

PERSPECTIVES

OPINION

Mix and match: how climate selects phytoplankton

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Abstract | Climate strongly influences the distribution and diversity of animals and plants, but its affect on microbial communities is poorly understood. By using resource competition theory, fundamental physical principles and the fossil record we review how climate selects marine eukaryotic phytoplankton taxa. We suggest that climate determines the equator-to-pole and continent-to-land thermal gradients that provide energy for the wind-driven turbulent mixing in the upper ocean. This mixing, in turn, controls the nutrient fluxes that determine cell size and taxa-level distributions. Understanding this chain of linked processes will allow informed predictions to be made about how phytoplankton communities will change in the future.

Analyses of the stable isotopic record for carbon, nitrogen and sulphur have suggested that, over the course of the Earth's history, all core microbial metabolic processes have survived sudden, forceful changes to the environment^{1–3} (P.G.F. and L. Godfrey, unpublished observations). This does not mean that the community structure or the relative abundance of key microorganisms has remained constant over geological time. However, because of the difficulty in documenting historical changes in the prokaryotic component of the microbial community, we currently have no pattern from the Earth's history on which to base prognostic models.

Relative to prokaryotes, many eukaryotic phytoplankton have a well-preserved fossil record^{4–6}. Several taxa within this polyphyletic group have reinforced cell walls that fossilize in marine sediments. Based on these fossils, and on data that were derived from geochemical analyses, it is possible to reconstruct the evolutionary history of morphologically defined species on geological timescales. Although such reconstructions might not conform perfectly to clocked phylogenetic trees⁷, which are based on molecular biological

information, they do allow for a robust interpretation of macro-evolutionary changes that can be related to specific geological indices, such as sea-level⁸ and ocean-thermal⁹ structures that are climate-driven⁶.

In this Perspective, we consider the climate-driven processes that influence turbulent mixing in the ocean, which, in turn, seems to have strongly influenced the diversity and relative abundance of the three major eukaryotic phytoplankton taxa — dinoflagellates, coccolithophores and diatoms — over the past 200 million years (FIG. 1). By analysing experiments that used extant representative species from these three groups, we consider how climatically driven physical processes in the ocean have selected phytoplankton taxa in the geological past that are still present in the contemporary ocean. We also evaluate how such processes might influence microbial community structures in the coming centuries, based on projections of global climate models¹⁰.

Our basic premise is that physical (turbulent) mixing is a strong ecological determinant of the taxonomic composition of eukaryotic phytoplankton. This premise reiterates, in the context of historical climate change, the empirical relationship

between turbulence, nutrient supply and taxonomic selection that was eloquently proposed by Ramon Margalef^{11,12}. Whether this fundamental principle holds for marine prokaryotes remains to be seen, because the spatial and temporal distribution of prokaryotic taxa, as well as their relevant ecophysiological attributes, is not yet well characterized.

Mixing and ocean environmental structure

We first consider some of the basic concepts of the oceanic environment in relation to mixing. The ocean is divided into two horizontal layers: the upper ocean and the ocean interior. These two layers are separated by a pycnocline, which reflects the differences in density between the upper ocean and the ocean interior. These differences result primarily from either the heating of the upper ocean by solar radiation or its cooling by precipitation, melting ice or the deep-ocean transport of cold polar waters to the lower latitudes^{13,14}. The upper ocean is a special environment. Surface waters receive sufficient solar energy to support photosynthetic organisms, such as cyanobacteria and eukaryotic phytoplankton. As these organisms grow, they deplete the ocean surface of inorganic nutrients, particularly fixed inorganic nitrogen (found primarily as ammonium and nitrate) and soluble phosphorus (found primarily as dissolved inorganic phosphate). A fraction of the phytoplankton that grow in the upper ocean sink downwards into the deep ocean (the global average is approximately 15%^{15,16}), where the cells are hydrolysed and their contents are oxidized by heterotrophic and chemoautotrophic microorganisms to the lowest thermodynamically stable molecules. The elemental composition of these molecules reflects that of the average sinking flux¹⁷. Consequently, the deep waters contain a large reservoir of inorganic nutrients, but little particulate organic matter (FIG. 2). If the influence of riverine and aeolian nutrient inputs are ignored, the nutrients that are removed from the upper ocean by the sinking flux of organic matter are equal to the nutrients that are supplied from the ocean interior by mixing into the upper ocean¹⁸. It should be noted that the hydrolysis and oxidation of the sinking

flux of organic matter depletes the surface waters and enriches the ocean interior with inorganic carbon, simultaneously^{15,19}. This phenomenon, which is commonly called the biological pump²⁰, is dependent on cell size and taxa^{21–23}. Larger cells sink faster than smaller cells; diatoms sink faster than flagellated eukaryotes^{24–26} (FIG. 2).

In the upper ocean, the combination of solar heating and the nutrient draw-down by photosynthetic microorganisms of nutrients supplied from the ocean interior sets up two crucial, vertically opposing resource gradients that select for specific phytoplankton groups²⁷. The degree of overlap between these two vertical gradients is mainly determined by the amount of mixing between the upper and deep ocean along density surfaces (isopycnal mixing)^{28,29}, and, to a lesser extent, across the pycnocline (diapycnal mixing)^{13,30}. More mixing results in a deeper pycnocline where cells are exposed to more nutrients and less light, whereas less mixing results in a shallow pycnocline where cells are exposed to less nutrients and more light³¹. This simple configuration of the ocean water column is a stable system, in which stability

is related to the vertical density gradient (see Equation 1).

$$E = -\frac{1}{\rho} \left(\frac{\delta \rho}{\delta z} \right) \quad (1)$$

In Equation 1, E is the stability per metre, z is the depth in metres and ρ is the density of seawater in kilograms per m³. The larger the density gradient, the more stable the water column, with more energy being required for mixing³². Solar radiation provides the energy that stabilizes and layers the ocean. However, solar radiation is also a source of the energy that erodes the stability of the ocean water column by the generation of the wind that mixes the ocean. Low latitudes are warmed by the sun more than the poles. This asymmetric heating pattern creates an atmospheric equator-to-pole pressure gradient, which, along with the rotation of the Earth, controls the global wind patterns. In addition, the continents warm and cool faster than the ocean owing to the latent heat of the water, which results in continent-to-ocean atmospheric pressure gradients and winds along the ocean margins. Together, these wind patterns are the major forces that control the circulation and mixing of the surface ocean³³, and which erode

the stability of the water column. The crucial point, is that the climate-driven processes that regulate the intensity and distribution of solar radiation on the Earth can significantly affect both the stability of the water column and the upper ocean circulation patterns.

So far, we have only discussed the major patterns of ocean circulation at one level. However, there are several other important ocean-mixing processes that are ultimately driven by solar radiation and wind patterns, such as convective overturn and eddy formation. It is also proposed that tidal forces are a significant source of the energy that controls ocean mixing. However, regardless of the source of the flow that is generated, all of these flows have a turbulent fate. Turbulent energy cascades from large-scale flow fields in the ocean to microscopic scales. For example, when wind blows on the surface of water the top layers move faster than the lower layers. The velocity differences between these layers in these ocean flow fields (known as shear) cause turbulent eddies to be formed that are at first large (metres to tens of metres in scale), but subsequently propagate throughout the fluid to sub-millimetre scales, with little energy loss³⁴. In general, the faster the flow fields the larger the shear and the greater the amount of turbulence that is produced. This process, sometimes referred to as the Kolmogorov cascade (BOX 1), functions to erode the stability of the pycnocline, and is responsible for transporting nutrients from the bulk fluid to the surface of a microbial cell. As we will discuss, when considering nutrient supply at the cellular level, nutrient concentrations at the cell surface become important to the ecological and community structure of marine phytoplankton.

Nutrient uptake kinetics and mixing

Our concepts of the role of mixing in the kinetics and selection of taxa are based primarily on resource competition theory³⁵, which, in turn, is derived from nutrient-uptake kinetic models, such as those proposed by Droop³⁶. In these models, nutrient uptake and growth can be described by two separate, but related equations (see Equation 2),

$$\begin{aligned} \text{growth} &= \mu_{\infty} \left(1 - \frac{Q_{\min}}{Q} \right) \\ \text{uptake} &= V_{\max} \frac{R}{K + R} \end{aligned} \quad (2)$$

where Q is the internal nutrient concentration (nutrient quota), Q_{\min} is the minimum quota (a mathematically derived value for when growth rate is equal to 0), μ_{∞} is the growth rate of a species at an infinite cell quota, V_{\max} is the maximum nutrient-uptake

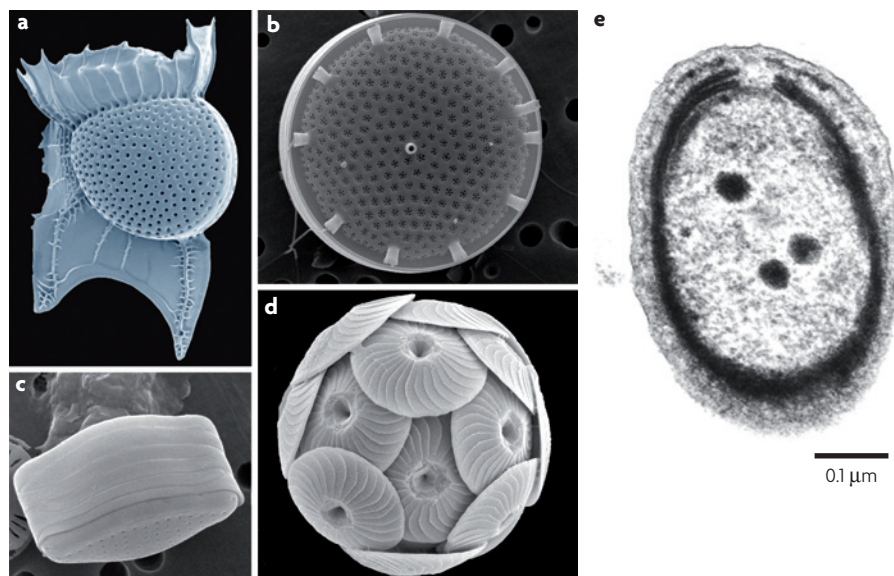


Figure 1 | Micrographs of representative eukaryotic phytoplankton taxa from the Phanerozoic period. **a** | A scanning electron micrograph of the thecate dinoflagellate *Ornithocercus* spp., 40 μm in diameter. **b** | A scanning electron micrograph showing a valve view of the centric diatom *Thalassiosira* spp., 6 μm in diameter. **c** | A scanning electron micrograph of the pinnate diatom *Fragilaria* spp., 5 μm in length. **d** | A scanning electron micrograph of the coccolithophorid *Calcidiscus quadriperforatus*, 15 μm in diameter. **e** | A transmission electron micrograph of a thin section taken across the length of an isolate of *Prochlorococcus marina*, the most abundant cyanobacterium in the oceans. The electron dense areas along the inner circumference of the cell are the photosynthetic membranes. Images **a** and **d** are courtesy of J. Young, Natural History museum, London, United Kingdom, images **b** and **c** are courtesy of A. Kahn, Rutgers University, New Jersey, USA and image **e** is courtesy of S. W. Chisholm, MIT (Massachusetts Institute of Technology), Massachusetts, USA.

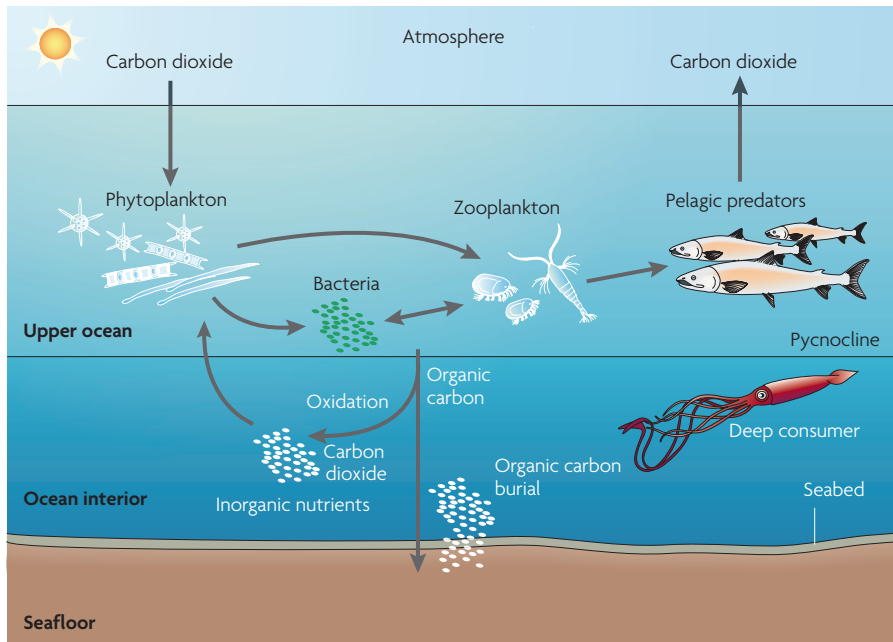


Figure 2 | A cartoon of the biological pump. Phytoplankton use solar energy in the upper ocean to fix carbon dioxide and form particulate organic carbon. Most of the organic carbon is consumed and respired in the upper ocean by herbivores and bacteria. Approximately 15% of the organic matter is exported below the thermocline to the ocean interior, where most is consumed and respired. The flux of the organic matter to the ocean interior, and its subsequent oxidation, enriches the inorganic nutrient pool below the thermocline. Consequently, the concentration of inorganic carbon in the ocean interior is more than the equilibrium concentration in the atmosphere. This enrichment of inorganic carbon, called the biological pump, is responsible for keeping the ocean approximately 300 parts per million by volume higher in carbon dioxide than the atmosphere. Only a small fraction (approximately 0.1%) of the organic matter that sinks into the ocean interior is subsequently buried in the seafloor and incorporated into marine sediments and sedimentary rocks. This burial represents a sequestration of reductant. On geological time scales, the consequence of carbon burial is the accumulation of oxygen in the Earth's atmosphere. Figure reproduced from one kindly provided by John Delaney, University of Washington, Washington, USA).

rate, K is the half-saturation constant for nutrient uptake and R is the external nutrient concentration. This model has been widely applied to phytoplankton and other microorganisms, and can be used to predict growth in the steady state or under the more realistic condition of external nutrient-concentration fluctuation^{37–39}.

The Droop model (see Equation 2) can be re-formulated to examine the competitive abilities of two or more species using the dimensionless parameter R^* (REF. 40), which describes the competitive fitness of an organism with regard to nutrients and is expressed in Equation 3,

$$R^* = \frac{K\mu_{\infty}Q_{min}m}{V_{max}(\mu_{\infty}-m)-\mu_{\infty}Q_{min}m} \quad (3)$$

where m is the specific mortality rate. At equilibrium, it is predicted that the species with the lowest R^* will out-compete all other species for a given nutrient. Low R^* values can be achieved in several ways that are not

necessarily mutually exclusive; these include an increase in V_{max} and/or μ_{∞} , or a decrease in Q_{min} , K and/or m . For example, cells with a low Q_{min} would have a competitive advantage when external nutrient concentrations are low, as this condition generally favours small cells. Conversely, cells that are exposed to high nutrient concentrations would have a competitive advantage if they had a high V_{max} , as such conditions generally favour larger cells. Resource competition theory provides a framework for understanding how nutrient-uptake kinetics, cell quotas and external nutrient concentrations select for specific microbial taxa and community size distributions. However, at the cellular scale there is significant heterogeneity, so that the limit of competitive exclusion is never reached and multiple species can coexist^{41–43}.

Maintaining high nutrient concentrations around their cell surface is a serious problem for microorganisms. For the length

scale of a typical eukaryotic phytoplankton cell (approximately 10 μm in diameter) the Reynolds number is small, and viscous forces dominate the local environment (BOX 2; FIG. 3). When nutrient uptake rates, which are dependent on both the size of the cell and its physiology, are high the cell can easily deplete its surrounding environment (that is, the boundary layer) of nutrients⁴⁴. The re-supply of nutrients from the bulk fluid through the boundary layer to the cell membrane follows Fick's second law of diffusion (see Equation 4),

$$\frac{\delta R}{\delta t} = D \frac{\delta^2 R}{\delta x^2} \quad (4)$$

where R is the external nutrient concentration, D is the diffusivity of resource R in m^2 per second, t is time in seconds and x is the thickness of the boundary layer that is just outside the cell membrane. Equation 4 describes diffusion in planar coordinates, but this can be re-formulated in spherical coordinates if the left hand side of the equation is proportional to the radius of the cell⁴⁵. The re-supply rate of nutrients to the boundary layer is dependent on the nutrient gradient across the boundary layer from the cell surface, where the concentration of R is extremely low, to the bulk fluid, where the concentration of R is maximal⁴⁵ (FIG. 3). For some motile phytoplankton, such as dinoflagellates, this gradient can be increased by swimming⁴⁶. However, for non-motile taxa (such as coccolithophores, diatoms and cyanobacteria), nutrients are re-supplied to the bulk fluid by turbulent mixing^{45,47}. Larger cells have a smaller surface area to volume ratio than small cells. Therefore, the larger the cell the more likely it is to be diffusion limited. To overcome this limitation, large cells must either decrease the thickness of their boundary layer at the cell surface or rely on turbulent mixing to re-supply nutrients to the environment just outside the boundary layer of the cell⁴⁸. Consequently, when nutrient concentrations and turbulent mixing are low, small cells are more likely to be selected.

This effect can be seen in the open tropical ocean, where the dissolved, fixed inorganic nitrogen and/or phosphate concentration can become extremely low, and can be reduced to nanomolar concentrations. In these regions, the phytoplankton community is dominated by small cells, particularly cyanobacteria such as *Prochlorococcus* and *Synechococcus* spp. In regions of the world's oceans where wind energy is high (for example, coastal upwelling areas or polar seas), the flux of nutrients from deep waters to the upper ocean frequently results in massive blooms

Box 1 | The Kolmogorov cascade

The length scale of turbulent eddies in the ocean is dependent on the energy dissipation rate that occurs in the ocean. The length scale of the largest turbulent eddies (Ozmidov length scales) can be estimated by Equation 5

$$L_o = \left(\frac{\varepsilon}{N^3} \right)^{0.5} \quad (5)$$

where L_o is the length scale of the Ozmidov turbulent eddy in metres, ε is the energy dissipation rate in $\text{m}^2 \text{s}^{-3}$ and N is the Brunt-Väisälä frequency, which is a measure of the stability of a water column and has units of inverse time (per second). The Brunt-Väisälä frequency is related to Equation 1 in the main text by Equation 6

$$N = (-gE)^{0.5} \quad (6)$$

where g is gravity and E is stability.

The length scale of the smallest turbulent eddies (Kolmogorov length scales) can be estimated by Equation 7

$$L_k = \left(\frac{\nu^3}{\varepsilon} \right)^{0.25} \quad (7)$$

where L_k is the length scale of the Kolmogorov turbulent eddy in metres and ν is the kinematic viscosity of water (10^{-6} per m^2 per second; ν should not be confused with velocity, which is represented by v). The more turbulent energy that is in the system, the larger the Ozmidov eddies and the smaller the Kolmogorov eddies.

The concept of the turbulence cascade was best summarized by Lewis F. Richardson⁷³:

“Big whorls have little whorls
That feed on their velocity,
And little whorls have lesser whorls
And so on to viscosity.”

of phytoplankton⁴⁹. These blooms are commonly dominated by large eukaryotic cells, and one of the major taxa that dominates such blooms is the diatoms (FIG. 4). Diatoms have a storage vacuole in which nutrients that are taken up from the environment can

be concentrated and used for cell division long after they are depleted in the bulk fluid⁵⁰. Storage vacuoles provide diatoms with a strong competitive advantage when nutrients are injected into the upper ocean in turbulent pulses³⁸. Pulsed nutrient supply is increased when wind stress is high and storms are frequent. On geological timescales, this type of climate occurs when equator-to-pole temperature gradients are at their largest, such as during glacial periods⁵¹. In regions where nutrient fluxes are intermediate — between the extremely oligotrophic conditions of the tropical ocean and nutrient-rich upwelling areas — dinoflagellates and/or carbonate-precipitating coccolithophores (neither of which has a true storage vacuole) tend to dominate the eukaryotic phytoplankton assemblage⁵¹. Because diatoms, coccolithophores and dinoflagellates occupy different mixing regimes in the modern ocean, we can use their fossil record to estimate previous environmental conditions and relate their success to geochemical parameters for ocean mixing.

Fossil record of phytoplankton

Although the fossil record of eukaryotic phytoplankton extends well into the Proterozoic period, the most detailed reconstructions have come from around the period of the Triassic–Jurassic boundary, approximately 200 million years ago (FIG. 5). The microfossil record from this period of the Earth’s history is better preserved in marine sediments compared with sedimentary rocks. The oldest marine sediments are approximately 200 million years old; older sediments are subducted as the seafloor spreads and, unless the sediments are uplifted onto continents to become sedimentary rocks, are lost to the geological and palaeontological record. This record can reveal the long-term trends in the distribution of the major taxa and their

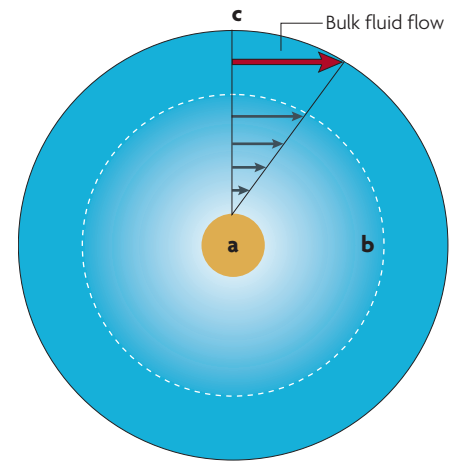


Figure 3 | An idealized diagram of the nutrient concentration and the flow field that immediately surrounds a cell. Flow near the cell surface decreases from bulk-fluid velocity to near zero at the cell surface. Uptake by the cell depletes the nutrient concentration around the cell (a), so setting up a strong nutrient gradient within the boundary layer (b). Because flow is low at the surface of the cell, nutrients must travel down the nutrient gradient from the bulk fluid (c), across the boundary layer, to the cell surface by diffusion. The dashed line represents the outer edge of the boundary layer. The size of the boundary layer is proportional to cell size but is exaggerated in the figure for illustrative purposes.

size structure. Geochemists can reconstruct a basic, although somewhat crude, picture of the ocean thermal structure from measurements of certain features of sediments, including: isotopes, such as oxygen, carbon and sulphur; specific taxa components, such as the protist group or foraminifera; and specific organic molecules, such as alkenones, which are derived from the coccolithophorids. For example, the oxygen isotopes in carbonates that are precipitated by foraminifera reflect the temperature of the water at the time of precipitation⁵². By comparing the oxygen isotopes in carbonate shells deposited by foraminifera that live in the upper ocean with those contained in shells from benthic species, we can estimate the difference in temperature between the upper mixed layer and the ocean interior, as well as the stability (see Equation 1) of the upper ocean–deep ocean system. In addition, the temperature of the ocean interior reflects the temperature at the poles, where the deep waters are formed. The measurement of carbon isotopes in carbonates and organic matter also permits estimates to be made of the atmospheric carbon-dioxide and oxygen concentrations, whereas other measurements allow estimates of ocean

Box 2 | The Reynolds number

The Reynolds number is a dimensionless metric that is useful in determining whether inertial or viscous forces dominate the motion of an object in a fluid⁷⁴ (see Equation 8),

$$\Re = \frac{av}{\nu} \quad (8)$$

where \Re is the Reynolds number, a is the length scale of the object in the fluid (in metres), ν is the kinematic viscosity of water (10^{-6} per m^2 per second) and v is the velocity (in metres per second). The \Re number is the ratio of inertial to viscous forces. When \Re is more than 1, inertial forces dominate the motion of the object in water. For example, a person who is 2 m in height swimming at 1 m per second has a Reynolds number of 2×10^6 . In this case, inertial forces dominate the motion of the swimmer. However, a 5 μm long dinoflagellate swimming at 100 μm per second has a Reynolds number of 5×10^{-4} . Clearly, viscous forces dominate the motion of this cell. For the swimmer to experience the same viscous forces as the dinoflagellate, the swimmer would have to swim in a fluid where ν is on the order of 4,000 m^2 per second; similar to the viscosity of hot tar.

salinity, sea level and the concentration of oxygen in the ocean interior to be made. Correlations between the geochemical and geophysical measurements of ocean circulation, and the chemistry and fossil record of phytoplankton, provide insights into how the physical–chemical ocean environment has selected for specific taxa in the geological past^{6,53,54}.

The fossil record over the past 200 million years for the three major armoured eukaryotic phytoplankton taxa — coccolithophores, dinoflagellates and diatoms — has revealed long-term trends. From the early Triassic period until the extinction event that occurred 65 million-years ago, the diversity of the carbonate-precipitating coccolithophores and armoured dinoflagellates increased. This period of the Earth's history was marked by warm polar seas, with no permanent ice and a single, extremely large continent (known as Pangea), which began to fragment during the Triassic period. Over the next 200 million years, continental fragmentation led to the formation of North America and Eurasia, a combined African–South American craton (known as Gondwana) and a massive (Panthalassic) ocean that eventually became the contemporary Pacific Ocean. During this period,

the export of organic matter to marine sediments increased slowly around the continental margins, leading to a long-term increase in atmospheric oxygen⁵⁵. However, oceanic productivity was probably low and comparable with that of the contemporary South Pacific Ocean, which is the most oligotrophic ocean basin in the world. The first fossilized diatom was recorded at approximately 146 Ma, but throughout the Mesozoic period diatoms were rare⁵⁶.

The extinction event that occurred at 65 Ma marked the beginning of the Palaeogene period, during which time a significant portion of the coccolithophore and dinoflagellate diversity was removed⁵³. For the next 10 million years, the deep ocean was relatively warm; temperatures reconstructed from benthic foraminifera oxygen isotopes indicate that values were as high as 18°C⁵⁷. Over the next 55 million years, temperatures slowly decreased to the contemporary value of 2°C⁹. Based on isotopic analysis, the thermal difference between the upper ocean and the ocean interior 65 million years ago was approximately 10°C. Today, the thermal difference in the tropical ocean is approximately 25°C. This implies that it required less energy to mix the oceans 65 million years ago than it does now; that is, in the past it was easier to bring nutrients from the ocean interior into the upper mixed layer of the ocean.

By approximately 34 Ma, the Drake Passage had opened between the southern tip of South America and the Antarctic continent, thereby isolating the Antarctic continent with a circumpolar sea. This tectonic shift in the continental configuration led to a major climatic shift, whereby permanent polar ice developed on the Antarctic continent, resulting in the contemporary ‘ice-house’ world⁵⁸; the last ice-house world occurred more than 250 million-years earlier, during the Permian period. This change in the ocean thermal structure, resulting from the formation of polar continental ice, was accompanied by a rapid increase in diatom diversity. This group of phytoplankton subsequently became one of the most successful that lived during the Cenozoic Era⁵⁹, and their proliferation was accompanied by a significant increase in the organic carbon that was exported to continental margins around the world⁴⁹.

Although the fossil record suggests that the diversity of diatoms increased rapidly over the past 34 million years, the average size of these organisms has decreased by a factor of almost three⁵⁹. This decline in size is correlated with an increase in thermal

Glossary

AEOLIAN

The continentally derived nutrient input that is transported by the wind.

Ma

(Mega-annum). A unit of time that is equal to 1 million (10⁶) years.

OLIGOTROPHIC

An aquatic environment that has low levels of nutrient and algal photosynthetic production (for example, high mountain lakes or the open ocean).

PRIMARY PRODUCER

An organism that is the original source of organic material in an ecosystem — plants, algae or chemosynthetic microorganisms.

RIVERINE

The continentally derived nutrient input that is transported by rivers and streams.

stratification (or stability), as inferred from the isotopic analyses of benthic and planktonic foraminifera. This long-term trend suggests that ocean mixing has a major role in determining the size of cells, even in a single eukaryotic taxon. In eukaryotic phytoplankton, cell size is positively correlated with genome size and genome-size evolution. Consequently, climate-driven changes in ocean physics potentially alter the genomic structure and tempo of the evolution of marine eukaryotic microorganisms^{60,61}.

MAKING PREDICTIONS

Can we use the historical data of macroevolutionary (secular) trends in the taxonomic compositions of eukaryotic phytoplankton and the ecological patterns that have been observed in the contemporary ocean as predictors for the coming centuries? The answer is clearly in the affirmative⁶². Robust models that are based on physical circulation and the taxa-based physiological parameterization of Equation 2 are being developed for that purpose^{39,63}. Fundamentally, these analyses predict that as greenhouse gases continue to accumulate in the Earth's atmosphere, the upper mixed layer of the ocean will become increasingly isolated from the deep ocean by a strong pycnocline⁶⁴, and the thermal contrast between the continents and the coastal oceans will increase. These analyses might indicate that wind-driven upwelling will be greater along coastal regions⁶⁵, thereby increasing the competitive advantage that diatoms have in such regions. However, throughout most of the open ocean, the increase in stratification will

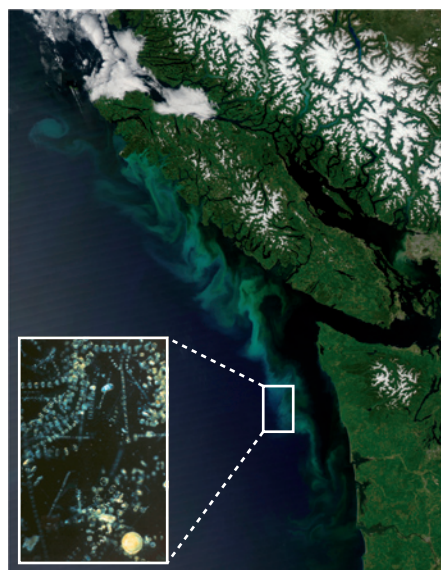


Figure 4 | A colour satellite image of a diatom bloom off the west coast of Vancouver Island, Canada. The inset shows a micrograph of the chain-forming diatoms that are characteristic of this area of the world's oceans. The image is courtesy of J. Schmaltz, MODIS Land Rapid Response Team at NASA Goddard Space Flight Center, Washington DC, USA. The inset was kindly provided by F. J. R. Taylor, University of Columbia, New York, USA.

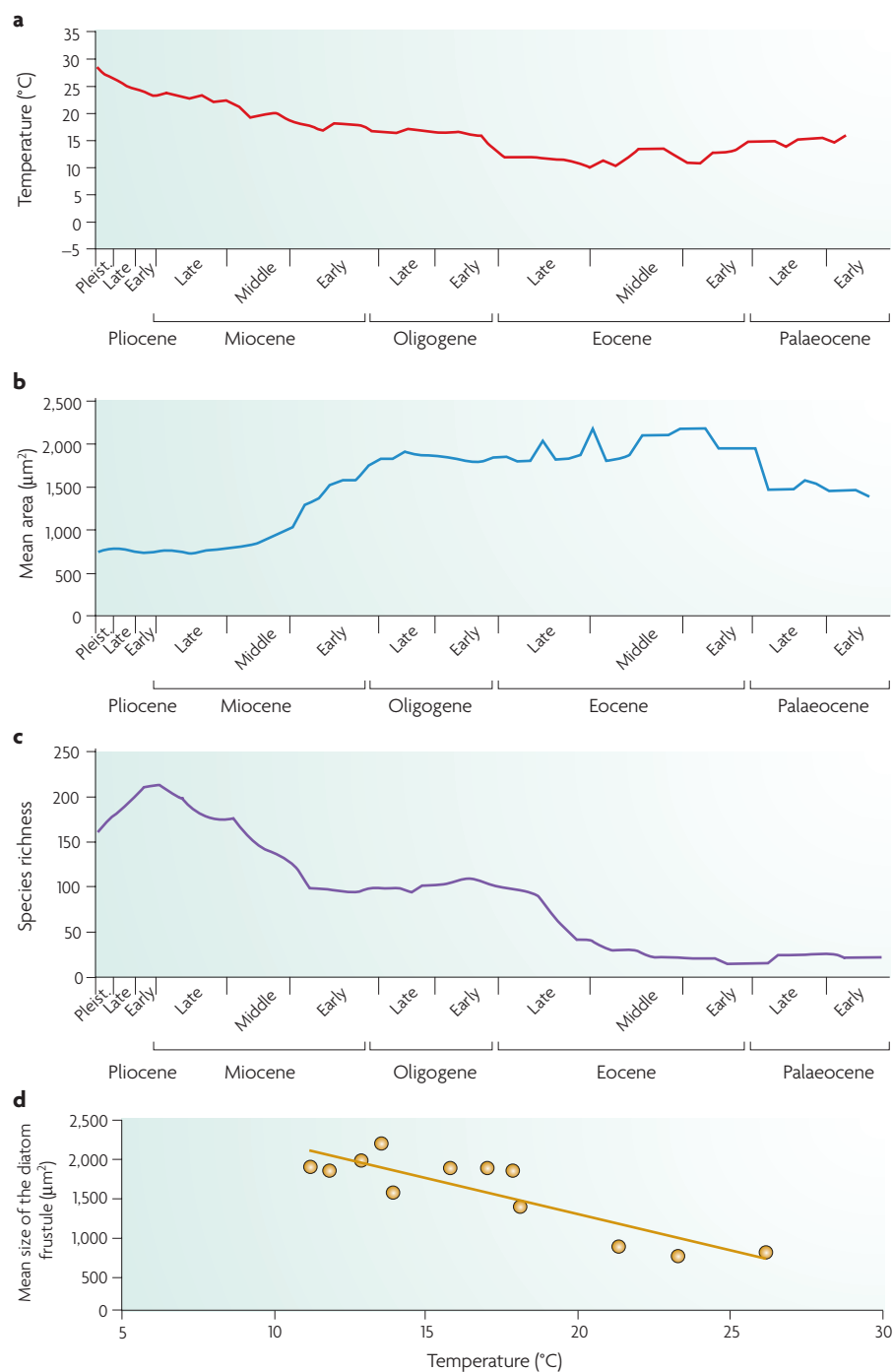


Figure 5 | Changes in ocean thermal structure and the size of diatoms in the Cenozoic period. Changes in temperature (a), the average size of marine diatom shells (frustules) (b) and the species richness of marine diatoms (c) over the past 65 million years. Correlation between temperature and the average size of marine diatoms over the past 65 million years (d). Pleist., Pleistocene.

probably result in a decrease in the average nutrient availability and, therefore, a reduction in the abundance of large cells and a low export production⁶⁶. The ‘winners’ in such a situation would potentially be the coccolithophorids⁵¹, small eukaryotic phytoplankton⁶⁷ and the ubiquitous

cyanobacteria. Indeed, these outcomes can be predicted with some certainty by analyses of the relevant taxa-level parameters shown in Equation 3. Such ecological ‘portraits’, coupled with general circulation models of the atmosphere and ocean, provide a powerful tool with which to examine

and explain the distribution of eukaryotic phytoplankton in the contemporary ocean^{63,66}. By assuming there will be continuity in the inheritance of taxa-specific traits in the coming decades, we can predict basic patterns for future decades and centuries. However, it is far more difficult to predict the effect that changes in the distribution of primary producers will have on the higher levels of marine food webs⁶² or on global biogeochemical fluxes²².

What about the non-photosynthetic microbial community? Microbial ecology — which has for decades been based on broad-brushed physiological tools, such as the measurement of total-cell abundance and the uptake of a labelled substrate^{68–70} — has been rapidly transformed to a molecular-based science, in which ribosomal DNA sequences can be quantitatively analysed for taxonomic composition, and whole shotgun and bacterial artificial-chromosome gene sequences can be derived for potential functionality. This has provided a means by which we can observe temporal and spatial changes in the contemporary marine (mainly prokaryotic) microbial community. However, without physiological analyses that are relevant to resource competition theory or an alternative mathematical model, the distributions of genes in time and space can be correlated with physical and chemical patterns, but cannot be analysed from an evolutionary adaptive perspective.

Our inability to infer microbial phenotypic characteristics from genomic information has prevented a more rigorous prediction of how prokaryotic microbial communities will respond to changes in climate in the coming centuries. However, regardless of how the microbial community responds, the ocean as a whole will not become net heterotrophic⁷¹; were that to occur the nutrients that would accumulate in the upper ocean would be assimilated by photoautotrophs, which would, in turn, generate oxygen. This feedback has continuously maintained oxygen in the Earth’s atmosphere for the past ~2.3 billion years⁷².

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Competing interests statement

The authors declare no competing financial interests.

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ALL LINKS ARE ACTIVE IN THE ONLINE PDF

ERRATUM

Mix and match: how climate selects phytoplankton

Paul G. Falkowski and Matthew J. Oliver

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In the above article, the legend to figure 5 should have indicated that the figure was first published in reference 59. We wish to apologize to the author, and to readers, for any confusion caused.

Diatoms in a future ocean — stirring it up

Francesc Peters

A recent review by Falkowski and Oliver¹ argues that coccolithophorid algae, and possibly cyanobacteria and other picoplankton and nanoplankton, should dominate the upper mixed layer of the open ocean in the future. A scenario that involves increased ocean temperature would result in greater water-column stability and reduced turbulent mixing that, consequently, would reduce the input of inorganic nutrients from the deep ocean. This situation favours the growth of small plankton that have high surface to volume ratios over larger organisms, such as diatoms. Here, I contend that the presence of other factors renders this prediction of a generalized picoplankton and nanoplankton ocean uncertain.

Let me first consider the assumption that a future upper open ocean will become more stabilized. Air temperature is increasing to an even greater extent than ocean-water temperature². Consequently, higher levels of water vapour in the atmosphere will more than likely increase storm frequency and intensity. Wind and storm events that temporarily increase turbulence in the upper mixed layer, and thus pulse nutrients into the euphotic zone, are the ideal growth conditions for diatoms. But, changes in the predominance of one type of 'life-form' (as defined by Margalef³) over an annual cycle are hard to predict, and the end result can be attributable to a trade off between the overall water-column stabilization and an increase in destabilization events. The uncertainty is large. Regionally, the global-warming trend is melting large areas of the Arctic, which is greatly reducing the summer ice-covered area; in summer 2007, the Arctic ice-free area was more than 10⁶ km² larger than the previous record of 2005 (REF. 4).

This exposes large areas of the ocean to high wind-energy inputs that should favour organisms such as diatoms. In addition, the differential warming between the poles and the equator seems to intensify the westerlies⁵, entraining further mechanical energy into the upper ocean. It is clear that if trends other than that of water warming are considered, future oceanic conditions do not seem unfavourable for diatoms.

Let me now assume that the increase in upper-ocean temperature would indeed result in stronger thermal stratification and greater stability of the water column on average. The average nutrient availability from deep waters would be reduced, and our current tropical oceans are templates of this situation, with deep chlorophyll maxima (DCM) developing where enough nutrients meet sufficient radiation energy. Modelling shows that reduced vertical diffusivity in the water column results in a more fluctuating nutrient field near the DCM and an increase in the diversity of organisms⁶. This is because of mismatches between vertical settling rates of particulate organic matter and upward-flow velocities. It also explains the increase in diatom diversity with increasing temperature that has been observed in the geological record, as shown by Falkowski and Oliver¹, and contradicts the conclusion that diatoms are 'losers' in such a situation.

In ocean areas of high nutrient, low chlorophyll (HNLC), export production after the pulsed addition of iron, which could represent an aeolian micronutrient input, is inversely related to the depth of the wind-mixed layer⁷. Diatoms take advantage of such pulsed

conditions, and are also primarily responsible for export because of their heavy silicate frustules. Shoaling of the mixed layer in the vast HNLC areas, punctuated by micronutrient pulses, should then increase the export of organic matter to the deep ocean. This would reduce the excess atmospheric carbon dioxide, resulting in a negative feedback that would alleviate further temperature rises. Whether pulsing events or background stability would dominate the budget at annual scales and, consequently, the relative importance of diatoms, is again uncertain.

Thus, fluctuations or pulses that are caused by meteorological fronts, storms or aeolian inputs would be expected to increase in a global-warming scenario, and therefore have to be considered as drivers in the open ocean. Diversity should increase if such fluctuations can be considered as system disturbances of the right frequency^{8,9}. Overall, future open-ocean scenarios do not point towards a decrease in the predominance of diatoms.

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Diatoms in a future ocean — stirring it up: reply from Falkowski and Oliver

Paul G. Falkowski and Matthew J. Oliver

We have suggested that future warming climate scenarios will result in a shift in the phytoplankton community in the central ocean gyres towards smaller cells, and that under such conditions, diatoms, especially large-celled species, would be at a competitive disadvantage¹. We also suggested that a warming climate will simultaneously enhance the productivity of large phytoplankton, such as diatoms, in coastal regions, owing to increased wind-driven upwelling¹. Peters claims that our suggestion is uncertain, arguing that climate and biological-modelling efforts show that future warming climate scenarios will result in conditions that favour diatoms.

First, we agree with Peters that our proposal of future phytoplankton-population dynamics is not certain. Unfortunately, certainty is not an attribute of future climate prediction, and therefore simply demonstrating that there is uncertainty in a prediction cannot be used as a test to reject our basic hypothesis. Rather, what is necessary is an assessment of climate-forced environmental conditions that allow one phytoplankton group to out-compete other phytoplankton groups. We suggest that future warming climate scenarios generally lead to increased stratification in the central gyres, which, if true, is predicted to reduce the competitive advantages of diatoms². If that happens, small-celled phytoplankton will have a competitive advantage over large-celled phytoplankton. This does not mean, however, that diatoms will be absent; rather, diatoms

will probably become a smaller component of the phytoplankton community.

Peters provides two examples of how warming climate scenarios might lead to a less-stable upper ocean that favours diatoms and an export flux of organic matter: increased storms and chaos in the upper mixed layer. Indeed, these two phenomena could increase the turbulent energy in the upper ocean, and thus potentially enhance export production; however, even if this were to occur, the feedback effect on the climate would be small. As Peters also points out, warming climate scenarios depend on the integrated balance of stabilizing versus destabilizing events in the open ocean. This is an onerous modelling task that can have uncertain results owing to the number of parameters that are required to estimate the balance of stabilizing and destabilizing events in future climate scenarios.

Ultimately, it is the geological record and ecological observations that inform models^{3,4}. The geological record suggests that as climate warms the upper ocean becomes more stabilized, with a greater abundance of small coccolithophorids and smaller diatoms⁵. It is possible that the current warming event might not unfold as historical record suggests; however, the geological record remains one of the best sources of empirical evidence from which to evaluate and predict the effect of climate change on the ocean environment. Similarly, during glacial–interglacial cycles, there seems to be an alteration between diatoms and coccolithophorids^{6,7}. Finally, recent ecological

observations suggest that the central gyres have become increasingly oligotrophic^{8–10}.

In summary, models are inevitably imperfect. However, based on the geological record and ecological observations, we contend that in the coming centuries the ocean will favour small cells and fewer diatoms than that observed prior to the industrial revolution.

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