ANNUAL REVIEWS

Annual Review of Marine Science

Phytoplankton in the *Tara* Ocean

Juan José Pierella Karlusich, Federico M. Ibarbalz, and Chris Bowler

Institut de Biologie de l'École Normale Supérieure (IBENS), Département de Biologie, École Normale Supérieure, CNRS, INSERM, Université de Recherche Paris Sciences et Lettres (Université PSL), 75005 Paris, France; email: cbowler@biologie.ens.fr

Annu. Rev. Mar. Sci. 2020. 12:233–65

The *Annual Review of Marine Science* is online at marine.annualreviews.org

https://doi.org/10.1146/annurev-marine-010419-010706

Keywords

diatoms, dinoflagellates, photosynthesis, primary production, *Prochlorococcus*, *Synechococcus*, *Tara* Oceans

Abstract

Photosynthesis evolved in the ocean more than 2 billion years ago and is now performed by a wide range of evolutionarily distinct organisms, including both prokaryotes and eukaryotes. Our appreciation of their abundance, distributions, and contributions to primary production in the ocean has been increasing since they were first discovered in the seventeenth century and has now been enhanced by data emerging from the *Tara* Oceans project, which performed a comprehensive worldwide sampling of plankton in the upper layers of the ocean between 2009 and 2013. Largely using recent data from *Tara* Oceans, here we review the geographic distributions of phytoplankton in the global ocean and their diversity, abundance, and standing stock biomass. We also discuss how omics-based information can be incorporated into studies of photosynthesis in the ocean and show the likely importance of mixotrophs and photosymbionts.

1. INTRODUCTION

Microscopic organisms dominate life in the world's ocean in terms of biomass, organism abundance, and diversity (Bar-On et al. 2018, de Vargas et al. 2015). Collectively called plankton, they compose the core of marine food webs and have major impacts on multiple biogeochemical cycles. Their critical roles are explained principally by the fact that a large fraction of them are photosynthetic primary producers.

The photosynthetic plankton, or phytoplankton, consist of unicellular organisms of diverse evolutionary history and ecology. Their composition in today's ocean consists mainly of the larger and hence more conspicuous diatoms and dinoflagellates, as well as smaller eukaryotes such as coccolithophores, pelagophytes, and prasinophytes, and the minuscule picocyanobacteria *Prochlorococcus* and *Synechococcus*. They live in the sunlit upper layer to depths where light can still pass, which can extend to depths of 200 m in transparent waters at low latitudes. Their biogeochemical roles include the generation of oxygen, the recycling of elemental nutrients, and the removal of CO_2 from the atmosphere to generate organic biomass through primary production.

Measurements of primary production and remote sensing of surface chlorophyll indicate that phytoplankton are responsible for generating more than 45% of global net primary production (approximately 50 Gt C y^{-1}) (Field et al. 1998). Remarkably, though, they represent only approximately 1% of Earth's photosynthetic biomass, due to their fast proliferation times and their rapid consumption through grazing and other means, and because all cells are photosynthetically active, unlike plants on land (see Section 3.4). The drawdown of atmospheric CO_2 through the activity of these organisms is called the biological carbon pump, which results in the generation of organic matter (and calcium carbonate in some taxa) that can be consumed by other organisms and/or sequestered in the deep ocean after sinking (Zhang et al. 2018). This biological carbon pump exports approximately 5–12 Gt C y^{-1} from the surface to the mesopelagic layer, from which approximately 0.2 Gt C y^{-1} is stored in sediment for millennia (Ciais et al. 2013), thus contributing to the vertical gradient of carbon in the ocean. The process also results in biological feedback on atmospheric CO_2 and thus Earth's climate because CO_2 is a greenhouse gas (Field et al. 1998, Joos et al. 1999).

Although our appreciation of phytoplankton in the ocean can be traced back to the seventeenth century, a clearer picture of their evolutionary history has emerged only in the past few decades, with the advent of molecular-based approaches. This picture is nonetheless not yet fully resolved, and even though we have made major advances in understanding the spatial and temporal patterns of phytoplankton, we are still far from deciphering the mechanisms underlying their adaptation and acclimation strategies, range of trophic modes (e.g., mixotrophy), and biological interactions (e.g., photosymbioses).

The *Tara* Oceans expedition circumnavigated the world's ocean to sample plankton ecosystems from 2009 to 2013. By applying state-of-the-art methodologies in microbial oceanography, the project has described plankton communities in their environmental context to an unprecedented level, with the purpose of advancing knowledge about the evolution and ecology of marine ecosystems and beyond. It provided an extensive depiction of ocean life at the beginning of the twenty-first century in an epoch characterized by profound global change caused by human activities. Here, we provide an extensive overview of what the *Tara* Oceans project has so far uncovered regarding the composition, diversity, and biogeography of phytoplankton. Finally, we identify potential areas of research for which such data sets could provide interesting insights and discuss limitations that still need to be addressed.

2. PHOTOSYNTHESIS IN THE OCEAN

2.1. The Origins and Evolution of Phytoplankton

Oxygenic photosynthesis is arguably the most important process in biology, as it changed the redox conditions on Earth and allowed the appearance of life forms based on oxygen respiration (Fischer et al. 2016) (**Figure 1*a***). It first evolved in the cyanobacteria at least 2.4 billion years ago and then was transferred to the eukaryotic domain of life approximately 1.5 billion years ago through a primary endosymbiotic event involving the engulfment of a cyanobacterium by the common ancestor of glaucophytes, red and green algae, and land plants (**Figure 1*a*,*b***). However, the photosynthetic protists that characterize today's ocean are derived predominantly from additional secondary or higher endosymbiotic events in which eukaryotic algae were incorporated into a eukaryotic cell, particularly events involving the incorporation of chloroplasts derived from red algae (Reyes-Prieto et al. 2007) (**Figure 1*b***). Thus, while land plants belong to a small corner of the tree of life that evolved roughly 450 million years ago, the marine photosynthetic community is composed of organisms with deep branches that are distributed throughout the eukaryotic tree of life (**Figure 1*b***).

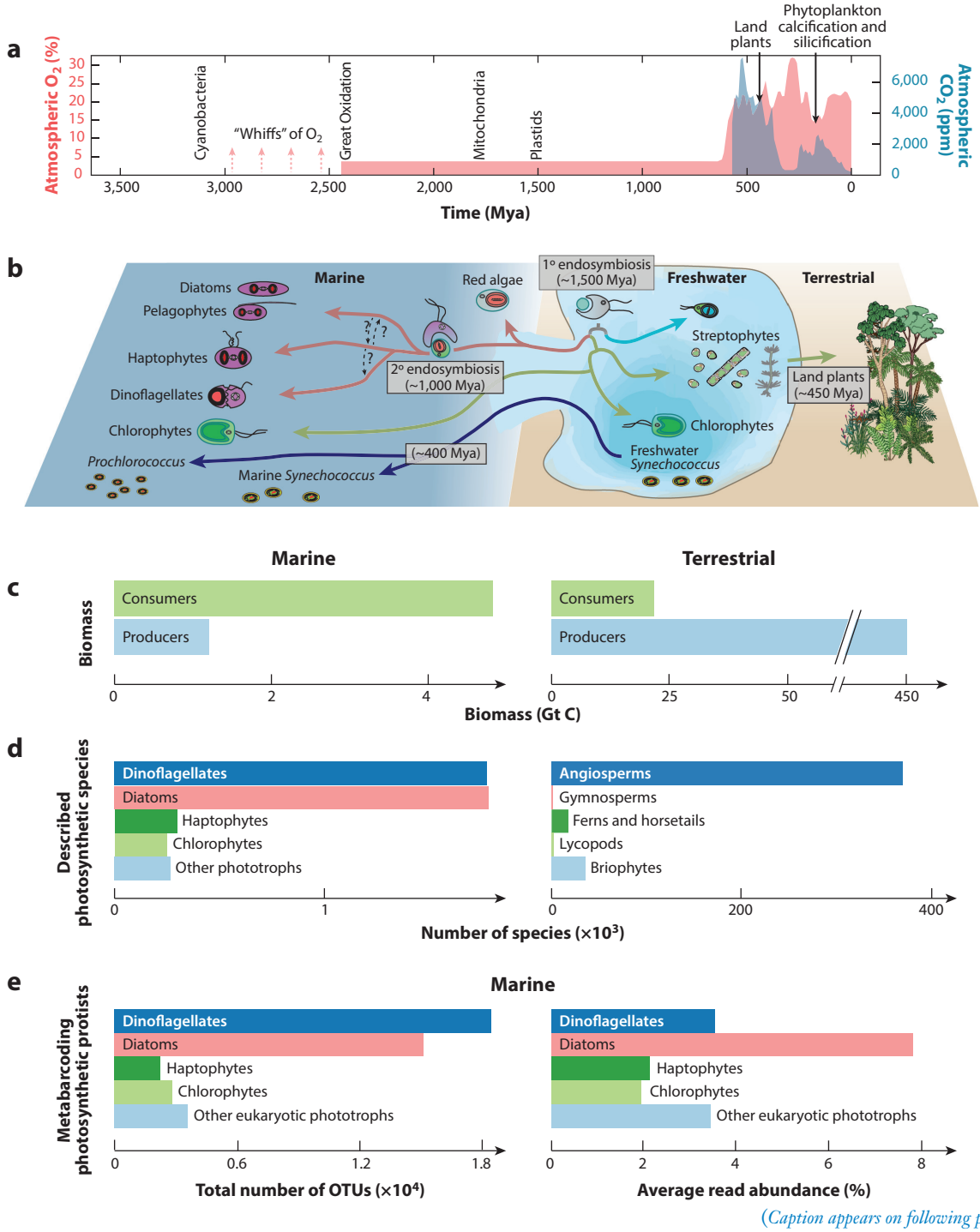
A further characteristic of current marine environments with respect to terrestrial ones is the abundance of the picocyanobacteria *Synechococcus* and *Prochlorococcus* (**Figure 2**). Sánchez-Baracaldo et al. (2019) have proposed that the main marine clades arose from a common ancestor that made a transition from fresh water to the ocean in the Cambrian approximately 500 million years ago. The split between these genera may then have occurred approximately 400 million years ago during the Devonian (Sánchez-Baracaldo et al. 2019) (**Figure 1*b***).

Morphological innovations among the phytoplankton have led to huge impacts on Earth's geochemistry. The appearance of diatoms, which have siliceous cell walls (frustules), and coccolithophores, which are armored with miniature plates of calcite (coccoliths; see both in **Figure 2**), has contributed to the precipitation of hard materials to the ocean interior and has affected the atmospheric levels of CO_2 (Benoiston et al. 2017, Falkowski 2012, Falkowski et al. 2008, Knoll et al. 2007, Smetacek 1999) (**Figure 1*a***). The evolutionary trajectories that led to the remarkable diversity of photosynthetic organisms in the ocean exceed the scope of this review, but other recent work has covered this topic extensively (see Coelho et al. 2013, de Vries & Gould 2018, Dorrell & Bowler 2017, Falkowski & Knoll 2011, Falkowski et al. 2004, Simon et al. 2009, and references therein).

2.2. Large-Scale Phytoplankton Surveys in the Ocean

Large-scale oceanographic expeditions have been used for the study of planktonic ecosystems since the nineteenth century. Although he did not focus on it, Charles Darwin was able to describe the diversity of marine microorganisms during his voyage on the HMS *Beagle* (1831–1836) (Costa 2017). However, modern oceanography is considered to have began with the first deep-sea exploration by the HMS *Challenger* from 1872 to 1876. Several planktonic organisms sampled by this expedition were described and drawn in detail by Ernst Haeckel, who coined the term ecology (Haeckel 1998).

During the twentieth century, the development of methods that use carbon radioisotopes to measure carbon fixation and satellite remote sensing of ocean color (principally chlorophyll) allowed the estimation of global net primary production rates in the marine environment, showing an annual yield comparable to that on land (Behrenfeld et al. 2005, Field et al. 1998, McClain 2009, Steemann Nielsen 1960). Further advances have come with ocean observing initiatives, such



(*Caption appears on following page*)

Figure 1 (*Figure appears on preceding page*)

Interplay between geochemical changes and biological evolution, together with estimates of current biomass and species distributions in marine and terrestrial environments. (*a*) Temporal relationships between trends in atmospheric O_2 and CO_2 concentrations and major evolutionary events during the evolution of life on Earth. (*b*) Schematic representation of the colonization of Earth's main habitats by the currently most abundant phototrophs and their diversification during evolution. This panel shows the wide diversity of photosynthetic groups that thrive in the marine environment in comparison with the exclusive dominance of land plants in terrestrial environments. For the sake of simplicity, we omit the multiple incursions across the freshwater–marine boundary near the evolutionary roots of *Synechococcus* (Sánchez-Baracaldo et al. 2019) and the multiple independent events of secondary endosymbiosis of green algae. Haptophytes, dinoflagellates, and stramenopiles (such as diatoms and pelagophytes) are distantly related, but they all harbor a red complex plastid that ultimately traces back to a monophyletic secondary endosymbiosis event. Nevertheless, the number and order of subsequent tertiary (or even quaternary) endosymbiosis events remain topics of intense investigation (de Vries & Gould 2018). (*c*) Comparison of the biomass distributions in marine and terrestrial environments. The biomass of producers (photoautotrophs) and consumers (heterotrophs, not including those in marine subseafloor sediment, oceanic crust, or terrestrial substratum that is deeper than 8 m and different from soil) is based on the yearly averaged estimates from Bar-On et al. (2018). Terrestrial producers consist of land plants, while marine producers are dominated by phytoplankton but also include macroalgae and seagrasses. The breakdown of phytoplankton biomass into different subgroups is an open issue due to huge uncertainties, biases, and under- and oversampling. (*d*) Number of photosynthetic species in the marine and terrestrial environments across high taxonomic levels (based on data from Sournia et al. 1991 for marine phytoplankton and R. Bot. Gard. Kew 2017 for land plants). (*e*) Diversity and composition of eukaryotic phytoplankton from *Tara* Oceans based on the complete 18S rRNA gene (V9 region) metabarcoding data set (de Vargas et al. 2015, Ibarbalz et al. 2019). The left side shows the total number of operational taxonomic units (OTUs) among all size fractions, and the right side shows the corresponding read abundances relative to total eukaryotic counts from the 0.8–2,000-μm size fraction. Panel *a* adapted from Benoiston et al. (2017).

as the worldwide network of Argo floats that provide key contextual information such as temperature and salinity. The Biogeochemical-Argo program is taking a further step by implementing a global network of floats equipped with bio-optical and biogeochemical sensors (Xing et al. 2018). An important output from these approaches is the recent advances in the understanding of phytoplankton bloom dynamics, which first came from satellite observations (Behrenfeld 2010) and later were supported by data from Biogeochemical-Argo floats (Boss & Behrenfeld 2010), showing that rates of accumulation of phytoplankton biomass do not necessarily correlate with cell division rates (Behrenfeld & Boss 2014, 2018) and thus leading to a reevaluation of traditional concepts.

Other ocean observing surveys have focused on plankton imaging. 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 methods, including the Continuous Plankton Recorder (CPR) (Reid et al. 2003).

Starting in the early twenty-first century, omics-based approaches began to be applied in the field of oceanography. Large-scale sampling began with J. Craig Venter's Global Ocean Sampling expedition, which collected bacteria-enriched samples in surface waters of the northwest Atlantic and eastern tropical Pacific from 2004 to 2006 and used Sanger sequencing to generate a set of 6.1 million genes (Rusch et al. 2007). Further omics projects of large spatial coverage came later with the Malaspina expedition, led by Carlos Duarte, which principally targeted the deep ocean in a worldwide sampling campaign in 2010 and 2011 (Duarte 2015), and the Ocean Sampling Day initiative, which began with a simultaneous global-sampling campaign on June 21, 2014, at 191 different sites, mostly in coastal areas (Kopf et al. 2015).

3. MARINE PHYTOPLANKTON THROUGH THE *TARA* OCEANS LENS

3.1. How Did *Tara* Oceans Assess Photosynthesis in the Ocean?

In the spirit of expeditions of discovery in previous centuries, in 2008 a consortium of scientists led by Eric Karsenti organized a circumglobal expedition aimed specifically at studying microscopic

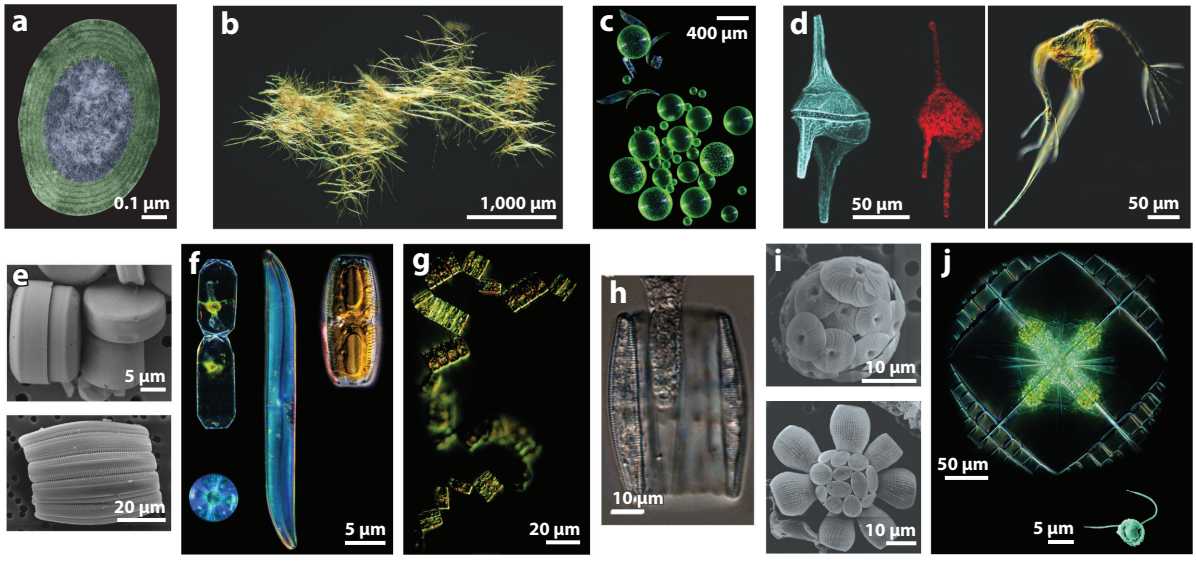


Figure 2

Examples of morphological and trophic complexity of marine plankton with photosynthetic capacity. (*a*) The picocyanobacterium *Prochlorococcus marinus*, which measures 0.5–0.7 µm in diameter and is the smallest and most abundant photosynthetic cell on the planet. The photosynthetic membranes are pseudocolored in green, and the DNA is in blue. (*b*) *Trichodesmium* colony collected in the equatorial Pacific during the *Tara* Oceans expedition. This genus of diazotrophic cyanobacteria can form large colonies (1–5 mm in diameter) composed of tens to hundreds of filaments (or trichomes) 5–20 µm in length, which consist of aggregates of approximately 100 cells. (*c*) Example of a green alga. The chlorophyte *Halosphaera* sp. (*large spherical cells*) is shown together with the diatom *Rhizosolenia* sp. (*cylindrically shaped cells*); these were the two predominant plankton species collected with a 0.1-mm mesh net during the winter in Roscoff, France. (*d*) The dinoflagellates *Ceratium candelabrum* (*left*) and *Ceratium ranipes* (*right*). Like many other dinoflagellates, *C. candelabrum* builds envelopes made of a delicately ornamented cellulose plate, the theca; blue fluorescence shows the theca, and red fluorescence shows the chloroplasts. (*e*) Electron micrographs of centric (*top*) and pennate (*bottom*) diatoms. Diatom cells are housed within an extracellular envelope called a frustule, consisting of two parts fitting one into the other. These shells are made of hydrated silicate oxides deposited onto a protein matrix synthesized inside the cell. (*f*) Light microscopy images of the diatoms *Cerataulina* sp. (*top left*), *Actinoptychus* sp. (*bottom left*), *Gyrosigma* sp. (*center*), and *Amphora* sp. (*right*). (*g*) The chain-forming pennate diatom *Thalassionema nitzschioides*. The cells, each measuring 10–20 µm, are joined together in chains by mucilaginous links. (*h*) The diatom *Fragilariopsis doliolus*. This species forms barrel-shaped chains that enable interaction with a tintinnid ciliate, as shown in this image, collected in the South Atlantic during the *Tara* Oceans expedition. (*i*) Electron micrographs of two coccolithophores: *Dicosphaera tubifera* (*top*) and *Scyphosphaera apsteinii* (*bottom*). These organisms (unicellular algae from the phylum Haptophyta) produce calcite plates (scales or coccoliths) that adorn the cell surface to form an exoskeleton (coccosphere). *S. apsteinii* is a larger cell with several kinds of coccoliths. (*j*) *Lithoptera fenestrata* collected during winter in the bay of Villefranche-sur-Mer. This unicellular zooplankton (order Acantharia) has a skeleton of strontium sulfate that grows in size with age. Cytoplasmic extensions are visible here. The four yellow masses are groups of photosynthetic symbionts of the genus *Phaeocystis* (phylum Haptophyta) living inside the cytoplasm. At the bottom right is an image of the cultured microalgae *Phaeocystis* sp. with its two flagella. Panel *a* is by William K.W. Li (Bedford Institute of Oceanography, Dartmouth, Canada) and Frédéric Partensky (CNRS, Station Biologique, Roscoff, France) (adapted from Sardet 2015); panels *b*, *c*, *f*, and *g* are by Christian Sardet (adapted from Sardet 2015); panel *d* is by Christian Rouviere, Marie-Dominique Pizay, John Dolan, and Rodolphe Lemée (CNRS, Observatoire Océanologique de Villefranche-sur-Mer, Laboratoire d'Océanographie de Villefranche-sur-Mer) (adapted from Sardet 2015); panels *e* and *i* are by Atsuko Tanaka and Chris Bowler (École Normale Supérieure, CNRS, France); panel *h* is adapted from Vincent et al. (2018); and panel *j* is by Fabrice Not and Johan Decelle (CNRS-SU, Station Biologique, Roscoff, France) (adapted from Sardet 2015).

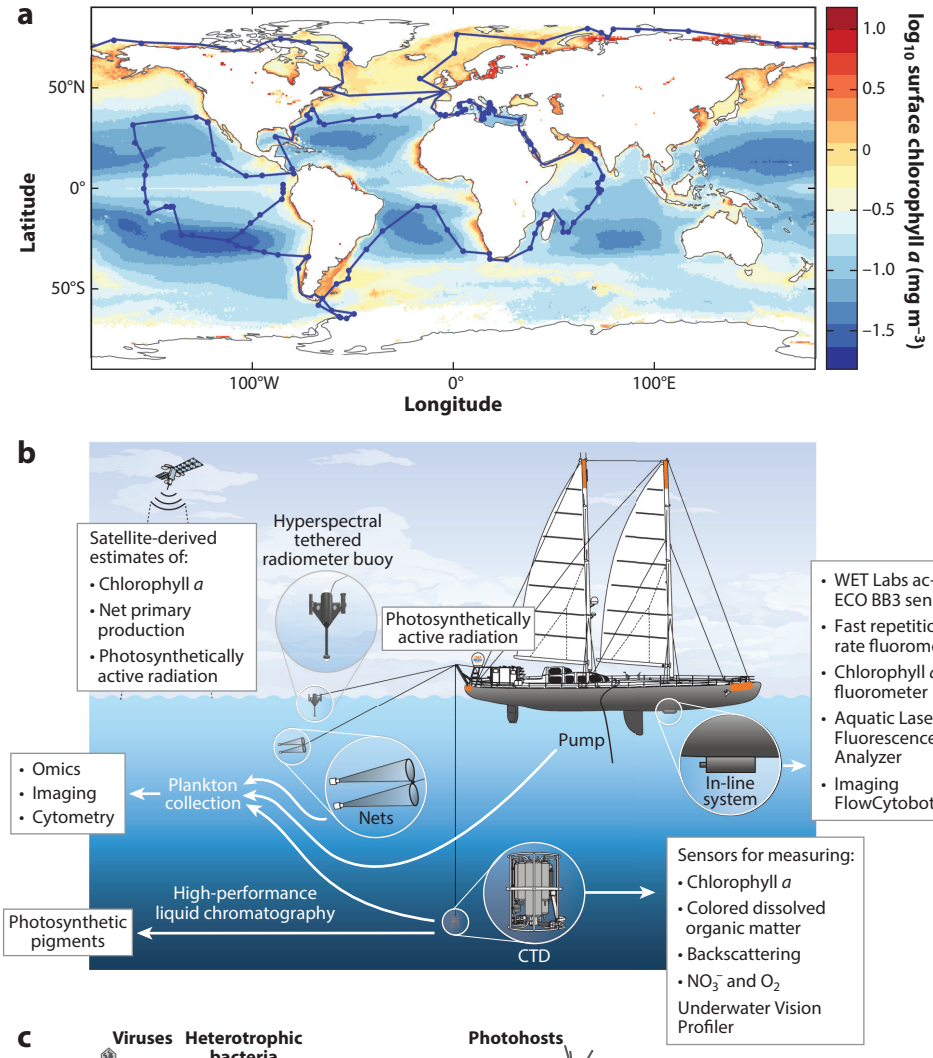
plankton ecosystems at a global scale. The *Tara* Oceans pan-oceanic expedition deployed a holistic sampling of plankton, ranging in size from viruses to fish larvae, and took comprehensive in situ biogeochemical measurements that provided the detailed environmental contexts necessary for ecological interpretation of marine microbial communities (Karsenti et al. 2011). *Tara* Oceans is in fact derived from two research expeditions performed between 2009 and 2013 using a 36-m-long schooner (SV *Tara*) refitted to operate state-of-the-art oceanographic and plankton sampling equipment within the limits of its size. 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 (**Figure 3*a***).

These two expeditions targeted a wide range of contrasting ecosystems and collected more than 35,000 discrete samples from 210 distinct sampling stations, together with more than 1,000 CTD (conductivity, temperature, and depth) profiles down to a depth of 1,000 m. Because the sampling protocols were highly standardized and consistent at each site, data intercomparisons can be performed to reveal a truly global view of entire plankton communities, from viruses to zooplankton (using genomics and cellular imaging), as demonstrated in a range of publications from *Tara* Oceans and other scientists (Brum et al. 2015, de Vargas et al. 2015, Guidi et al. 2016, Louca et al. 2016, Sunagawa et al. 2015, Villar et al. 2015). Moreover, the in-line optical equipment used in *Tara* Oceans provided continuous measurements for particle absorption, scattering, and attenuation that were highly consistent with chlorophyll extraction. These measurements have enriched observations for oligotrophic areas of the ocean (Boss et al. 2013) and represent an opportunity for satellite calibration and validation (Werdell et al. 2013). In combination with pigment data from high-performance liquid chromatography, optical measurements have also proved valuable for estimating phytoplankton accessory pigments from hyperspectral reflectance spectra, testing its potential and limitations (Chase et al. 2017). As such, the sampling, data organization, and analysis protocols (Alberti et al. 2017, Pesant et al. 2015) can be inspirational for future ocean observation projects to address ecosystem change over time. **Figure 3*b*** and **Table 1** provide a general overview of sampling on the schooner, particularly with respect to what is relevant for measuring photosynthesis and quantifying phytoplankton; further information is provided in the **Supplemental Appendix**. In the following sections, we discuss current knowledge about phytoplankton distributions in the ocean, in particular highlighting the contribution of information from *Tara* Oceans.

Supplemental Material >

3.2. The Diversity of Marine Phytoplankton

The ocean harbors a wide range of photosynthetic groups derived from different evolutionary trajectories (**Figure 1*b***). Dinoflagellates display tremendous morphological and functional diversity, with approximately half of their species containing chloroplasts (**Figure 2*d***). Haptophytes include the coccolithophores, which are characterized by the presence of calcified scales (**Figure 2*i***) and form massive blooms in temperate waters, as well as the genus *Phaeocystis*, which can be found as free-living single cells, colonies, or endosymbionts (**Figure 2*j***). Cryptophytes dwell in coastal marine habitats and are still understudied. The photosynthetic groups among stramenopiles form a monophyletic clade known as ochrophytes, which besides diatoms include prominent groups such as pelagophytes and dictyochophytes (silicoflagellates). The characteristic, highly elaborate siliceous cell walls of diatoms, known as frustules, are easily recognizable (**Figure 2*e–h***). Other stramenopiles, such as dictyochophytes, are also silicifiers. New ribogroups are now recognized within Ochrophyta and have been named marine Ochrophyta (MOCH) (Massana et al. 2014). MOCH-1 and MOCH-2 contain single-cell amplified genomes sorted as plastidic cells,



(*Caption appears on following page*)

Figure 3 (*Figure appears on preceding page*)

Tara Oceans expedition and sampling strategy with respect to photosynthesis and phytoplankton. (*a*) Route of the *Tara* Oceans expeditions from 2009 to 2013. The background color corresponds to surface chlorophyll *a* concentrations estimated from satellite (multiannual average data from the Moderate Resolution Imaging Spectroradiometer instrument, 2002–2018). (*b*) Devices on board SV *Tara* for sampling phytoplankton and assessing photosynthesis. Phytoplankton were sampled using nets towed vertically or horizontally, Niskin bottles on the CTD (conductivity, temperature, and depth) instrument, or a peristaltic pump (down to 70-m depth). Once collected, plankton samples were shipped to land and analyzed by imaging, omics (metabarcoding, metagenomics, and metatranscriptomics), and flow cytometry. Measurements relevant to photosynthesis were generated on board via in-line instrumentation and from CTD casts (see the **Supplemental Appendix**). Satellite-based observations were also collected both in real time at each sampling station and from historical records. (*c*) Plankton sampling by size classes. Several filtration steps were performed using membranes with different pore sizes to obtain size-fractionated samples enriched in viruses (<0.1 μm and 0.1–0.2 μm), prokaryotes (0.2–3 μm), and eukaryotes (0.8–5, 5–20, 20–180, and 180–2,000 μm). Data for giant viruses (0.2–3 μm) are also available but not shown here. The lower part of the graph shows the obtained average abundances for the main phytoplankton groups in the different size fractions based on 16S miTags (metagenomic Illumina tags, i.e., 16S rDNA fragments derived from metagenomes sequenced with an Illumina platform) for prokaryotes (Sunagawa et al. 2015) and 18S rRNA gene (V9 region) metabarcoding for eukaryotes (de Vargas et al. 2015, Ibarbalz et al. 2019). These general results confirm that diatoms and dinoflagellates are the predominant groups of microphytoplankton, whereas haptophytes, chlorophytes, and pelagophytes are smaller groups, but they also reveal the unexpected abundance of diatoms in pico- and nanoplankton fractions, as recently confirmed by Leblanc et al. (2018). Panel *b* designed by Noan le Bescot (Ternog Design).

and MOCH-5 includes two cultures of phototrophs (no longer available) (Massana et al. 2014). Another prominent group is the chrysophytes, several of which have lost their capacity to photosynthesize or have even lost their chloroplast genome altogether (Dorrell et al. 2019). Among chlorophytes (**Figure 2*c***), the most prominent lineages correspond to clade VII prasinophytes and Mamiellophyceae, which include well-studied members such as *Ostreococcus*, considered to be the smallest free-living eukaryote (0.95 μm) (Derelle et al. 2006).

Compared with the wide diversity at a high taxonomic level, the total species diversity in marine phytoplankton appears to be extremely low, especially in relation to the almost 400,000 species of terrestrial plants (R. Bot. Gard. Kew 2017) (**Figure 1*d***). Approximately 4,000 species of marine phytoplankton had formally been described by the end of the 1980s (Sournia et al. 1991). Diatoms, dinoflagellates, and to a lesser extent haptophytes and chlorophytes were the most diversified groups (with approximately 40%, 40%, 10%, and 6% of the described phytoplanktonic eukaryote species, respectively; **Figure 1*d***). In comparison, the marine planktonic cryptophytes, chlorarachniophytes, and euglenophytes appear to be far less diversified (less than 2% for each group). However, due to the comparatively limited sampling, the relative paucity of distinctive morphological features, and the scarcity of taxonomists, the current number of phytoplankton species is almost certainly underestimated, while the known numbers of higher plants probably do reflect their actual diversity.

DNA-based approaches have been instrumental in defining phytoplankton taxa in the absence of morphological features. Indeed, several new phytoplankton lineages that are quite distantly related from well-known taxa have been discovered in the last few decades (Simon et al. 2009). Communities of microscopic organisms can be examined by amplicon sequencing, where a fragment of the small subunit of the rRNA gene (16S for prokaryotes, 18S for eukaryotes) is universally amplified and massively sequenced from an environmental sample. This approach enabled a tremendous expansion of richness estimates in the microscopic realm, in spite of recurrent and unresolved problems (e.g., definition of species in the absence of data from sexual crosses, artifacts from polymerase chain reaction and sequencing methods; see the **Supplemental Appendix**). In *Tara* Oceans, the sequencing of approximately 1.7 million reads belonging to the 18S rRNA gene (V9 region) from 334 samples from 47 different geographical sites of the expedition revealed the occurrence of approximately 110,000 distinct eukaryotic operational taxonomic units (OTUs, a proxy for species in molecular surveys), of which fewer than 20% could

Supplemental Material >

Table 1 ***Tara*** **Oceans measurements with respect to photosynthesis and phytoplankton (and their communities)**

Method	Target
Plankton diversity	
18S rRNA gene (V9 region) metabarcoding	Eukaryotes (size fractions of 0.8–2,000 μm, 0.8–3 or 0.8–5 μm, 3–20 or 5–20 μm, 20–180 μm, and 180–2,000 μm) (de Vargas et al. 2015, Ibarbalz et al. 2019)
16S rRNA gene miTags	Prokaryotes and chloroplasts (0.22–1.6 or 0.22–3 μm) (Sunagawa et al. 2015, Salazar et al. 2019)
petB gene miTags	Picocyanobacteria (0.22–1.6 or 0.22–3 μm) (Farrant et al. 2016)
Plankton gene and genome catalogs	
Global Ocean Viromes 2.0	Viruses (Brum et al. 2015, Gregory et al. 2019, Roux et al. 2016)
Ocean Microbial Reference Gene Catalog version 2	Viruses, prokaryotes, and picoeukaryotes (Sunagawa et al. 2015, Salazar et al. 2019)
Marine Atlas of *Tara* Oceans Unigenes version 1	Protists (size fractions of 0.8–2,000 μm, 0.8–3 or 0.8–5 μm, 3–20 or 5–20 μm, 20–180 μm, and 180–2,000 μm) (Carradec et al. 2018)
Single-amplified genomes	Pico- and nanoeukaryotic plankton (Alberti et al. 2017, Seeleuthner et al. 2018)
Plankton imaging	
Quantitative transmission electron microscopy	Viruses (Brum et al. 2015)
Transmission electron microscopy and scanning electron microscopy	Nanoplankton (5–20 μm) and microplankton (20–180 μm)
Inverted light microscopy	Eukaryotes (unfiltered samples) and microplankton (20–180 μm)
Environmental high-content fluorescence microscopy	Nanoplankton (5–20 μm) and microplankton (20–180 μm) (Colin et al. 2017)
Flow cytometry	Picophytoplankton and heterotrophic bacteria (Hingamp et al. 2013, Ibarbalz et al. 2019)
FlowCam	Protists, small metazoans, and larval stages of larger metazoans (50–300 μm); only *Tara* Oceans Polar Circle
Imaging FlowCytobot	Microplankton (20–180 μm); only *Tara* Oceans Polar Circle
Underwater Vision Profiler 5	Particles larger than 100 μm; suited for fragile aggregates such as marine snow and organisms that tend to break when sampled with nets, such as gelatinous metazoans (Biard et al. 2016, Guidi et al. 2016)
ZooScan	Suited for large hard-shelled protists (e.g., Rhizaria) and metazoans captured with nets (Ibarbalz et al. 2019)
Optical parameters	
High-performance liquid chromatography	Photosynthetic pigments (Chase et al. 2013)
WET Labs ac-s spectrophotometry	Photosynthetic pigments (Boss et al. 2013, Chase et al. 2013)
Fast repetition rate fluorometry	Photosynthetic efficiency (Kolber et al. 1998, Pesant et al. 2015)
Fluorescence emission (Aquatic Laser Fluorescence Analyzer)	Photosynthetic efficiency; only *Tara* Oceans Polar Circle
Surface photosynthetically active radiation sensor	Only *Tara* Oceans Polar Circle (during *Tara* Oceans, photosynthetically active radiation was predicted based on data from the Advanced Moderate Resolution Imaging Spectroradiometer)
Optical backscattering (three wavelengths)	Only *Tara* Oceans Polar Circle
Physicochemical parameters	
SeaBird temperature and conductivity sensor	Temperature and conductivity
Nutrient	NO_2^-, PO_4^{3-}, NO_2^-/NO_3^-, O_2, and Si
Carbonate system parameters	pHT, CO_2, pCO_2, fCO_2, HCO_3^-, CO_3^{2-}, total alkalinity, total carbon, and aragonite and calcite saturation states
Organic carbon	Dissolved organic carbon, fluorescence colored dissolved organic matter, and dissolved oxygen isotopes; only *Tara* Oceans Polar Circle

be assigned to phytoplankton and known hosts of photosymbiosis (de Vargas et al. 2015). Among phytoplankton, the largest numbers of OTUs were assigned to dinoflagellates and diatoms, followed by green algae (more precisely prasinophytes) and haptophytes (**Figure 1*e***). The relative diversity of each group is consistent with morphology-based estimates, although the actual numbers of taxa based on OTUs are consistently approximately 10-fold higher (**Figure 1*d*,*e***). Other photosynthetic groups, such as the cryptophytes, chlorarachniophytes, and ochrophytes other than diatoms, were also found. Note that assigning photosynthetic capacity based solely on the rRNA gene is challenging and limited to what we know from experts and the literature (e.g., groups such as dinoflagellates contain members that have been subjected to multiple independent events of chloroplast gains and losses) (Dorrell & Smith 2011).

As for the microeukaryotes, the global diversity of cyanobacteria is difficult to assess in terms of species number. AlgaeBase (**http://www.algaebase.org**) currently contains more than 4,500 cyanobacterial species, mostly distributed in freshwater/terrestrial (67%) and marine (14%) habitats, including benthic and planktonic lifestyles. The taxonomic diversity of free-living, planktonic cyanobacteria in present-day marine waters is surprisingly low, with few major genera, such as *Prochlorococcus* (**Figure 2*a***) and *Synechococcus* and the nitrogen fixers *Trichodesmium* (**Figure 2*b***) and *Crocosphaera*. At the level of species, if one uses the classical bacterial taxonomy yardstick of less than 3% divergence in the 16S rRNA sequence, all members of *Prochlorococcus* belong to the same "species" called *Prochlorococcus marinus*, while *Synechococcus* is composed of several species. Molecular phylogenetic analyses have revealed different clades for these two genera. Approximately 13 clades were defined for *Prochlorococcus* and approximately 20 for *Synechococcus*, but few of them predominate in the environment. To overcome their low sequence variability at the 16S rRNA gene, Farrant et al. (2016) analyzed their diversity with a genetic marker with higher resolution (*petB*, a gene encoding cytochrome b_6) retrieved from the *Tara* Oceans metagenomes. They defined ecologically significant taxonomic units—that is, organisms belonging to the same clade and occupying a common oceanic niche—which revealed a significant diversity at a finer resolution than the currently defined clades. Overall, however, marine photosynthetic bacteria appear to be far less diversified than their eukaryotic counterparts.

For years we have realized that photosynthesis in plankton is not a sharply defined box, but rather a continuum that fades into heterotrophy (see the sidebar titled Mixotrophs). Faure et al. (2019) carried out a search for mixotrophs in the 18S rRNA gene (V9) metabarcoding data set through 659 samples across 122 geographical sites of the *Tara* Oceans transect, obtaining 318,054 mixotrophic OTUs belonging to 133 lineages (**Figure 4*a***). Among phytoplankton, they retrieved phagotrophic members of chrysophytes (including species of the genera *Chrysolepidomonas*, *Chrysoxys*, *Ochromonas*, and *Poterioochromonas*), haptophytes (*Exanthemachrysis*, *Exanthemachrysis*, *Pavlova*, *Chrysochromulina*, and *Prymnesium*), and dinoflagellates (members of the Prorocentrales order, including species from *Alexandrium*, *Gonyaulax*, *Lingulodinium*, *Fragilidium*, *Gymnodinium*, *Karenia*, *Karlodinium*, *Akashiwo*, *Gyrodinium*, *Cochlodinium*, *Scrippsiella*, *Heterocapsa*, and *Prorocentrum*) (**Figure 4*a***). Their study indicates that mixotrophy appears to be ubiquitous and that the largest number of OTUs corresponds to photohosts among radiolarians (**Figure 4*a***).

3.3. Composition of Marine Phytoplankton

Tara Oceans relied on the quantification of marker genes to analyze the composition of the plankton community. A taxon-specific fraction of reads out of the total number of reads is typically used as a proxy for the abundance fraction of that taxon (although affected by multiple factors, such as copy-number variation of the marker gene among species; see de Vargas et al. 2015 and the **Supplemental Appendix**). 16S rDNA fragments derived from metagenomes were identified and assembled, generating the so-called miTags (metagenomic Illumina tags, i.e., 16S

Supplemental Material >

MIXOTROPHS

Marine plankton have been traditionally classified into two groups depending on their trophic strategy: the photosynthetic plankton (phytoplankton) and the heterotrophic plankton (zooplankton). But from very early on it was evident to shrewd observers such as Charles Darwin that this dichotomy was highly problematic (Costa 2017). It is now clear that mixotrophy—the ability to combine autotrophy and heterotrophy—has been largely underestimated and is commonly found in the plankton (Caron 2016, Flynn et al. 2013, Mitra et al. 2016, Selosse et al. 2017, Stoecker et al. 2017).

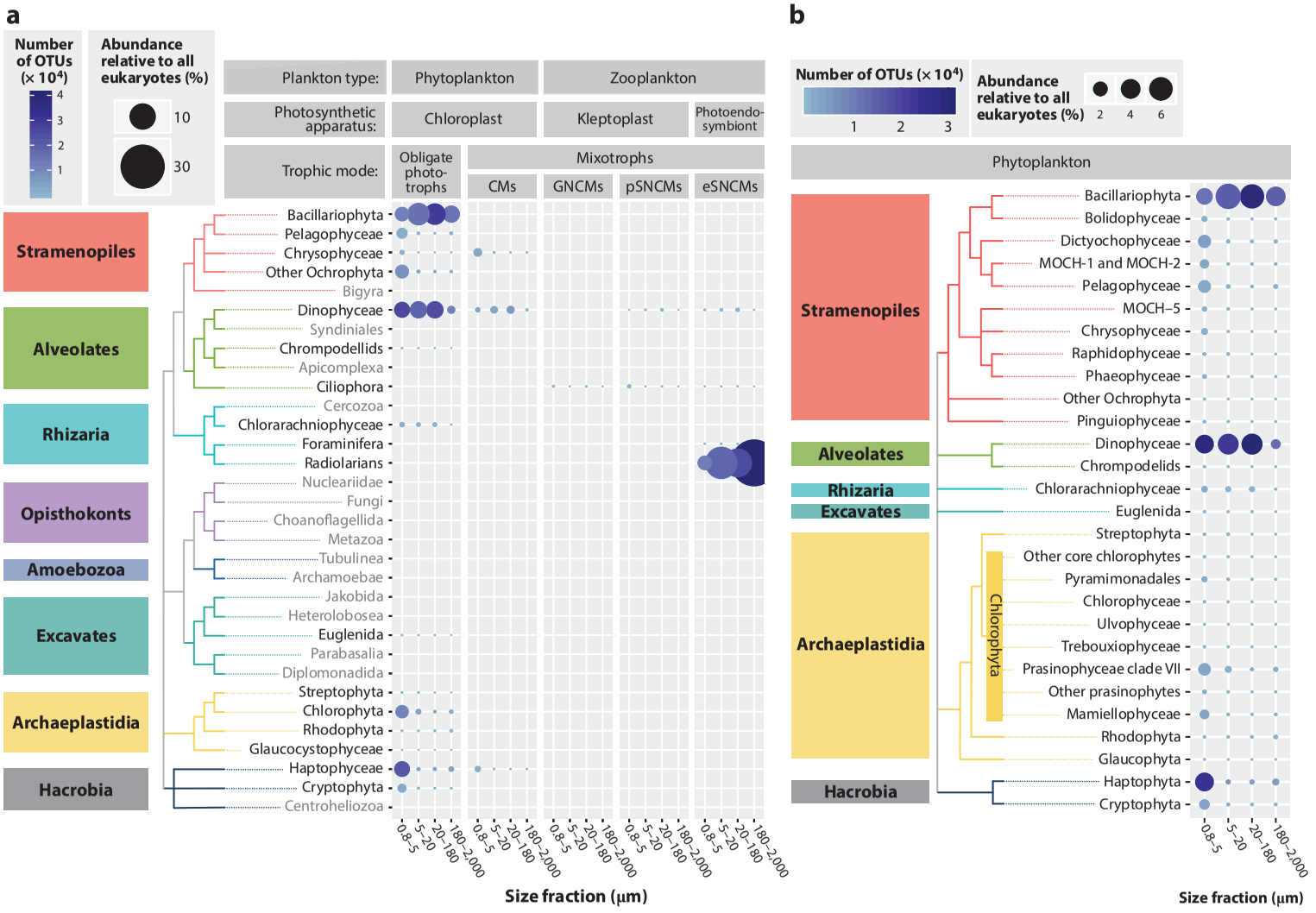
Mitra et al. (2016) proposed a new functional classification for marine protists to aid exploration of the new mixotroph-centric paradigm in marine ecology. According to this classification, marine protists are divided into six groups: two that align with the traditional nonphagotrophic phytoplankton (notably diatoms) and nonphototrophic microzooplankton, and four that represent contrasting mixotroph functional groups, or mixotypes. The constitutive mixotrophs are photosynthetic organisms that are capable of phagotrophy and were also denoted "phytoplankton that eat." The group includes most mixotrophic nanoflagellates (e.g., *Prymnesium parvum* and *Karlodinium micrum*). At the opposite end of the scale, the nonconstitutive mixotrophs, or photosynthetic zooplankton, are heterotrophic organisms that have developed the ability to acquire energy through photosynthesis (Stoecker et al. 2017). This ability can be acquired in three different ways: (*a*) The generalist nonconstitutive mixotrophs steal the chloroplasts of their prey (kleptoplastidy) (e.g., most plastid-retaining oligotrich ciliates, such as *Laboea strobila*), (*b*) the plastidic specialist nonconstitutive mixotrophs steal the chloroplasts from a specific type of prey (e.g., *Mesodinium rubrum* or *Dinophysis* spp.), and (*c*) the endosymbiotic specialist nonconstitutive mixotrophs contain photosynthetically active endosymbionts (most mixotrophic Rhizaria from Collodaria, Acantharia, Polycystinea, and Foraminifera, as well as dinoflagellates such as *Noctiluca scintillans*; see **Figure 2*j***).

Osmotrophy—the uptake of dissolved organic substances—has not been included in this classification because it appears to be ubiquitous in protists and therefore is not useful in discriminating among trophic strategies (Flynn et al. 2013, Mitra et al. 2016). Osmotrophy is also ubiquitous in prokaryotes, which lack the ability to internalize food particles by phagotrophy. Bacteria and archaea that additionally use light energy, such as cyanobacteria, are called mixotrophs by some authors (Eiler 2006).

Supplemental Material >

rDNA fragments derived from metagenomes sequenced with an Illumina platform), to capture the prokaryotic abundance and diversity in the 0.22–3-μm size fraction (although chloroplasts are detected as well; see Sunagawa et al. 2015 and the **Supplemental Appendix**). For the eukaryotic fractions, 18S rRNA gene metabarcoding was performed, targeting the V9 variable region (see the **Supplemental Appendix**).

Figure 3*c* shows an overview of the global phytoplankton composition by size fraction. *Prochlorococcus* and *Synechococcus* are by far the dominant cyanobacteria in the 0.22–3-μm size fractions, while sequences from diatoms and dinoflagellates are the most frequent among eukaryotic phototrophs, especially in the size fractions 5–20 μm and 20–180 μm. Between 180 and 2,000 μm, diatoms are still abundant due to the presence of chain-forming (e.g., *Hyalosira* and *Fragilaria*) and epizoic (e.g., *Pseudohimantidium*) species. Abundance in the smaller 0.8–5-μm size fraction is much more heterogeneous between the different groups. **Figure 4*b*** illustrates this heterogeneity at a deeper taxonomic resolution, with haptophytes, dinoflagellates, diatoms (see, e.g., Leblanc et al. 2018), chlorophytes (especially clade VII prasinophytes and Mamiellophyceae), pelagophytes, dictyochophytes, and cryptophytes. As shown in **Figure 4*a***, phagotrophic phytoplankton lineages of dinoflagellates, haptophytes, and chrysophytes are also detected, particularly for the size fractions 5–20 μm and 20–180 μm. As described in the **Supplemental Appendix**, there is an inverse



(Caption appears on following page)

Figure 4 (*Figure appears on preceding page*)

Abundance, richness, and taxonomic distribution of 18S rRNA metabarcodes from protists with photosynthetic capacity in surface waters. (*a*) Taxonomic distribution of phototrophic and mixotrophic capacities in marine protists within the eukaryotic tree of life and corresponding abundances and richness based on 18S rRNA gene (V9 region) metabarcoding on four different size fractions. The trophic mode is divided into obligate phototrophs and four mixotrophic groups (Mitra et al. 2016; see the sidebar titled Mixotrophs): constitutive mixotrophs (CMs), generalist nonconstitutive mixotrophs (GNCMs), plastidic specialist nonconstitutive mixotrophs (pSNCMs), and endosymbiotic specialist nonconstitutive mixotrophs (eSNCMs). (*b*) Taxonomic distribution, abundance, and richness of eukaryotic phytoplankton based on 18S rRNA gene (V9) metabarcoding on four different size fractions. For both panels, the area of each circle corresponds to the average abundance relative to total eukaryotic read counts, while the color gradient varies according to the number of operational taxonomic units (OTUs). Data are derived from the complete *Tara* Oceans data set for 18S rRNA gene (V9 region) metabarcoding (de Vargas et al. 2015, Ibarbalz et al. 2019).

relationship between plankton size and abundance, so small size fractions represent the numerically dominant organisms in terms of cell abundance (but not necessarily in terms of total biomass).

The analysis also indicates that the most abundant mixotrophs correspond to photosymbiotic hosts among radiolarians, which account on average for 34% of eukaryotic reads in the 180–2,000-μm size fraction, although these values might be overestimated due to their high 18S rRNA gene copy number (**Figure 4*a***). Radiolarians have often been overlooked in traditional morphological surveys of plankton net-collected material because of their delicate gelatinous and/or easily dissolved structures, but microscope-based and in situ imaging studies have now shown that they are highly abundant (Biard et al. 2016, Dennett 2002, Michaels et al. 1995, Stemmann et al. 2008). Other zooplankton with photosymbionts or with a capacity for kleptoplasty (i.e., the retention of functional plastids from ingested algal prey) are detected among dinoflagellates and members of Foraminifera and Ciliophora (**Figure 4*a***). Note, however, that the contributions of these organisms to primary production are largely unexplored because the actual extent of photosymbiosis within different taxonomic groups has not been fully defined and because we do not yet know the extent of facultative photosymbiotic interactions.

Tara Oceans also used quantitative methods to determine cell abundance. For example, picocyanobacterial cell abundance was measured at each sampling site by flow cytometry. In addition, size-fractionated samples were fixed on board and analyzed by confocal microscopy for automated high-content imaging (Colin et al. 2017). The 5–20-μm size fraction was recently classified at a high taxonomic level (with an estimated accuracy of 93.8% at the phylum or class level), with the following average cell abundances among the eukaryotic phytoplankton: 35% diatoms, 34% dinoflagellates, 16% haptophytes, and 14% other eukaryotic phytoplankton (Colin et al. 2017). These results exhibit some marked differences with the metabarcoding method, particularly regarding the low read abundances for haptophytes in the same size fraction (5–20 μm) (**Figures 3*c*** and **4*b***). These discrepancies highlight the need for further comparative studies of imaging- and sequence-based data and a better assessment of their limitations.

3.4. Phytoplankton Biomass

Marine net primary production is approximately 50 Gt C y^{-1}, not far from that of terrestrial ecosystems (55–60 Gt C y^{-1}), even though the ocean has more than twice as much surface area (Field et al. 1998). The lower marine productivity per area is explained largely by the poorer light penetration in water (Field et al. 1998). Even though the land and the ocean have similar total primary production, there is approximately 80 times more biomass on land (Bar-On et al. 2018) (**Figure 1*c***). Land plants make up most of this difference, constituting approximately 80% of all biomass on Earth.

When split by trophic levels, the biomass of primary producers on land constitutes more than 95% of all biomass (Bar-On et al. 2018) (**Figure 1*c***). In stark contrast, approximately 1 Gt C of

primary producers supports approximately 5 Gt C of consumer biomass in the ocean, resulting in an inverted standing biomass distribution (**Figure 1*c***), in which consumers make up more than 80% of biomass (Bar-On et al. 2018). Such inverted biomass distributions can occur when primary producers have a rapid turnover of biomass (a few days; Zubkov 2014), while consumer biomass turns over much more slowly (a few years in the case of mesopelagic fish; Catul et al. 2011).

The difference between total biomass in the ocean and on land also reflects the contrasting energetic efficiencies of their food chains. An average 10% of energy is transferred from one trophic level to the next in the ocean (Barbier & Loreau 2019, Trebilco et al. 2013), whereas on land herbivores assimilate as little as 1% of primary production (Hairston & Hairston 1993). This order-of-magnitude difference arises mostly from the presence of woody and stem structures in plants (Swenson & Enquist 2007) to help them rise above their competitors and reach the light in the absence of buoyancy in a liquid environment. These structures are relatively inaccessible to consumers and make up the bulk of land plant biomass (Bar-On et al. 2018). Woody land plants also have a slow turnover, and their biomass represents the accumulation of years to decades of primary production, compared with much shorter timescales in ocean producers.

The biomass of all phytoplankton can be assessed based on satellite detection of global depth-integrated chlorophyll, as in the reports by Antoine et al. (1996) and Behrenfeld & Falkowski (1997). These studies estimated the global phytoplankton biomass at approximately 0.75 Gt C. Based on the MAREDAT database (Buitenhuis et al. 2013), which includes data from flow cytometry, microscopy, and bottle and net sampling counts, Bar-On et al. (2018) summed up the contributions of all phytoplankton and reached a figure of approximately 1.3 Gt C, which is approximately double yet within the same order of magnitude as the remote sensing estimates. The contribution of seagrasses is approximately 0.1 Gt C (Fourqurean et al. 2012), and although there are insufficient data for macroalgae, estimates indicate that phytoplankton are the main component of the global biomass of marine producers (Bar-On et al. 2018). How this biomass is distributed among the different phytoplankton groups is still unresolved due to sampling biases and uncertainties. For example, MAREDAT contains data only for picophytoplankton, diatoms, and *Phaeocystis* (and has a *Phaeocystis* sampling bias toward coastal environments, where dense blooms of this genus regularly occur), but it does not account for nanophytoplankton (phytoplankton between 2 and 20 μm) or autotrophic dinoflagellates (Buitenhuis et al. 2013). Resolving this issue is key to increasing our understanding of the main groups involved in global primary production.

3.5. Spatial Patterns of Phytoplankton Composition and Diversity

A fundamental paradox that has challenged oceanographers for decades is how the ocean, which, superficially at least, is relatively homogeneous, can support so much diversity; this concept was formalized as the "paradox of the plankton" by Hutchinson (1961). We now know that this paradoxical diversity is supported at least in part by the spatial and temporal heterogeneity of factors influencing plankton (e.g., light, nutrients, turbulence, and particles), which results in a mosaic of shifting niches rather than a homogeneous ocean.

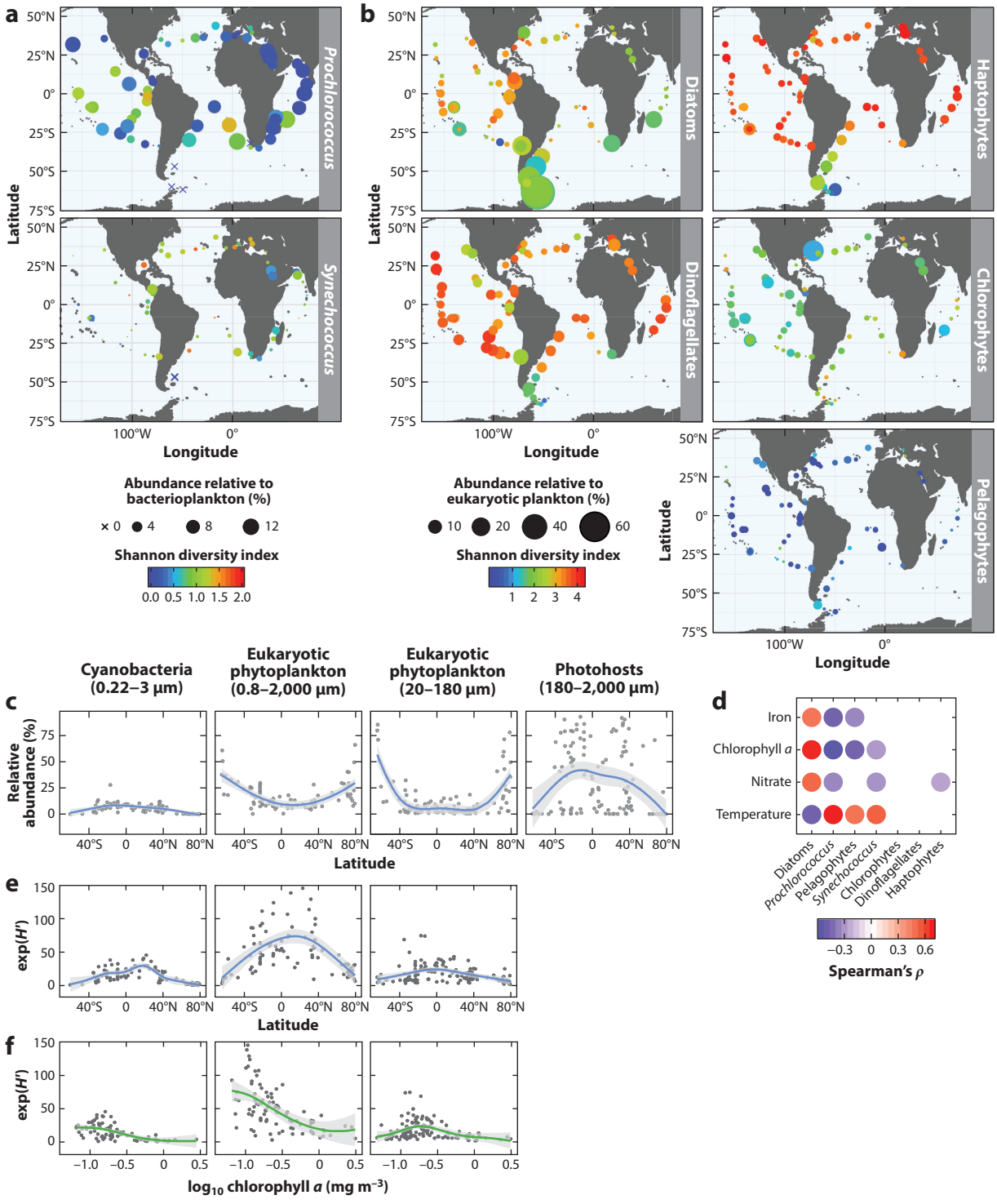
3.5.1. Biogeography and community variation across environmental gradients. Satellite-derived observations together with pigments and microscopy data retrieved worldwide by multiple cruises have provided over the years an overall understanding of the global distribution and composition of phytoplankton. In general terms, picophytoplankton (0.2–2 μm, mainly picocyanobacteria *Prochlorococcus* and *Synechococcus*) are found in warm, nutrient-poor waters in the tropical and subtropical ocean, while nanophytoplankton (2–20 μm) can be detected potentially year-round in

temperate regions (**Figure 5*a*,*c***). By contrast, microphytoplankton (20–200 μm) bloom mainly at higher latitudes at the beginning of spring and sometimes also in the late summer, as well as in upwelling regions (**Figure 5*a*,*c***).

Follows et al. (2007) were able to summarize this knowledge in a global circulation model of the ocean seeded with tens of phytoplankton types, each with a set of traits regarding nutrient preference, growth, sinking, dispersal, and losses due to grazing. The global sampling of *Tara* Oceans can also assess these patterns for phytoplankton, albeit in the context of the whole plankton community. The *Tara* Oceans sampling allowed exploration of the patterns of mixotrophic groups as well, revealing the photohost preference for low and middle latitudes (Biard et al. 2016) (**Figure 5*c***). **Figure 5*a–d*** compare the biogeographic trends for the abundances of the main phytoplankton groups based on *petB* and 18S rRNA counts as well as environmental and biotic factors. *Prochlorococcus* dominates in warm, oligotrophic areas of the open ocean between 40°N and 40°S, beyond which the population size declines (**Figure 5*a*,*d***). This is reflected by the correlation of abundance with temperature and the anticorrelation with chlorophyll and nutrient concentrations. By contrast, *Synechococcus* is especially abundant in near-coastal waters and in areas enriched by local upwellings (**Figure 5*a***). It has a wider geographical distribution that covers both polar and high-nutrient waters (Partensky et al. 1999). Flombaum et al. (2013) found that temperature is the main control on the regional distributions of both *Prochlorococcus* and *Synechococcus*, with a lower temperature boundary for *Synechococcus*, which exhibits populations in Arctic waters but is absent in subzero waters around Antarctica (Letelier & Karl 1989, Robineau 1999).

At the other extreme in terms of distribution and size, diatoms are particularly prevalent at high latitudes and in upwelling environments (**Figure 5*b*,*d***), where they are able to bloom and outcompete other marine phytoplankton when nitrate and silicate are abundant (Malviya et al. 2016). In between, while pelagophytes cluster close to picocyanobacteria, the abundance patterns of chlorophytes, dinoflagellates, and haptophytes are less straightforward to contextualize. In some cases, a closer analysis of the taxonomic composition reveals contrasting trends among subgroups, as observed for *Phaeocystis* (Haptophyta; data not shown in **Figure 5**), whose colonies become dominant and relatively abundant toward colder latitudes (lower Shannon diversity index and larger circles in the corresponding panel of **Figure 5*b***). In the case of chlorophytes, results from *Tara* Oceans and the Ocean Sampling Day initiative show that Mamiellophyceae are prominent in coastal waters (Monier et al. 2016, Vannier et al. 2016), while clade VII prasinophytes dominate oceanic waters (Lopes Dos Santos et al. 2017). Such subgroup variations might induce nonmonotonic responses at the higher taxonomic level shown here, and this is generally not captured by our correlation analyses (**Figure 5*d***). Further analyses will be needed to retrieve biogeographical patterns of coccolithophores. Their relevance in the oceanic ecosystem, particularly at low to middle latitudes (O'Brien et al. 2012), was not well represented by the metabarcoding survey in *Tara* Oceans. However, a broad trend emerged across latitudes, with a switch from order Isochrysidales (which includes *Emiliania huxleyi* as well as many noncalcifying species) to order Coccolithales (calcifying) toward the cold waters of the Southern Ocean (data not shown in **Figure 5**). Regarding dinoflagellates, the fact that they contribute to a major fraction of the photosynthetic community and display a regular distribution (Le Bescot et al. 2016) (**Figure 5*b***) is indicative of the broad ecological strategies employed by different genera.

3.5.2. Large-scale gradients of alpha-diversity. Marine phytoplankton are embedded in a complex ecosystem, from which patterns are expected to emerge at the large scale. The latitudinal diversity gradient is a pervasive macroecological pattern on land and in the ocean, for primary producers as well as for animals and heterotrophic microbes (Ibarbalz et al. 2019, Kreft & Jetz 2007, Tittensor et al. 2010) (**Figure 5*e***). This gradient consists of a decrease in the number of



(*Caption appears on following page*)

Figure 5 (*Figure appears on preceding page*)

Global biogeographical and diversity patterns for the most abundant marine photosynthetic groups in surface samples across *Tara* Oceans stations. (*a*) Abundance and diversity of the main picocyanobacteria genera based on *petB* miTags (metagenomic Illumina tags, i.e., *petB* gene fragments derived from metagenomes sequenced with an Illumina platform) retrieved from the 0.22–3-μm size fraction (Farrant et al. 2016). Abundance is normalized to total bacterial counts based on 16S miTags. (*b*) Abundance and diversity of the major photosynthetic protists based on 18S rRNA gene (V9 region) metabarcoding data from the 0.8–2,000-μm size fraction (de Vargas et al. 2015). Abundances are normalized to total eukaryotic read counts. In panels *a* and *b*, the size of each circle corresponds to the abundance at each location, and the fill color refers to the Shannon diversity index (*blue* for low diversity and *red* for high diversity). (*c*) Relative abundance of groups with photosynthetic capacity across latitudes. Cyanobacteria derive from 16S rRNA gene miTags and are normalized to total prokaryotic read counts. Photohosts are nonphotosynthetic protists that carry photosynthetic endosymbionts [endosymbiotic specialist nonconstitutive mixotrophs (eSNCMs) in **Figure 4**]. For eukaryotes, abundance values derive from the 18S rRNA gene (V9) metabarcoding survey and are normalized to the total eukaryotic read counts. (*d*) Correlation analysis among relative abundances of the main phytoplankton groups and a selection of productivity-related parameters. Color represents Spearman's rho. Empty spaces refer to nonsignificant correlation values ($p > 0.05$). Temperature and chlorophyll *a* concentration derive from in situ measurements, whereas nitrate and iron concentrations were retrieved from models and represent annual averages (see the **Supplemental Appendix**). (*e*) Phytoplankton diversity across latitudes. (*f*) Phytoplankton diversity in relation to chlorophyll *a* concentration ($\log_{10}$ transformed). In panels *e* and *f*, exp(H') stands for exponentiated Shannon index, calculated for the first three groups in panel *c*. In panels *c*, *e*, and *f*, the solid lines correspond to generalized additive model smoothings, and the 95% confidence intervals are shown as gray shading. Data for panels *c*–*f* are from the complete *Tara* Oceans data sets for 16S miTags (Salazar et al. 2019, Sunagawa et al. 2015) and 18S rRNA gene (V9 region) metabarcoding (de Vargas et al. 2015, Ibarbalz et al. 2019).

Supplemental Material >

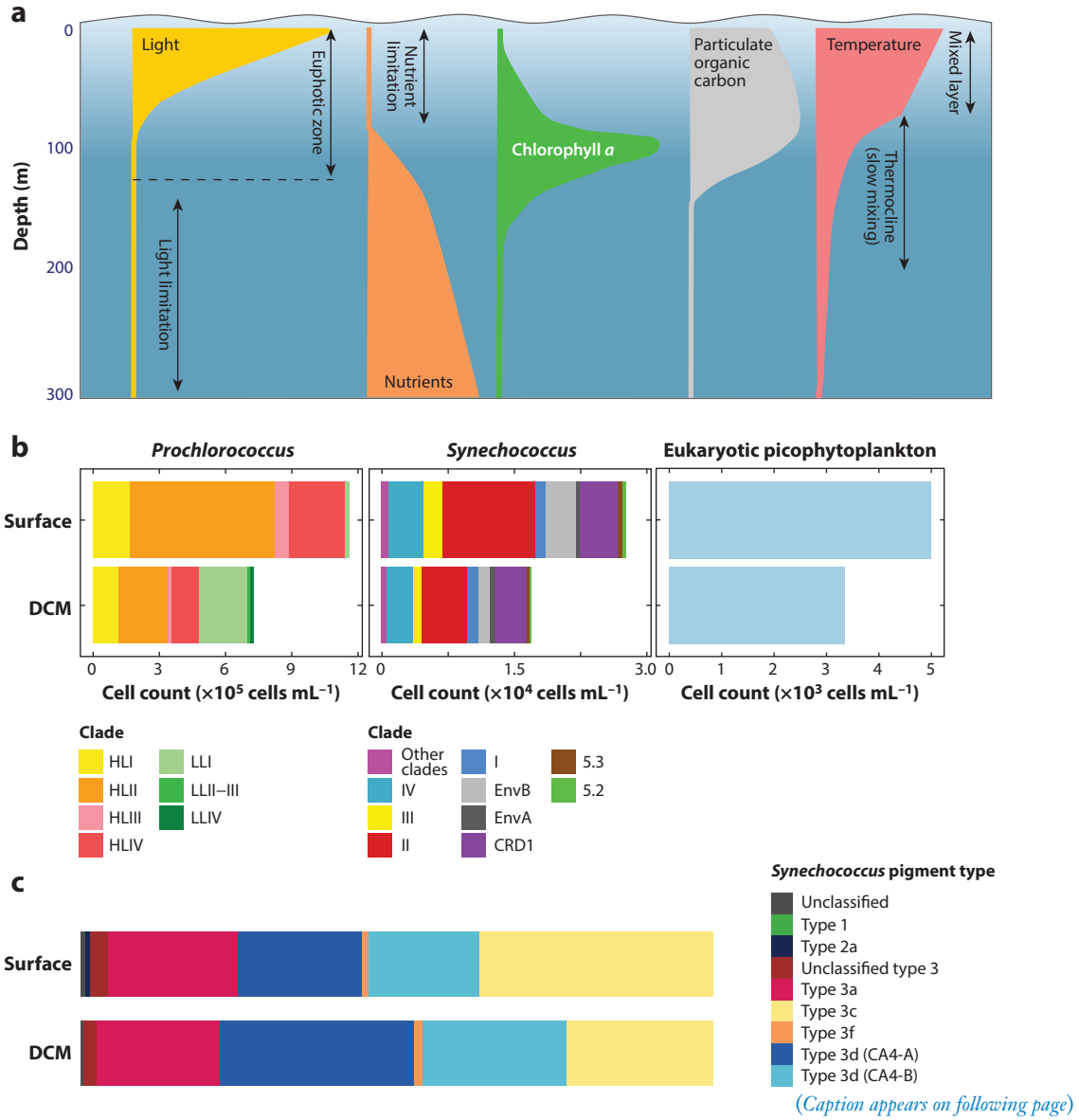
species toward the poles and is thought to be generated by a combination of processes that operate at both ecological and evolutionary scales (reviewed in Pontarp et al. 2019). Among them, solar radiation and temperature have been identified as major drivers (Brown 2014, Clarke & Gaston 2006). On land and at a global scale, vascular plants exhibit a clear latitudinal diversity gradient, although interrupted by large deserts such as those in Africa and Australia (Kreft & Jetz 2007).

Also at a global scale, plant diversity covaries with annual primary production, with both peaking near the equator. As a side note, if only the growing season at temperate latitudes is considered, then primary production might not differ significantly between tropical and temperate areas; for more local scales, different shapes for this relation have been observed (Oehri et al. 2017, Šímová & Storch 2017). The observed agreement between diversity and annual primary production underlies the so-called productivity hypothesis for the latitudinal diversity gradient, which states that the abundance of resources (light and water for land plants) in tropical areas promotes species coexistence through the support of larger population sizes, hence limiting local extinction (reviewed in Clarke & Gaston 2006).

In the ocean, primary production is limited by light and nutrients and is highest in coastal and in upwelling regions or seasonally at temperate and subpolar latitudes. Past studies at a global scale have often reported a unimodal trend of phytoplankton local diversity in response to increasing phytoplankton biomass, and this pattern has been interpreted with a focus on the minima at the beginning and the end of the biomass gradient, by mechanisms including turbulence variation, nutrient concentrations, and competitive exclusion (Irigoien et al. 2004, Li 2002, Vallina et al. 2014). In general, these studies have excluded the smallest phytoplankton groups from their analysis. DNA-based approaches, by contrast, can be significantly more sensitive for detection of small and low-abundance organisms and exhibit a much higher taxonomic resolution (Ibarbalz et al. 2019), perhaps explaining the emergence of the patterns found by *Tara* Oceans. While photosynthetic protists in the size fraction 20–180 μm seem to follow the above-mentioned bell-shaped trend, photosynthetic organisms in smaller size fractions appear to instead show a decrease from high to low diversity as chlorophyll *a* concentration increases (**Figure 5*f***). Even in low-production areas in the ocean, small phytoplankton cells are still growing and reproducing (Chavez et al. 2011). Presumably the high surface-area-to-volume ratio of tiny phytoplankton allows them to cope with

nutrient-poor conditions and shifts the maximum toward lower biomass levels with respect to the microphytoplankton.

3.5.3. Community variation with depth. One of the best-described gradients in the ocean is the vertical structure of the water column, where phytoplankton are subjected to opposing trends of two vital resources for them: light, which penetrates from above and diminishes with depth, and nutrients, which are often supplied from below and decrease toward the surface (**Figure 6*a***). In stratified waters, phytoplankton frequently form a peak of chlorophyll known as the deep chlorophyll maximum, typically located at approximately 50–120 m, toward the base of the pycnocline



(*Caption appears on following page*)

Figure 6 (*Figure appears on preceding page*)

Environmental and biological features across the water column of stratified oceans. (*a*) Schematic of the vertical features at the Bermuda Atlantic Time-Series Station in July 2008. From a purely bottom-up perspective, the dynamics are as follows: The thermocline stratifies the upper water column, and the new supply of major nutrients is limited by the slow mixing across the upper thermocline. Within the upper thermocline, the slow nutrient supply is completely consumed by phytoplankton in their growth. This growth leads to the accumulation of particulate organic carbon in the surface ocean, some of which is respired by bacteria and zooplankton, and a small fraction is exported as sinking material. The deep chlorophyll maximum (DCM) occurs at the depth where there is adequate light for photosynthesis and significant nutrient supply from below. However, additional mechanisms such as top-down processes might also be at play. See also Sigman & Hain (2012); data are from the Bermuda Bio-Optics Project (**http://www.oceancolor.ucsb.edu/bbop** and **http://bats.bios.edu/bats-data**). (*b*) Picophytoplankton partitioning in the water column of *Tara* Oceans stations. The graphs show the average cell counts based on flow cytometry and the disaggregation of distinct *Prochlorococcus* and *Synechococcus* clades based on *petB* counts (see Farrant et al. 2016). There is a clear depth partitioning of *Prochlorococcus* populations but not of *Synechococcus* populations. There is also a larger number of picophytoplankton cells in surface layers than at the DCM in these samples. Although we do not know the average carbon content per cell, these data show that the DCM should not be strictly interpreted as a depth maximum in phytoplankton biomass, as the phytoplankton at the DCM have particularly high internal chlorophyll concentrations due to light shading. For *Prochlorococcus*, HL refers to high-light-adapted clades, and LL refers to low-light-adapted clades. (*c*) Distribution of *Synechococcus* pigment types in the water column of *Tara* Oceans stations. The graph shows the corresponding relative abundance from metagenomes based on the marker genes *cpcBA*, *mpeBA*, and *mpeW* (Grébert et al. 2018). There is no apparent correlation with genetic (panel *b*) or pigment (panel *c*) diversity in this genus.

and strongly coupled to the nutricline (Cullen 1982, 2015) (**Figure 6*a***). It is formed and maintained by a range of interacting processes, including enhanced growth of phytoplankton under an optimal combination of light and nutrients, physiologically controlled swimming behavior or buoyancy regulation, and low-light acclimation by increasing chlorophyll content relative to biomass—all strongly influenced by trophic interactions (grazing, viral lysis, and cell death) and hydrodynamics (sinking and physical mixing) (Cullen 1982, 2015).

Phytoplankton communities at the deep chlorophyll maximum and in the overlying layer can be different, reflecting particular characteristics of each environment. *Prochlorococcus* generally extends to greater depths than *Synechococcus* (Buitenhuis et al. 2012). There is a well-known depth partitioning of phylogenetically distinct *Prochlorococcus* populations, with high-light-adapted populations in the upper layer and low-light-adapted populations located further down the water column (Johnson et al. 2006) (**Figure 6*b***). By contrast, no clear depth partitioning has been observed for *Synechococcus* clades (**Figure 6*b***), while changes in *Synechococcus* pigment types with depth have been observed along the *Tara* Oceans transect (Grébert et al. 2018) (**Figure 6*c***). Indeed, there is no apparent correlation with genetic and pigment diversity in this genus (Six et al. 2007). In the case of eukaryotic phytoplankton, community differences in diatoms, dinoflagellates, and coccolithophores were observed during the Malaspina expedition (Estrada et al. 2016) and in tropical and subtropical coccolithophore species during the Atlantic Meridional Transect cruises (Poulton et al. 2017). The analysis of diatoms during the *Tara* Oceans expedition also shows differences of genera by depth (Malviya et al. 2016), corroborating studies at a regional scale (Beers et al. 1975, Estrada 1991, Kemp & Villareal 2013, Venrick 1988). In addition, phytoplankton community may change within fine-scale layers of the deep chlorophyll maximum, suggesting that the deep chlorophyll maximum is not a single, homogeneous ecological entity in which phytoplankton groups are equally distributed (Barnett et al. 2019, Latasa et al. 2017) but may be composed of a range of ephemeral layers. The diatoms from these ephemeral layers appear to have a significant impact on the export of fixed carbon to the deep ocean in the North Pacific Subtropical Gyre at station ALOHA (Kemp & Villareal 2013).

3.6. Adaptation and Acclimation Strategies in Phytoplankton

The response of phytoplankton to their environment on short timescales (over the lifetime of the cell) is called acclimation and includes the modulation of gene expression. By contrast, adaptation

to an environmental niche refers to genetic changes (e.g., in gene copy number) that accumulate over many generations. Responses to environmental cues also include shifts in the phytoplankton community structure, including changes of broad taxonomic groups as well as changes of genotypes of the same species adapted to local conditions.

The interaction of phytoplankton with the micronutrient iron is a good model to study the processes of adaptation and acclimation. Photosynthetic species have particularly high iron demands, as approximately half of their intracellular iron is bound to photosynthesis proteins (Raven et al. 1999). Caputi et al. (2019) investigated the changes in the average copy number and expression of iron-responsive genes in the phytoplankton community, particularly in picocyanobacteria and diatoms. The strongest response was with diatom genes encoding the iron starvation–induced protein family, whose abundance and expression displayed strong negative correlations with iron. This study also examined the patterns of the iron storage protein ferritin. Ferritin was only recently identified in diatoms and seems to have been acquired by horizontal gene transfer from a bacterium donor, with subsequent differential losses in multiple lineages that resulted in a patchy distribution (Cohen et al. 2018, Marchetti et al. 2009). At the community level, Caputi et al. (2019) found no clear patterns in diatom ferritin gene abundance or expression as a function of iron levels, in agreement with recent laboratory studies that showed how ferritin function can vary among diatoms, either as an intracellular iron buffering system when iron availability is limiting or as a long-term iron storage molecule when iron is replete (Cohen et al. 2018). One of the exceptions, however, was *Pseudo-nitzschia*, in which the biogeographical patterns of ferritin gene expression indicated a positive correlation with iron (Caputi et al. 2019). This might be one of the reasons for their success in chronically low-iron regions that receive intermittent iron inputs.

In addition to analyzing specific genes, Caputi et al. (2019) performed broad studies using network analysis. They detected subnetworks of prokaryotic genes correlated in abundance, and five of these subnetworks strongly tracked iron availability. Although these subnetworks have genes whose functions related to iron are evident, most of the genes are of unknown function. These results provide a useful context to explore new patterns of adaptation. When Caputi et al. (2019) analyzed prokaryotes at the taxonomic level, they detected no subnetworks associated with iron, suggesting a low level of specialization. In accordance with a recent study based largely on *Tara* Oceans data (Louca et al. 2016), this result advocates for the use of prokaryotic functional signals rather than standard taxonomic criteria to study environmental responses of prokaryotes in the global ocean, at least with the resolution allowed by the 16S rRNA marker gene. In fact, the analysis of picocyanobacteria with a higher-resolution genetic marker (the *petB* gene, encoding cytochrome b_6) displayed a remarkable strain-dependent sensitivity to iron availability (Caputi et al. 2019). These observations indicate the need for methods with higher taxonomic resolution and a better assignation of functional taxonomy in prokaryotes (i.e., how functions are distributed over taxa).

The processes of adaptation and acclimation that enable mixotrophy in the ocean are also beginning to be explored (see the sidebar titled Mixotrophs). The assimilation of organic nutrients has been demonstrated in *Prochlorococcus* and *Synechococcus*. Metagenomic data from the *Tara* Oceans expedition indicate that the genetic potential for mixotrophy in picocyanobacteria is globally distributed and differs among clades, with a gradual organic nutrient transporter gene loss from low-light clade IV to high-light clade II *Prochlorococcus* (Yelton et al. 2016) and an increase in the rate of gene diversification for sugar metabolism (Delmont & Eren 2018). Also using *Tara* Oceans data but in relation to eukaryotes, Carradec et al. (2018) observed that obligate autotrophs, such as diatoms and chlorophytes, exhibited a high positive correlation between conditions of high productivity and the expression of gene families containing members involved in photosynthesis and carbon fixation. Haptophytes and dinoflagellates (which contain mixotrophic representatives)

showed weak or no correlations. Indeed, dinoflagellates showed high positive correlation for the expression of gene families encoding cell lytic components, such as proteases and lipases (Carradec et al. 2018). Such changes may be due to differences in the dominant dinoflagellates in the community or switches in trophic strategy in mixotrophic species. However, further functional annotation efforts, which are particularly challenging in eukaryotes, will be required to address this issue properly. The application of methods based on comparative genomics is a promising strategy that is already being implemented (Burns et al. 2018).

3.7. Biotic Interactions in Phytoplankton

A major feature that has emerged from *Tara* Oceans is the importance of biotic interactions in shaping plankton community structure. Lima-Mendez et al. (2015) created a species interaction network that includes prokaryotes, viruses, and eukaryotes, which revealed that environmental conditions are insufficient for predicting the composition of ocean communities and emphasized the role of top-down biotic interactions, such as symbiosis and parasitism, in the epipelagic zone.

3.7.1. Phytoplankton in the context of their community. The response of phytoplankton to bottom-up processes (light and nutrient availability) has a direct effect on the population dynamics of higher trophic levels. Using a network analysis approach, Caputi et al. (2019) identified more than 30 eukaryotic subcommunities in which organisms within global co-occurrence networks displayed a high degree of covariation. Four of these assemblages were (positively or negatively) correlated with iron estimates. They contain organisms with varying nutritional modes (such as autotrophs, heterotrophs, mixotrophs, and parasites), suggesting that a multitude of strategies are used to overcome iron limitation and that these strategies are highly dependent on organismal interactions. One particular iron-associated assemblage contained many diatoms that are commonly found in the most severely iron-limited regions of the ocean and included members of the pennate diatom genus *Pseudo-nitzschia*. These species potentially represent a stable supply of resources for others and thus probably have a central role in the assemblage.

Viruses have gained important attention in the last few decades because they seem to play a large role in marine ecosystems. Viruses are credited with lysing approximately 20–40% of bacteria per day and releasing carbon and other nutrients that affect the food web (reviewed in Suttle 2007). In addition, they could have a potential impact by complexing micronutrients such as iron (Bonnain et al. 2016). A survey of the *Tara* Oceans metagenomes for genes encoding viral structural proteins with putative iron-binding sites showed that they are widespread and abundant (Caputi et al. 2019). Viruses can also alter biogeochemical cycling by metabolically reprogramming metabolism. During infection, they can express auxiliary metabolic genes that alter host metabolism toward pathways that maximize production of new viral particles. This phenomenon has been well characterized in cyanobacteria–cyanophage systems, in which these genes supplement photosynthetic electron transport while redirecting energy from carbon fixation to the pentose phosphate pathway (Puxty et al. 2016). A comprehensive map of the auxiliary metabolic gene content of marine viral communities has been published based on the samples from the *Tara* Oceans and Malaspina research expeditions (Roux et al. 2016), where both photosynthesis and carbon metabolism appear among the most abundant functions.

Nucleocytoplasmic large DNA viruses are a group of eukaryotic viruses with a large double-stranded DNA genome ranging from 100 kb to 1.26 Mb (Mihara et al. 2018). They are also capable of affecting algal host metabolism (Monier et al. 2017). Some of them are known to have important roles in marine ecosystems, affecting the population dynamics of bloom-forming algae (Pagarete et al. 2011). Their absolute abundances have been estimated across a section of the *Tara* Oceans transect, showing that the ratio of nucleocytoplasmic large DNA viruses to eukaryotes is within

the range of the ratio of phages to bacteria in seawater (Hingamp et al. 2013). Their large global richness indicates that they might affect a broad range of hosts (Mihara et al. 2018). Together, these findings suggest that viral auxiliary metabolic genes influence numerous pathways of microbial metabolism and that viral communities in general have the potential to influence primary production in the ocean.

3.7.2. Specific cases of symbioses among phytoplankton. Protists can harbor photosynthetic symbionts of eukaryotic and prokaryotic origin inside (endosymbiosis) and/or outside (ectosymbiosis) their cells. Such photosymbioses sometimes involves a dinitrogen-fixing cyanobacterium.

The combination of imaging and molecular data sets from *Tara* Oceans has revealed new interactions and the potential benefits underlying such associations. One example is the epibiotic association between the diatom *Fragilariopsis doliolus* and genera of tintinnid ciliates (Vincent et al. 2018) (**Figure 2*b***). The study revealed that *F. doliolus*, one of the most abundant diatoms in the global ocean, is able to form barrel-shaped chains that enable interactions with tintinnids. The consortia were particularly prevalent in nutrient-replete conditions, which are rich in potential predators, supporting the hypothesis of a mutualistic symbiosis wherein diatoms acquire enhanced motility and tintinnids benefit from the armor-like protection of the silicified barrel. Exciting research is ahead for exploring the physics and the chemistry of such interactions and its biological underpinnings.

Another example is the photosynthetic dinoflagellate genus *Symbiodinium*, which sustains coral reefs by establishing mutualistic endosymbioses with a wide diversity of benthic hosts. Mordret et al. (2016) reported one of the few examples of symbiosis within oceanic plankton; the pelagic host is a new calcifying ciliate species closely related to *Tiarina fusus* (Colepidae). In addition, Decelle et al. (2018) reported the first global picture of the diversity and activity of *Symbiodinium* in the open ocean. *Symbiodinium* clades A and C were by far the most prevalent and widely distributed lineages (representing 0.1% of phytoplankton reads), were transcriptionally active, and expressed core metabolic pathways (e.g., photosynthesis, carbon fixation, glycolysis, and ammonium uptake). They were detected in small and large plankton size fractions, suggesting the potential existence of a free-living population and a symbiotic lifestyle within planktonic hosts, respectively (Decelle et al. 2018).

The uncultivated unicellular 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 prymnesiophyte closely related to *Braarudosphaera bigelowii* (Thompson et al. 2012). Sequences from UCYN-A and the identified hosts were also found in the metagenomic and metatranscriptomic data sets from the *Tara* Oceans and Malaspina expeditions (Cabello et al. 2016; Cornejo-Castillo et al. 2016, 2019), revealing new information about the diversity, abundance, and evolution of this diazotrophic group.

Finally, Radiolaria is the most diverse group of planktonic hosts harboring eukaryotic microalgal symbionts (see Section 3.2 and **Figure 4*a***). All of the main radiolarian lineages (Spumellaria, Collodaria, Nassellaria, and Acantharia) include numerous species with obligate eukaryotic microalgal symbionts (Suzuki & Not 2015), making them a type of nonconstitutive mixotroph (see the sidebar titled Mixotrophs). Recent studies have estimated the abundance and diversity of these groups across the *Tara* Oceans transect (Biard et al. 2016, 2017; de Vargas et al. 2015; Decelle et al. 2013). In the Spumellaria, Collodaria, and Nassellaria, the most commonly occurring symbiont appears to be *Brandtodinium nutricula*, a dinoflagellate that was first described as *Zooxanthella nutricula* more than a century ago (Krueger 2017) but was only recently cultured and morphologically

characterized, leading to its placement in the new genus *Brandtodinium* (Probert et al. 2014). Finally, for the main monophyletic clade of symbiotic Acantharia, Decelle et al. (2012) found that the microalgal symbionts are members of the haptophyte genus *Phaeocystis* (**Figure 2*g***).

Symbiotic microorganisms therefore represent an important component of marine ecosystems and play a role in the food web and biogeochemical cycling (e.g., carbon and nitrogen). The combination of genomic and imaging approaches is starting to improve our knowledge of their diversity, distribution, and metabolic exchanges.

4. PERSPECTIVES

In the spirit of former oceanographic expeditions and with state-of-the-art protocols, *Tara* Oceans has accessed the diversity and complexity of phytoplankton in the ocean like never before. Despite having a fair initial understanding of the collected data, it seems we are only scratching the surface regarding phytoplankton distributions, community composition, genomic content, and ecological and evolutionary relatedness. While this review has focused on the dominant and hence best-studied groups of marine phytoplankton, it is by no means exhaustive. Our view is further muddied by the enormous taxonomic diversity of photosynthetic groups and by the fact that many are only facultatively phototrophic. While the extent of mixotrophy in the ocean is beginning to be uncovered (Faure et al. 2019, Knoll & Follows 2016), we still have much to learn.

Considering that genetic studies of photosynthesis extend back to the 1950s (Sager & Zalokar 1958), one could assume that its components and process are well known. However, a recent high-throughput functional screen in *Chlamydomonas* identified 303 candidate photosynthesis genes (Li et al. 2019), suggesting that a large fraction of genes required for photosynthesis remain uncharacterized. The recent observation that photosynthesis in diatoms is configured differently with respect to respiration compared with plants and green algae (Bailleul et al. 2015) further supports the notion that much needs to be learned about ocean photosynthesis and cannot be ignored when trying to balance carbon budgets.

In comparison with cyanobacteria, major gaps in our understanding remain for photosynthetic protists. In part this is a technical challenge—eukaryotic genomes are more difficult to characterize—but eukaryotic adaptations are also more dependent on morphology and behavior than they are on the metabolic diversity that typifies bacteria, and these adaptations cannot be readily inferred from genomic data (Keeling & del Campo 2017). The use of high-throughput imaging by *Tara* Oceans has begun to provide insights into the eukaryotic morphological complexity and into new biotic interactions (Colin et al. 2017, Mordret et al. 2016, Vincent et al. 2018). Moreover, prior to *Tara* Oceans, eukaryotic metagenomics and metatranscriptomics had not been deployed at a global scale, as doing so would require considerable sequencing efforts. The first pictures are emerging (Caputi et al. 2019, Carradec et al. 2018), and more accurate annotation methods are being applied (Burns et al. 2018). In this sense, an important step forward might come from the identification of individual genomes (denoted metagenome-assembled genomes). Although this approach is already successful for prokaryotes (Delmont & Eren 2018), the size and complexity of eukaryotic genomes make it more challenging and will necessitate further innovation in bioinformatic algorithms and/or sequencing technologies. Data should not become limiting, as omics samples from a third expedition called *Tara* Pacific (2015–2018) are on their way.

A full understanding of primary production in the ocean should be a current fundamental objective, as primary production represents a globally important flux of carbon between the atmosphere and the biosphere. From an ecological perspective, it represents the rate at which solar energy is stored by phototrophs as organic matter and therefore is made available to the rest of the food chain. In biogeochemical terms, it connects the biosphere and the climate system through the

global cycling of carbon and nutrients. Improved estimates of the contributions of different phytoplankton groups to global net primary production are therefore important. In this regard, there is a need to improve abundance estimates of phytoplankton groups and reduce the uncertainty of global variation in carbon fixation rates. Measurement of photosynthesis by the radioisotope ^{13}C or ^{14}C remains a well-established standard (López-Sandoval et al. 2018) because it is the only method that directly measures the fixation of inorganic carbon into its organic form (even if it is still difficult to discriminate between net and gross primary production); other methods represent proxies. The development of a method that is not based on radioactivity would be a major breakthrough for the field.

The relative importance of bottom-up (light and nutrient availability) and top-down (viral lysis, parasitism, pathogenesis, and grazing) processes in the regulation of phytoplankton communities has profound implications for our understanding of the interannual variability, food web structure, and population dynamics of higher trophic levels in the ocean. Interestingly, observations at large temporal and spatial scales over the past few decades have called for the reevaluation of well-established concepts (Behrenfeld 2010; Behrenfeld & Boss 2014, 2018; Boss & Behrenfeld 2010; Kemp & Villareal 2018). Numerical simulations of ocean processes aimed at capturing the fluxes of key elements are currently based on just a handful of plankton functional types (Le Quéré et al. 2005) or functional genes (Coles et al. 2017). Despite not having accounted for cell turnover, nutrient uptake, or primary production rates, *Tara* Oceans might offer concrete insights to improve numerical models of the oceanic ecosystem (Stec et al. 2017). The results from Caputi et al. (2019) highlight the need to incorporate the response of entire plankton assemblages to more accurately determine responses at different levels, such as gene expression, gene copy numbers, or community composition. To determine the relevance of such processes, omics should become a routine component of ocean observation, and as Caputi et al. (2019) demonstrated, it can contribute to assessing the validity of ecosystem models by complementing biogeochemical measurements in the field and adding critical information about the actual bioavailability of nutrients, which is currently difficult to measure. In the case of photosynthesis, mathematical models have been developed successfully for specific microalgae under culture conditions (De-Luca et al. 2018). The challenge is now transferring these approaches to the field. This might be hampered by the fact that, for the moment, in comparison with the high-resolution view of temperature, salinity, and broad biogeochemical variables, the spatial resolution of genomic data is low due to financial budgets and technology constraints (Santoro 2019) and a lack of protocols for accurate quantitative results. *Tara* Oceans has made attempts to move these aspects forward by combining sequencing with abundance measurements from flow cytometry for nucleocytoplasmic large DNA viruses and picocyanobacterial clades (Caputi et al. 2019, Hingamp et al. 2013), as well as from phytoplankton microscopy counts (Colin et al. 2017).

Phytoplankton have evolved a diverse set of physiological tools to cope with the variable growth conditions imposed by the environment (e.g., photoacclimation and photoinhibition). Differences of photosynthetic efficiencies among organisms can potentially lead to shifts in the community under certain environmental conditions. The continued mechanistic refinement of the description of these photophysiological aspects is critical not only for the interpretation of global chlorophyll changes but also for assessments of ocean productivity, organic carbon export to the deep ocean, and performance evaluations of modern coupled ocean ecosystem models. Accurate photoacclimation models are also required for quantifying phytoplankton photoprotection under supersaturating light (that is, nonphotochemical quenching), which is the dominant signal registered in satellite-retrieved chlorophyll fluorescence quantum yield data (Behrenfeld et al. 2009). The combination of the rich information from meta-omics with that obtained from the in-line optical equipment used in *Tara* Oceans represents a basis for future efforts to address these needs.

Regarding large timescales, even though *Tara* Oceans collected data only from the contemporary ocean, Lewitus et al. (2018) recently used the extensive sequence data from metabarcodes to identify diversification events during the evolutionary history of diatoms over the last 200 million years. The combination of DNA metabarcoding data with paleo-environmental data and phylogenetic models of diversification shed new light on the diversity dynamics of diatoms since their origins in the Mesozoic. It showed, for example, how geological events have likely been essential in allowing the rise of diatoms in the Southern Ocean, and also suggested how a changing climate could favor some clades at the expense of others.

Today, phytoplankton are being exposed to multiple stressors triggered by increasing CO_2 in the atmosphere. These stressors are all expected to increase in intensity throughout the twenty-first century and beyond (Bopp et al. 2013). Sea surface warming, nutrient scarcity due to mixing disruptions, deoxygenation, and acidification are imposing new abiotic pressures. Although it is difficult to refer to a consistent trend for total marine net primary production, the consensus is that phytoplankton will confront new conditions at the local and regional scale (Boyd et al. 2014). A recent study points to potential increases in diversity, particularly in temperate and cold oceans (Ibarbalz et al. 2019), although these increases could result in less productive plankton communities and hence represent a major threat to higher trophic levels.

This review has covered the current appreciation of phytoplankton diversity, biogeography, phylogenies, symbioses, and the continuum of trophic modes, with a focus on the data set and results from *Tara* Oceans. Modern biological oceanography stands not only on the shoulders of giants, but also on terabytes of data now available to be mined and appraised to reveal fundamental aspects of the marine ecosystem and, more generally, of life on Earth. While we have begun to gain an appreciation of the different biomass partitionings in the ocean compared with those on land, we are nonetheless far from understanding key questions of how chlorophyll standing stocks relate to photosynthetically derived organic biomass throughout the photic zone of the ocean at different times of the year, at different latitudes, and with respect to nutrient availability and the activity of pathogens, predators, and parasites. How the contributions of different taxonomic groups of phytoplankton compare with the activities of photosymbionts, which likely span the range from facultative to obligate, is also unresolved. The new generation of Biogeochemical-Argo floats will address some of these questions (Xing et al. 2018), but omics and imaging approaches will also need to become much more prevalent in oceanography to truly understand who is there, what they are doing, and how they are contributing to the functioning of trophic interactions, biogeochemical cycles, and the Earth system as a whole.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We would like to thank all of our colleagues from the *Tara* Oceans consortium as well as the *Tara* Oceans Foundation for their inspirational vision. We are also grateful to Andy Knoll, Ron Milo, Yinon Bar-On, Emmanuel Boss, Lee Karp-Boss, Laurence Garczarek, and Richard Dorrell for their valuable comments during the preparation of this review. Work in our laboratory has been funded by European Research Council Advanced Awards Diatomite and Diatomic under the European Union's Horizon 2020 research and innovation program (grant agreements 294823 and 835067), the Fonds Français pour l'Environnement Mondial, the French government

"Investissements d'Avenir" Programmes MEMO LIFE (grant ANR-10-LABX-54), Université de Recherche Paris Sciences et Lettres (Université PSL) (grant ANR-1253 11-IDEX-0001-02), and OCEANOMICS (grant ANR-11-BTBR-0008). The Bowler laboratory is a member of the CNRS Research Federation for the study of Global Ocean Systems Ecology and Evolution, FR2022/*Tara* Oceans GOSEE, 3 rue Michel-Ange, 75016 Paris, France. This article is contribution number 89 of *Tara* Oceans.

LITERATURE CITED

Alberti A, Poulain J, Engelen S, Labadie K, Romac S, et al. 2017. Viral to metazoan marine plankton nucleotide sequences from the *Tara* Oceans expedition. *Sci. Data* 4:170093

Antoine D, André J-M, Morel A. 1996. Oceanic primary production: 2. Estimation at global scale from satellite (Coastal Zone Color Scanner) chlorophyll. *Glob. Biogeochem. Cycles* 10:57–69

Bailleul B, Berne N, Murik O, Petroutsos D, Prihoda J, et al. 2015. Energetic coupling between plastids and mitochondria drives CO_2 assimilation in diatoms. *Nature* 524:366–69

Barbier M, Loreau M. 2019. Pyramids and cascades: a synthesis of food chain functioning and stability. *Ecol. Lett.* 22:405–19

Barnett ML, Kemp AES, Hickman AE, Purdie DA. 2019. Shelf sea subsurface chlorophyll maximum thin layers have a distinct phytoplankton community structure. *Cont. Shelf Res.* 174:149–57

Bar-On YM, Phillips R, Milo R. 2018. The biomass distribution on Earth. *PNAS* 115:6506–11

Beers JR, Reid FMH, Stewart GL. 1975. Microplankton of the North Pacific central gyre. Population structure and abundance, June 1973. *Int. Rev. Gesamt. Hydrobiol.* 60:607–38

Behrenfeld MJ. 2010. Abandoning Sverdrup's Critical Depth Hypothesis on phytoplankton blooms. *Ecology* 91:977–89

Behrenfeld MJ, Boss ES. 2014. Resurrecting the ecological underpinnings of ocean plankton blooms. *Annu. Rev. Mar. Sci.* 6:167–94

Behrenfeld MJ, Boss ES. 2018. Student's tutorial on bloom hypotheses in the context of phytoplankton annual cycles. *Glob. Change Biol.* 24:55–77

Behrenfeld MJ, Boss ES, Siegel DA, Shea DM. 2005. Carbon-based ocean productivity and phytoplankton physiology from space. *Glob. Biogeochem. Cycles* 19:GB1006

Behrenfeld MJ, Falkowski PG. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol. Oceanogr.* 42:1–20

Behrenfeld MJ, Westberry TK, Boss ES, O'Malley RT, Siegel DA, et al. 2009. Satellite-detected fluorescence reveals global physiology of ocean phytoplankton. *Biogeosciences* 6:779–94

Benoiston A-S, Ibarbalz FM, Bittner L, Guidi L, Jahn O, et al. 2017. The evolution of diatoms and their biogeochemical functions. *Philos. Trans. R. Soc. Lond. B* 372:20160397

Biard T, Bigeard E, Audic S, Poulain J, Gutierrez-Rodriguez A, et al. 2017. Biogeography and diversity of Collodaria (Radiolaria) in the global ocean. *ISME J.* 11:1331–44

Biard T, Stemmann L, Picheral M, Mayot N, Vandromme P, et al. 2016. In situ imaging reveals the biomass of giant protists in the global ocean. *Nature* 532:504–7

Bonnain C, Breitbart M, Buck KN. 2016. The Ferrojan Horse hypothesis: iron-virus interactions in the ocean. *Front. Mar. Sci.* 3:82

Bopp L, Resplandy L, Orr JC, Doney SC, Dunne JP, et al. 2013. Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences* 10:6225–45

Boss E, Behrenfeld M. 2010. In situ evaluation of the initiation of the North Atlantic phytoplankton bloom. *Geophys. Res. Lett.* 37:L18603

Boss E, Picheral M, Leeuw T, Chase A, Karsenti E, et al. 2013. The characteristics of particulate absorption, scattering and attenuation coefficients in the surface ocean; contribution of the *Tara* Oceans expedition. *Methods Oceanogr.* 7:52–62

Boyd PW, Sundby S, Pörtner H-O. 2014. Cross-chapter box on net primary production in the ocean. In *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*,

ed. CB Field, VR Barros, DJ Dokken, KJ Mach, MD Mastrandrea, et al., pp. 133–36. Cambridge, UK: Cambridge University Press
Brown JH. 2014. Why are there so many species in the tropics? *J. Biogeogr.* 41:8–22
Brum JR, Ignacio-Espinoza JC, Roux S, Doulcier G, Acinas SG, et al. 2015. Patterns and ecological drivers of ocean viral communities. *Science* 348:1261498
Buitenhuis ET, Li WKW, Vaulot D, Lomas MW, Landry MR, et al. 2012. Picophytoplankton biomass distribution in the global ocean. *Earth Syst. Sci. Data* 4:37–46
Buitenhuis ET, Vogt M, Moriarty R, Bednaršek N, Doney SC, et al. 2013. MAREDAT: towards a world atlas of MARine Ecosystem DATa. *Earth Syst. Sci. Data* 5:227–39
Burns JA, Pittis AA, Kim E. 2018. Gene-based predictive models of trophic modes suggest Asgard archaea are not phagocytotic. *Nat. Ecol. Evol.* 2:697–704
Cabello AM, Cornejo-Castillo FM, Raho N, Blasco D, Vidal M, et al. 2016. Global distribution and vertical patterns of a prymnesiophyte-cyanobacteria obligate symbiosis. *ISME J.* 10:693–706
Caputi L, Carradec Q, Eveillard D, Kirilovsky A, Pelletier E, et al. 2019. Community-level responses to iron availability in open ocean plankton ecosystems. *Glob. Biogeochem. Cycles* 33:391–419
Caron DA. 2016. Mixotrophy stirs up our understanding of marine food webs. *PNAS* 113:2806–8
Carradec Q, Pelletier E, Da Silva C, Alberti A, Seeleuthner Y, et al. 2018. A global ocean atlas of eukaryotic genes. *Nat. Commun.* 9:373
Catul V, Gauns M, Karuppasamy PK. 2011. A review on mesopelagic fishes belonging to family Myctophidae. *Rev. Fish Biol. Fish.* 21:339–54
Chase AP, Boss E, Cetinić I, Slade W. 2017. Estimation of phytoplankton accessory pigments from hyperspectral reflectance spectra: toward a global algorithm. *J. Geophys. Res. Oceans* 122:9725–43
Chase AP, Boss E, Zaneveld R, Bricaud A, Claustre H, et al. 2013. Decomposition of in situ particulate absorption spectra. *Methods Oceanogr.* 7:110–24
Chavez FP, Messié M, Pennington JT. 2011. Marine primary production in relation to climate variability and change. *Annu. Rev. Mar. Sci.* 3:227–60
Ciais P, Sabine C, Bala G, Bopp L, Brovkin V, et al. 2013. Carbon and other biogeochemical cycles. In *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, ed. TF Stocker, D Qin, G-K Plattner, M Tignor, SK Allen, et al., pp. 465–570. Cambridge, UK: Cambridge Univ. Press
Clarke A, Gaston KJ. 2006. Climate, energy and diversity. *Proc. Biol. Sci.* 273:2257–66
Coelho SM, Simon N, Ahmed S, Cock JM, Partensky F. 2013. Ecological and evolutionary genomics of marine photosynthetic organisms. *Mol. Ecol.* 22:867–907
Cohen NR, Mann E, Stemple B, Moreno CM, Rauschenberg S, et al. 2018. Iron storage capacities and associated ferritin gene expression among marine diatoms. *Limnol. Oceanogr.* 63:1677–91
Coles VJ, Stukel MR, Brooks MT, Burd A, Crump BC, et al. 2017. Ocean biogeochemistry modeled with emergent trait-based genomics. *Science* 358:1149–54
Colin S, Coelho LP, Sunagawa S, Bowler C, Karsenti E, et al. 2017. Quantitative 3D-imaging for cell biology and ecology of environmental microbial eukaryotes. *eLife* 6:e26066
Cornejo-Castillo FM, Cabello AM, Salazar G, Sánchez-Baracaldo P, Lima-Mendez G, et al. 2016. Cyanobacterial symbionts diverged in the late Cretaceous towards lineage-specific nitrogen fixation factories in single-celled phytoplankton. *Nat. Commun.* 7:11071
Cornejo-Castillo FM, Muñoz-Marín MDC, Turk-Kubo KA, Royo-Llonch M, Farnelid H, et al. 2019. UCYN-A3, a newly characterized open ocean sublineage of the symbiotic N-fixing cyanobacterium *Candidatus* Atelocyanobacterium thalassa. *Environ. Microbiol.* 21:111–24
Costa JT. 2017. *Darwin's Backyard: How Small Experiments Led to a Big Theory*. New York: Norton
Cullen JJ. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. *Can. J. Fish. Aquat. Sci.* 39:791–803
Cullen JJ. 2015. Subsurface chlorophyll maximum layers: enduring enigma or mystery solved? *Annu. Rev. Mar. Sci.* 7:207–39
de Vargas C, Audic S, Henry N, Decelle J, Mahé F, et al. 2015. Ocean plankton. Eukaryotic plankton diversity in the sunlit ocean. *Science* 348:1261605

de Vries J, Gould SB. 2018. The monoplastidic bottleneck in algae and plant evolution. *J. Cell Sci.* 131:jcs203414
Decelle J, Carradec Q, Pochon X, Henry N, Romac S, et al. 2018. Worldwide occurrence and activity of the reef-building coral symbiont *Symbiodinium* in the open ocean. *Curr. Biol.* 28:3625–33.e3
Decelle J, Martin P, Paborstava K, Pond DW, Tarling G, et al. 2013. Diversity, ecology and biogeochemistry of cyst-forming Acantharia (Radiolaria) in the oceans. *PLOS ONE* 8:e53598
Decelle J, Probert I, Bittner L, Desdevises Y, Colin S, et al. 2012. An original mode of symbiosis in open ocean plankton. *PNAS* 109:18000–5
Delmont TO, Eren AM. 2018. Linking pangenomes and metagenomes: the *Prochlorococcus* metapangenome. *PeerJ* 6:e4320
De-Luca R, Bernardi A, Meneghesso A, Morosinotto T, Bezzo F. 2018. Modelling the photosynthetic electron transport chain in *Nannochloropsis gaditana* via exploitation of absorbance data. *Algal Res.* 33:430–39
Dennett MR. 2002. Video plankton recorder reveals high abundances of colonial Radiolaria in surface waters of the central North Pacific. *J. Plankton Res.* 24:797–805
Derelle E, Ferraz C, Rombauts S, Rouzé P, Worden AZ, et al. 2006. Genome analysis of the smallest free-living eukaryote *Ostreococcus tauri* unveils many unique features. *PNAS* 103:11647–52
Dorrell RG, Azuma T, Nomura M, de Kerdrel GA, Paoli L, et al. 2019. Principles of plastid reductive evolution illuminated by nonphotosynthetic chrysophytes. *PNAS* 116:6914–23
Dorrell RG, Bowler C. 2017. Secondary plastids of stramenopiles. *Adv. Bot. Res.* 84:57–103
Dorrell RG, Smith AG. 2011. Do red and green make brown? Perspectives on plastid acquisitions within chromalveolates. *Eukaryot. Cell* 10:856–68
Duarte CM. 2015. Seafaring in the 21st century: the Malaspina 2010 Circumnavigation Expedition. *Bull. Limnol. Oceanogr.* 24:11–14
Eiler A. 2006. Evidence for the ubiquity of mixotrophic bacteria in the upper ocean: implications and consequences. *Appl. Environ. Microbiol.* 72:7431–37
Estrada M. 1991. Phytoplankton assemblages across a NW Mediterranean front: changes from winter mixing to spring stratification. In *Homage to Ramon Margalef; Or, Why There Is Such Pleasure in Studying Nature*, Vol. 10, ed. J Ros, N Pratt, pp. 157–85. Barcelona: Univ. Barcelona
Estrada M, Delgado M, Blasco D, Latasa M, Cabello AM, et al. 2016. Phytoplankton across tropical and subtropical regions of the Atlantic, Indian and Pacific Oceans. *PLOS ONE* 11:e0151699
Falkowski PG. 2012. Ocean science: the power of plankton. *Nature* 483:S17–20
Falkowski PG, Fenchel T, DeLong EF. 2008. The microbial engines that drive Earth's biogeochemical cycles. *Science* 320:1034–39
Falkowski PG, Katz ME, Knoll AH, Quigg A, Raven JA, et al. 2004. The evolution of modern eukaryotic phytoplankton. *Science* 305:354–60
Falkowski PG, Knoll AH. 2011. *Evolution of Primary Producers in the Sea*. San Diego, CA: Academic
Farrant GK, Doré H, Cornejo-Castillo FM, Partensky F, Ratin M, et al. 2016. Delineating ecologically significant taxonomic units from global patterns of marine picocyanobacteria. *PNAS* 113:E3365–74
Faure E, Not F, Benoiston A-S, Labadie K, Bittner L, Ayata S-D. 2019. Mixotrophic protists display contrasted biogeographies in the global ocean. *ISME J.* 13:1072–83
Field CB, Behrenfeld MJ, Randerson JT, Falkowski P. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281:237–40
Fischer WW, Hemp J, Johnson JE. 2016. Evolution of oxygenic photosynthesis. *Annu. Rev. Earth Planet. Sci.* 44:647–83
Flombaum P, Gallegos JL, Gordillo RA, Rincón J, Zabala LL, et al. 2013. Present and future global distributions of the marine cyanobacteria *Prochlorococcus* and *Synechococcus*. *PNAS* 110:9824–29
Flynn KJ, Stoecker DK, Mitra A, Raven JA, Glibert PM, et al. 2013. Misuse of the phytoplankton–zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton functional types. *J. Plankton Res.* 35:3–11
Follows MJ, Dutkiewicz S, Grant S, Chisholm SW. 2007. Emergent biogeography of microbial communities in a model ocean. *Science* 315:1843–46

Fourqurean JW, Duarte CM, Kennedy H, Marbà N, Holmer M et al. 2012. Seagrass ecosystems as a globally significant carbon stock. *Nat. Geosci.* 5:505–9
Grébert T, Doré H, Partensky F, Farrant GK, Boss ES, et al. 2018. Light color acclimation is a key process in the global ocean distribution of *Synechococcus* cyanobacteria. *PNAS* 115:E2010–19
Gregory A, Zayed A, Conceição-Neto N, Temperton B, Bolduc B, et al. 2019. Marine DNA viral macro- and micro-diversity from pole to pole. *Cell* 177:1109–23
Guidi L, Chaffron S, Bittner L, Eveillard D, Larhlimi A, et al. 2016. Plankton networks driving carbon export in the oligotrophic ocean. *Nature* 532:465–70
Haeckel E. 1998. *Art Forms in Nature: The Prints of Ernst Haeckel*. New York: Prestel
Hairston NG, Hairston NG. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *Am. Nat.* 142:379–411
Hingamp P, Grimsley N, Acinas SG, Clerissi C, Subirana L, et al. 2013. Exploring nucleo-cytoplasmic large DNA viruses in *Tara* Oceans microbial metagenomes. *ISME J.* 7:1678–95
Hutchinson GE. 1961. The paradox of the plankton. *Am. Nat.* 95:137–45
Ibarbalz FM, Henry N, Brandão MC, Martini S, Busseni G, et al. 2019. Global trends in marine plankton diversity across kingdoms of life. *Cell*. In press
Irigoien X, Huisman J, Harris RP. 2004. Global biodiversity patterns of marine phytoplankton and zooplankton. *Nature* 429:863–67
Johnson ZI, Zinser ER, Coe A, McNulty NP, Woodward EMS, Chisholm SW. 2006. Niche partitioning among *Prochlorococcus* ecotypes along ocean-scale environmental gradients. *Science* 311:1737–40
Joos F, Plattner GK, Stocker TF, Marchal O, Schmittner A. 1999. Global warming and marine carbon cycle feedbacks on future atmospheric CO_2. *Science* 284:464–67
Karsenti E, Acinas SG, Bork P, Bowler C, de Vargas C, et al. 2011. A holistic approach to marine eco-systems biology. *PLOS Biol*. 9:e1001177
Keeling PJ, del Campo J. 2017. Marine protists are not just big bacteria. *Curr. Biol.* 27:PR541–49
Kemp AES, Villareal TA. 2013. High diatom production and export in stratified waters – a potential negative feedback to global warming. *Prog. Oceanogr.* 119:4–23
Kemp AES, Villareal TA. 2018. The case of the diatoms and the muddled mandalas: time to recognize diatom adaptations to stratified waters. *Prog. Oceanogr.* 167:138–49
Knoll AH, Follows MJ. 2016. A bottom-up perspective on ecosystem change in Mesozoic oceans. *Proc. Biol. Sci.* 283:20161755
Knoll AH, Summons RE, Waldbauer JR, Zumberge JE. 2007. The geological succession of primary producers in the oceans. In *Evolution of Primary Producers in the Sea*, ed. PG Falkowski, AH Knoll, pp. 133–63. San Diego, CA: Academic
Kolber ZS, Prášil O, Falkowski PG. 1998. Measurements of variable chlorophyll fluorescence using fast repetition rate techniques: defining methodology and experimental protocols. *Biochim. Biophys. Acta Bioenerg.* 1367:88–106
Kopf A, Bicak M, Kottmann R, Schnetzer J, Kostadinov I, et al. 2015. The ocean sampling day consortium. *Gigascience* 4:27
Kreft H, Jetz W. 2007. Global patterns and determinants of vascular plant diversity. *PNAS* 104:5925–30
Krueger T. 2017. Concerning the cohabitation of animals and algae – an English translation of K. Brandt's 1881 presentation "Ueber das Zusammenleben von Thieren und Algen." *Symbiosis* 71:167–74
Latasa M, Cabello AM, Morán XAG, Massana R, Scharek R. 2017. Distribution of phytoplankton groups within the deep chlorophyll maximum. *Limnol. Oceanogr.* 62:665–86
Le Bescot N, Mahé F, Audic S, Dimier C, Garet M-J, et al. 2016. Global patterns of pelagic dinoflagellate diversity across protist size classes unveiled by metabarcoding. *Environ. Microbiol.* 18:609–26
Le Quéré C, Harrison SP, Prentice IC, Buitenhuis ET, Aumont O, et al. 2005. Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. *Glob. Change Biol.* 11:2016–40
Leblanc K, Queguiner B, Diaz F, Cornet V, Michel-Rodriguez M et al. 2018. Nanoplanktonic diatoms are globally overlooked but play a role in spring blooms and carbon export. *Nat. Commun.* 9:953
Letelier RM, Karl DM. 1989. Phycoerythrin-containing cyanobacteria in surface waters of the Drake Passage during February 1987. *Antarct. J. U.S.* 24:185–88

Lewitus E, Bittner L, Malviya S, Bowler C, Morlon H. 2018. Author correction: clade-specific diversification dynamics of marine diatoms since the Jurassic. *Nat. Ecol. Evol.* 2:1993

Li WKW. 2002. Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. *Nature* 419:154–57

Li X, Patena W, Fauser F, Jinkerson RE, Saroussi S, et al. 2019. A genome-wide algal mutant library and functional screen identifies genes required for eukaryotic photosynthesis. *Nat. Genet.* 51:627–35

Lima-Mendez G, Faust K, Henry N, Decelle J, Colin S, et al. 2015. Ocean plankton. Determinants of community structure in the global plankton interactome. *Science* 348:1262073

Lopes Dos Santos A, Gourvil P, Tragin M, Noël M-H, Decelle J, et al. 2017. Diversity and oceanic distribution of prasinophytes clade VII, the dominant group of green algae in oceanic waters. *ISME J.* 11:512–28

López-Sandoval DC, Delgado-Huertas A, Agustí S. 2018. The ^{13}C method as a robust alternative to ^{14}C-based measurements of primary productivity in the Mediterranean Sea. *J. Plankton Res.* 40:544–54

Louca S, Parfrey LW, Doebeli M. 2016. Decoupling function and taxonomy in the global ocean microbiome. *Science* 353:1272–77

Malviya S, Scalco E, Audic S, Vincent F, Veluchamy A, et al. 2016. Insights into global diatom distribution and diversity in the world's ocean. *PNAS* 113:E1516–25

Marchetti A, Parker MS, Moccia LP, Lin EO, Arrieta AL, et al. 2009. Ferritin is used for iron storage in bloom-forming marine pennate diatoms. *Nature* 457:467–70

Massana R, del Campo J, Sieracki ME, Audic S, Logares R. 2014. Exploring the uncultured microeukaryote majority in the oceans: reevaluation of ribogroups within stramenopiles. *ISME J.* 8:854–66

McClain CR. 2009. A decade of satellite ocean color observations. *Annu. Rev. Mar. Sci.* 1:19–42

Michaels AF, Caron DA, Swanberg NR, Howse FA, Michaels CM. 1995. Planktonic sarcodines (Acantharia, Radiolaria, Foraminifera) in surface waters near Bermuda: abundance, biomass and vertical flux. *J. Plankton Res.* 17:131–63

Mihara T, Koyano H, Hingamp P, Grimsley N, Goto S, Ogata H. 2018. Taxon richness of "Megaviridae" exceeds those of Bacteria and Archaea in the ocean. *Microbes Environ.* 33:162–71

Mitra A, Flynn KJ, Tillmann U, Raven JA, Caron D, et al. 2016. Defining planktonic protist functional groups on mechanisms for energy and nutrient acquisition: incorporation of diverse mixotrophic strategies. *Protist* 167:106–20

Monier A, Chambouvet A, Milner DS, Attah V, Terrado R, et al. 2017. Host-derived viral transporter protein for nitrogen uptake in infected marine phytoplankton. *PNAS* 114:E7489–98

Monier A, Worden AZ, Richards TA. 2016. Phylogenetic diversity and biogeography of the Mamiellophyceae lineage of eukaryotic phytoplankton across the oceans. *Environ. Microbiol. Rep.* 8:461–69

Mordret S, Romac S, Henry N, Colin S, Carmichael M, et al. 2016. The symbiotic life of *Symbiodinium* in the open ocean within a new species of calcifying ciliate (*Tiarina* sp.). *ISME J.* 10:1424–36

O'Brien CJ, Peloquin JA, Vogt M, Heinle M, Gruber N, et al. 2012. Global marine plankton functional type biomass distributions: coccolithophores. *Earth Syst. Sci. Data* 5:259–76

Oehri J, Schmid B, Schaepman-Strub G, Niklaus PA. 2017. Biodiversity promotes primary productivity and growing season lengthening at the landscape scale. *PNAS* 114:10160–65

Pagarete A, Le Corguillé G, Tiwari B, Ogata H, de Vargas C, et al. 2011. Unveiling the transcriptional features associated with coccolithovirus infection of natural *Emiliania huxleyi* blooms. *FEMS Microbiol. Ecol.* 78:555–64

Partensky F, Blanchot J, Vaulot D. 1999. Differential distribution and ecology of *Prochlorococcus* and *Synechococcus* in oceanic waters: a review. *Bull. Inst. Oceanogr. Monaco.* No. Spéc. 19:457–76

Pesant S, Not F, Picheral M, Kandels-Lewis S, Le Bescot N, et al. 2015. Open science resources for the discovery and analysis of *Tara* Oceans data. *Sci. Data* 2:150023

Pontarp M, Bunnefeld L, Cabral JS, Etienne RS, Fritz SA, et al. 2019. The latitudinal diversity gradient: novel understanding through mechanistic eco-evolutionary models. *Trends Ecol. Evol.* 34:211–23

Poulton AJ, Holligan PM, Charalampopoulou A, Adey TR. 2017. Coccolithophore ecology in the tropical and subtropical Atlantic Ocean: new perspectives from the Atlantic Meridional Transect (AMT) programme. *Prog. Oceanogr.* 158:150–70

Probert I, Siano R, Poirier C, Decelle J, Biard T, et al. 2014. *Brandtodinium* gen. nov. and *B. nutricula* comb. nov. (Dinophyceae), a dinoflagellate commonly found in symbiosis with polycystine radiolarians. *J. Phycol.* 50:388–99

Puxty RJ, Millard AD, Evans DJ, Scanlan DJ. 2016. Viruses inhibit CO_2 fixation in the most abundant phototrophs on Earth. *Curr. Biol.* 26:1585–89

R. Bot. Gard. Kew. 2017. *State of the world's plants 2017*. Rep., R. Bot. Gard. Kew, Richmond, UK

Raven JA, Evans MCW, Korb RE. 1999. The role of trace metals in photosynthetic electron transport in O_2-evolving organisms. *Photosynth. Res.* 60:111–50

Reid PC, Colebrook JM, Matthews JBL, Aiken J. 2003. The Continuous Plankton Recorder: concepts and history, from Plankton Indicator to undulating recorders. *Prog. Oceanogr.* 58:117–73

Reyes-Prieto A, Weber APM, Bhattacharya D. 2007. The origin and establishment of the plastid in algae and plants. *Annu. Rev. Genet.* 41:147–68

Robineau B. 1999. Ultraphytoplankton abundances and chlorophyll *a* concentrations in ice-covered waters of northern seas. *J. Plankton Res.* 21:735–55

Roux S, Brum JR, Dutilh BE, Sunagawa S, Duhaime MB, et al. 2016. Ecogenomics and potential biogeochemical impacts of globally abundant ocean viruses. *Nature* 537:689–93

Rusch DB, Halpern AL, Sutton G, Heidelberg KB, Williamson S, et al. 2007. The *Sorcerer II* Global Ocean Sampling expedition: northwest Atlantic through eastern tropical Pacific. *PLOS Biol.* 5:e77

Sager R, Zalokar M. 1958. Pigments and photosynthesis in a carotenoid-deficient mutant of *Chlamydomonas*. *Nature* 182:98–100

Salazar G, Paoli L, Alberti A, Huerta-Cepas J, Ruscheweyh H-J, et al. 2019. Gene expression changes and community turnover differentially shape the global ocean metatranscriptome. *Cell*. In press

Sánchez-Baracaldo P, Bianchini G, Di Cesare A, Callieri C, Chrismas NA. 2019. Insights into the evolution of picocyanobacteria and phycoerythrin genes (*mpeBA* and *cpeBA*). *Front. Microbiol.* 10:45

Santoro AE. 2019. Crystal ball: the microbial map of the ocean. *Environ. Microbiol. Rep.* 11:35–37

Sardet C. 2015. *Plankton: Wonders of the Drifting World*. Chicago: Univ. Chicago Press

Seeleuthner Y, Mondy S, Lombard V, Carradec Q, Pelletier E, et al. 2018. Single-cell genomics of multiple uncultured stramenopiles reveals underestimated functional diversity across oceans. *Nat. Commun.* 9:310

Selosse M-A, Charpin M, Not F. 2017. Mixotrophy everywhere on land and in water: the grand écart hypothesis. *Ecol. Lett.* 20:246–63

Sigman DM, Hain MP. 2012. The biological productivity of the ocean. *Nat. Educ. Knowl.* 3:21

Simon N, Cras A-L, Foulon E, Lemée R. 2009. Diversity and evolution of marine phytoplankton. *C. R. Biol.* 332:159–70

Šímová I, Storch D. 2017. The enigma of terrestrial primary productivity: measurements, models, scales and the diversity-productivity relationship. *Ecography* 40:239–52

Six C, Thomas JC, Garczarek L, Ostrowski M, Dufresne A, et al. 2007. Diversity and evolution of phycobilisomes in marine *Synechococcus* spp.: a comparative genomics study. *Genome Biol.* 8:R259

Smetacek V. 1999. Diatoms and the ocean carbon cycle. *Protist* 150:25–32

Sournia A, Chrdtiennot-Dinet MJ, Ricard M. 1991. Marine phytoplankton: how many species in the world ocean? *J. Plankton Res.* 13:1093–99

Stec KF, Caputi L, Buttigieg PL, D'Alelio D, Ibarbalz FM, et al. 2017. Modelling plankton ecosystems in the meta-omics era. Are we ready? *Mar. Genom.* 32:1–17

Steemann Nielsen E. 1960. Productivity of the oceans. *Annu. Rev. Plant Physiol.* 11:341–62

Stemmann L, Youngbluth M, Robert K, Hosia A, Picheral M, et al. 2008. Global zoogeography of fragile macrozooplankton in the upper 100–1000 m inferred from the underwater video profiler. *ICES J. Mar. Sci.* 65:433–42

Stoecker DK, Hansen PJ, Caron DA, Mitra A. 2017. Mixotrophy in the marine plankton. *Annu. Rev. Mar. Sci.* 9:311–35

Sunagawa S, Coelho LP, Chaffron S, Kultima JR, Labadie K, et al. 2015. Structure and function of the global ocean microbiome. *Science* 348:1261359

Suttle CA. 2007. Marine viruses—major players in the global ecosystem. *Nat. Rev. Microbiol.* 5:801–12

Suzuki N, Not F. 2015. Biology and ecology of Radiolaria. In *Marine Protists*, ed. S Ohtsuka, T Suzaki, T Horiguchi, N Suzuki, F Not, pp. 179–222. Tokyo: Springer

Swenson NG, Enquist BJ. 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *Am. J. Bot.* 94:451–59

Thompson AW, Foster RA, Krupke A, Carter BJ, Musat N, et al. 2012. Unicellular cyanobacterium symbiotic with a single-celled eukaryotic alga. *Science* 337:1546–50

Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, et al. 2010. Global patterns and predictors of marine biodiversity across taxa. *Nature* 466:1098–101

Trebilco R, Baum JK, Salomon AK, Dulvy NK. 2013. Ecosystem ecology: size-based constraints on the pyramids of life. *Trends Ecol. Evol.* 28:423–31

Vallina SM, Follows MJ, Dutkiewicz S, Montoya JM, Cermeno P, Loreau M. 2014. Global relationship between phytoplankton diversity and productivity in the ocean. *Nat. Commun.* 5:4299

Vannier T, Leconte J, Seeleuthner Y, Mondy S, Pelletier E, et al. 2016. Survey of the green picoalga *Bathycoccus* genomes in the global ocean. *Sci. Rep.* 6:37900

Venrick EL. 1988. The vertical distributions of chlorophyll and phytoplankton species in the North Pacific central environment. *J. Plankton Res.* 10:987–98

Villar E, Farrant GK, Follows M, Garczarek L, Speich S, et al. 2015. Ocean plankton. Environmental characteristics of Agulhas rings affect interocean plankton transport. *Science* 348:1261447

Vincent FJ, Colin S, Romac S, Scalco E, Bittner L, et al. 2018. The epibiotic life of the cosmopolitan diatom *Fragilariopsis doliolus* on heterotrophic ciliates in the open ocean. *ISME J.* 12:1094–108

Werdell PJ, Proctor CW, Boss E, Leeuw T, Ouhssain M. 2013. Underway sampling of marine inherent optical properties on the Tara Oceans expedition as a novel resource for ocean color satellite data product validation. *Methods Oceanogr.* 7:40–51

Xing X-G, Claustre H, Boss E, Chai F. 2018. Toward deeper development of Biogeochemical-Argo floats. *Atmos. Ocean. Sci. Lett.* 11:287–90

Yelton AP, Acinas SG, Sunagawa S, Bork P, Pedrós-Alió C, Chisholm SW. 2016. Global genetic capacity for mixotrophy in marine picocyanobacteria. *ISME J.* 10:2946–57

Zehr JP, Waterbury JB, Turner PJ, Montoya JP, Omoregie E, et al. 2001. Unicellular cyanobacteria fix N_2 in the subtropical North Pacific Ocean. *Nature* 412:635–38

Zhang C, Dang H, Azam F, Benner R, Legendre L, et al. 2018. Evolving paradigms in biological carbon cycling in the ocean. *Natl. Sci. Rev.* 5:481–99

Zubkov MV. 2014. Faster growth of the major prokaryotic versus eukaryotic CO_2 fixers in the oligotrophic ocean. *Nat. Commun.* 5:3776