and natural storage by tidal flat diatoms globally. To estimate the global CO_2 equivalent (CO_2e) removal by tidal flat diatoms, the NPP was multiplied by the tidal flat area while factoring in their carbon accumulation ratios. The total annual estimate ranges from 11,160,040–12,739,772 tons C yr^{-1}, constituting 0.11–0.13% of the global greenhouse gas emissions despite tidal flats covering only 0.0025% of Earth's surface and diatoms being less than 0.5% of global photosynthetic plants by weight.

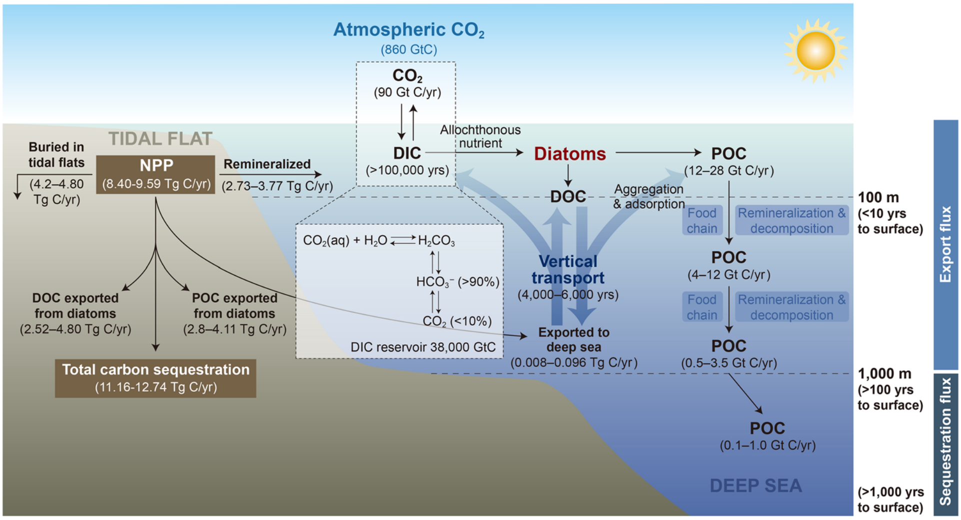


Figure 4. Schematic of the marine carbon cycle and role of marine diatoms. To calculate the annual estimated CO_2e removal potential of tidal flat diatoms globally, we multiplied their NPP by the tidal flat area within each longitudinal range (10° increments) and then the corresponding carbon accumulation rate. The sum was expressed as the total annual global estimated CO_2e removal potential of tidal flat diatoms globally, namely, 11,160,040 ton C yr^{-1} (assuming the NPP = 65.7 g C m^{-2} yr^{-1}) or 12,739,772 ton C yr^{-1} (assuming the NPP = 75 g C m^{-2} yr^{-1}). Our calculations of the NPP, carbon removal potential, POC, DOC, remineralization, and buried carbon amount were based on the literature (please see Supplementary Information 1). DOC, dissolved organic carbon; DIC, dissolved inorganic carbon; NPP, net primary productivity; POC, particulate organic carbon.

5. Challenges for integrating diatoms into the BC system

Diatoms, crucial components of marine ecosystems, play a pivotal role in marine food chains and contribute to the sequestration of atmospheric CO_2, akin to the Amazon rainforest. They are estimated to be responsible for approximately 40% of exported organic matter that sinks to depths exceeding 1,000 m, where it can persist for centuries, thereby significantly contributing to long-term planetary-scale CO_2 reduction (Hill et al., 2015; Tréguer et al., 2018; Trevathan-Tackett et al., 2015) (Figure 4). Furthermore, diatoms function as carbon donors by supplying particulate organic carbon (POC) to BC ecosystems, facilitating effective carbon sequestration.

Nevertheless, the complete integration of diatoms into the BC paradigm faces several substantial challenges. Specifically, these encompass the documentation of carbon sequestration beyond BC habitats, the tracking of carbon back to its source habitats, and the demonstration of habitat-level management strategies that can enhance sequestration within sinks (Macreadie et al., 2019). Quantifying inputs of organic matter and distinguishing between external (allochthonous) and local (autochthonous) organic carbon sources present further significant hurdles. This complexity arises from policy frameworks, such as the Verified Carbon Standard Methodology VM0033, which restrict the allocation of offset credits for allochthonous organic carbon because of the potential duplication of carbon sequestration gains that might have already been accounted for in adjacent ecosystems (Cox et al., 2012).

Coastal systems store substantial amounts of carbon in their sediments that is either locally produced (autochthonous) or coming from elsewhere (allochthonous) through tidal and fluvial transport and atmospheric deposition (Duarte et al., 2013; Hayes et al., 2017). Allochthonous carbon can contribute significantly to the growth of different trophic levels of the receiving habitats (Garcia et al., 2019; Polis et al., 1997). Almost half of the world's buried organic carbon is of allochthonous origin (Duarte et al., 2013; Temmink et al., 2022). Therefore, it can be hypothesized that separating blue carbon ecosystems (BCEs) into autochthonous and allochthonous environments would allow more accurate prediction of their organic carbon accumulation potential, which could better inform the development of coastal management strategies to conserve BCEs (Macreadie et al., 2019). However, the relative importance of autochthonous vs. allochthonous carbon inputs to the coastal carbon budget is difficult to determine. Moreover, the magnitude of organic carbon preservation is constrained by nitrogen (N) and phosphorus (P) limitations in response to climate and anthropogenic changes (Li et al., 2023). Data are still lacking to examine the responses of global sediment N or P to organic carbon accumulation in salt marshes, mangroves, and seagrasses. More importantly, the respective fractions of buried organic carbon and nutrients remain largely unconstrained (Deegan et al., 2012; Reef et al., 2010), limiting our ability to quantitatively predict organic carbon accumulation potentials. In the future, assessing how nutrient limitation patterns regulate organic carbon stocks requires an understanding of the tradeoffs between accumulation and fluvial transit.

It is known that coastal salt marshes store up to 1,700 g $m^{-2} yr^{-1}$ of organic carbon, making them one of the most carbon-rich environments on Earth (Mcleod et al., 2011). Half of all marine carbon sequestration occurs in wetlands, although they represent only 0.2% of the area available for marine carbon sequestration (Duarte et al., 2013). Due to the high amount of stored carbon, coastal marshes are considered BCEs, leading to intensive studies of marsh carbon burial rates over the past few decades (Chmura et al., 2003; Duarte et al., 2005; Mcleod et al., 2011; Ouyang & Lee, 2014). On the other hand, although salt marsh plants are likely to be the main contributors to this carbon pool, algae may be a significant source of organic carbon in salt marsh sediments. Indeed, stable carbon isotope values of marsh sediments indicate that a major source of carbon in the sediments may originate from planktonic or benthic photosynthetic microorganisms (Middelburg et al., 1997). In addition, stable isotopes have identified biofilms as an important source of carbon in salt marsh food webs (Galván et al., 2008; Johnson et al., 2019; Lee et al., 2021; Nelson et al., 2019).

Microphytobenthos, or biofilms, have been suggested to be an important contributor to carbon storage in marsh systems (Connor et al., 2001). Furthermore, while marsh productivity is often driven by plants, gross primary production by biofilms can be similar to that of plants. It is noteworthy that diatoms are a major component of microphytobenthos, and that the net primary production of biofilms can be greater than 90% of their gross primary production (Pomeroy, 1959), suggesting that most of the carbon produced by biofilms is not respired but available for decomposition, transfer to other trophic levels, or burial. Although the organic matter produced by biofilms, particularly extracellular polymeric substances (EPS), is relatively labile compared to marsh plants (McKew et al., 2011), the sheer volume of carbon produced by the rapid turnover rate of these microorganisms can contribute significantly to the carbon pool of marsh sediments. In marshes, biofilms are either degraded by heterotrophic bacteria, buried, resuspended, or consumed by other organisms (Middelburg et al., 2000). Furthermore, biofilms can be a CO_2 sink on the sediment surface, suggesting that they can accumulate carbon (Chen et al., 2019). Notably, biofilms that are rapidly buried may decompose more slowly in an anaerobic environment than at the surface, allowing for greater carbon storage.

In tidal flats, benthic diatoms (epiphyte, epipelon, and epipsammon) are considered autochthonous, whereas typical marine and freshwater diatoms are considered allochthonous. Analysis of diatom composition, total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), and carbon isotopic signatures ($\delta^{13}C$) indicated that the carbon stored in intertidal flats was predominantly autochthonous. Further, the TOC content of the sediment was significantly correlated with the relative abundance of diatoms (El-Hacen et al., 2022).

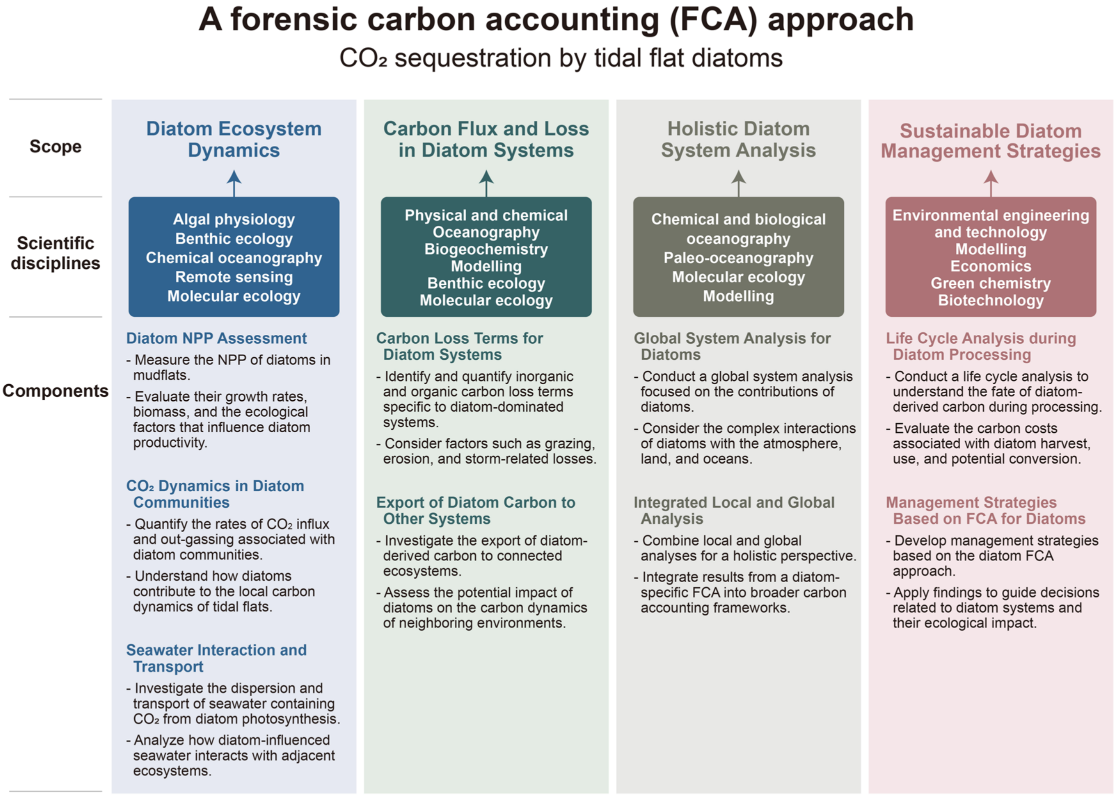
It is estimated that the total (photoautotrophic) primary production globally is 104.9 Pg C yr^{-1}. Much of the organic carbon buried in marine sediments originates from photosynthetic activity in the terrestrial (NPP = 56.4 Pg C yr^{-1}) or marine biosphere (NPP = 48.5 Pg C yr^{-1}) (Field et al., 1998). The proportion of organic carbon of marine origin in marine sediments globally is, therefore, 46.2%. Diatoms account for 40% of total global marine primary carbon production, of which benthic diatoms are the most species-rich and abundant, forming a major component of the microphytobenthos on sediments (Evrard et al., 2012; Lohrer et al., 2004; Snoeijs-Leijonmalm et al., 2017). Benthic diatoms can, therefore, contribute up to 86.6% (40/46.2) of the organic carbon sequestration in marine sediments and are likely central to this CO_2 removal process. However, determining the extent of the diatoms' contributions to carbon storage and export is demanding, necessitating the identification and classification of diatom species based on morphological traits, next-generation sequencing, and carbon export analysis utilizing high-throughput DNA databases (Tréguer et al., 2018).

The existing assumptions regarding the fate of POC in oceanic systems, where it sinks into the deep sea, must be reevaluated within the context of tidal flats. In tidal flat environments, diatoms experience regular mixing because of currents and tides, leading to the resuspension or burial of a portion of the biomass (De Jonge, 1985). Additionally, tidal flats exhibit low rates of organic matter decomposition because of reduced oxygen availability and salinity, resulting in the accumulation of organic matter in sediments (Pendleton et al., 2012). These phenomena should be considered when investigating the destiny and recycling of organic matter in tidal flat systems.

Similar to seaweeds, tidal diatoms hold untapped potential in climate change mitigation but accurately quantifying their CO_2 removal potential is difficult. To address this issue, we propose the adoption of the forensic carbon accounting (FCA) approach, which has been successfully applied to seaweed (Hurd et al., 2022), to assess their CO_2 removal potential and the distribution of the sequestered carbon. The FCA approach for diatoms entails the strategic integration of physical, biogeochemical, biological, ecological, and mathematical methodologies on both local and global scales. This comprehensive approach is designed to predict the fate and function of diatoms, serving as a robust foundation for developing management strategies related to carbon credits or offset initiatives. By utilizing FCA, we can systematically and accurately assess the amount of CO_2 removed and the distribution of carbon sequestered by diatoms in tidal flats, similar to its successful application for studies of seaweed.

Further, integration into the BC system is vital, necessitating future research initiatives within an international and multidisciplinary consortium. The focus should encompass tidal flat diatom ecosystem dynamics, diatom carbon flux and loss in tidal flat systems, holistic diatom system analyses, and sustainable diatom management strategies. Such a comprehensive approach can aim to fill existing research gaps and pave the way for effective tidal diatom-based climate change mitigation strategies (Table 1).

Table 1. Forensic Carbon Accounting (FCA): An approach for assessing diatoms' CO_2 removal potential and carbon distribution.



A forensic carbon accounting (FCA) approach

CO_2 sequestration by tidal flat diatoms

Scope	Diatom Ecosystem Dynamics	Carbon Flux and Loss in Diatom Systems	Holistic Diatom System Analysis	Sustainable Diatom Management Strategies
Scientific disciplines	Algal physiology Benthic ecology Chemical oceanography Remote sensing Molecular ecology	Physical and chemical Oceanography Biogeochemistry Modelling Benthic ecology Molecular ecology	Chemical and biological oceanography Paleo-oceanography Molecular ecology Modelling	Environmental engineering and technology Modelling Economics Green chemistry Biotechnology
Components	Diatom NPP Assessment - Measure the NPP of diatoms in mudflats. - Evaluate their growth rates, biomass, and the ecological factors that influence diatom productivity. CO_2 Dynamics in Diatom Communities - Quantify the rates of CO_2 influx and out-gassing associated with diatom communities. - Understand how diatoms contribute to the local carbon dynamics of tidal flats. Seawater Interaction and Transport - Investigate the dispersion and transport of seawater containing CO_2 from diatom photosynthesis. - Analyze how diatom-influenced seawater interacts with adjacent ecosystems.	Carbon Loss Terms for Diatom Systems - Identify and quantify inorganic and organic carbon loss terms specific to diatom-dominated systems. - Consider factors such as grazing, erosion, and storm-related losses. Export of Diatom Carbon to Other Systems - Investigate the export of diatom-derived carbon to connected ecosystems. - Assess the potential impact of diatoms on the carbon dynamics of neighboring environments.	Global System Analysis for Diatoms - Conduct a global system analysis focused on the contributions of diatoms. - Consider the complex interactions of diatoms with the atmosphere, land, and oceans. Integrated Local and Global Analysis - Combine local and global analyses for a holistic perspective. - Integrate results from a diatom-specific FCA into broader carbon accounting frameworks.	Life Cycle Analysis during Diatom Processing - Conduct a life cycle analysis to understand the fate of diatom-derived carbon during processing. - Evaluate the carbon costs associated with diatom harvest, use, and potential conversion. Management Strategies Based on FCA for Diatoms - Develop management strategies based on the diatom FCA approach. - Apply findings to guide decisions related to diatom systems and their ecological impact.

6. Prospects: Monitoring and conservation

Since 1984, there has been a notable 16.02% decline in bare tidal flats, indicating a potential global loss exceeding 20,000 km^2 (Murray et al., 2019). This reduction raises concerns about the carbon sequestration capacity of intertidal zones, which is expected to further decline by at least 13.10 Tg C yr^{-1} if vegetated habitats continue to transition into unvegetated mudflats, a decrease equivalent to 1% of global carbon emissions resulting from land use changes (Lin et al., 2020).

The significance of any changes in carbon sequestration within tidal flats extends to the global carbon budget due to the global coverage of such habitats. Unfortunately, tidal flats are currently overlooked in global carbon budget models, resulting in a substantial gap in our understanding (Lin et al., 2020). Addressing this oversight is crucial, as a comprehensive understanding of the carbon sequestration in tidal flat areas would provide valuable insights for the wider scientific community. Further, in the context of escalating human impacts and climate change threats, there is an urgent need to quantify the carbon sequestration capacity of tidal flat diatoms and investigate the factors that regulate it.

We pose that human intervention to artificially boost the carbon sequestration potential of tidal flat diatoms is unwarranted except when required to ensure the health and maintenance of their natural activity, particularly photosynthesis. This cautious approach is based on historical precedents that highlight the potential unforeseen consequences that can occur when human intervention disrupts delicate ecological balances, such as the case of the Kaibab deer in Arizona from 1907 to 1939 and the Nile perch in Lake Victoria during the 1950s. Given the potential role of tidal flat diatoms in global carbon management, prioritizing conservation efforts and implementing effective management practices is essential for maintaining and restoring the biodiversity and ecological functions of diatom-rich tidal flats. To optimize the carbon sequestration potential of diatoms, it is crucial to protect their habitats—tidal flats—from the escalating impacts of climate change and pollution (Chen & Lee, 2022).

One of the most practical and cost-effective strategies for marine conservation may be the establishment of marine-protected areas (MPAs), where five key characteristics (being a no-take zone, well-enforced, well-established (≥ 10 years old), large (≥ 100 km^2), and isolated) have been shown to provide the greatest conservation benefits (Edgar et al., 2014). The proactive creation of small MPAs by local people offers a practical way to sustainably manage their natural resources while enhancing their potential to adapt to climate change, independent of global, national, or regional targets. Combining these bottom-up approaches with large, partially protected MPAs established together with local communities can yield both local and global benefits. Encouraging and supporting, such approaches through legal, financial, and social incentives, are crucial for their upscaling to achieve regional and global impacts, aligning with national and international climate change adaptation and mitigation commitments.

A multi-purpose monitoring system based on a combination of satellite technology and field surveys is also necessary for the effective conservation of tidal flats (Figure 5). The problem of distinguishing diatoms from other photosynthetic organisms in tidal flats can be addressed using Sentinel-2 MSI data, which contain additional spectral bands that allow for the distinction between benthic diatoms and other algae at a high spatial resolution of 10 m (Daggers et al., 2018). Further, diatom photosynthetic activity as an indirect estimate of carbon sequestration can be estimated from satellite-based chlorophyll data, which is generally based on the empirical relationship with the normalized difference vegetation index (Daggers et al., 2018; Kromkamp et al., 2006; Van der Wal et al., 2008).

Satellite data should be calibrated using field campaigns because benthic diatoms on intertidal tidal flats usually disappear at the end of emersion and either become buried or reappear through resuspension by incoming tides (Consalvey et al., 2004; Easley et al., 2005). For a more accurate estimation of benthic photosynthetic activity, information on diatom biomass (mg chlorophyll *a* m^{-2}) must be combined with an estimate of tidal zone emersion times, light availability, and

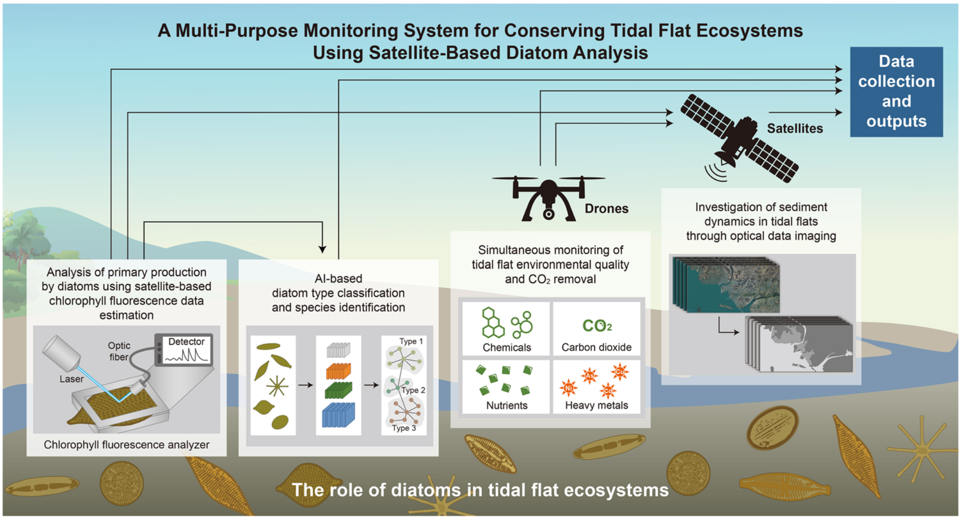


Figure 5. Satellite-based diatom analysis for multi-purpose tidal flat monitoring.

temperature (Daggers et al., 2018). Here, automated sensors on platforms, buoys, or gliders can provide data on many such factors, including meteorological variables, tidal amplitude, wave height, currents, turbidity, conductivity, temperature, salinity, nutrient concentration, and biomass with high temporal resolution (Eide & Westad, 2018).

Notably, several variables can be measured to estimate the photosynthetic carbon fixation of diatoms, including inorganic ^{14}C radiotracer fixation (Nielsen, 1952), O_2 evolution (Delieu & Walker, 1972; Pomeroy, 1959; Qlark, 1956), and variable chlorophyll fluorescence (Papageorgiou, 2004). Of these, variable chlorophyll fluorescence-based measurements of photosynthetic activity are most commonly used because they are noninvasive, allow for repeated measurements of the same sample, and enable rapid assessment of a range of photosynthetic parameters. A previous study reported a strong correlation between ^{14}C incorporation and chlorophyll fluorescence in the diatom *Coscinodiscus granii* (Trampe et al., 2015). Such *in situ* fluorometry-based measurements are also consistent with optical remote sensing-based production rates (Daggers et al., 2018). Therefore, chlorophyll *a* fluorescence measurements appear to be a novel, ideal baseline and a suitable monitoring method for estimating the primary production of tidal flat diatoms.

Stable isotopes such as ^{13}C,^{15}N, and ^{34}S, which have been used to identify and quantify organic carbon sources, can be used to monitor the distribution of carbon sequestered by tidal flat diatoms. The cost of this approach is low, sample preparation and analysis are relatively simple, and the technique's validity has been extensively tested (Bianchi et al., 2016). However, organic matter diversity can result in complex organic carbon mixtures that cannot be accurately determined using isotopic source separation. The isotopic values of different species may be similar, whereas those of one species may vary depending on microhabitat, season, growth cycle, or tissue type (Canuel & Hardison, 2016; Kramer et al., 2017). Therefore, the use of stable bulk isotopes should be improved using additional analyses of individual compounds with specific taxonomic origins. Biomarkers, such as lignin, lipids, alkanes, and amino acids, are useful in distinguishing inputs from different sources in coastal sediments (Bianchi et al., 2016; Upadhayay et al., 2017). Further, various studies have investigated compound-specific stable isotopes *via* natural and radiocarbon analyses by adding age to taxonomic specificity (Canuel & Hardison, 2016; Wakeham & McNichol, 2014). Stable oxygen and hydrogen isotopes can also be used to improve the resolution power. However, they are mainly used in food web studies, and their utility in determining sediment sources in coastal systems has not been validated (Duarte et al., 2005). Lastly, environmental DNA and barcoding based on 16S rRNA sequencing have been successfully employed to obtain relevant information on the chemical and species composition of diatoms (Hicks et al., 2018; Tréguer et al., 2018).

Biomonitoring constitutes a fundamental aspect of ecosystem conservation, management, and restoration efforts. In contemporary environmental stewardship, biomonitoring has become an imperative undertaking and is typically orchestrated by governmental bodies. Among the various biological indicators employed in biomonitoring, diatoms have emerged as a widely recognized tool for assessing the environmental quality of aquatic ecosystems (Lavoie et al., 2018; Pandey et al., 2017). In its most basic form, diatom biomonitoring entails the systematic documentation of species diversity and population abundances across diverse locations and timeframes. This process employs a repertoire of ecological census techniques and taxonomic identification methodologies. However, over the past decade, the field of diatom biomonitoring has evolved to encompass additional parameters beyond species diversity and abundance. These newer parameters, including lipid bodies (LBs), morphological anomalies, and size reductions, have found utility in both biological assessments and ecotoxicological studies (Pandey et al., 2017; Park, Bergey, et al., 2020; Park, Lee, et al., 2020). Under favorable conditions, diatoms grow rapidly and with a relatively low lipid content, whereas they show reduced growth and increased lipid accumulation under environmental stress. Specifically, diatoms produce more and larger LBs when exposed to various environmental and human disturbances (Hildebrand et al., 2012; Ramachandra et al., 2009). This biomarker is correlated with environmental pollution (Figure 6) (Pandey et al., 2017), and its analysis does not require taxonomic expertise, as lipids can be quantified using dyes and fluorescence staining, providing a simple and rapid endpoint for ecological assessments and biological monitoring of river and marine ecosystems.

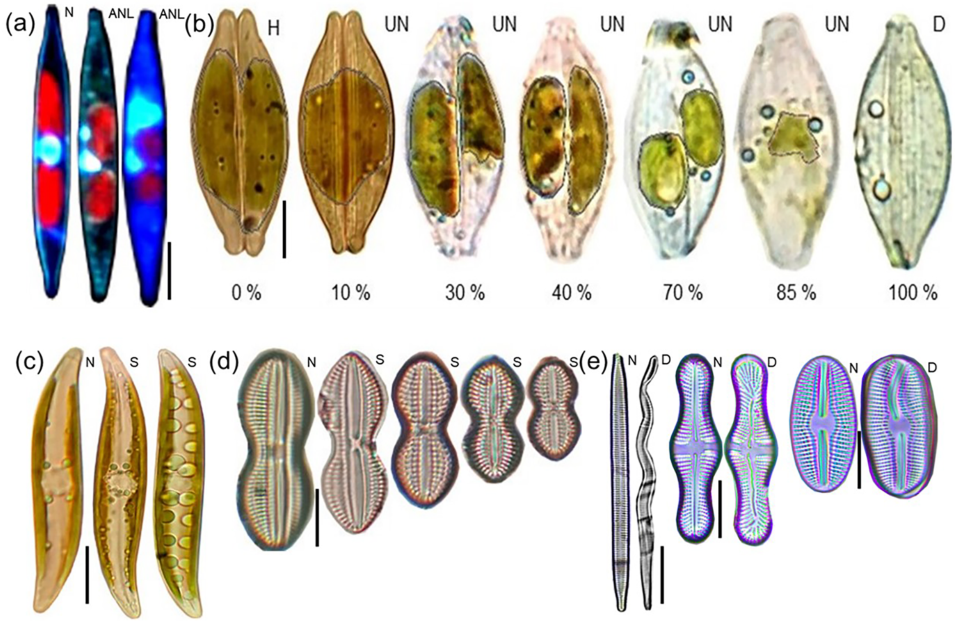


Figure 6. Analysis of diatom responses to environmental and anthropogenic stressors. (a) Alterations in cell integrity present as nuclear anomalies in *Nitzschia* with normal (N) and abnormal nuclear locations (ANLs). The scale bar represents 10 µm. (b) Alteration in the cell membrane and cytoplasmic content: the percent decrease in the photosynthetic apparatus of live *Amphora* under copper stress in healthy (H) and unhealthy (UN) laboratory conditions. The scale bar represents 8 µm. (c) Light micrographs of lipid bodies in *Gyrosigma spencerii*. The scale bar represents 5 µm. (d) Alteration in frustule size in *Diploneis interrupta* in response to different environmental and anthropogenic disturbances. The scale bar represents 5 µm. (e) Morphological deformities are observed in living diatom frustules in response to various environmental and anthropogenic perturbations. *Ulnaria ulna* is shown, with the first frustule being normal and subsequent frustules exhibiting deformities. The scale bar represents 8 µm. All materials in this figure were adapted from Pandey et al. (2017).

Furthermore, diatoms are known for their robust, species-specific, ornate silica frustules, which occasionally change in response to different environmental (Winder et al., 2009) and anthropogenic stressors. The occurrence of various morphological forms, size reduction, and frustule deformations can be used as endpoints for environmental studies (Cox et al., 2012; Morin et al., 2012). Although size reduction is common and distinguishing the effects of stress-induced reduction from those of naturally occurring reduction following successive cell divisions is difficult, it could be a valuable biomonitoring tool, provided that a strategy is developed to ensure that any significant size reduction is confirmed to have been caused by environmental stress (Figure 6).

In addition, significant relationships have been reported between anthropogenic stress and anomalies in diatom frustules. Diatoms can reflect sublethal responses to environmental stressors through valve deformities (teratologies) (Lavoie et al., 2017). Falasco et al. (2009) quantified deformities by broadly classifying them according to where they occur: in valves (type I), striae (type II), raphe (type III), and multiple locations (type IV). However, it is also important to better understand the indicator potential of different species, the severity of deformities, the transmission of teratologies to subsequent generations, species-specific susceptibility to deformities, and the "ecological signal" provided by a biomarker (Lavoie et al., 2017) before using a metric based on diatom deformities as an environmental stress indicator.

Diatom metrics such as LBs and frustule deformities are relatively quick, easy, and inexpensive to identify, reproducible, and based on globally accepted protocols. Furthermore, they are independent of taxonomic specificity or endemism, allowing direct comparisons between sites over large geographical scales (e.g., countries and continents). Therefore, they are useful for early stress detection below critical levels that induces cell death (Renzi et al., 2014). Applying these metrics for environmental monitoring of the health of tidal flat diatoms could help to ensure that tidal flat ecosystems remain stable and well-conserved. Promoting the popularization and diffusion of marine ecosystem health assessment technology can offer new growth engines for national environmental projects, stimulating a future market stabilized by green innovation and reviving local economies through ecotourism. Showcasing the excellent state of local tidal flat ecosystems and fostering a clean tidal flat image through recovering tidal flat ecosystem health and marine biodiversity can result in significant benefits.

7. Future perspectives

Utilizing natural tidal flat diatoms for CO_2 sequestration opens up promising prospects. An emerging approach involves collecting and cultivating diatoms on land to achieve substantial biomass production. This can be followed by the production of fine chemicals utilizing biorefinery techniques, a shift that aligns with the evolving concept of marine blue biotechnology, which aims for zero-waste circular processing of marine resources. The overarching goal is to ensure the cleanliness and safety of marine systems through continuous monitoring of marine biomass and the derivation of biofuels and other high-value materials from marine biomass for industrial applications.

Tidal flat diatoms can be diversely applied in large-scale biomass production and biorefinery processes. They can be sampled using methods like sediment surface scraping, the lens-tissue technique, or density gradient centrifugation. Culture strains are then created through traditional methods or advanced techniques like flow cytometry, optical tweezers, and laser microdissection. Clonal cultures are initiated using standard media with careful monitoring of silicate concentrations for optimal diatom growth. Diatoms stand out for their high, continuous growth rates, with reported yields exceeding 120 MT dry diatoms per hectare annually (Wang & Seibert, 2017). Further, productivity in photobioreactor systems is twice that of open pond systems, supporting their candidacy for large-scale biomass production (Buono et al., 2016; Marella & Tiwari, 2023; Weisz, 2004).

Diatoms have bio-compound synthesis abilities, making them ideal for biorefineries. Their biosynthesis of valuable compounds, including ω-3 fatty acids and chlorophyll derivatives, makes them versatile for applications in food, feed, cosmetics, pharmaceuticals, aquaculture, agriculture, and bioenergy (Marella et al., 2020; Tiwari et al., 2022). Further, hydrothermal liquefaction can convert approximately one-third of diatom dry weight into biocrude. Thus, diatoms prove to be a sustainable source for biofuel production, with potential applications in a biorefinery context (Sharma et al., 2021). The entire U.S. oil demand could potentially be satisfied using only 3–5% of the country's land (Levitan et al., 2014). The Jawkai Bioengineering R&D Center has achieved sustained diatom yields, aligning with commercial biofuel production predictions (Wang & Seibert, 2017). Moreover, diatoms used for liquid fuel production generate minimal waste, allowing for effective recycling of the growth medium (Wang & Seibert, 2017), and their frustules, adorned with nano-sized holes, can extract heavy metals from industrial wastewater (Wang, 2015). As such, diatoms have diverse applications in nanotechnology and materials science, including the biosynthesis of cytotoxic nanoparticles (Gutu et al., 2009; Sharma et al., 2021; Yamazaki et al., 2010).

Additionally, the adaptability of diatoms to changes in their frustule structure based on environmental factors and silicon uptake efficiency offers a unique advantage (Knight et al., 2016). This characteristic can be harnessed to tailor the frustule shape and pore size, allowing for applications in various industries, including nanotechnology and drug delivery. In drug and gene delivery, the diatoms' intricate frustule characteristics make them potential substitutes for traditional tools (Knight et al., 2016; Martin-Jézéquel et al., 2000). Their natural 3D porous structure should be explored for efficient biomedical applications. Innovative designs, such as magnetically guided drug carriers, showcase enhanced drug delivery performance, emphasizing the potential of diatoms in pharmaceutical advancements (Aw et al., 2011; Gnanamoorthy et al., 2014; Ragni et al., 2017). Therefore, through land-based cultivation, diatoms have the potential to revolutionize large-scale biomass production for biorefinery processes. Their versatility, coupled with their ability to adapt to controlled environments like PBRs, positions diatoms as valuable contributors to the sustainable production of biomass and the development of biorefinery technologies (Dhanker et al., 2024).

In line with this, over the past decade, substantial investments have been directed toward projects focused on the production of high-value materials, including biofuels derived from microalgae (Okeke et al., 2022; Uma et al., 2023; Yadav et al., 2022; Khan et al., 2023; Maghzian et al., 2023). However, challenges have emerged, including the need for sufficient biomass, economically viable biorefinery platforms, and alignment of these technologies with existing value chains. To overcome these challenges, several strategic approaches can be adopted. These encompass selecting, retaining, and mass cultivating suitable diatom species through integrated multidisciplinary research and technological development, spanning areas such as taxonomy, genetic engineering, physiology, ecology, engineering, and informatics. Additionally, life cycle assessment (LCA) can play a pivotal role in enhancing the economic viability of the entire process. This is complemented by implementing efficient and cost-effective new technologies for individual processes. Furthermore, developing a recycling closed-loop process can effectively transform waste into high-value materials, supplemented by marketability analysis, target material type and function profiling, and artificial amplification.

Amidst pressing global challenges related to climate change, increasing energy demands, and the depletion of petroleum resources, biorefinery technologies offer a promising solution for a sustainable future. Grounded in principles such as the supply of safe food and energy, continuous resource utilization, zero environmental impact, job creation, and market competitiveness, biorefineries serve as an integrated system of processes and technologies that convert biomass into high-value products while minimizing waste production (IEA Bioenergy Task 42). In marine blue biotechnology, applying biorefinery principles to marine biomass holds the potential to usher in a new era of marine resource utilization. Diatoms, with their capacity to produce

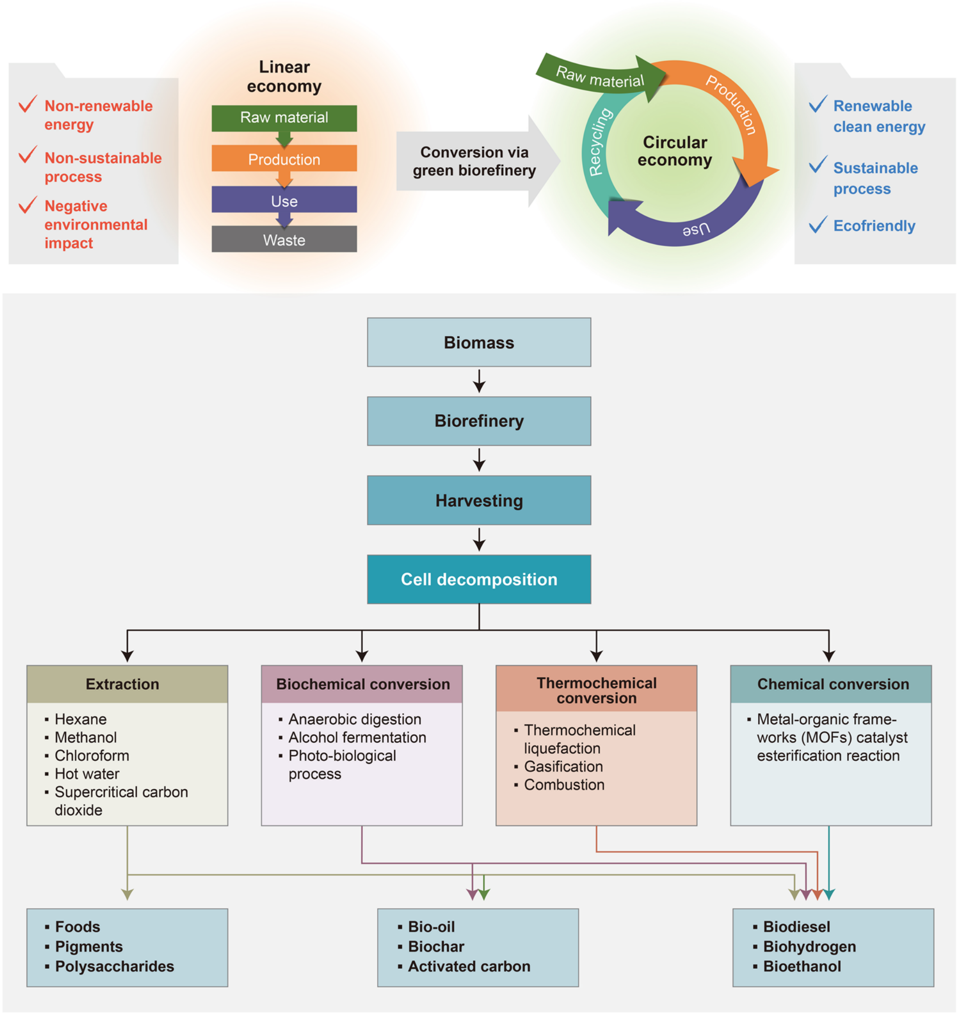


Figure 7. A bio-based circular economy including an exemplary biorefinery using diatoms.

biofuels, fine chemicals, and other valuable materials, stand poised to become pivotal contributors to the bioeconomy (Figure 7).

Collaboration among experts from diverse disciplines, including molecular biology, cell biology, genetics, physiology, ecology, and engineering, is imperative to realize these future perspectives. Additionally, integrating green technology and artificial intelligence (AI) advancements can enhance the efficiency and precision of diatom cultivation and biorefinery processes, propelling marine blue biotechnology to new heights.

From an economic perspective, establishing a bioprospecting platform and an automatic-control biomass production system for industrial applications of diatom fine chemicals can yield crucial insights into diatom genetic resources. This integration can involve synthetic biology, green refinery techniques, AI/ICT, and bioinformatics technologies, potentially positioning the industry for global market dominance in diatom-related sectors. This holds the potential for bioenergy (biofuels) production with international competitive advantages and explores opportunities for international bioenergy businesses beyond domestic commercialization. Furthermore, the industry's indirect economic effects can be substantial, driven by the development of a bio-industrial complex and reduced environmental protection costs associated with developing and restoring tidal flat ecosystems.

8. Conclusions

Diatoms, having evolved over millions of years, have a remarkable potential for CO_2 sequestration. Despite their minute contribution to the total weight of global photosynthesizing plants, they annually produce organic carbon at a rate equivalent to that of all terrestrial plants combined. Furthermore, diatoms form the foundation of marine food chains, and evidence from current and paleocean data suggests their capacity to transport substantial amounts of organic carbon into the deep ocean, highlighting their significance in addressing contemporary climate change challenges.

This review underscores the intrinsic value of tidal flats and their diatom inhabitants as carbon reservoirs and biological pumps. It outlines their potential role in shaping tidal flat conservation policies, particularly in light of the increasing attention to BC and the substantial carbon stocks estimated in Korean tidal flats. However, from a carbon storage perspective, it is paramount to ascertain the fate of converted organic carbon, whether stored within tidal flats or exported from the euphotic intertidal zone to the deep ocean layers, which can provide a long-term solution to climate change mitigation.

Therefore, a multidisciplinary approach, encompassing physical, biogeochemical, biological, ecological, oceanographic, and mathematical dimensions, must be cultivated to unravel the mechanisms governing the biological carbon pumping functions of our oceans and forecast future scenarios at local and global scales. Additionally, developing a robust technical foundation for assessing the bio-pumping and storage functions of diatoms in intertidal ecosystems is imperative to quantify their BC potential effectively.

Moreover, recognizing the pivotal role of BC systems in tidal flats will engender diligent conservation monitoring and streamlined management and regulation of these vital ecosystems. This will serve as the groundwork for incentivizing their preservation or restoration, thereby supporting climate change mitigation initiatives. We recommend advocating for interdisciplinary research, bridging ecological and economic domains, to establish standardized methodologies for monitoring and quantifying carbon inputs. Such an approach will substantiate the valuation of tidal flat diatoms as a BC source. Simultaneously, it will acknowledge the added value of BC ecosystem conservation, encompassing benefits such as enhanced fisheries, nutrient cycling, livelihood support for coastal communities, and coastal protection, offering a cost-effective alternative to hard engineering solutions.

Comprehensive international collaborations are indispensable for gathering and leveraging region-specific data, fostering the development of pragmatic models for predicting carbon flux mitigation in tidal flats worldwide and aiming to achieve global integration. The future of marine blue biotechnology lies in the innovative and sustainable utilization of natural tidal flat diatoms. By combining their role in native tidal flat habitats with land-based cultivation for extensive biomass production and biorefinery processes, diatoms can be the cornerstone of a zero-waste circular processing system for marine resources. Through interdisciplinary research, technological advancements, and global partnerships, the vision of a diatom-based biorefinery can be realized, offering a promising pathway toward a greener and more prosperous future for humanity and the marine ecosystems upon which we depend.

CRediT author statement

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Data availability statement

All data associated with this review can be found within the main manuscript and original sources are stated.

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