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REVIEW

Exploration of marine phytoplankton: from their historical appreciation to the omics era

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Marine phytoplankton are believed to account for more than 45% of photosynthetic net primary production on Earth, and hence are at the base of marine food webs and have an enormous impact on the entire Earth system. Their members are found across many of the major clades of the tree of life, including bacteria (cyanobacteria) and multiple eukaryotic lineages that acquired photosynthesis through the process of endosymbiosis. Our understanding of their distribution in marine ecosystems and their contribution to biogeochemical cycles have increased since they were first described in the 18th century. Here, we review historical milestones in marine phytoplankton research and how their roles were gradually understood, with a particular focus on insights derived from large-scale ocean exploration. We start from the first observations made by explorers and naturalists, review the initial identification of the main phytoplankton groups and the appreciation of their function in the influential Kiel and Plymouth schools that established biological oceanography, to finally outline the contribution of modern large-scale initiatives to understand this fundamental biological component of the ocean.

KEYWORDS: phytoplankton; primary production; microbial oceanography; omics; HMS *Challenger*; Plankton Expedition; *Tara* Oceans

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INTRODUCTION

Marine phytoplankton have shaped life on Earth throughout their extensive evolutionary history. First, by providing gaseous oxygen they gradually changed the composition of Earth's atmosphere and its redox status (Lyons *et al.*, 2014). Second, because of the carbon that is fixed during photosynthesis, they have the critical role of supplying organic matter to marine food webs, accounting for more than 45% of the photosynthetic net primary production on the whole planet (Field *et al.*, 1998). Hence, by providing both oxygen and the source of organic carbon into the water column they sustain the existence of most marine life. Thirdly, their acquired capacity to build mineral structures (e.g. silica frustules, calcite and aragonite plates (coccoliths) and spicules), in combination with their enormous population sizes, has resulted in huge deposits that can be observed in the geological record (Knoll, 2003). Finally, either by the sinking of individual or aggregated cells or via trophic interactions and the microbial loop, phytoplankton contribute overall to the biological carbon pump, by which carbon dioxide is removed from the atmosphere and sequestered in the deep ocean for millennia (Turner, 2015; Boyd *et al.*, 2019).

Phytoplankton composition in the ocean spans two domains of life. On the eukaryotic side, they consist mainly of the larger and hence more conspicuous diatoms and dinoflagellates, as well as numerous smaller microorganisms including haptophytes, pelagophyceans, prasinophyceans, cryptophyceans, euglenoids and chlorarachniophyceans. On the bacterial side, they are dominated by the minuscule picocyanobacteria *Prochlorococcus* and *Synechococcus*, and the nitrogen fixers *Trichodesmium*, *Crocosphaera* and *Richelia*. The majority are found as free-floating single cells, although many form chains (e.g. some diatoms), some form colonies (e.g. *Phaeocystis* and *Trichodesmium*) and many live in symbiosis with other species (e.g. *Richelia*). Furthermore, the classic view that catalogs them as simple autotrophic organisms has been increasingly challenged by the fact that many are mixotrophs, e.g. capable of phagotrophy of bacteria and small protists or uptake of dissolved organic substances (Sanders, 1991; Jones, 1997; Stoecker, 1998; Mitra *et al.*, 2016).

Formal knowledge of marine phytoplankton was gained gradually after the invention of the microscope and the inclusion of naturalists in marine expeditions on sailing ships. It was only in the 19th century that the first dedicated global expedition to study the oceans was launched (HMS *Challenger*; see below). Even if it was not specifically aimed at studying marine phytoplankton, it represented a major step in the creation of what we know today as biological oceanography. Much later, towards the end of the 20th century, we were able to monitor phytoplankton global contributions to primary production through satellite-based observations at large spatial and temporal scales. Even more recently, the beginning of the 21st century has witnessed the advent of high-throughput DNA sequencing that has increased the resolution at which we can study microscopic communities to an unprecedented level.

Here, we attempt to review the historical path of research on phytoplankton, since their first description up to today's global appreciation. Historical references were traced mostly through available online literature (research and review articles), a limited number of printed books and the help of colleagues, but the breadth of the topic makes it impossible for a single review to be fully exhaustive. We did our best to select milestones in this path, starting with the initial steps that laid the foundations to understand the nature of marine phytoplankton, their spatial distributions, morphologies and ecological roles. Next, we attempt to document their first distinction into different major groups. A brief overview of the use of microscopy, pigments, radioisotopes and remote sensing is offered mainly as a transition into the final section, in which we highlight the contribution of high-throughput sequencing and advanced imaging in large-scale initiatives. However, we acknowledge the omission of hundreds of men and women, institutions and achievements that were fundamental for the advancement of this highly interdisciplinary field but that we cannot include here due to lack of space. We do not cover the history of many important topics in biological oceanography (e.g. nutrients, water column, upwelling, trophic interactions and numerical modelling), biogeochemistry or biology (e.g. photobiology, paleobiology, ecology), which represent central areas in the study of phytoplankton. Instead, we advise readers to consult Sverdrup and Armbrust (2009), Falkowski and Knoll (2007), Deacon *et al.*, (2001) and Cullen (2015). Further information about the early history of phytoplankton studies and the development of biological oceanography in general in the Kiel and Plymouth schools are treated comprehensively by Mills (2012) in his scholarly volume: *Biological Oceanography: An Early History, 1870–1960*, as well as in numerous recent publications (see Dolan, 2020 and references within). Algal taxonomy's past, present and future is presented in De Clerck *et al.*, 2013 and an overview about harmful algal blooms can be found in Anderson *et al.*, 2002.

HISTORICAL APPRECIATION OF PHYTOPLANKTON IN THE OCEAN

Our knowledge of phytoplankton came initially from studies of freshwater ecosystems, particularly due to their presence in lakes. It can be traced back to the invention

of one of the first practical microscopes by the Dutch tradesman Antoni van Leeuwenhoeck, based on the more elaborate design of Robert Hooke (Ball, 1966; Gest, 2004). In a letter dated 7 September 1674, van Leeuwenhoeck describes looking at material forming green streaks in a Dutch lake as "spirally wound serpent-wise earthy particles." These were most likely from a bloom of the charophyte *Spirogyra* (Dobell, 1958; Fogg, 1990), as well as organisms that are "green in the middle and before and behind white," apparently the euglenoid *Euglena viridis* (Dobell, 1958). Moreover, two years earlier, an English gentleman named Christopher Kirkby reported the presence of a "hairy efflorescence" in a Polish lake with toxic effect on animals, which likely represents the first communication about a harmful algal bloom (probably a cyanobacteria; see this and further historical references in Codd *et al*., 2015).

The first reports of phytoplankton in the open ocean came only in the following century. During James Cook's voyage to the South Seas on the *Endeavour* from 1768 to 1771, the now famous naturalist Joseph Banks described what the sailors called "sea sawdust," which we now know as colonies of the cyanobacterium *Trichodesmium* (Fogg, 1990). The later design and use of specific nets was a key for plankton sampling. To our knowledge, their first recorded use was by French naturalists Francois Péron and Charles-Alexandre Lesueur during an expedition to Australia from 1801 to 1804 (Egerton, 2012; West-Sooby, 2015). The whaler/explorer William Scoresby Junior is also likely to have used a plankton net for his researches off Greenland at a similar time, although he has left no details about it, whereas the unequivocal use of a plankton net was described by John Vaughan Thompson in 1816, returning to England from Mauritius (Egerton, 2012; Damkaer, 2016). Charles Darwin was another of the earliest users, first discussing it on 10 January 1832 in his Beagle diary. The following day he wrote in his diary: "*I am quite tired having worked all day at the produce of my net—The number of animals that the net collects is very great & fully explains the manner so many animals of a large size live so far from land*" (Darwin, 1988). A few years later, another famous naturalist, Joseph Dalton Hooker, then assistant surgeon on the Antarctic voyage of HM Discovery Ships *Erebus* and *Terror* led by Captain James Clark Ross from 1839 to 1843, appreciated the ecological significance of phytoplankton in the ocean. He noted extremely large numbers of a range of different species of *Diatomaceae* in net tows, as well as within the pack-ice, in the guts of marine animals, and in the sediments. His studies thus led him to understand that (i) although invisible they must be extremely abundant, as evidenced by the accumulation of their siliceous frustules at the seafloor, (ii) they were distributed throughout the oceans including in the polar regions, (iii) they constitute the food source that sustains the larger marine animals (many explorers at that time had been puzzled by the abundance of animal life in the seas without any obvious source of food), and (iv) like trees and grass on land, they were also "purifiers of the vitiated atmosphere" (Hooker, 1847; Ross, 1847; Fogg, 1990).

At the time of the voyage, *Diatomaceae* were known as one component of a microscopic community referred to as animalculae or infusoria and were considered by the world authority of protozoology at the time, the German Christian Gottfried Ehrenberg, to be animals (misled by their ability to move and believing that the chloroplasts were ovaries) classified as "siliceous polygastrics." It was only afterwards that Hooker realized their "vegetable origin," following consultation with expert cryptogamists, notably George Henry Kendrick Thwaites (Hooker, 1847). Similar confusion might have existed when Thomas Henry Huxley, while on board HMS *Rattlesnake* in the Pacific Ocean in 1851, first described the existence of minute yellow–green cells within large protists (Radiolaria), which he thought were organelles (Huxley, 1851). Later on, it was Karl Brandt who established that these small coloured cells were photosynthetic endosymbionts (Brandt, 1881).

The subsequent development of improved nets for sampling led to an increased appreciation of the diversity of microscopic life in the oceans, a fact revealed most dramatically by the expedition of HMS *Challenger* from 1872 to 1876 (Figs 1A and 2). Although focused on deep-sea exploration, this project that we would now define as big science was also the first to bring attention to "the world of free floating animals that inhabit the open sea" (Egerton, 2012), and samples from the expedition were used by Ernst Haeckel, the founder of the term ecology, for some of his magnificent drawings (Fig. 3A) (Haeckel, 1904).

The first expedition specifically devoted to the study of marine microscopic organisms was performed in the North Atlantic in 1889 by Victor Hensen from Kiel University under the patronage of the German Emperor Wilhelm II (Fig. 1A) (Fogg, 1990). It was carried out using the 58 m 835 ton steamer SMS *National* and is now known as the Plankton Expedition (Fig. 1A) (Mills, 2012). Hensen recognized the importance of plankton as the base of all marine life, describing them as "this blood of the sea." He is credited with laying the foundations of biological oceanography through his view that plankton should be studied quantitatively by determining rates of production rather than taxonomically or through measures of standing stocks (Mills, 2012). It was he who first used the term plankton in 1887, from the Greek "planktos" (to wander or drift). The Plankton Expedition was

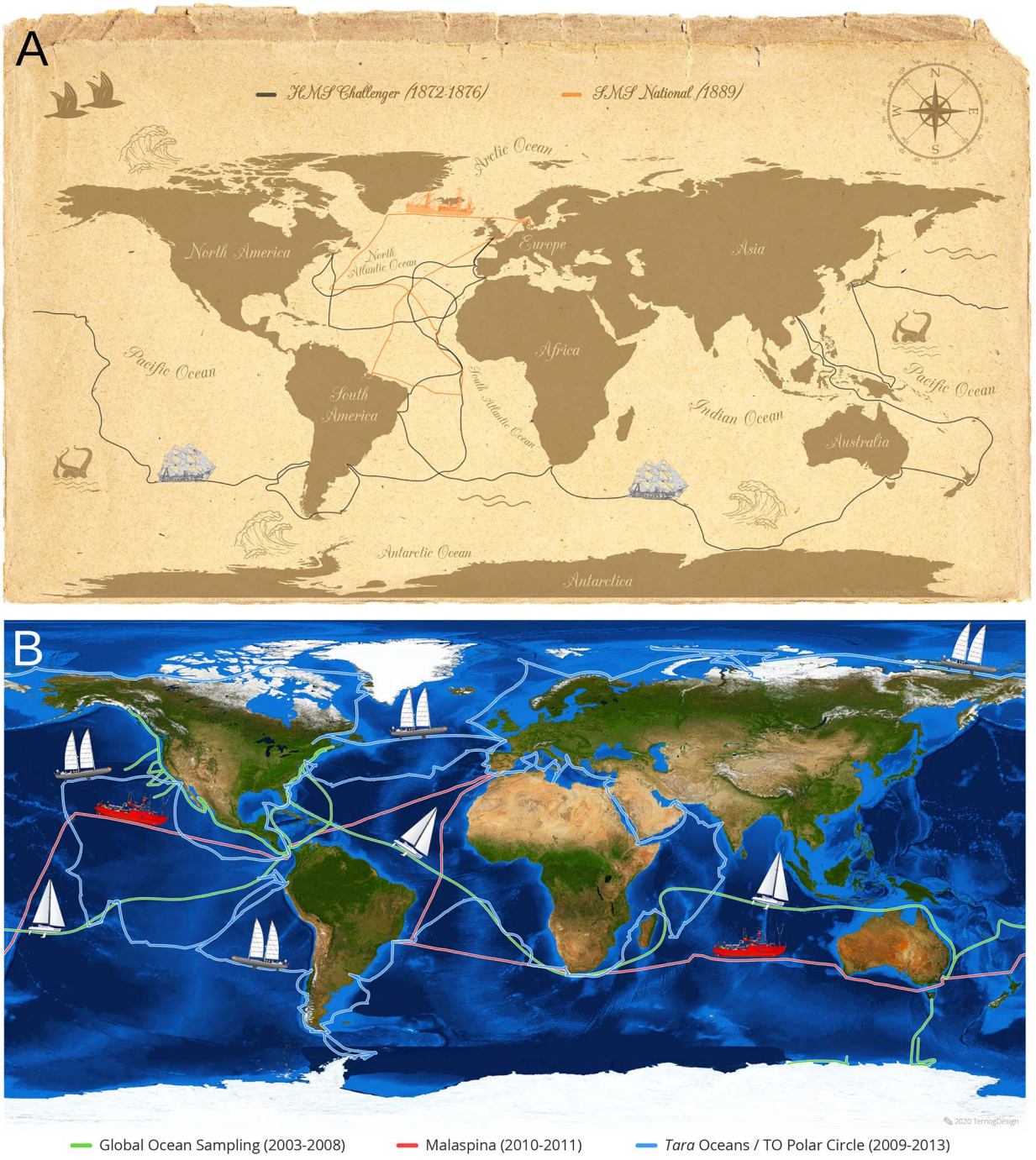

Fig. 1. Routes of HMS *Challenger* (1872–1876) and SMS *National* (1889) (panel **A**), and Global Ocean Sampling (2003–2008), Malaspina (2010–2011) and *Tara* Oceans expeditions (2009–2013) (panel **B**). The HMS *Challenger* expedition can claim to be the foundation of modern oceanographic studies. This historic voyage was the first to specifically gather data on a broad range of ocean features, including ocean temperature, seawater chemistry, currents, marine life, bathymetry, and the geology of the seafloor. The first expedition specifically devoted to the study of plankton was later performed in the North Atlantic by Victor Hensen on SMS *National* and is now known as the Plankton Expedition. Hensen coined the term plankton and laid the basis for biological oceanography. At the beginning of the 21st century, large-scale expeditions incorporated -omics technologies, as in the cases of the Global Ocean Sampling, Malaspina and *Tara* Oceans expeditions. Figure designed by Noan le Bescot (Ternog Design).

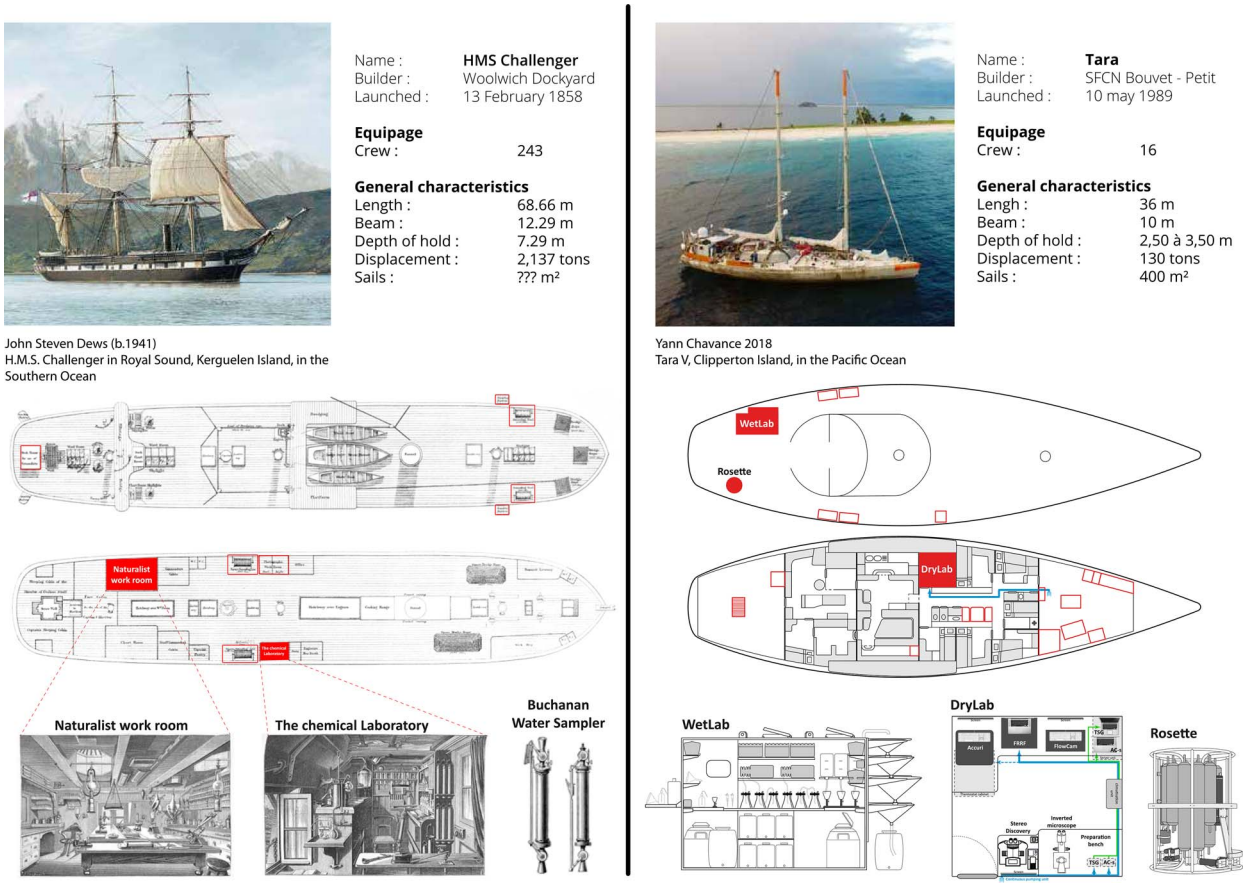

Fig. 2. Comparison between sampling devices and working areas on board HMS *Challenger* and SV *Tara*. Figure designed by Noan le Bescot (Ternog Design).

an important milestone in plankton research, although Haeckel was highly critical of the sampling methods used and the overall scientific approach being promoted by Hensen (Mills, 2012). As an example, Haeckel and many other contemporary researchers argued that oceanic food webs are based on organic material from macroalgae and aquatic plants as well as terrestrial plant debris washed into the open sea from shores and rivers (Smetacek, 1999; Barber and Hilting, 2002; Smetacek *et al.*, 2002). Hensen, vehemently promoting the idea that Hooker, A. S. Ørsted and G. O. Sars had introduced, insisted that microscopic planktonic plants were the major producers and it was his lifelong goal to measure the planktonic production of the ocean (Smetacek, 1999; Barber and Hilting, 2002; Smetacek *et al.*, 2002). Further arguments essentially centred around the distributions of plankton at different latitudes and in terms of their patchiness, and the relation between distributions, species richness, and productivity. With hindsight, both provided important insights into debates that even today have not yet been fully resolved. Furthermore, both Hensen and Haeckel, as well as others from the *Challenger* expedition, defined different categories of plankton: the plant plankton or phytoplankton (plants), the zooplankton (animals) and the temporary meroplankton (only part of an organism's life cycle) (Gran, 1912; Egerton, 2012; Mills, 2012). Discovery of smaller classes of plankton in addition to the more readily observable microplankton of 20–200 microns, now known as nanoplankton (3–20 microns) and picoplankton (0.2–3 microns), was driven by the need to improve quantification in order to relate plankton abundance with productivity and was initially pioneered by Hans Lohmann (Mills, 2012). Charles Atwood Kofoid at the Illinois Biological Station further confirmed their numerical abundance by using centrifugation as a means of collection, but appreciation of these smaller plankton only really began in the 1970s following the introduction of fluorescence microscopy (see the next section; Johnson and Sieburth, 1979; Waterbury *et al.*, 1979; Fogg, 1990). Lohmann was an ambitious young scientist at the Zoological Institute in Kiel and had participated in the Plankton Expedition. Overall, under the leadership of Karl Brandt,

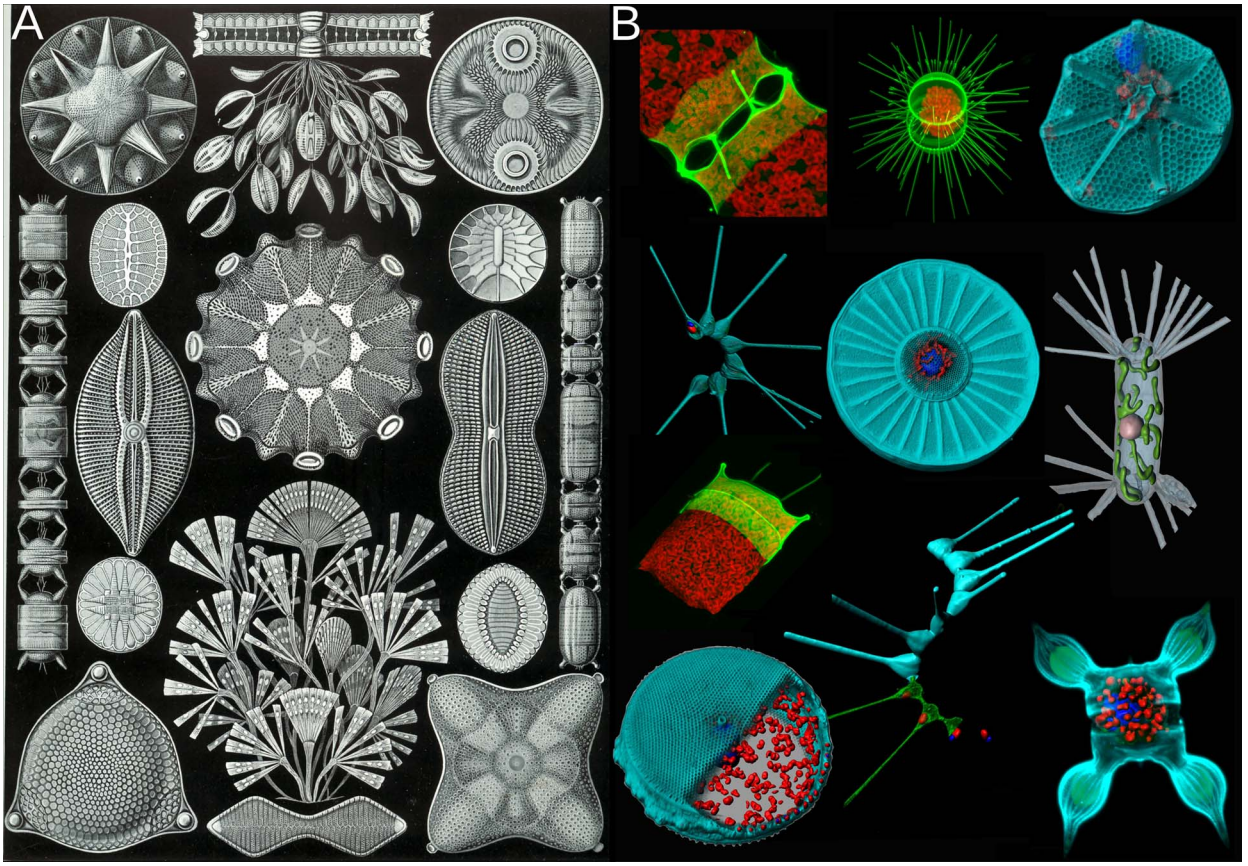

Fig. 3. Drawings by Ernst Haeckel for his book Kunstformen der Natur (known in English as Art Forms of Nature; Haeckel, 1904) showing various species of diatoms (panel **A**) are compared with the confocal microscopy images generated from samples collected during the *Tara* Oceans expeditions (2009–2013) or off the coast of Brittany near Roscoff (panel **B**).

he and the other scientists at the Zoological Institute made the first major contributions to understanding the role of phytoplankton in the ocean from 1887 through to the 1920s (Mills, 2012).

The Plymouth Marine Laboratory, established in 1886, is considered to have continued on from the Kiel scientists to further consolidate the roots of biological oceanography, but only following the decline of the Kiel school (Mills, 2012). Although originally mandated, in the words of the Duke of Argyll at the founding meeting, to perform research "*leading to the improvement of zoological and botanical science, and to an increase of our knowledge as regards the food, life, conditions and habits of British food fishes, and molluscs in particular, and the animal and vegetable resources of the sea in general*" (Mills, 2012), i.e. to improve management of the fishing industry that had become unpredictable in UK waters due to overfishing, it was only during the period between the two world wars that major contributions were made. Scientists such as E. J. Allen, W. R. G. Atkins, H. W. Harvey and F. S. Russell are considered to have made the most important insights into understanding the environmental constraints on fish stocks, in particular through the study of plankton dynamics. One important contribution of the Plymouth scientists was to establish phytoplankton isolation and culturing techniques with which they could study growth constraints, e.g. by light and nutrients. The quantitative approaches established by the Plymouth school and the objective to relate plankton productivity with fish stocks opened up the development of modelling of marine ecosystems based on nutrient flow through marine food webs, an approach subsequently pioneered by Gordon A. Riley at Yale University in the US from the 1930s (Mills, 2012).

The contributions of female scientists to the beginnings of plankton research are more difficult to determine. They were not able to participate in early ocean exploration, and prominent positions in scientific research establishments were typically reserved for male scientists until relatively recently. Notwithstanding, several women have been noted as making important contributions during this early period, including E. Catherine Herdman at Port Erin Marine Laboratory in the Isle of Man, Sheina

Marshall at the Scottish Marine Biological Association's lab at Millport, Birgithe Ruud Foyn at the University of Oslo in Norway, and Penelope Jenkin and Marie V. Lebour in Plymouth. Marie Lebour made extensive use of light microscopy to describe diatom and dinoflagellate taxonomy as well as marine metazoan life cycles (Mills, 2012). The light microscopy characterization of phytoplankton was facilitated by the setting up of isolation and culturing techniques, but many phenotypic features are too small to be accurately confirmed by it. The later deployment of the electron microscope for studies of plankton after World War II allowed to visualize, e.g. the ultrastructural details of diatom frustules (Hendey, 1959; Lewin and Guillard, 1963), the morphology of coccoliths that surround coccolithophores (Watabe and Wilbur, 1966), and the ultrastructure of the minute organic scales that cover many small flagellate taxa of prasinophyceans and haptophytes (Parke *et al.*, 1955; Manton, 1959; Manton and Parke, 1960). This new degree of structural resolution made possible a much better discrimination at the species level that is still deployed today, permitting many cases of taxonomic reassignment (particularly with small species, see next section for the example of *Micromonas pusilla*).

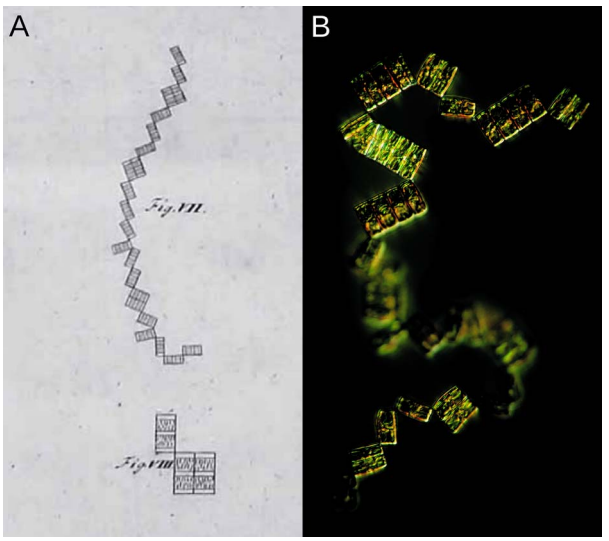

Fig. 4. The first unambiguous depiction of a diatom in 1703 (panel **A**), which was indisputably the diatom *Tabellaria* and was probably made by Charles King (Dolan, 2019), is compared with a modern microscopy image of a diatom with similar morphology, the chain-forming pennate *Thalassionema nitzschioides* (panel **B**; cell culture from the Mediterranean Culture Collection of Villefranche-sur-Mer; adapted from Sardet, 2015). The cells are joined together in chains by mucilaginous links.

Historical references for the main phytoplankton groups

The first illustrations of diatoms (Bacillariophyta) are found in an article from 1703 in Transactions of the Royal Society showing unmistakable drawings of *Tabellaria* (Fig. 4) (Dolan, 2019). Although the publication was authored by an unnamed English gentleman, there is recent evidence that he was Charles King of Staffordshire (Dolan, 2019). It is only 80 years later that we find the first formally identified diatom, the colonial *Bacillaria paxillifera*, discovered and described in 1783 by Danish naturalist Otto Friedrich Müller, who characterized many infusoria during his life. Like many others after him, he wrongly thought that it was an animal due to its ability to move (Mann, 2002). Even Darwin saw diatom remains in dust whilst in the Cape Verde Islands, although he was not sure what they were. It was only later that they were identified for him by Ehrenberg (as siliceous polygastrics) (Ehrenberg, 1844). The infusoria that Darwin later noted in the face paint of Fueguinos, native inhabitants of Tierra del Fuego in the southern end of South America, were later identified in the same way (Williams, 2011). During his lifetime, the siliceous polygastrics were clarified as belonging to the *Diatomaceae*, and Darwin struggled to understand the reasons underpinning their beauty. He exchanged opinions with the noted cryptogamist G. H. K. Thwaites on the topic. In the fourth edition of On the Origin of Species he stated that "*Few objects are more beautiful than the minute siliceous cases of the diatomaceae: were these created that they might be examined and admired under the high powers of the microscope*"? and reasoned that their exquisite morphologies must have functional underpinnings rather than having been created purely for humans to admire (Darwin, 1866). Subsequently, a diatom was named after Darwin (*Asteromphalus darwinii)*, probably by Ehrenberg (Ehrenberg, 1844). Diatom samples obtained by Ehrenberg were used for making one of the first photomicrographs of these organisms by Gustav Theodor Fritsch (1838–1927), as a result of his improvements of an apparatus for photomicrography (Fig. 5A) (Ehrenberg, 1870).

Dinoflagellates (Dinoflagellata) were first described in 1753 by Henry Baker as "Animalicules that cause the sparkling light in sea water" (Baker, 1753) and were formally named by Otto Friedrich Müller in 1773 (Müller, 1773). Darwin was also enchanted by the phenomenon of bioluminescence, stating in his journal while on HMS *Beagle* in 1833 "... *on one very dark night, the sea presented a wonderful and most beautiful spectacle. There was a fresh breeze, and every part of the surface, which during the day is seen as foam, now glowed with a pale light. The vessel drove before her bows two billows of liquid phosphorus, and in her wake she was followed by a milky train. As far as the eye reached, the crest of every wave was bright, and the sky*

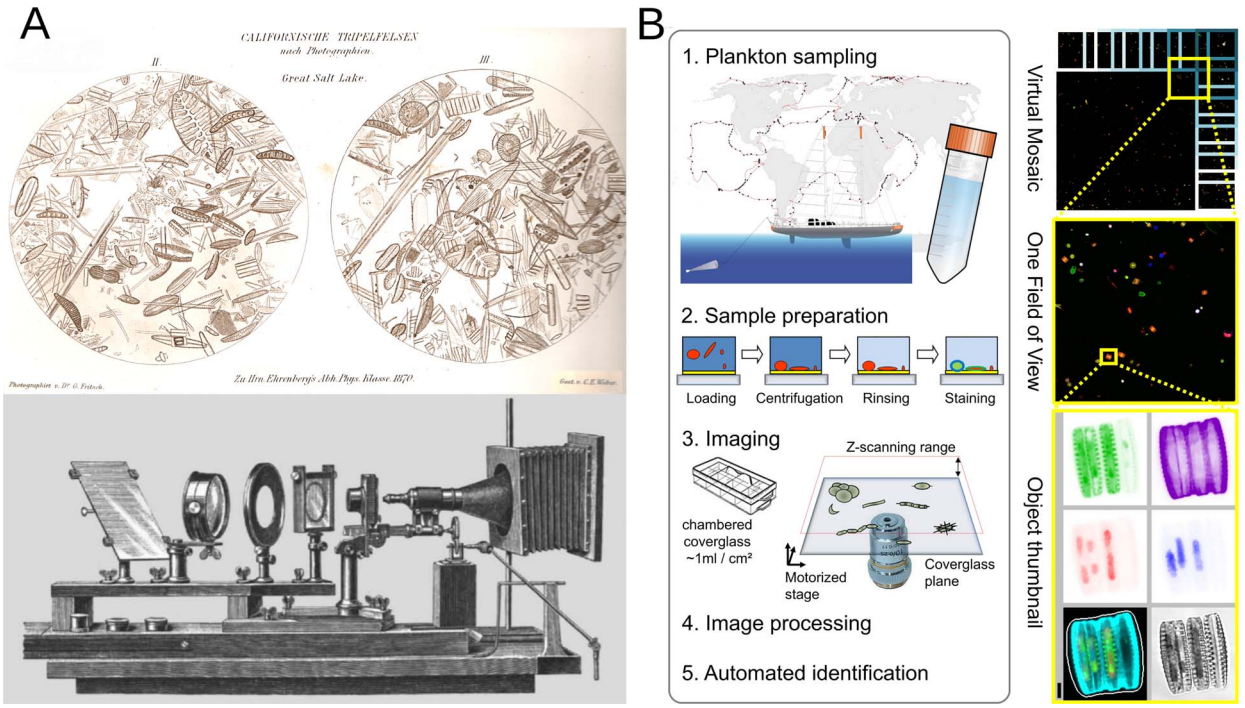

Fig. 5. Comparison between early and modern photomicrographs and devices. (**A**) Upper figure probably corresponds to one of the first photomicrographs of diatoms (probably benthic) by Gustave Theodor Fritsch (1838–1927), using samples obtained by Christian G. Ehrenberg (Ehrenberg, 1870). Lower figure shows Fritsch's photomicrographic horizontal camera (adapted from Overney and Overney, 2011). (**B**) High-throughput workflow for generating confocal microscopy images from *Tara* Oceans samples (adapted from Colin *et al.*, 2017). An example of micrograph is shown for a diatom of the *Fragilariopsis* genus, including different subcellular compartments.

above the horizon, from the reflected glare of these vivid flames, was not so utterly obscure, as over the rest of the heavens" (Darwin, 1845). Bioluminescence is present in a number of ecologically important dinoflagellate species, including both phototrophs and, mainly, heterotrophs (Valiadi and Iglesias-Rodriguez, 2013). Although dinoflagellates are not the only bioluminescent organisms, they are the most celebrated in the ocean. Some species can further form highly resistant spores (known as cysts) that are preserved in the geological record, and that go back at least to the Triassic Period. Indeed, already in the 1830s, Ehrenberg not only examined many living samples and proposed several dinoflagellate genera that are still in use today (including *Peridinium*, *Prorocentrum* and *Dinophysis*), he also noted the first fossil forms from flint of Cretaceous age (Ehrenberg, 1841).

Coccolithophores are haptophytes covered by small regular calcareous plates (coccoliths) and are extremely important in biogeochemical cycles because they are responsible for about half of all modern precipitation of $CaCO_3$ in the ocean (Milliman, 1993). The first register of coccoliths corresponds to Ehrenberg in 1836 during a microscopic analysis of chalk. Back then and throughout his career, he was convinced that they were of inorganic origin. It was Henry Clifton Sorby in 1860 who first suggested their biological nature (Winter and Siesser, 2006). The most well-known representative is *Emiliania huxleyi*, which has arisen only recently in evolutionary history to become the most numerically abundant and widespread coccolithophore species. It was originally named as *Pontosphaera huxleyi* by Lohmann in 1902 but was renamed in 1967 by Hay and Mohler (Young and Westbroek, 1991), in recognition of Thomas Huxley (who was the first to examine sea-bottom sediment and discover the coccoliths within it in 1858) and Cesare Emiliani (credited with founding the field of paleo-oceanography). In addition to coccolithophores, non-calcifying haptophyte lineages such as the genus *Phaeocystis* are also abundant. *Phaeocystis* usually blooms in polar regions, forming floating colonies, but they also include members, which are endosymbionts of the protist *Acantharia* (Decelle *et al.*, 2012). The colonies of *Phaeocystis* can reach diameters of up to 2 mm and were first observed by G. O. Sars in 1878 in the vicinity of Jan Mayen island in the Arctic Ocean (Gran, 1902). More than a decade later, *Phaeocystis pouchetii* became the first described species of this genus (Pouchet, 1892; Lagerheim, 1896).

Species from the phylum Cryptophyta were also first reported by Ehrenberg (1831). This is no surprise considering he belongs to the few algal scientists that identified more than 1 000 species (De Clerck *et al.*, 2013). Regarding euglenoids, as mentioned in the previous section, *Euglena viridis* is supposedly one of the first described protists. O. F. Müller gave a more complete description of the organism in 1786 and Ehrenberg gave its current name in 1830 (Ehrenberg, 1830a). Therefore, taxa of all the currently recognized phytoplankton phyla were discovered prior to 1850, with the exception of Chlorarachniophyta, whose type species (*Chlorarachnion reptans*) was originally described in 1930 (Geitler, 1930).

The role of picophytoplankton in the ocean emerged mainly in the second part of the 20th century with the work by Butcher (1952). He isolated and described several species less than 3 μm in diameter, including *Chromulina pusilla*, initially classified using light microscopy as a member of the Chrysophyceae (Butcher, 1952). However, this species was recognized as a chlorophyte by Irene Manton and Mary Parke using electron microscopy and by careful pigment analysis (Manton, 1959; Manton and Parke, 1960). It was later renamed as *Micromonas pusilla*, now known to be one of the most widespread species in temperate latitudes, and further classified within the prasinophyceans, a paraphyletic group of green microalgae that are currently classified either at the class, order or family level, or as clades without formal taxonomic description (Tragin *et al.*, 2016). The two major groups of prasinophyceans are Mamiellales (*Micromonas*, *Bathycoccus* and *Ostreococcus*, which includes the smallest free-living eukaryote *O. tauri* (Courties *et al.*, 1994), and clade VII, both prominent in oceanic waters (Guillou *et al.*, 2004; Lopes Dos Santos *et al.*, 2017). Prasinophyte clade VII are naked coccoid cells with no specific morphological feature and remain without formal description, despite the fact that cultured representatives exist since 1965 (Potter *et al.*, 1997). The taxonomy of prasinophyceans has proved particularly challenging in part due to the small size and uniform morphology of many of their members, but modern molecular and phylogenetic approaches have been particularly informative (see below; see also Daugbjerg *et al.*, 2020 for a recent example).

Before 1970, cyanobacteria were known to occur widely in freshwater and terrestrial habitats, but they were thought to be relatively unimportant in the modern ocean. This perception changed dramatically in the late 1970s and 1980s with the discovery of *Synechococcus* and *Prochlorococcus*, which are among the most abundant organisms on the planet. *Synechococcus*, 0.8–1.5 μm in diameter, was discovered in 1979 when small coccoid cells were observed in a fluorescent microscope during an expedition in the Arabian Sea (Johnson and Sieburth, 1979; Waterbury *et al.*, 1979). *Prochlorococcus* is even smaller, at just 0.5–0.7 μm in diameter, and was discovered in 1986 by Sallie W. (Penny) Chisholm and collaborators following the introduction of flow cytometry into oceanographic research (Chisholm *et al.*, 1988). Besides these two prominent genera of cyanobacteria, at least two nitrogen-fixing genera are also known: the filamentous *Trichodesmium* and the coccoid *Crocosphaera*, both restricted to tropical waters (Zehr *et al.*, 2007). While *Crocosphaera* was only recently discovered and characterized, *Trichodesmium* colonies have been known by sailors since at least the 18th century (see earlier) and was described by Ehrenberg (1830b). Additionally, nitrogen-fixing cyanobacteria are known to enter into symbiotic associations with a range of eukaryotes, including *Richelia* with a few diatoms (Venrick, 1974). The earliest reports of these associations came from microscopic observations in the late nineteenth and early twentieth centuries (Ostenfeld and Schmidt, 1901; Lemmermann, 1905), although it was only recently shown that nitrogen is fixed and transferred to the diatom host (Foster *et al.*, 2011).

The use of molecular and phylogenetic approaches to define species was a key innovation that provided novel insights into the diversity and evolutionary history of different phytoplankton groups (De Clerck *et al.*, 2013). It was first applied to cultivated individual strains: the first marine plankton sequence corresponds to the 5S and 5.8S rDNA from the nonphotosynthetic dinoflagellate *Crypthecodinium cohnii* (Hinnebusch *et al.*, 1981). The technique was very laborious, but other sequences were steadily obtained such as those from the photosynthetic dinoflagellate *Prorocentrum micans* (Maroteaux *et al.*, 1985; Herzog and Maroteaux, 1986). The subsequent development of the polymerase chain reaction (Saiki *et al.*, 1985) facilitated the work and thus the number of available phytoplankton sequences increased sharply. Thus, cultured taxa without distinctive morphological features were defined as novel groups thanks to these DNA-based phylogenetic methods, such as the pelagophyceans (Andersen *et al.*, 1993) and the bolidophyceans (Guillou *et al.*, 1999).

The discoveries of new phytoplankton taxa of ecological significance extend to today, thanks to the application of culture independent genetic surveys in marine samples (see also last section). The uncultivated unicellular diazotrophic cyanobacterium "Candidatus *Atelocyanobacterium thalassa*," commonly known as UCYN-A, was first detected through the amplification of transcripts of the *nifH* gene (encoding the dinitrogenase reductase subunit of nitrogenase) (Zehr *et al.*, 2001). It lives in a mutualistic partnership with an uncultivated unicellular alga, a calcifying prymnesiophycean closely related to *Braarudosphaera bigelowii* (Zehr *et al.*, 2001). Other examples are found

among ochrophytes, a monophyletic clade covering the whole range of photosynthetic stramenopiles (although a few species have lost their capacity to photosynthesize). Besides prominent stramenopile groups such as diatoms, pelagophyceans and dictyochophyceans (silicoflagellates), five new uncultured groups are now recognized and have been named marine Ochrophyta (MOCH) and three of them are likely to be photosynthetic (Massana *et al.*, 2014). The five MOCHs are not closely related but are scattered among the ochrophytes (Massana *et al.*, 2014).

DETECTING PHYTOPLANKTON AND MEASURING PRIMARY PRODUCTIVITY IN THE OCEAN

While we have known about microscopic phytoplankton for several centuries and have studied their importance for sustaining marine food webs since the end of the 19th century, precisely how much production they sustain, how this compares with land plants, and which phytoplankton groups contribute where and when has been an active debate since then and has not yet been fully resolved. Remarkably, even the most astute observers on the early oceanographic expeditions cited above apparently failed to notice the importance of the spring bloom, and Mills found no references from early fishermen that noted the relevance of the phenomenon to fish stocks either. He considers rather that appreciation of the spring bloom arose steadily in the late 19th/early 20th century as a result principally of the work in the Kiel and Plymouth schools (Mills, 2012). The combined knowledge from their work led to an appreciation that the phenology underlying productivity in the ocean appeared to be different to what is observed on land, in that productivity is maximal during the spring bloom, whereas it is generally highest in the summer months on land, and that annual productivity is most pronounced at higher latitudes in the open ocean whereas tropical regions display maximal annual productivity on land.

Methods for measuring phytoplankton abundance and/or productivity have continually been developed since the 19th century. In 1865, Father Pietro Angelo Secchi, when in charge of mapping the clarity of the Mediterranean Sea for the Papal Navy, invented the simplest of oceanographic instruments: a 20-cm-wide white disk that is lowered until the observer loses sight of it. Secchi-depth determinations assess light penetration in the upper ocean and can be related to phytoplankton abundance, and even today, they are a routine part of oceanographic observations (Tyler, 1968; Preisendorfer, 1986; Wernand, 2010). Besides plankton net catches and microscopy examination of seawater samples (Utermöhl, 1958), more specific approaches came only in the middle of the 20th century, when spectrophotometric and fluorometric techniques were adapted for estimating chlorophyll concentration in seawaters (Yentsch and Menzel, 1963; Lorenzen and Jeffrey, 1980). The subsequent development of thin layer chromatography eventually allowed the recognition of the full spectrum of chlorophylls, carotenoids and chlorophyll degradation products (Jeffrey, 1974). Photosynthetic pigments consist of chlorophyll *a* as the major component, plus a suite of other light-absorbing organic molecules (e.g. carotenoids) with accessory functions. As broad phytoplankton groups vary in their accessory pigments, determining their content and composition in a sample can inform on the actual community structure. Pigments present in a seawater sample are nowadays measured directly by extraction and subsequent high-performance liquid chromatography (HPLC) (Jeffrey *et al.*, 1999), and extensive datasets are available across the global ocean (Jeffrey *et al.*, 1999; Peloquin *et al.*, 2013). In order to move from purely qualitative analyses to more quantitative results, a few algorithms based on pigment ratios have been developed (e.g. CHEMTAX; Mackey *et al.*, 1996).

During the 20th century, *in situ* chemical measurements shed light on net primary productivity (NPP)—the rate at which phytoplankton populations incorporate organic matter through photosynthesis after meeting their own energy needs. A major step came with the development of the detection of the assimilated ^{14}C tracer and its use on the global Danish expedition Galathea (Nielsen, 1952). Slowly, figures for global net primary production in the seas in the order of tens of gigatons carbon per year started to emerge, making it comparable with the annual yield on land (Nielsen, 1960).

A major advance started in the 1980s with remote sensing of the colour of the ocean (Gordon *et al.*, 1980), which provides synoptical information at large spatial and temporal scales (Field *et al.*, 1998; Karl and Church, 2014). It relies on the estimation of near-surface chlorophyll *a* concentrations through bio-optical algorithms with the use of satellites (McClain, 2009). Initially used to estimate standing stocks of phytoplankton, it then developed into estimates of net primary productivity at regional and global scales (Platt and Sathyendranath, 1988; Morel, 1991; Longhurst *et al.*, 1995; Antoine *et al.*, 1996; Behrenfeld and Falkowski, 1997; Field *et al.*, 1998; McClain, 2009). In addition, the retrievals of backscattering, a proxy of phytoplankton carbon (Graff *et al.*, 2015), allowed for estimation of phytoplankton growth rate and the generation of carbon-based algorithms for net primary productivity (Behrenfeld *et al.*, 2005; Westberry *et al.*, 2008). This global understanding was used to partition the oceanic

ecosystem into ecological provinces (IOCCG, 2009) and to better appreciate the biogeochemical processes shaping coastal and open-ocean environments. Remote sensing further supports the importance of ocean phytoplankton for global primary productivity, leading to our current estimation that the ocean contributes around 45% of the global total (Field *et al.*, 1998). Our view from space has furthermore revealed that NPP of some regions is higher compared to others, e.g. the high latitudes of the North Atlantic and North Pacific Oceans, as well as the Southern Ocean (Tréguer *et al.*, 2018).

Satellite-based detection of chlorophyll is now used extensively to estimate primary production, and further developments are being explored to access different aspects of phytoplankton communities, such as the taxonomic composition (Alvain *et al.*, 2005; Uitz *et al.*, 2006; El Hourany *et al.*, 2019) or the distribution of specific taxa (Balch *et al.*, 1991; Subramaniam *et al.*, 2002; Simis *et al.*, 2005; Lubac *et al.*, 2008), size groups (Bricaud *et al.*, 2007), or their physiological status (Behrenfeld *et al.*, 2008; Blondeau-Patissier *et al.*, 2014). Importantly, advances in understanding phytoplankton bloom dynamics have come from satellite observations (Behrenfeld, 2010), later also supported by data from Biogeochemical-Argo floats (see next section) (Boss and Behrenfeld, 2010), showing that rates of phytoplankton biomass accumulation do not necessarily correlate with cell division rates (Behrenfeld and Boss, 2014, 2018). In addition, it has been possible to study the link between phytoplankton and ocean biogeochemistry by, for example, assimilating satellite chlorophyll data into biogeochemical models (Doron *et al.*, 2013) or by using it to estimate the production of the climate active gas dimethylsulfide (DMS), which is the cleavage product of dimethylsulfoniopropionate (DMSP), synthesized by different phytoplankton groups (Gali *et al.*, 2015, 2019).

Obtaining precise estimates of biomass or primary production at different depths of the photic layer still represents a challenge, since the signal is derived mainly from the very first surface layers (Morel and Berthon, 1989; Uitz *et al.*, 2006). Notwithstanding, remote sensing of the ocean by satellites represents a milestone as it revealed seasonal and interannual variabilities in phytoplankton features at the global scale (Racault *et al.*, 2012), which constitutes a fundamental aspect in the study of ecosystem status in the context of climate dynamics (Arrigo and van Dijken, 2015).

OCEAN OBSERVING PROGRAMS IN THE AGE OF GENOMICS AND BIG DATA

The study of marine phytoplankton started with a focus on the organisms using microscopy and cultivated strains, but then—for several decades—the attention moved strongly towards bulk properties such as pigments and satellite remote sensing. Nowadays, even if the focus on individual organisms has never been lost, it has been revitalized, in part due to the better appreciation of their taxonomic diversity, but also due to the development of genomics and advanced imaging systems that allow to understand their evolutionary origins, their functional diversity and their complex interactions in planktonic communities with enormous amounts of new data.

The complete genomes of several marine phytoplanktonic species were published at the beginning of the 21st century, including *Prochlorococcus* (Dufresne *et al.*, 2003; Rocap *et al.*, 2003), *Synechococcus* (Palenik *et al.*, 2003), the diatoms *Thalassiosira pseudonana* (Armbrust *et al.*, 2004) and *Phaeodactylum tricornutum* (Bowler *et al.*, 2008), and the prasinophyceans *Ostreococcus tauri* (Derelle *et al.*, 2006), *O. lucimarinus* (Palenik *et al.*, 2007), *Micromonas commoda* and *M. pusilla* (Worden *et al.*, 2009). More recently, the Marine Microbial Eukaryote Transcriptome Sequencing Project (MMETSP) sequenced expressed genes from cultured protists. It resulted in over 650 assembled and functionally annotated transcriptomes within 210 different genera from undersampled branches of the eukaryotic tree of life, most of them corresponding to phytoplankton species (Keeling *et al.*, 2014).

Community assessment of plankton samples based on DNA metabarcoding started in the 1990s (Giovannoni *et al.*, 1990; Fuhrman *et al.*, 1993), but bloomed with the advent of high-throughput sequencing in the 2000s. A global-scale metagenomic sampling of the ocean began years later with J. Craig Venter's Global Ocean Sampling (GOS) expeditions between 2003 and 2008 (Fig. 1B), which included the collection of "bacterial" size fractions from surface waters from the North–West Atlantic and Eastern Tropical Pacific Oceans from 2004 to 2006 (Fig. 1B), generating a 6.1 million gene set using Sanger sequencing (Rusch *et al.*, 2007). Of relevance to photosynthesis and global ocean energy budgets, this expedition was instrumental in revealing the widespread occurrence of proteorhodopsin-driven phototrophy in bacterioplankton (Béjà *et al.*, 2000, 2001), which has been recently also found in archaea (Frigaard *et al.*, 2006), protists (Slamovits *et al.*, 2011; Marchetti *et al.*, 2015) and viruses (Yutin and Koonin, 2012), although it is still unclear to what extent this process actually contributes to transforming energy (Finkel *et al.*, 2013). Later, in the context of the Census of Marine Life (http://www.coml.org/), a consortium of researchers deployed the International Census of Marine Microbes (ICoMM, http://icomm.mbl.edu/; Amaral-Zettler *et al.*, 2010) to provide a detailed inventory of marine microbial diversity. Further projects of large spatial coverage came subsequently with the Malaspina expedition, led by

Carlos Duarte, which targeted principally the deep ocean but also the epipelagic layers in a worldwide sampling campaign from 2010 to 2011 (Fig. 1B) (Duarte, 2015), and the Ocean Sampling Day initiative, which began with a simultaneous global sampling campaign on 21 June 2014 at 191 different sites, mostly in coastal areas (Kopf *et al.*, 2015). The latter projects relied mainly on metabarcoding by amplicon sequencing of rRNA genes (16S for prokaryotes, 18S for eukaryotes).

Another large-scale and long-term observatory is the Atlantic Meridional Transect (AMT), a north–south transect in the Atlantic Ocean from England to the Malvinas/Falkland Islands, which has been performed regularly since 1995 (Robinson *et al.*, 2006). Although genetic data are still limited from this programme, it has revealed important information regarding the distribution of *Prochlorococcus* and *Synechococcus* at ocean basin scale (Zubkov *et al.*, 1998). Conversely, hundreds of single cell genomes from these picocyanobacteria have been generated from the Pacific and Atlantic Oceans thanks to further projects (Berube *et al.*, 2018; Biller *et al.*, 2018; Pachiadaki *et al.*, 2019), in particular the BioGEOTRACES component of GEOTRACES (Anderson *et al.*, 2014). In parallel, the generation of genomic data has been expanding rapidly at ocean time-series sites, e.g. the Bermuda Atlantic Time Series, http://bats.bios.edu/, the Integrated Marine Observing System, http://imos.org.au/, the Hawaii Ocean Time series, http://hahana.soest.hawaii.edu/hot/, the Carbon Retention In A Colored Ocean program, http://imars.marine.usf.edu/cariaco, the FRAM observatory, https://www.awi.de/en/expedition/observatories/ocean-fram.html, and the Marine Biodiversity Observation Network, https://ioos.noaa.gov/project/bio-data/. These and other programmes have accelerated the availability of genetic data of microbes from the ocean.

Databases relying on microscopic observations of plankton are also proving to be extremely valuable. Of note, the MARine Ecosystem biomass DATa (MAREDAT) initiative has quantified global biomass of different plankton groups (Buitenhuis *et al.*, 2013). The MAREDAT database derives principally from light microscopy and automated imaging sampling, including the Continuous Plankton Recorder (see below) (Reid *et al.*, 2003). Another resource is found in the collaborative web application and repository EcoTaxa (Picheral *et al.*, 2017) that allows for the storage and analysis of imaging datasets, typically acquired by automated, high-throughput methods. It includes, amongst others, data obtained through confocal microscopy (e.g. Figs 3B and 5B, Colin *et al.*, 2017), UVP5 (Guidi *et al.*, 2016), FlowCam and ZooScan (Gorsky *et al.*, 2010; Ibarbalz *et al.*, 2019), collected during the *Tara* Oceans expeditions (see below). It offers a range of tools for the rapid validation by specialists with the help of automatic recognition algorithms.

Ocean continuous monitoring initiatives are fundamental strategies to understand and follow the dynamics of the largest ecosystem on Earth. The Continuous Plankton Recorder (CPR) survey is one of the longest running marine biological surveys. Since the first CPR tow in the North Sea in 1931 by Alister Hardy (Warner and Hays, 1994), the methodology has been applied worldwide, although the core CPR programme of monthly, synoptic sampling has focused on the North Atlantic Ocean. To date, it has resulted in more than 5 million nautical miles of ocean sampled at a depth of ~10 m by voluntary "ships of opportunity" carrying the towed CPR machines, generating more than 250 000 phyto- and zooplankton data sets, including the Phytoplankton Colour Index (Batten *et al.*, 2003). Additional initiatives include the worldwide use of Argo floats to profile key physical parameters, while the Biogeochemical-Argo Program is implementing a global network of floats equipped with bio-optical and biogeochemical sensors (Xing *et al.*, 2018). They represent a key complement to the continuous monitoring performed by satellites. For example, the implementation of miniature fluorometers on Biogeochemical-Argo floats makes possible the systematic collection of vertical profiles of chlorophyll *a* (Claustre *et al.*, 2020).

In 2008, Eric Karsenti led a consortium of scientists that organized a circumglobal expedition on board the 36-m-long schooner SV *TARA* (Figs 1B and 2). The expedition was specifically designed for studying microscopic plankton ecosystems at global scale. Based on a holistic approach, the *Tara* Oceans pan-oceanic expedition sampled plankton ranging in size from viruses to small metazoans, coupled with comprehensive *in situ* biogeochemical measurements, which are key for ecological interpretation of marine microbiomes (Karsenti *et al.*, 2011). A wide range of contrasting ecosystems were targeted, using sampling protocols that were highly standardized and consistent at each site. *Tara* Oceans is in fact derived from two research expeditions performed between 2009 and 2013. The first expedition (named *Tara* Oceans) lasted two years and eight months and sampled all of the principal ocean basins with the exception of the Arctic Ocean, and the second (named *Tara* Oceans Polar Circle) lasted seven months and circumnavigated the Arctic Circle (Fig. 1B). These two expeditions consisted in the collection of >35 000 plankton samples from 210 sampling sites, which were used for generating >60 terabases of DNA and RNA sequenced and ~7 million images (Sunagawa *et al.*, 2020). A further expedition, called *Tara* Pacific, has recently finished (2015–2018) and included the sampling of corals and plankton mainly across the

Pacific Ocean (Gorsky *et al.*, 2019; Planes *et al.*, 2019). The *Tara* Oceans sampling related to photosynthesis and phytoplankton has been recently reviewed in detail (Pierella Karlusich *et al.*, 2020).

The value of sample preservation following global expeditions such as those discussed is highlighted in a recent study that compares samples from the HMS *Challenger* expedition with those from *Tara* Oceans, designed to assess whether ocean acidification has increased since the beginning of the industrial age by examining the shells of calcifying foraminifera hosting photosymbionts (Fox *et al.*, 2020). The study focused on the central Pacific Ocean, where the sampling was carried out during the same month in both cases (Fig. 1) and detected up to 76% reduction in shell thickness, pointing to the potential effect of decreasing pH during the 140-year period that separated both expeditions. Although we do not have records of what depths the *Challenger* samples were taken from, and the differences may be compounded by multiannual processes such as El Niño—La Niña cycles, this study illustrates the value of archiving samples for future use.

CONCLUSION

Our appreciation of phytoplankton in the ocean can be traced back to the eighteenth century, while large-scale oceanographic expeditions dedicated to their study have been deployed since the nineteenth century. Throughout that extended period of time, the focus has moved from the individual organisms to the collective properties at a global scale. However, a clearer picture of phytoplankton ecology and their evolutionary histories has emerged only in the last decades, with the burst of omics and advanced imaging technologies that has brought the individualities back to the spotlight. Thus, observations at multiple scales, from the naked eye to microscopes and from satellite-remote sensing to molecular surveys, have made this an inspiring scientific journey, resulting in the discoveries of new taxa, new functions and interactions, and in major advances in the understanding of their spatial and temporal patterns. The picture is not yet fully resolved and we are still far from deciphering the mechanisms of adaptation and acclimation, range of trophic modes (e.g. mixotrophy), and biological interactions (e.g. photosymbioses). In the context of global change and anthropogenic pressure on ocean ecosystems, the study of phytoplankton and marine ecosystems in general needs to continue to provide an understanding of the ecological and evolutionary responses that underlie the functioning of the ocean. Records (and sometimes even samples) from previous expeditions furthermore represent a treasure trove that can be used to compare today's highly modified modern ocean with that of former centuries.

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