

# The life of diatoms in the world's oceans

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**Marine diatoms rose to prominence about 100 million years ago and today generate most of the organic matter that serves as food for life in the sea. They exist in a dilute world where compounds essential for growth are recycled and shared, and they greatly influence global climate, atmospheric carbon dioxide concentration and marine ecosystem function. How these essential organisms will respond to the rapidly changing conditions in today's oceans is critical for the health of the environment and is being uncovered by studies of their genomes.**

About one-fifth of the photosynthesis on Earth is carried out by microscopic, eukaryotic phytoplankton known as diatoms<sup>1</sup>. These photosynthetic workhorses are found in waters worldwide, wherever there is sufficient light and nutrients. Their name is derived from the Greek *diatomos*, meaning 'cut in half', a reference to their distinctive two-part cell walls made of silica (Fig. 1). Each year, diatom photosynthesis in the sea generates about as much organic carbon as all the terrestrial rainforests combined<sup>1,2</sup>. But unlike much of the carbon generated by trees, the organic carbon produced by diatoms is consumed rapidly and serves as a base for marine food webs. In coastal waters, diatoms support our most productive fisheries. In the open ocean, a relatively large proportion of diatom organic matter sinks rapidly from the surface, becoming food for deep-water organisms<sup>3</sup>. A small fraction of this sinking organic matter escapes consumption and settles on the sea floor, where it is sequestered over geological timescales in sediments and rocks and contributes to petroleum reserves. Given the crucial role of diatoms in the global carbon cycle, plans have been made, controversially, to reduce atmospheric levels of the greenhouse gas carbon dioxide by fertilizing large regions of the ocean with iron to generate huge blooms of diatoms<sup>4</sup>.

Fresh insight into the mechanisms underlying the global impact of diatoms came from the availability of the roughly 34 megabases (Mb) of DNA sequence for the nuclear, plastid and mitochondrial genomes of the cosmopolitan diatom *Thalassiosira pseudonana*<sup>5</sup>. Whole-genome sequence of a second model diatom, *Phaeodactylum tricornutum* (27 Mb), soon followed<sup>6</sup>, and draft sequence is now available for the polar species *Fragilariopsis cylindrus* (80 Mb) and the toxigenic coastal species *Pseudo-nitzschia multiseries* (300 Mb). One of the more intriguing outcomes of the sequencing projects thus far is a recognition of the unique combination of genes and metabolic pathways that distinguish diatoms from the evolutionarily distinct plant and animal lineages. Enormous amounts of diversity are encapsulated within diatoms. For example, *T. pseudonana* and *P. tricornutum* probably diverged from one another only about 90 million years (Myr) ago, yet their genomes are about as different as those of mammals and fish, which diverged about 550 Myr ago<sup>6</sup>.

Here I explore the intersection of diatom ecology, biogeochemistry and genomics, with a focus on the roles of diatoms in past and contemporary oceans. What emerges is a genomics-based reflection of the complex interactions that define marine ecosystems, in which metabolites and capabilities are shared across different kingdoms of organisms. The goal is twofold: first, to provide a window into the fascinating world of this unusual group of organisms that has such a crucial role in regulating the stability of our planet; and second, to gain a deeper understanding of how diatoms may fare under future ocean conditions.

This is crucial because alterations in diatom populations resulting from climate change could have a dramatic effect on Earth's atmosphere.

## Life in the ocean waves

Marine microbial communities are incredibly diverse, consisting of interconnected groups of cyanobacteria, heterotrophic Bacteria, Archaea, viruses, eukaryotic phytoplankton and protists. The most abundant phytoplankton in the sea are the marine cyanobacteria of the genus *Prochlorococcus*. The most diverse group of phytoplankton is the diatoms, with an estimated 200,000 different species, ranging in size from a few micrometres to a few millimetres and existing either as single cells or as chains of connected cells<sup>7</sup> (Fig. 1). Diatoms reproduce primarily by mitotic divisions interrupted infrequently by sexual events (Box 1). They bloom quickly, increasing in cell number by many orders of magnitude in just a few days. Diatoms tend to dominate phytoplankton communities in well-mixed coastal and upwelling regions, as well as along the sea-ice edge, where sufficient light, inorganic nitrogen, phosphorus, silicon and trace elements are available to sustain their growth<sup>8</sup>. In polar environments, where glaciers and permafrost limit photosynthesis on land, diatoms are critical components of the food webs that sustain both marine and terrestrial ecosystems. Larger species of diatoms can move up and down through the water column by controlling their buoyancy. Certain open-ocean species can move between well-lit but nutrient-depleted surface waters, in which they photosynthesize, and nitrate-rich waters at a depth of about 100 m, where they take up and store the nutrients necessary to keep dividing<sup>9</sup>. Diatoms seem to have exquisite communication capabilities, using a nitric-oxide-based system that mediates signalling between and within cells and regulates the production of aldehydes<sup>10</sup>, which can be harmful to grazing copepods<sup>11</sup>.

## Mix-and-match genomes

Diatoms have a complex evolutionary history that is distinct from plants, the dominant photosynthetic organisms on land<sup>12</sup>. Oxygenic photosynthesis had its origins in cyanobacteria, but different endosymbiotic events gave rise to plants and diatoms (Fig. 2). The initial, primary, endosymbiosis occurred about 1.5 billion years ago, when a eukaryotic heterotroph engulfed (or was invaded by) a cyanobacterium to form the photosynthetic plastids of the Plantae, the group that includes land plants and red and green algae<sup>13</sup>. Genes were subsequently transferred from the symbiotic cyanobacterial genome to the host nucleus, with about 10% of Plantae nuclear genes being derived from the cyanobacterial endosymbiont<sup>14</sup>. About 500 million years later, a secondary endosymbiosis occurred, in which a different eukaryotic heterotroph captured a red alga. Over time, the red-algal

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endosymbiont was transformed into the plastids of the Stramenopiles, the group that includes diatoms, brown macroalgae and plant parasites. Gene transfer continued from the red-algal nuclear and plastid genomes to the host nucleus<sup>5</sup>. At least 170 red-algal genes have been identified in the nuclear genome of diatoms, most of which seem to encode plastid components<sup>6</sup>. As in Plantae plastids, photosynthesis and the biosynthesis of fatty acids, isoprenoids and amino acids are carried out in diatom plastids.

Diatoms have a distinctive range of attributes that can be traced to this union between heterotrophic host and photosynthetic red alga. For example, unlike plants, diatoms have a complete urea cycle, although it remains to be seen how they use this pathway. The urea cycle was previously thought to be restricted to organisms that consume complex organic nitrogen compounds and excrete nitrogenous waste products<sup>5</sup>. Diatoms also combine an animal-like ability to generate chemical energy from the breakdown of fat with a plant-like ability to generate metabolic intermediates from the breakdown, a combination that probably allows diatoms to survive long periods of darkness, as occurs at the poles, and resume division and growth when they return to the light<sup>5</sup>. Numerous examples of this mix-and-match compilation of characteristics reiterate the simple fact that diatoms are neither plants nor animals.

More recent analyses suggest additional contributions to the mixture that defines diatom genomes. One unexpected twist was revealed by comparative analyses with the Chlamydiae, a group of intracellular bacteria that today exist only as pathogens or symbionts. The presence of some chlamydial genes in both plants and red algae, but not in cyanobacteria, suggests that a chlamydial endosymbiont also tagged along during the early stages of the primary endosymbiosis<sup>15</sup>. Further analysis suggests that in addition to the red alga, a green alga may have contributed to the mix of nuclear genes in diatoms<sup>16</sup>.

A second twist is the finding that at least 587 genes in the *P. tricornutum* nuclear genome seem to share a history with diverse lineages of bacteria in addition to the Chlamydiae<sup>6</sup>. Some bacterial genes replaced homologous genes found in other phototrophs, whereas others provided new functions to the diatoms<sup>17</sup>. Less than half the bacterial genes in *P. tricornutum* are shared with *T. pseudonana*, and only 10% are shared between *T. pseudonana* and the distantly related oomycete *Phytophthora*<sup>6</sup>, suggesting that independent gains and losses of bacterial genes by diatoms are ongoing. Finally, viruses also seem to mediate gene transfer to diatoms<sup>18</sup>, although the extent of this process is still unclear<sup>12</sup>.

The emerging picture is that the different species of diatoms are characterized by a complex combination of genes and pathways acquired from a variety of sources (Fig. 2). Endosymbiotic events defined the overall capabilities of diatoms, but subsequent gains (or losses) of specific genes, largely from bacteria, presumably helped them adapt to new ecological niches. What factors might underlie this constantly evolving mixture of attributes? Bacteria in the sea outnumber diatoms by many orders of magnitude, ensuring that diatoms are never free of bacterial influences. There are numerous examples of diatom dependency on bacterial metabolites such as vitamins<sup>19,20</sup> and of bacterial dependency on released diatom metabolites<sup>21,22</sup>. Some bacteria attach to diatoms by embedding themselves in the crevices of diatom cell walls<sup>23</sup>. Open-ocean diatoms can harbour nitrogen-fixing cyanobacteria under their silica cell wall, whereas other nitrogen-fixing cyanobacteria attach to silica spines protruding from the walls<sup>24</sup>. In the most extreme example, bacteria have been reported to live between the third and fourth outermost membranes of the plastids of a freshwater diatom<sup>25</sup>. All this was possible because diatoms evolved in a dilute world where essential metabolites are shared across kingdoms. Redundancy, reliability and ease of transfer of different components of this metabolic soup in different environments probably influence whether the cross-kingdom interaction is opportunistic or an obligate symbiosis, perhaps with the incorporation of critical bacterial genes as an end point. Studying diatoms in the sterile environment of the laboratory is an important first step in predicting responses to environmental change, but new sequencing technologies that yield greater amounts of information at a lower cost provide opportunities to study these organisms in laboratory consortia that may more closely mimic the real world. Ultimately, metagenomic tools amenable to studying organisms with large genomes will be essential for understanding how diatoms function in nature.

### The rise of diatoms

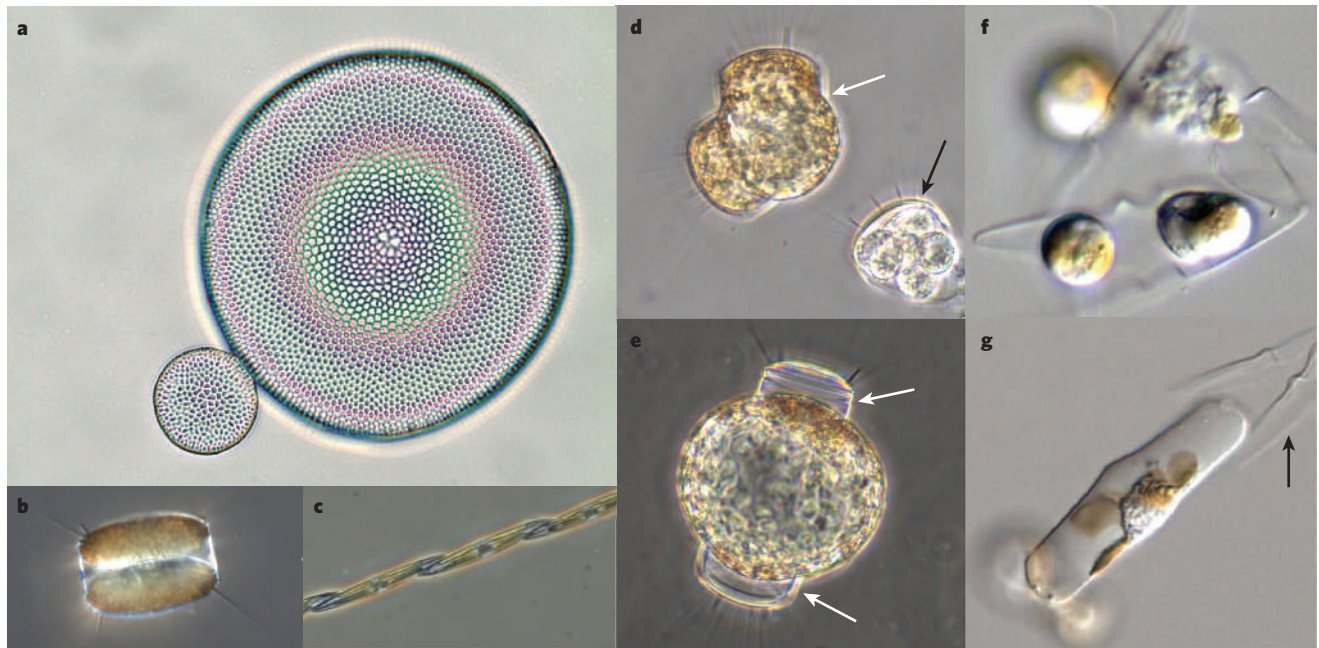
Molecular-clock-based estimates suggest that diatoms arose in the Triassic period, perhaps as early as 250 Myr ago<sup>26</sup>, although the earliest well-preserved diatom fossils come from the Early Jurassic, some 190 Myr ago<sup>27</sup>. Before the diatoms, the phytoplankton consisted primarily of cyanobacteria and green algae only slightly larger than bacteria<sup>28</sup>. The emergence of diatoms and two other groups of larger eukaryotic phytoplankton, the dinoflagellates and coccolithophorids, resulted in a major shift in global organic carbon cycling. This initiated an era of declining atmospheric CO<sub>2</sub> concentrations and increasing atmospheric



**Figure 1 | Micrographs of different diatom species.** **a–c**, Diatoms can exist as single cells or chains of cells, as illustrated in a concentrated field sample (**a**). The two main morphological categories of diatoms are pennate (**b**, *Pseudo-nitzschia*) and centric (**c**, *Thalassiosira*). The two halves of the cell wall (valves) fit together like a Petri dish (**c**) that appears round (or oval) when viewed from the top and rectangular when viewed from the side. **d**, The two valves (arrows) are held together by a series of siliceous hoops, or girdle bands (brackets), seen in more detail in this scanning electron

micrograph of *Thalassiosira pseudonana*. New girdle bands are laid down during cell growth. The patterns of pores and other cell-wall structures are species specific. **e, f**, Photosynthesis takes place in membrane-bound plastids that appear as small discs within the cell (**e**) and contain the photosynthetic pigment chlorophyll *a*, which fluoresces red when illuminated with blue light (**f**). (Images courtesy of K. Holtermann, University of Washington, Seattle (**a, c, e, f**), P. von Dassow, Station de Biologique de Roscoff, France (**b**) and N. Kröger, Georgia Institute of Technology, Atlanta (**d**).

## Box 1 | The sex life of diatoms



Living in a glass box has created some interesting life-cycle attributes for diatoms. Physical and developmental constraints associated with replication of the cell wall mean that in each mitotic division, one daughter cell is slightly smaller than the other. Over successive divisions, cells of dramatically different sizes are found within a population (**a**, *Coccosira*). Cell size is ultimately restored through sexual reproduction, which occurs differently in centric (**b**) and pennate (**c**) diatoms. In centric diatoms (**b**, *Thalassiosira*), only small cells are receptive to an environmental trigger and can become either sperm (**d**, white arrow), which break free of the wall, or eggs, which remain encased within the wall (**d**, black arrow). Sperm swim to an egg, gain entry past the glass wall, and fertilize the egg nucleus. The resultant zygote swells to form a specialized cell known as the auxospore (**e**), sheds its old cell walls (**e**, arrows) and produces a much larger wall, restoring cell size. This is risky for a centric diatom because if sperm are

unable to find eggs in the dilute ocean, the gametes will die. Pennates (**c**, *Pseudo-nitzschia*) also have a size requirement for the initiation of sexual reproduction, but seem to form gametes only when they find an appropriate mate of the opposite sex, a seemingly less risky option. When paired, pennate cells produce morphologically identical gametes (**f**), which are unable to swim and instead move towards one another in an amoeba-like fashion and fuse to create the zygote and auxospore (**g**), which breaks free of the old cell wall (arrow). The sexual cycle of most diatoms cannot be controlled in the laboratory, hindering the development of classical genetic studies. Instead, genetic manipulation of diatoms has relied primarily on the addition of new versions of genes (transformation)<sup>12</sup> or on reduced expression of targeted genes (RNA interference)<sup>12</sup>. (Images courtesy of J. Koester, University of Washington, Seattle (**a**), P. von Dassow, Station Biologique de Roscoff, France (**b**, **d**, **e**) and K. Holtermann, University of Washington, (**c**, **f**, **g**.)

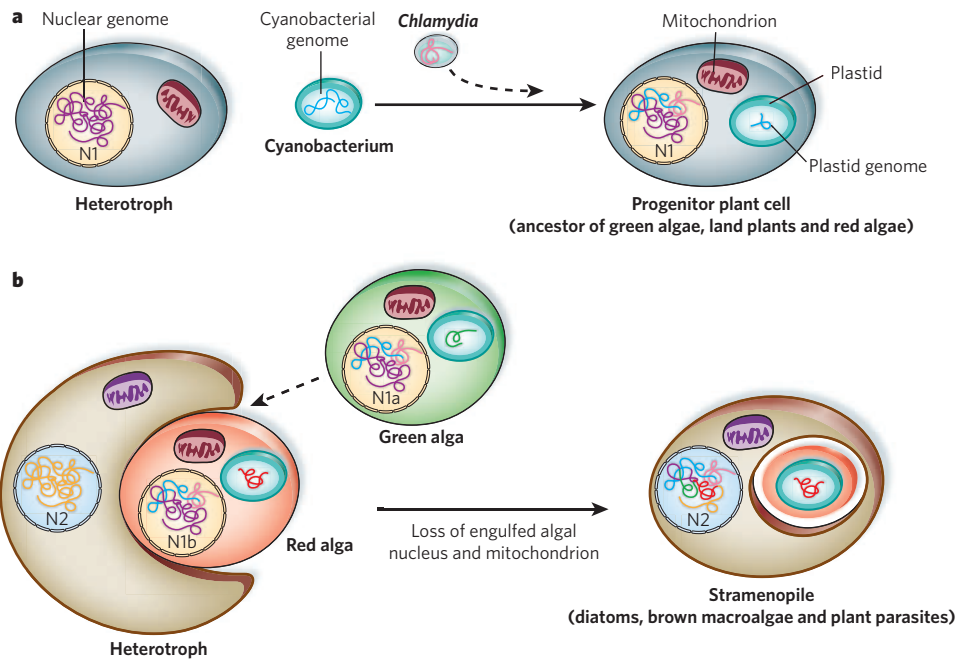
O<sub>2</sub> concentrations<sup>29</sup>. The increased sinking rates associated with these large phytoplankton led to enhanced burial of organic carbon in continental margins and shallow seas, creating most of the petroleum reserves known today<sup>30</sup>. Consider that the early Mesozoic ocean differed dramatically from modern oceans. Atmospheric concentrations of CO<sub>2</sub> were almost eight times higher than today<sup>31</sup>; the average global temperature was significantly higher; and Africa and Europe were beginning to separate, leading to extensive flooding of continental shelves. This probably led to increased continental weathering and released large amounts of nutrients, which increased phytoplankton activity<sup>29,32</sup>. Additionally, the absence of polar ice caps and the smaller pole-to-equator temperature gradient reduced ocean circulation and increased stratification of the water column. Together, these factors decreased the oxygenation of the oceans and contributed to ocean anoxic events. Fossil records reveal that the earliest diatoms, known as radial centrics (Fig. 3), had a heavy, highly silicified cell wall that initially restricted them to a benthic lifestyle in shallow, near-shore waters.

Diatoms assumed their dominant role in the carbon cycle about 100 Myr ago, during the Cretaceous period, when atmospheric CO<sub>2</sub> levels were still about five times higher than they are today<sup>31</sup> and O<sub>2</sub> levels were increasing<sup>30</sup>. Ocean stratification was decreasing as the nutrient supply to surface waters increased. The proliferation of diatoms and other photosynthetic organisms during this period increased the oxygenation of surface waters with a concomitant decrease in iron availability. These conditions coincided with the divergence of a second

major lineage of diatoms, the bipolar and multipolar centrics, which includes members of *Thalassiosira*, the genus first chosen for whole-genome sequencing (Fig. 3).

The mass extinction at the end of the Cretaceous, about 65 Myr ago, led to loss of about 85% of all species, including substantial reductions in the diversity of marine dinoflagellates and coccolithophorids<sup>28</sup>. Diatoms survived this event relatively unscathed and began to colonize offshore areas, including the open ocean. Centric species that migrated into the open ocean were able to survive despite the reduced nutrient levels there, further increasing their impact on the global carbon cycle. A third group of diatoms, the araphid pennates, are detected in the fossil record from this period (Fig. 3).

By 50 Myr ago, atmospheric O<sub>2</sub> concentrations had stabilized to today's levels, further reducing iron concentrations in the open ocean, and atmospheric CO<sub>2</sub> concentrations continued to decline to near today's levels<sup>31</sup>. Diatom diversity peaked at the Eocene/Oligocene boundary, some 30 Myr ago<sup>33</sup>, and a fourth group of diatoms, the raphid pennates, emerged (Fig. 3). These are distinguished by a slit (raphe) in their walls that allows them to glide along surfaces<sup>7,27</sup>. The evolution of the raphe greatly expanded the ecological niches available and probably had as profound an impact on diatom diversification as the evolution of flight had on birds<sup>27</sup>. Today, the raphid species *Fragilariopsis kerguelensis* dominates the diatom community in the Southern Ocean, the largest region of diatom-based carbon export<sup>34</sup>. Three of the four diatoms with complete or draft genome sequences are raphid pennates. Genome-based detection of differences in the regulation of



**Figure 2 | Endosymbiosis in diatoms.** Representation of the origin of diatom plastids through sequential primary (a) and secondary (b) endosymbioses, and their potential effects on genome evolution. **a**, During primary endosymbiosis, a large proportion of the engulfed cyanobacterial genome is transferred to the host nucleus (N1), with few of the original genes retained within the plastid genome. The potential for invasion of the host by a chlamydial parasite is indicated with a dashed arrow, and the ensuing transfer of chlamydial genes to the host nucleus is indicated in pink. The

progenitor plant cell subsequently diverged into red and green algae and land plants, readily distinguished by their plastid genomes. **b**, During secondary endosymbiosis, a different heterotroph engulfs a eukaryotic red alga. Potential engulfment of a green algal cell as well is indicated with a dashed arrow. The algal mitochondrion and nucleus are lost, and crucial algal nuclear and plastid genes (indicated in blue, purple and pink) are transferred to the heterotrophic host nucleus, N2. Additional bacterial genes are gained and lost throughout diatom evolution, but for simplicity this is not indicated here.

carbon fixation by the bipolar centric *T. pseudonana* and the raphid pennate *P. tricorutum*<sup>35</sup> may reflect the different atmospheric CO<sub>2</sub> and O<sub>2</sub> conditions, and the resultant seawater chemistries, when the two lineages emerged.

### The need for iron

Primary productivity in 30–40% of the world's contemporary oceans is limited by the availability of iron, particularly in open-ocean regions of the Southern Ocean, equatorial Pacific Ocean and north Pacific Ocean<sup>36</sup>. These high-nutrient, low-chlorophyll (HNLC) regions are characterized by exceedingly low concentrations of iron and high concentrations of other essential nutrients, such as nitrate, phosphate and silicic acid. Diatoms in the open ocean reduce their iron requirements under iron-limiting conditions<sup>37,38</sup>. Open-ocean centric species of *Thalassiosira*, for example, seem to have permanently modified their photosynthetic apparatus to require less iron<sup>39</sup> and have replaced iron-requiring electron-transport proteins with equivalent ones that need copper<sup>40</sup>. These changes seem to have compromised their ability to deal with the rapidly fluctuating light fields more characteristic of coastal environments<sup>39</sup>. Raphid pennate diatoms can also greatly reduce their iron requirements<sup>41</sup>, but they seem to do so using more flexible modifications, avoiding irreversible compromises. When starved of iron, *P. tricorutum* downregulates processes that require a lot of iron, such as photosynthesis, mitochondrial electron transport and nitrate assimilation<sup>42</sup>. By way of compensation, these iron-limited cells restructure their proteome, upregulate alternative pathways for dealing with oxidative stress, and upregulate additional iron-acquisition pathways<sup>42</sup>. The presence of different iron-responsive genes suggests that raphid pennate and bipolar centric diatoms have fundamentally different systems for acquiring iron<sup>41,42</sup>.

Centric and pennate diatoms also differ in their ability to store iron, a critical attribute for existence in the open ocean, where the iron supply is sporadic<sup>43</sup>. Members of the raphid pennate genera *Pseudo-nitzschia*,

*Fragilariopsis* and *Phaeodactylum* all produce ferritin, an iron-storage molecule that also protects against oxidative stress<sup>44</sup>. No other members of the Stramenopiles seem to encode ferritin, including *T. pseudonana*, and it seems that this gene may have arisen in the restricted subset of pennate diatoms through a lateral gene transfer from another organism<sup>44</sup>. The enhanced iron storage provided by ferritin in *Pseudo-nitzschia* probably underlies its numerical dominance in the massive diatom blooms that result from iron fertilization (Fig. 4) and helps to explain the importance of raphid diatoms in regulating the flux of CO<sub>2</sub> into surface waters<sup>44</sup>. So far, the *T. pseudonana* genome has provided no clues to how centric diatoms store iron, suggesting that novel mechanisms are used.

### Living in glass houses

One of the most striking features of diatoms is their beautiful cell wall made essentially of hydrated glass (SiO<sub>2</sub>.*n*H<sub>2</sub>O)<sup>45</sup> (Fig. 1 and Box 1). In creating these walls from silicon dissolved in sea water as silicic acid, diatoms control the biogenic cycling of silicon in the world's oceans to such an extent that every atom of silicon entering the ocean is incorporated into a diatom cell wall on average 39 times before being buried on the sea floor<sup>46</sup>. Depending on the conditions<sup>1</sup>, cell walls from dead diatoms can accumulate on the sea floor as immense deposits of silica up to 1,400 metres thick, as found on Seymour Island in the eastern Antarctic Peninsula<sup>27</sup>. The resulting diatomaceous earth has a variety of uses, including as flea powder, insulation and toothpaste ingredients.

The elaborate species-specific patterns of nano-scale to micro-scale pores, ridges and tubular structures are genetically controlled, although external factors such as salinity influence the density and pore size of the precipitated silica<sup>47</sup>. Their ability to produce silica structures in three dimensions has made diatoms attractive models for nanotechnology<sup>45</sup> and has prompted extensive searches for components of the necessary genetic machinery. The cell wall is produced in an acidic silica-deposition vesicle and encased in an organic matrix that is rich in proteins and

sugars, preventing the silica from dissolving in sea water. Consumption of this matrix by bacteria accelerates the recycling of silicon within surface waters<sup>48</sup>. Three categories of molecule normally embedded directly within the wall can precipitate silica in artificial systems: silaffins, which are highly modified phosphoproteins<sup>49</sup>; long-chain polyamines<sup>50</sup>; and silacidins, which are acidic proteins<sup>51</sup>. Both the amount and structure of each type of molecule differ between species, consistent with them having a critical role in the species-specific patterns of cell-wall nanostructures. More than 150 additional gene products potentially required for silicon biomanipulation have been identified in *T. pseudonana*<sup>52</sup>. Half of the genes are upregulated when cells are starved of either silicon or iron, suggesting that the iron and silicon pathways are linked. A similar connection between iron and silicon pathways was not reported for *Phaeodactylum*<sup>42</sup>, although it is not yet clear whether this reflects another difference between centric and pennate diatoms or the fact that *Phaeodactylum* is the only known diatom that lacks an obligate requirement for silicon.

Interactions between iron availability and silicon usage by diatoms in the Southern Ocean are thought to explain, in part, the reduction in atmospheric concentrations of CO<sub>2</sub> during glacial periods<sup>53</sup>, when iron concentrations were higher. Under iron-rich conditions, diatom communities use less silicon relative to nitrogen, leaving excess silicate in surface waters. This excess then circulates out of the Southern Ocean and fuels diatom, rather than coccolithophorid, productivity in the subtropics<sup>54</sup>. During glacial intervals, the increased amount of organic matter produced by diatoms is thought to sink into deep waters, resulting in long-term sequestration of atmospheric CO<sub>2</sub> (ref. 54).

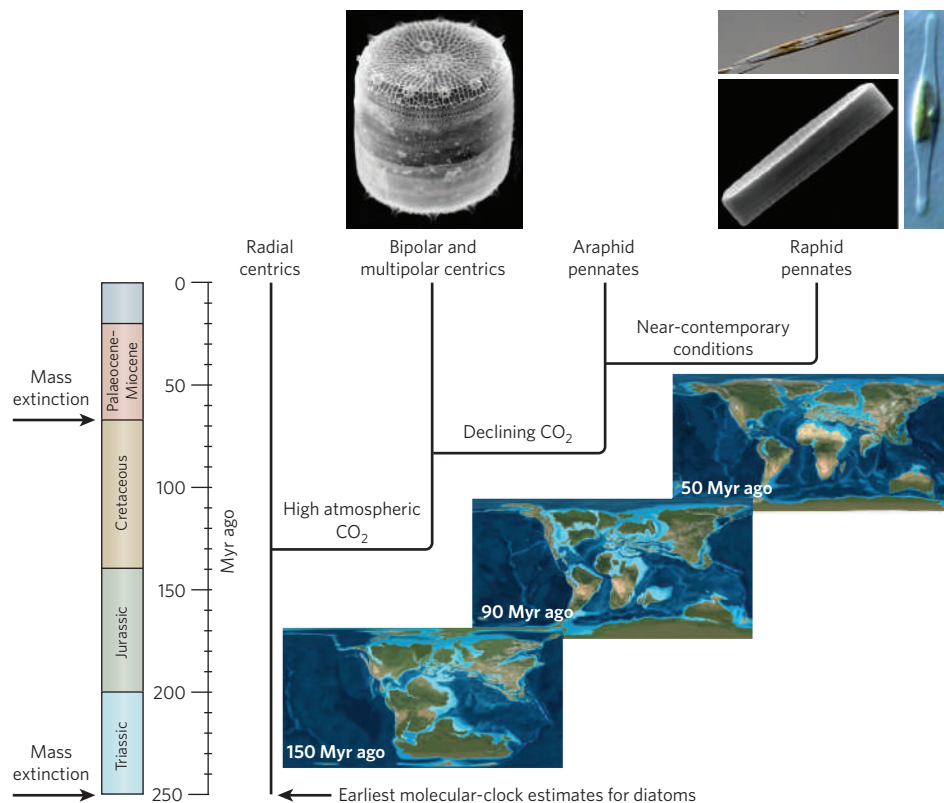
Several studies have mimicked these glacial-interval effects of iron

on diatoms by fertilizing iron-limited regions of the ocean with iron. The hope of some is that this will increase the export of carbon from surface waters and thus slow the rising levels of atmospheric CO<sub>2</sub> generated by the burning of fossil fuel. Iron-enrichment experiments done so far confirm that iron fertilization does produce the expected diatom blooms (Fig. 4), but most of the organic carbon generated by the bloom is consumed and recycled in surface waters. There is a relatively small increase in the amount that sinks to deep waters<sup>55</sup>. Even large-scale fertilization projects can be expected to draw down just a small fraction of the accelerating amounts of CO<sub>2</sub> entering the atmosphere, and even this has the potential to shift community composition and generate other greenhouse gases<sup>4</sup>. If we want to sequester large amounts of CO<sub>2</sub>, we must look elsewhere for a solution.

**Deadly diatoms**

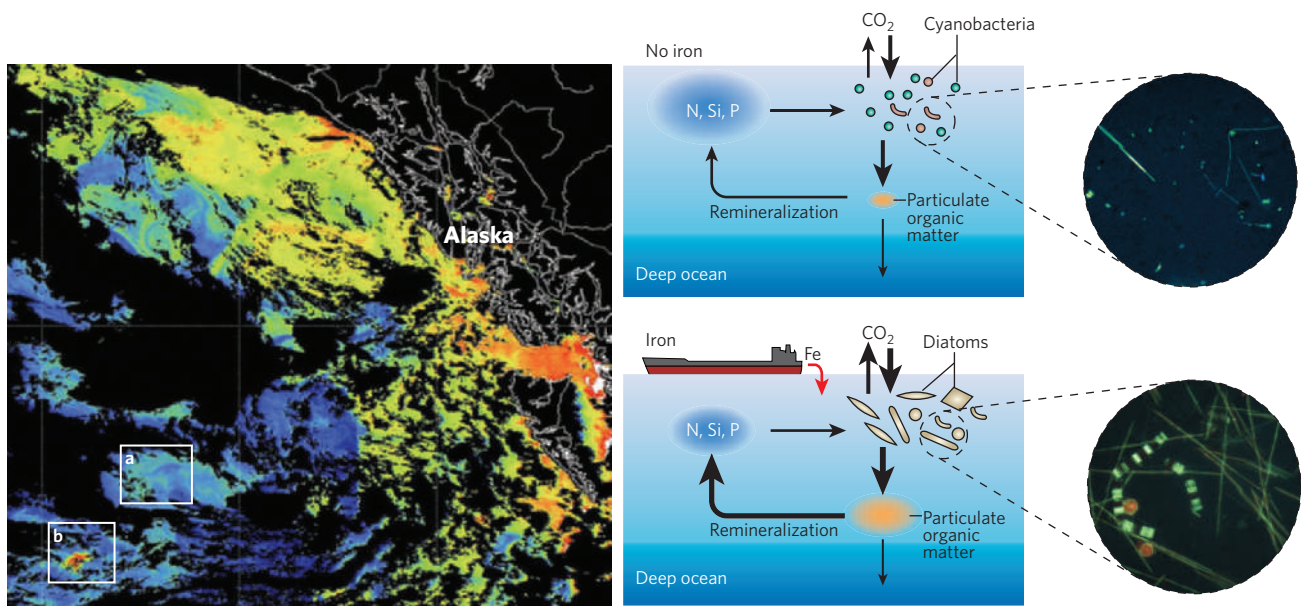
The ability of diatoms to affect humans is not limited to their role in the global carbon cycle. In 1987, 107 people became ill and 3 people died after eating mussels contaminated with the powerful neurotoxin domoic acid. Detective work showed that the toxin was produced by the diatom *P. multiseriis*<sup>56</sup>, whose genome is currently being sequenced. Domoic acid is water soluble and binds to glutamate receptors, causing a massive depolarization of nerve cells, particularly in the hippocampus. Crustaceans, bivalves and fish all serve as vectors of domoic acid to humans and other vertebrates<sup>56</sup>. Careful monitoring of shellfish has prevented further documented incidents in humans, but wild animals, including birds and mammals, are increasingly being affected by domoic acid<sup>57</sup>.

The genus *Pseudo-nitzschia*, which is the chief culprit, comprises at



**Figure 3 | Estimated timing of divergence of the four major diatom lineages and coincident events in Earth's history.** Shown above two of the branches are images of the four species for which the whole genome sequence is available: the multipolar centric *Thalassiosira pseudonana* (courtesy of N. Kroger, Georgia Institute of Technology, Atlanta), and the raphid pennates (from left to right) *Pseudo-nitzschia multiseriis* (top; courtesy of K. Holtermann, University of Washington, Seattle), *Fragilariopsis cylindrus* (bottom; courtesy of G. Dieckmann, Alfred-Wegener-Institut für

Polar- und Meeresforschung, Bremerhaven, Germany) and *Phaeodactylum tricoratum* (right; courtesy of C. Bowler, Ecole Normale Supérieure, Paris). To date, neither a representative radial centric nor an araphid pennate has been chosen for whole-genome sequencing. Maps (courtesy of R. C. Blakey, Northern Arizona University, Flagstaff) are palaeogeographic reconstructions of continent locations during the emergence of the diatom lineages. Shallower depths in the ocean are indicated by lighter blues. Timing of divergence in Myr ago compiled from refs 7 and 26.



**Figure 4 | The effect of iron fertilization on diatoms.** The left panel shows a SeaWiFS satellite image of a phytoplankton bloom resulting from iron fertilization in the northeast Pacific Ocean during the SERIES iron-enrichment experiment. The coast of Alaska is shown. Warm colours (reds and yellows) indicate high concentrations of chlorophyll *a* and thus high phytoplankton biomass; cool colours (blues) indicate low chlorophyll *a* concentrations. Dark areas over the ocean result from cloud cover. White boxed regions indicate areas of no iron addition (**a**) and a 700-km<sup>2</sup> region of high chlorophyll *a* concentration, resulting from the addition of iron (**b**). Middle panels show representations of phytoplankton communities and the relative nutrient concentrations present before (top) and after (bottom) the addition of iron to surface waters. The thicker arrows in the bottom panel

reflect enhanced carbon fluxes after the addition of iron. The right panels show micrographs of the resultant phytoplankton communities before and after the addition of iron to surface water, collected from a site near that in **b**. In both cases, most of the newly fixed carbon is consumed and respired as CO<sub>2</sub> in the upper ocean. The addition of iron shifts the community from one dominated by small cyanobacteria to one dominated by raphid pennate diatoms such as *Pseudo-nitzschia* (needle-like cells) and centric diatoms (other red or green cells). Both communities were stained with a dye that localizes to newly precipitated silica to illustrate actively dividing diatoms. N, nitrate; P, phosphate; Si, silicic acid. (Left panels courtesy of J. Gower, Orbimage/NASA. Right panels courtesy of C. Durkin and A. Marchetti, University of Washington, Seattle.)

least 30 described coastal and open-ocean species, including some that dominate iron-enrichment experiments in HNLC regions<sup>58</sup>. Only about one-third of known *Pseudo-nitzschia* species and one species of the closely related *Nitzschia* have been shown to produce domoic acid; no other diatoms are known to make toxins. Domoic acid production can be controlled under laboratory conditions, although the absolute concentration produced varies between species, as well as between different strains of the same species; for example, open-ocean strains have not been found to produce significant amounts of domoic acid<sup>59</sup>. Numerous explanations for the observed variation have been proposed<sup>56</sup>. Variation in toxin production among strains could reflect differences in their associated bacterial communities<sup>23</sup>, possibly representing another example of interaction between kingdoms<sup>60</sup>. Alternatively, initial analysis of the *Pseudo-nitzschia* genome indicates the presence of a large number of transposable elements, or 'jumping genes'. Movement of these elements to positions near important regulators of domoic acid production could also result in apparently random changes in different strains. The availability of the genome sequence for *P. multiseriata* should provide more insights into domoic acid biosynthesis, allowing researchers to profile production capabilities across different species, to better characterize their responses to environmental triggers, and to examine the molecular interactions between toxin-producing cells and bacteria. The genomic data should also help to determine whether toxin production by *Pseudo-nitzschia* is a further example of capabilities being gained directly from another organism.

### Seas of change

The oceans are constantly changing. Every day, about 22 million tonnes of atmospheric CO<sub>2</sub> dissolves in the oceans, lowering the pH and changing the chemistry, potentially making it harder for organisms such as bivalves, corals and coccolithophorids to create their calcium carbonate shells<sup>61</sup>. Seasonal variability in the upwelling of

deep CO<sub>2</sub>-rich waters amplifies the acidification, particularly in the Southern Ocean<sup>62</sup> and coastal upwelling systems<sup>61</sup>, where productivity tends to be dominated by diatoms. Ocean waters are also warming<sup>63</sup>, wind patterns are shifting, and ocean circulation is changing<sup>64</sup>, which together shift turbulent mixing and the delivery of nutrients from deep waters to surface waters<sup>32</sup>. In addition, low-nutrient open-ocean regions seem to be expanding<sup>65</sup>. Rapid warming in the Arctic has thinned and melted sea ice, potentially enhancing phytoplankton productivity as more light penetrates to deeper waters but potentially dampening diatom productivity through changes in the delivery of silicate-rich or nitrate-rich waters to the Arctic. In the Southern Ocean, wind intensity is increasing, affecting the Antarctic Circumpolar Current<sup>64,66</sup>. Wind-driven changes in the speed of this current could shift the delivery of both phytoplankton nutrients and CO<sub>2</sub> from deep waters to surface waters. Globally, populations of apex predators are declining, and nutrient inputs into coastal waters continue to rise<sup>67</sup>, giving concern that these changes may be linked to more frequent blooms of toxin-producing phytoplankton<sup>57</sup>. Couple these human-induced changes with the effect of natural climatic oscillations<sup>68</sup> and the urgent need for better monitoring of marine ecosystems becomes clear<sup>69,70</sup>.

How will critical components of marine food webs, such as diatoms, respond to such large changes occurring over a relatively short time? Some predict that diatoms will have a greatly reduced role in future phytoplankton communities. In this scenario, the ocean would be dominated by cyanobacteria, green algae<sup>32</sup> and coccolithophorids<sup>71</sup>, groups well adapted to compete in the low-nutrient environments characteristic of a less turbulent ocean. A shift away from diatom-based communities would bring a dramatic reduction in the ability of ocean biota to sequester CO<sub>2</sub> from the atmosphere, exacerbating climate change<sup>71</sup>. However, diatoms are masters at surviving in a wide variety of conditions, including in highly stratified, nutrient-poor regions such as the North Pacific Gyre<sup>72</sup>. Even so, there will be changes to the distribution

of some species of diatom and perhaps to the timing of diatom blooms. Many species will adapt to the changing ocean environment, but others will decline in abundance and some will disappear.

### The future of diatom research

It is important to know how diatoms affect ocean ecology and biogeochemistry at any given time in any given region. Sequencing the genomes of additional representative diatoms, in combination with analysing the genomes of diatom communities in nature, will identify the core attributes that allowed these organisms to cope with past conditions and will help to interpret responses to today's conditions. Next-generation ecogenomic sensors (see page 180), which continuously monitor the presence of sentinel species or the expression of sentinel genes, are needed to provide information about global patterns of biologically relevant physicochemical properties. Continuously monitoring the genes encoding the iron-storage molecule ferritin, for example, would provide information about the presence and the biological availability of iron in surface waters, which both seem to be changing<sup>73</sup>. This increasingly genomic approach will make it possible to move beyond speculation about the state of the environment to instead document the changes actually occurring in critical groups such as diatoms before they become the new canaries in the coal mine.

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