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Influence of diatom diversity on the ocean biological carbon pump

Paul Tréguer¹, Chris Bowler², Brivaela Moriceau¹, Stephanie Dutkiewicz³, Marion Gehlen⁴, Olivier Aumont⁵, Lucie Bittner⁶, Richard Dugdale⁷, Zoe Finkel⁸, Daniele Iudicone⁹, Oliver Jahn³, Lionel Guidi¹⁰, Marine Lasbleiz¹¹, Karine Leblanc¹¹, Marina Levy⁵ and Philippe Pondaven¹

Diatoms sustain the marine food web and contribute to the export of carbon from the surface ocean to depth. They account for about 40% of marine primary productivity and particulate carbon exported to depth as part of the biological pump. Diatoms have long been known to be abundant in turbulent, nutrient-rich waters, but observations and simulations indicate that they are dominant also in meso- and submesoscale structures such as fronts and filaments, and in the deep chlorophyll maximum. Diatoms vary widely in size, morphology and elemental composition, all of which control the quality, quantity and sinking speed of biogenic matter to depth. In particular, their silica shells provide ballast to marine snow and faecal pellets, and can help transport carbon to both the mesopelagic layer and deep ocean. Herein we show that the extent to which diatoms contribute to the export of carbon varies by diatom type, with carbon transfer modulated by the Si/C ratio of diatom cells, the thickness of the shells and their life strategies; for instance, the tendency to form aggregates or resting spores. Model simulations project a decline in the contribution of diatoms to primary production everywhere outside of the Southern Ocean. We argue that we need to understand changes in diatom diversity, life cycle and plankton interactions in a warmer and more acidic ocean in much more detail to fully assess any changes in their contribution to the biological pump.

Through photosynthesis, the primary producers build biomass by taking up CO₂ and thus influence its concentration in Earth's atmosphere¹. Among the microscale planktonic primary producers, diatoms are unique because of their silicified cell walls, which provide mechanical protection from grazers². Since the early Cenozoic, diatoms have become the most abundant and diverse siliceous marine microorganisms³, and have emerged as key drivers of the silicon cycle⁴. Their fast growth rates in high-nutrient environments^{5–7} (Supplementary Section 1) and comparatively large sizes also make them important contributors to organic carbon production in the euphotic zone⁸. They have been estimated to contribute as much as 20% of the total primary production on Earth, and up to 40% of the total marine primary production⁹ (Supplementary Section 1). The organic carbon synthesized by photosynthesis in the surface oceans is transferred to the trophic network, and may then be exported to depth, where most of it is remineralized to CO₂. This export is termed the biological carbon pump¹⁰. Diatoms are also believed to contribute ~40% of particulate organic carbon export¹¹, which can reach either the mesopelagic layer (the lower limit of which is ~1,000 m, coinciding with the nitrate maximum) or deeper, into the bathypelagic layer, which is also known as the 'CO₂ sequestration layer'. Carbon reaching bathypelagic depths is removed from the atmosphere for at least 100 years, and carbon will ultimately reach sediments at the seafloor and be buried.

An important concept in marine-plankton ecology is Margalef's mandala¹², which posits that diatoms characteristically thrive in nutrient-rich surface layers and turbulent conditions, and are thus typically found at high latitudes and in coastal upwelling regions (Fig. 1). Through remote sensing, new observation tools and models, abundant diatoms have also been identified in meso/submesoscale fronts^{13,14} (Fig. 1) and shown to contribute significantly to the 'shade flora' found at the deep chlorophyll maximum (DCM)¹⁵. The use of molecular biology techniques has further revealed that diatoms may be more relevant in oligotrophic systems than generally considered¹⁶. Herein we address the following questions: what factors control the distribution of diatoms in the ocean? What is the contribution of diatoms in carbon export from the photic layer? Are diatoms efficient transporters of organic carbon to the CO₂ sequestration layer? Can we predict the fate of diatoms in the future ocean impacted by climate change?

Controls of the distribution of diatoms in the ocean

Large-scale patterns of diatom distributions from ocean-colour remote sensing^{17,18} along with field observations^{19–21} reveal that they are an important component of phytoplankton biomass at high latitudes during spring (that is, in April–June in the Northern Hemisphere and October–December in the Southern Ocean) and in equatorial and coastal upwelling regions. They are present at lower

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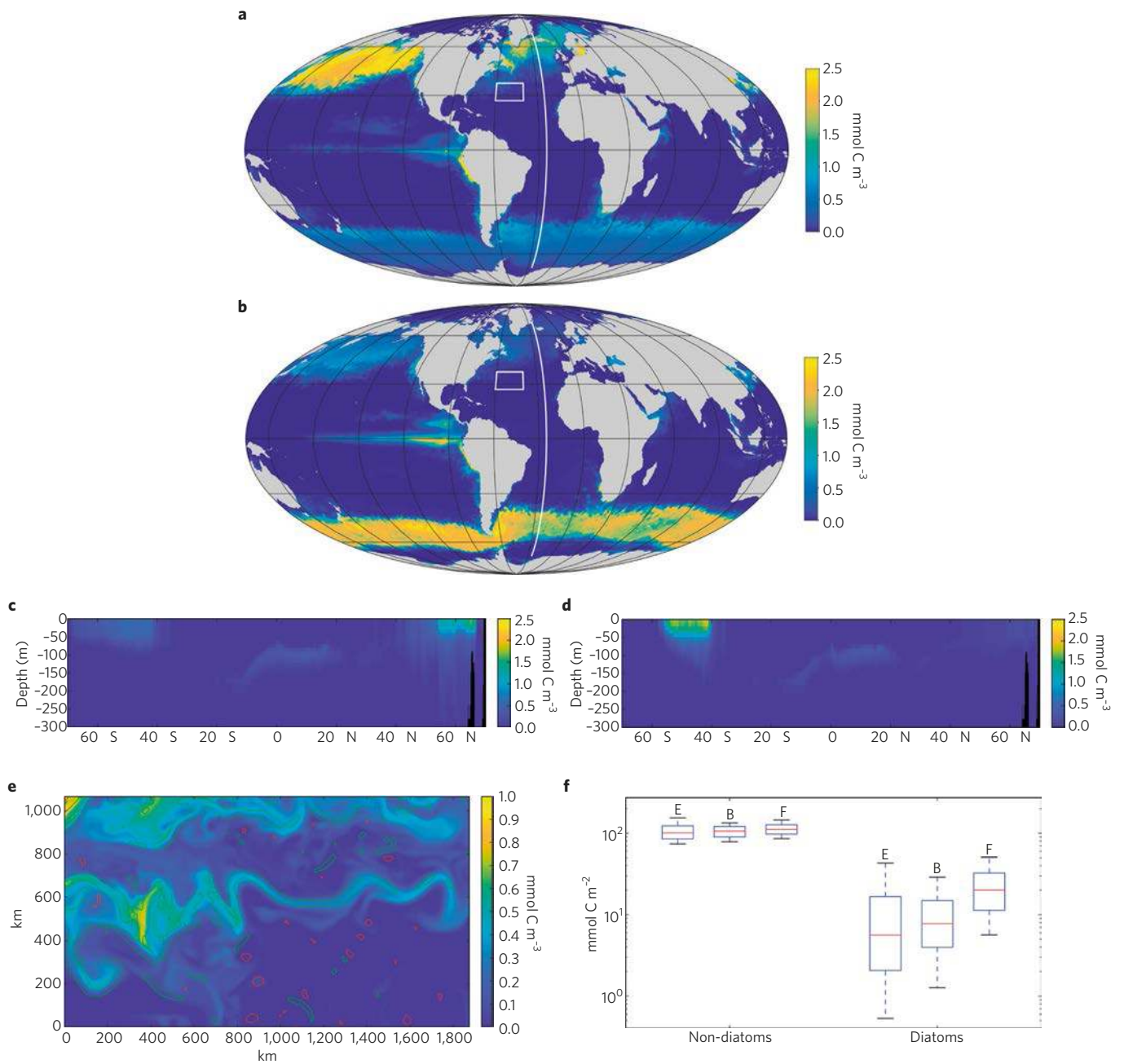


Fig. 1 | Diatom biogeography illustrated with the results of the MIT ecosystem model. a-d, Global model: Diatom concentrations at the surface for April-June (**a**) and October-December (**b**), and along transects (**c,d**) along lines in **a** and **b**. **e-f**, Higher-resolution regional model (nominally in squares in **a** and **b**). **e**, Diatom concentrations in January. Contours indicate fronts (green) and cores of eddies (red). **f**, Median concentrations of depth-integrated phytoplankton abundances (boxes are quartiles, whiskers are 9th and 91st percentiles) at fronts (F) and in eddies (E) compared to background conditions (B). For more details and limitations of the model, see Supplementary Section 8.

levels in mid-ocean subtropical gyres where smaller phytoplankton such as cyanobacteria dominate, but are found periodically at higher abundance^{8,15,22,23} even in these stratified regimes. In particular, symbiotic diatom-diazotroph assemblages (DDAs) appear to allow diatoms to periodically be important components of plankton communities in oligotrophic regions²². It is likely that diatoms are also important players at the DCM in oligotrophic gyres^{15,24} and also seasonally at higher latitudes²⁵. They furthermore appear well suited to thrive at the sea-ice edge²⁶. A recent synthesis of observations suggests that, over scales ranging from 1–10°, diatoms are patchier than other functional groups of phytoplankton²⁰.

Many of the large-scale diatom distribution patterns inferred from satellite and in situ observations can be captured by ecosystem models^{21,27–29} where diatom analogues are given traits, such as a requirement for silicic acid, as well as higher maximum growth rates^{7,30,31} and lower nutrient affinities relative to other non-diatom analogues (Fig. 1a,b). Diatom proliferation can occur independently from grazers and viruses early in the spring, and their high growth rates allow them to dominate during spring blooms^{32,33} (Supplementary Section 2). Additionally, in regions of high nutrient supply, such as equatorial and coastal upwelling regions and DCM (Fig. 1a–d), their relatively low affinity for nutrients is

compensated for by their high maximum growth rates and probably by their defensive silica frustules². The relative importance of bottom-up versus top-down controls on diatoms is, as of yet, unknown, especially as there are few mortality rate measurements or top-down studies explaining the demise of diatom blooms (Supplementary Section 2). It is noteworthy that in a large-scale analysis of plankton–plankton interactions, diatoms emerged as the only group of phytoplankton with a large exclusion signal towards other planktonic groups³⁴, implying their ability to successfully outcompete congeners.

Observations also suggest strong heterogeneity at small spatial scales in the distribution of diatoms, particularly in relation with mesoscale eddies and submesoscale fronts. Eddies show either enhanced or reduced abundances in their core^{35,36}, whereas fronts generally appear as diatom hotspots^{37,38}. Small-scale diatom patches have been identified from individual high-resolution ocean-colour images and can be related to stirring by mesoscale circulation³⁹. Transient diatom blooms in oligotrophic regions could be driven by turbulence prompted by storms, meso- or submesoscale features, seeded by deep populations¹⁵, or driven by symbiotic relationships with nitrogen-fixing symbionts²³.

The heterogeneity of diatoms as a result of submesoscale features has been explored using a high-resolution model representing the highly turbulent transition between subtropical and subpolar gyres (Fig. 1e). Statistically, the model shows an enhancement of diatom biomass in submesoscale fronts and, to a lesser extent, a reduction in the core of mesoscale eddies relative to background conditions (Fig. 1f). On average, diatoms almost double their biomass at fronts relative to other phytoplankton. This is in agreement with previous model results for opportunistic phytoplankton types (for example, fast-growing diatoms and other large phytoplankton types^{13,14}), and links to observational evidence (provided above). However, the model highlights that the enhancement at fronts is particularly strong for diatoms compared to all other non-diatom phytoplankton types. This enhancement is believed to result from the larger supplies of nutrients driven by particularly intense vertical motions over such fronts⁴⁰.

The distribution of diatoms is tightly coupled with the physics of the ocean, the supply of nutrients (including iron⁴¹) from the macro- to submesoscale (and probably also the microscale), as well as their interaction with predators, pathogens and parasites^{42,43} and, in some cases, symbionts²². The diatom-specific traits of high maximum growth rate, relatively low nutrient affinities and protection from grazers allow them to occupy niches that are more turbulent¹² and encompass deeper mixed layers, and higher nutrient concentrations^{44,45} than other phytoplankton. On top of these controls, the requirement for silicic acid further delineates their biogeography, especially for heavy versus light silicifiers⁴⁶.

All diatoms are not equal in the export of carbon

In the wake of Martin's particulate organic carbon attenuation curves concept⁴⁷, the bulk amount of carbon produced in the surface layer was classically considered to be the only factor influencing the export of organic carbon to depth. However, the subsequent discovery of high-biomass, low-export ecosystems⁴⁸ indicates that this concept is not a sufficient descriptor of the transfer of carbon to the deep ocean. Indeed, changes in both phytoplankton and zooplankton communities can affect the transfer of carbon out of the photic zone through their effects on the quantity and the quality of particulate matter. This, in turn, influences the lability of particles, their sinking and remineralization, and the transfer of carbon to higher trophic levels⁴⁹. As such, diatoms play a central role through a combination of factors including their large sizes⁵⁰, their significant contribution to oceanic primary production, their bloom forming ability and subsequent grazing, and the essential role of the opal cell wall in ballasting sinking particles⁵¹.

Given its direct and quantifiable impact on sinking rates, the diatom cellular Si/C quota represents one of the first variables that need to be better parameterized (Fig. 2). Based on the iron hypothesis on the control of carbon export to the ocean interior⁵², it is generally considered that iron-limited diatom species are more heavily silicified than diatom species in iron-replete regions^{53,54}. Yet silica contents are sometimes higher in iron-replete diatom cells than under iron-limiting conditions⁵⁵ and the range of variations of frustule thickness appears highly dependent on environmental conditions and taxonomic level⁵⁶ (Fig. 2). One likely explanation is the variability in the number and expression of genes related to frustule formation and silicon transport in evolutionarily distinct genera of diatoms⁵⁷.

Attempts at classification within the diatom functional group based on growth rates and degree of silicification are recent^{46,58}. Specifically, two similar diatom sub-groups were conceptualized. The species in C-sinkers/Group 1 consist of small, lightly silicified, fast growing and chain-forming diatoms (for example, *Chaetoceros* and *Pseudo-nitzschia*) that are dominant in iron-enriched regions. Si-sinkers/ Group-2 species are — on the contrary — large, slow-growing species that are heavily silicified, and thus resistant to grazing by large zooplankton: these species are mostly found in iron-limited areas (for example, *Fragilariopsis kerguelensis* and *Thalassiothrix antarctica*). This classification is in good agreement with a palaeoceanographic study linking the role of sea-ice extent, nutrient and iron inputs to the relative dominance of each group in the glacial Southern Ocean, with proposed analogue species in the Northern Hemisphere⁵⁹. Yet, these classifications into carbon and silicon sinkers clearly represent end members along a spectrum of Si:C ratios as illustrated in Fig. 2. The advent of molecular and phylogenetic studies — as well as cellular level understanding of the silicification process and its control factors — should help experimentalists refine diatom distinctions in the coming years (Box 1).

The wide size range of diatoms also impacts their fate in the water column: interspecific variations in the volume and carbon contents of diatom cells span over nine orders of magnitude¹⁹. They also exhibit incredible morphological diversity, including solitary cells (round or elongated), colonies (flat or spiral shaped) and the presence or absence of spines and setae. Certain shapes, especially when combined with the production of transparent exopolymer particles (TEP), are conducive to the formation of large aggregates⁶⁰ that can sink when incorporated silica results in a density high enough to compensate for the low density of TEP⁶¹.

Diatoms also exhibit complex and elusive life cycles, which affect size, morphology, Si/C quotas and export. The production of auxospores through diatom sexual reproduction has been shown to considerably alter silicon versus carbon export rates⁶², whereas the production of resting spores as a survival strategy, often dominated by the *Chaetoceros* and *Thalassiosira*, is a substantial contributor to C export in numerous coastal, upwelling and open ocean regions⁶³.

Mortality processes can be equally important for export rates. These include senescence and programmed cell death, which will result in passive sedimentation events, or direct consumption by other plankton groups. The demise of diatom blooms may occur due to a variety of top-down regulations, such as viral lysis⁶⁴, bacterial attack, zoospore parasite infection (Supplementary Section 3), tube feeding by heterotrophic flagellates⁶⁵, and grazing by copepods or euphausiacea, all leading to distinct export modes^{66–68}.

Other much less studied processes that could potentially modulate silicon and carbon export rates include biological interactions such as symbioses. Along with DDAs⁶⁹, infochemical signalling between copepods has been shown to alter diatom silicification or chain length^{70–72}. Other types of associations where diatoms serve as hosts also exist (Fig. 2).

Sinking diatom particles clearly need to be better described and assigned to different pathways such as the gravitational sinking

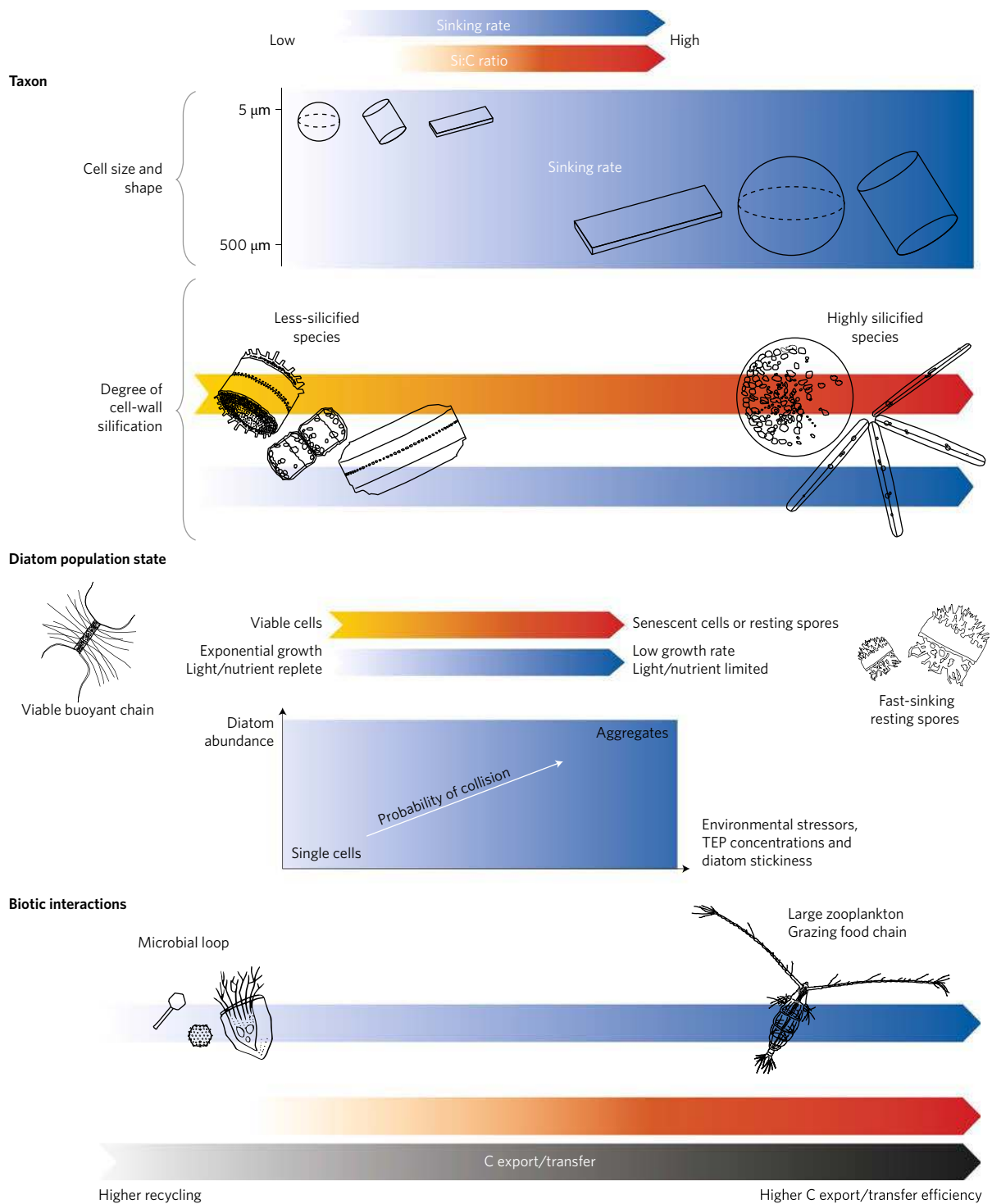


Fig. 2 | Key processes influencing the contribution of diatoms to carbon export/transfer efficiency (CE/TE) potential. Higher contribution of diatoms to this potential is driven by taxonomic differences in cell size, shape or the degree of cell-wall silification. This CE/TE potential is, however, modulated by changes in diatom population states: environmental stresses favour senescence, production of transparent exopolymers (TEP), or resting spores, providing higher probability of collision, scavenging, and aggregate formation. Diatom abundance and stickiness favour sedimentation of silica-balled carbon-rich marine snow. It is also modulated by biotic interactions: grazing of diatoms by large-size zooplankton generates silica ballasted faecal pellets of higher CE/TE. For more details, see Supplementary Section 9.

of single cells, the various types of aggregates and faecal pellets, or mediated through vertical zooplankton migrations⁷³. To better understand fluxes from the photic layer, we must stop considering diatoms as a single functional group and intensify our efforts to understand their diversity, abundance and interactions with other

plankton compartments (Box 2). Advances in high-throughput sequencing, combined with bioinformatics analyses such as have been deployed using Tara Oceans meta-barcoding data (Box 1), can offer a global and improved vision of the differential contribution of specific diatom groups to both net primary production

Box 1 | Insights from genomics

The first complete genome sequence from a diatom was reported in 2004, and nine other genomes have since been sequenced, as well as transcriptomes from a total of 99 species¹⁰¹. For some species, molecular tools to assess the functions of each of the >10,000 genes encoded in each genome have also been developed and applied. The analysis of these genomes and some of the genes they encode¹⁰² has not been fully exploited in an oceanographic context. Diatoms exhibit huge genetic and functional diversities¹⁶, and many species representatives are not readily cultured. So far, specific features of diatom gene repertoires that have been proposed to underpin their ecological success include: (1) an overabundance of cyclins and heat shock transcription factors that may facilitate the capacity of diatoms to bloom rapidly and respond to changing environments¹⁰³; (2) a urea cycle integrated within diatom primary metabolism for a broader utilization of nitrogenous compounds and for redirecting nitrogen towards essential diatom-specific processes such as frustule biogenesis¹⁰⁴; (3) novel components for iron capture and storage from the environment¹⁰⁵; and (4) a capacity to couple photosynthesis and respiration in an obligately interdependent manner¹⁰⁶.

Genes governing simple metabolisms responding to nitrogen, sulfur and iron have been identified. However, the challenge¹⁰⁷ is identifying the genes underpinning the more complex biogeochemical processes, including those that affect the potential for carbon export.

We also lack gene markers for key stages in diatom life histories, such as for assessing cell size, proliferation and death rates, chain/colony formation, sexual reproduction, spore and resting stage formation. It is also important to assess the extent to which diatoms adapt to their environment through irreversible changes in their genomes versus more flexible approaches based on changes in gene expression. Evidence is emerging that diatoms are able to change their gene expression profile to microscale turbulence¹⁰⁸ and that some may have evolved permanent, genome-level adaptations to certain conditions such as iron bioavailability¹⁰⁹), whereas others

have retained more flexible responses that allow acclimation to a wider range of conditions¹¹⁰. A further challenge is to evaluate the importance of epigenetic processes¹¹¹, which may be transmissible across generations and permit responses over shorter timescales¹¹². Such processes may underlie the extensive allele-specific gene expression patterns observed in the polar diatom *Fragilariopsis cylindrus*¹¹³. Yet ecosystem models are only now beginning to incorporate species evolvability^{114,115}.

Moreover, short-term observations of gene expression need to be placed in the context of long-term observations of ocean processes to assess the tempo of adaptation.

The monitoring of gene expression can improve estimates of primary production and nutrient cycling in a wide range of diverse conditions. A recent example using holistic approaches developed for systems biology provides a useful methodological framework to derive useful information from the immense DNA sequence-based datasets¹¹⁶. In particular, whereas current models generally define plankton functional types (PFTs) based on evolutionary relatedness of organisms, network-based approaches¹¹⁶ are used to identify modules of species based on their co-occurrences with respect to a particular parameter (in their case carbon export in the oligotrophic ocean). Although having no predetermined taxonomic affiliations with each other, the strict co-occurrence patterns were considered to imply that the organisms within each module form a tight sub-community within the larger ecosystem that is involved in performing a particular process. A different approach is seen in the combination of meta-transcriptomics and cellular physiology data with a global ecosystem model¹¹⁷, which used genomics to incorporate cellular metabolism. This approach could be taken further in the context of PFTs¹¹⁸. Such approaches are necessary to combat the growing gap between genomics and oceanography, and provide examples of how modelling efforts can be enabled by genomics to incorporate cellular metabolism, biodiversity and more accurate representations of organism interactions.

(NPP) and carbon export (CE) as a function of environmental factors (Fig. 3).

Efficiency of organic carbon transport and sequestration

The efficiency of the diatomaceous pathway for transporting organic carbon down to the CO₂ sequestration layer is under debate. Indeed, at the global-ocean scale, abyssal sediments rich in biogenic opal, which are located below silicic-acid-rich diatom-dominated surface waters (for example, the Southern Ocean), generally do not accumulate a high proportion of organic carbon⁷⁴. This would suggest that diatoms are not efficient transporters of organic carbon to the bathypelagic ocean. For different biomes of the world's ocean, PE_{eff} (proportion of primary production exported from the surface to subsurface waters) and T_{eff} (fraction of exported organic matter that survives remineralization during sinking to reach depths >2,000 m) were calculated to provide additional constraints on model development⁷⁵ from available satellite data, isotopic techniques and sediment trap data⁷⁶. In the highest northern and southern latitudes where diatoms usually dominate phytoplankton blooms^{46,77}, PE_{eff} is high but T_{eff} is low. However, a recent study⁷⁸, which reconstructed particle fluxes from the rate of nutrient accumulation along transport pathways in a data-constrained ocean circulation model — combined with estimates of organic matter export from the surface ocean — calculates high (about 25%) T_{eff} to 1,000 m at high northern and southern latitudes. The authors linked this T_{eff} with specific phytoplankton community structure and export of ballast minerals.

Importantly, numerous observations both at small and large scales for the modern and the past ocean show that the siliceous pathway is capable of organic carbon transport to the CO₂ sequestration layer, sometimes through episodic massive flux. In the modern ocean, deep carbon transport has been identified beneath both silicic-acid-rich and -poor surface waters. For example, in silicic-acid-rich systems dense siliceous- and pigment-rich fluffs were collected⁷⁹ at the sediment–water interface (3,600 and 4,700 m) in the autumn of 1993 at two stations located in the Crozet–Kerguelen basin (Southern Ocean) in the permanently open ocean zone (POOZ). These fluffs consisted of diverse living diatoms including a large fraction of *Chaetoceros* resting spores. In addition, high²³⁴Th excesses in subsurface waters indicates strong export of particles to the subsurface of the POOZ⁷⁹, and the presence of chlorophyll *a* in surficial sediments confirms that deposits of fresh material occur in this ecosystem⁷⁹. The deposition of fresh material resulted from fast sinking rates not reachable by single cells but similar to what has been measured for particles such as faecal pellets or aggregates that have been ballasted. Such observations are consistent with those reported^{80,81} for Southern Ocean iron-fertilized blooms and for the North Atlantic Porcupine Abyssal Plain⁸². Regarding silicic-acid-poor systems, during the Malaspina 2010 circumnavigation, the microphytoplankton communities collected in the deep sea (from 2,000–4,000 m) were dominated (81.5%) by diatoms (mostly centric forms), whereas 18% of phytoplankton cells were still alive⁸³. The presence of ubiquitous healthy diatoms in the deep sea confirms

Box 2 | Importance of incorporating diversity of diatom into numerical models

During the last decades, there has been a significant development in coupled physical–biogeochemical–ecosystem models. Biogeochemical models focus on stocks and exchange fluxes between reservoirs, usually within the first two trophic levels. The representation of ecosystems in these models often relies on reducing plankton diversity to a limited number of PFTs representative of key biogeochemical functions¹¹⁹. Diatoms are gathered or ‘proxied’ within a single PFT¹¹⁹ that requires silicic acid. However, models developed for more ecologically related questions have attempted to include the diversity within PFTs^{29,120}.

Future model developments need to strike a balance between the required incorporation of key traits, diversity, and computational cost. The limited amount of field observations^{20,121} to evaluate the models and our incomplete understanding of the controls on carbon export put additional constraints on model development.

Although some traits of diatoms that influence carbon export to the deep ocean — such as cell size³² and degree of silicification²⁸ — are beginning to be incorporated into models, other traits such as chain, spore or TEP formation are not yet understood sufficiently for them to be parameterized. Additionally, the development of a greater understanding of biotic interactions (for example, phytoplankton competition, symbiosis, grazing, virus infection) that shape plankton communities is needed. Theoretical approaches^{114,115,122} can provide a promising framework for including adaptation traits in models.

A first step for allowing modelled biogeochemical cycles to include the impact of diatom diversity could consist in refining parameterizations linking the fate of export production to the size distribution and composition of particles produced (for example, particulate organic carbon, siliceous and carbonate debris), as well as a better representation of zooplankton and microbial processes. The diversity of diatoms could thus be linked to their degree of

silicification; for instance by breaking the single PFT into Si-sinkers and C-sinkers.

Including diatom-diazotroph assemblages in the MIT ecosystem model allows seasonal blooms of large diatoms and subsequent increase in carbon export in some oligotrophic regions (Supplementary Fig. 1), reminiscent of the observed export pulses observed in the Pacific subtropical gyre⁸⁴. A version of the MIT model (Fig. 1) that includes size classes within diatoms (as well as other PFTs) finds a significant difference in the patterns of the mean size of phytoplankton, especially in the subtropical gyres, than a model with a more traditional two PFT (diatoms and picophytoplankton) framework (Supplementary Fig. 2). The more complex patterns from the size-based model impact the patterns of carbon export relative to the simpler community, and will probably be important in the response to climate change. Indeed, preliminary results from the MIT ecosystem coupled to a climate model suggest that including a range of size classes within PFTs allows for a more nuanced shift within communities than current climate models capture. For instance, a shift from large to small diatoms will have less impact on carbon export than a shift from a single diatom PFT to a small PFT.

Increased complexity in the representation of diatoms will need to be matched with developments of the other compartments to allow for shifts between phytoplankton groups, competition, and changes in grazing pressure under global climate change. Yet the inclusion of a large diversity of phytoplankton might not be computationally tractable in the Earth system models used for climate studies in the foreseeable future. We suggest that an avenue forward would be in a hierarchy of models: using those that include diverse, adaptive plankton communities to guide parameterizations of the carbon export impact of these additional complexities in the models.

the occurrence of deep carbon injection by the silica pathway. In addition, summer increases in biomass and productivity of DDAs have been identified as the main cause of carbon export events and sequestration observed at 4,000 m in the North Pacific Subtropical Gyre at station ALOHA⁸⁴. Further supplementary information more, during summer 2012 a widespread deposition of ice algal biomass corresponding to an average of 9 gC m⁻² to the abyssal floor of the central Arctic (>4,000 m) was observed, principally consisting of the diatom *Melosira arctica* which grows as meter-long filaments anchored under ice floes⁸⁵.

Abundant and carbon-rich diatom deposits have also been identified in ancient marine sediments¹⁶. For instance, the giant *Thalassiothrix* frustules in Neogene sediments of the Equatorial Pacific, *Rhizosolenid* diatoms in Pleistocene sapropel flora of the Mediterranean Sea, and exceptional diatom concentrations in Late Cretaceous Arctic Ocean sediments. Such deposits have been explained^{15,79} by physical and environmental processes that can generate massive, pulsed and short-lived export of large-sized or giant diatoms, either from convergence zones⁸⁶ or from the DCM in stratified surface waters, for instance involving DDAs such as *Hemiaulus hauckii*-*Richelia intracellularis*¹⁵. The rise of diatoms in ancient oceans is generally accompanied by the establishment of petroleum source rocks. The often spatial coincidence of silica and fossil fuels, together with surveys of biomarkers (such as 24-norcholestane or C28–C29 steranes) in sediments and source rocks indicate a close link between diatoms and the formation of petroleum reserves⁸⁷.

In summary, the patchy nature of diatom blooms makes it very likely that the sparse sediment trap observations are under

sampling these events. Our ability to quantify large-scale spatial and temporal variations in transfer efficiency of the siliceous and non-siliceous pathways is limited by the scarcity and uncertainties of particle flux data^{76,78}. Consequently, the fate of diatomaceous carbon remains largely unknown and depends on the interplay between the processes controlling export, remineralization and timescales of water mass subduction. Recent advances in collecting mesopelagic sinking particles⁸³ together with in situ imaging and genomics approaches (Box 1) provide new tools to study the biology of the oceans at scales relevant to meso/submesoscale processes. Combined with bioinformatics approaches they provide new opportunities to better understand the role of diatom communities in the export of carbon to the deep ocean.

The fate of diatoms in a future warm and acidified ocean

The ocean mitigates global anthropogenic climate change by absorbing excess heat and CO₂ from the atmosphere. As a result, the world ocean has warmed, acidified and lost oxygen since the onset of the industrial revolution⁸⁸ and these changes have consequences for marine ecosystems. Most current model projections suggest a decrease in global NPP compared to contemporary values⁸⁸, and a restructuring of phytoplankton communities, but with important regional heterogeneity^{29,89–91}. The decrease in global NPP largely occurs in the mid- and low-latitudes in response to increased stratification and decreased nutrient supply to the surface ocean⁸⁸. The relative reduction tends to be larger for diatoms than for nano/picophytoplankton. A detailed analysis of fully coupled Earth system models⁸⁹ suggests that a direct temperature effect on biological rates causes the NPP reduction, with increasing phytoplankton

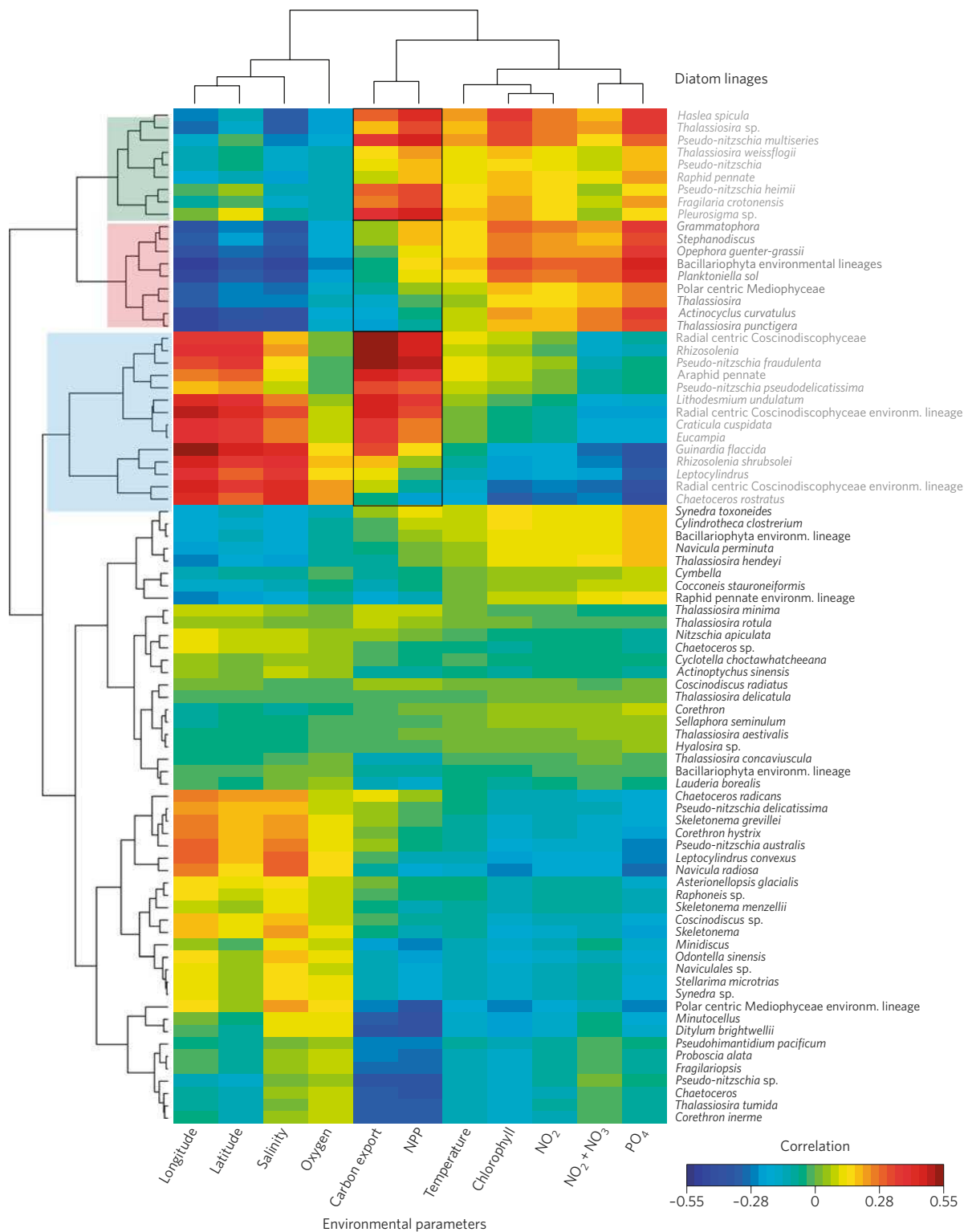


Fig. 3 | Diatom lineages and their role in net primary production (NPP) and carbon export (CE) as revealed by high-throughput DNA datasets.

Regression-based modelling was used to study correlations between meta-barcoding data and environmental parameters. A heatmap highlights groups of lineages, which are the best statistical predictors of CE and/or NPP in the oligotrophic low-latitude oceans. The blue and green groups show a significant positive correlation to NPP and CE, whereas the red group is only contributing to CE. Such analysis highlights the potential contribution of specific lineages to different aspects of the biological carbon pump. For more details, see Supplementary Section 10.

growth being kept in check by amplified zooplankton grazing. In contrast to low and mid-latitudes (Fig. 4a), most models project that the Southern Ocean will experience an increase in NPP and diatom biomass (Fig. 4b). Temperature is the consistent primary driver of

this increase, modulated variously by light, nutrient availability and grazing pressure across the different models⁸⁹.

The consistency of the sign of projected changes in global NPP, export production and differential responses of phytoplank-

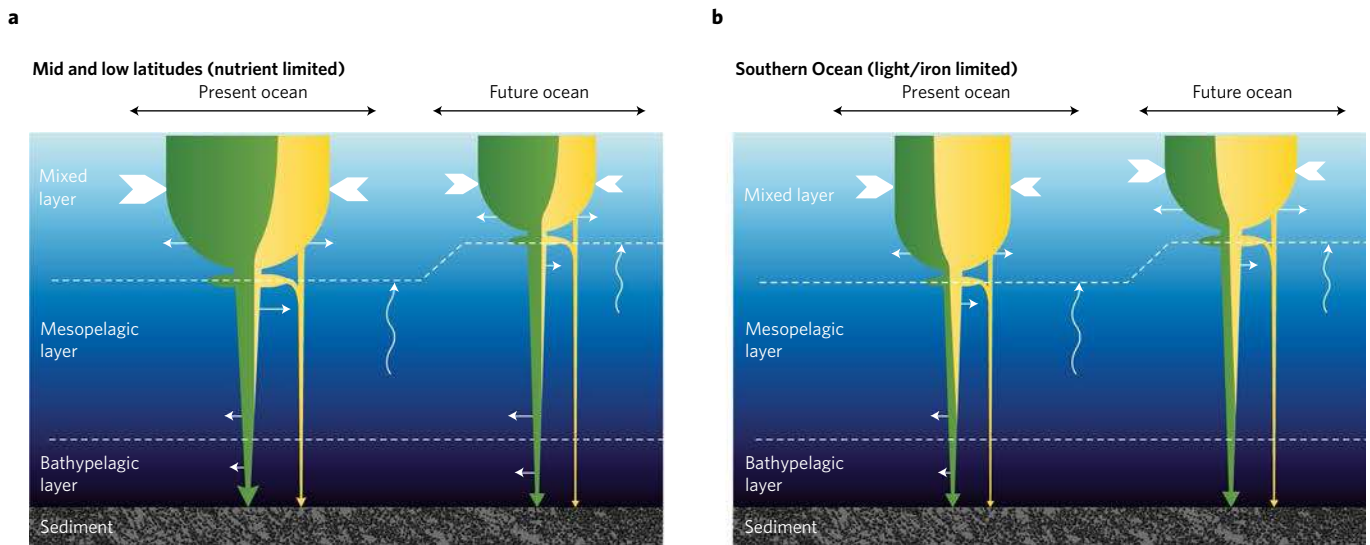


Fig. 4 | Schematic views on the role of diatoms in the biological carbon pump in the present and future ocean. Diatom pathway (yellow) and non-diatom pathway (green). **a**, Mid and low latitudes (nutrient limited). Present-day ocean: the diatom pathway exports particulate organic carbon to the bathy mesopelagic layer; specific environments trigger massive sedimentation that is able to reach the bathypelagic layer. Future ocean: in a warm, stratified and acidified ocean, most models predict a decrease in primary/export production. **b**, Southern Ocean (light/iron limited). Present-day ocean: labile organic carbon transported by the diatom pathway is mostly recycled within the mesopelagic layer; however, from frontal systems or 'shade flora', massive sedimentation of organic-carbon-rich siliceous matter can reach the bathypelagic layer. Future ocean: diatoms might double their growth rates primarily in response to rising temperatures and iron availability; impact on export production remains an open question. For more details, see Supplementary Section 11.

ton groups should, however, be interpreted with caution. Using Margalef's mandala¹² as a framework, most current climate models include only two phytoplankton size classes. Diatoms correspond to the large size class and are parameterized to thrive under nutrient-rich and low stratified regimes, while small cells contribute the background productivity under nutrient-poor and stratified conditions. Since diatoms are parameterized as the main carbon exporters in these models, their relatively greater reduction in response to increasing stratification compared to nano/picophytoplankton amplifies the decrease in export production^{29,92}. Projections of NPP are thus critically dependent on community structure and emerging top-down and bottom-up controls^{89,92}.

Fully coupled Earth system models (IPCC-class models) in general do not include impacts of ocean acidification on phytoplankton community structure and carbon export. The response of diatoms to altered surface ocean carbonate chemistry (increasing surface ocean P_{CO_2} and decreasing pH) has been the focus of numerous studies⁹³. However, a synthesis of many of these experiments on how various growth metrics responded to elevated P_{CO_2} suggests a large range of potential species-specific responses. On average, diatoms appear to have a statistically significant increase in growth rate in response to ocean acidification⁹⁴. Such differing responses to elevated P_{CO_2} have the potential to alter competitive fitness sufficiently to significantly alter community structure in a future high CO_2 world⁹⁴.

Additionally, larger diatom species tend to have a more pronounced growth rate enhancement in response to elevated P_{CO_2} than smaller species⁹⁵. An increase in the competitive fitness of larger diatom species could result in a change in community size structure and the efficiency of carbon and silicon export into the deep ocean⁹⁵. An increase in competitive fitness is also suggested by experimental studies that focus on the response of high-latitude diatoms to a combination of stressors⁹⁶. Southern Ocean diatoms might double growth rates primarily in response to rising temperature and increased iron availability^{96,97}. Experimental evidence detailing the response of diatoms to multiple stressors is still scarce and mostly regional (Supplementary Section 7). Including the effects of ocean

acidification and explicitly including multi-factor stress responses in coupled physical-biogeochemical-ecological models is likely to alter future projections of community structure, ocean productivity, and export.

The impacts of climate change on phytoplankton species⁹⁰ and their adaptive potential⁹⁸ can be explored with the help of statistical models. A species distribution model of North Atlantic diatoms and dinoflagellates projects a northward and eastward shift of ecological niches for a majority of organisms in the second half of the twenty-first century⁹⁰. However, evidence for rapid evolutionary adaptations of phytoplankton traits might promote changes in niche occupation over decadal to century scales and thus mitigate projected changes^{98,99} (Supplementary Section 7). We speculate that the expected alteration in carbon export, especially in response to a global reduction in diatoms^{28,29,100} and flow through the food web to upper trophic levels, might offset efforts of CO_2 emission mitigation and have consequences on higher trophic levels; this effect is not apparently captured in climate models that resolve biogeochemical fluxes. Projected changes in phytoplankton community structure are in line with our understanding of the underlying physical and chemical constraints, yet how community structure and biological processes contribute to community robustness and adaptive potential³⁴ have not yet been incorporated into such models.

The key role of diatoms

There is growing evidence for the key role diatoms play in the biological carbon pump in the modern ocean. In many regions of the world's ocean, they appear able not only to transfer particulate organic carbon to the mesopelagic layer but also to the CO_2 sequestration layer. However, the total amount of organic carbon annually exported to depth at different levels, as well as the transfer efficiency, remain to be quantified and parameterized accurately in models. Biogeochemical and physiological studies together with the use of genomics at a global ocean scale show the incredible diversity of diatoms and of their traits, which directly affect their potential for exporting organic carbon to depth. To better under-

stand and predict the fate of diatoms in a changing ocean (both in nutrient-limited systems and in light-or iron-limited systems) we need integrated strategies that combine physical, biogeochemical and biological approaches at different scales from local to global.

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Author contributions

P.T. coordinated the manuscript and figures. P.T., C.B., B.M., S.D., M.G., K.L., O.A., L.B., R.D., Z.F., L.G., D.I., M.La., M.Le., & P.P. all contributed to writing the manuscript. P.T., B.M., S.D., K.L., L.B., O.J. & P.P. worked on the figures. All authors read and approved the manuscript.

Competing interests

The authors declare no competing financial interests.