Minireview

Eukaryotic versus prokaryotic marine picoplankton ecology

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Summary

Marine microorganisms contribute markedly to global biomass and ecosystem function. They include a diverse collection of organisms differing in cell size and in evolutionary history. In particular, microbes within the picoplankton are similar in size but belong to two drastically different cellular plans, the prokaryotes and the eukaryotes. Compared with larger organisms, prokaryotes and picoeukaryotes share ecological features, such as high specific activity, large and constant abundances, and high dispersal potential. Still, there are some aspects where their different cell organization influences their ecological performance. First, prokaryotes have a huge metabolic versatility and are involved in all biogeochemical cycles, whereas picoeukaryotes are metabolically less flexible but can exploit diverse predatory life strategies due to their phagocytic capacity. Second, sexual reproduction is absent in prokaryotes but may be present in picoeukaryotes, thus determining different evolutionary diversification dynamics and making species limits clearer in picoeukaryotes. Finally, it is plausible that picoeukaryotes are less flexible to enter a reversible state of low metabolic activity, thus picoeukaryote assemblages may have fewer rare species and may be less resilient to environmental change. In summary, lumping together pico-sized microbes may be convenient for some ecological studies, but it is also important to keep in mind their differences.

Introduction

A major scientific achievement in the past century has been the discovery of the invisible microbial world (Maloy and Schaechter, 2006). Microorganisms are known to play a fundamental role in many scientific disciplines, including ecology, evolution, medicine and biotechnology. Life originated at microbial scales, and stayed there for most of the Earth's geological age, during which all metabolic innovations and many structural designs evolved before the appearance of macroorganisms through multicellularity (Gould, 1996). Microbes have shaped and are regulating the atmosphere and oceans we observe today by playing unique roles in all biogeochemical cycles and are large reservoirs of taxonomic and genetic biodiversity (Whitman *et al.*, 1998; Falkowski *et al.*, 2008). They have also interacted with humanity since its origins by establishing beneficial interactions (symbiosis, mutualism), causing major diseases, and being essential agents in many biotechnological processes in the food and pharmaceutical industry.

Microbes as small as prokaryotes were already observed centuries ago, but the recognition of their ecological importance is relatively recent. Developments in microscopy, radiotracer techniques and molecular tools have been pivotal to understand their abundance, activity and diversity. Now we know that microorganisms are the most abundant living beings on Earth and represent a significant share of biomass and ecosystem functions. This role is magnified in pelagic marine ecosystems, where food webs are based on microorganisms. Indeed, minute phytoplankton cells contribute to half global primary production, while representing only 1% of global biomass (Field *et al.*, 1998). Thus, the emerging field of microbial ecology has found the marine habitat as a central study system, where many new approaches have been first applied (Giovannoni *et al.*, 1990). However, microbial ecology has been mostly descriptive, and it is not straightforward to assess how ecological and evolutionary theories derived from the study of animals, plants or fungi fit with microorganisms. There is now a big effort to place microbes in the place they deserve in the map of

natural sciences, and this necessarily requires a better understanding of their functional and taxonomic diversity.

It is tempting to treat microorganisms as a more or less homogeneous ecological assemblage. However, this is an anthropocentric perspective, as we oversimplify an amazing amount of evolutionary and metabolic diversity only because microbes remain invisible to the human naked eye. An operational way to classify the huge microbial diversity is according to cell organization and body size. Most microbes are unicellular and belong to one of the two main cell designs, prokaryotes or eukaryotes, each with different metabolic and structural features. With respect to body size, aquatic microorganisms are traditionally separated in three logarithmic classes, pico (0.2–2 μm), nano (2–20 μm) and micro (20–200 μm). The two larger size classes are composed essentially by eukaryotes (although symbiotic or attached prokaryotes can be found in these larger fractions), whereas the picoplankton, first thought to be composed by prokaryotes only, was soon recognized to contain also eukaryotic unicells (Johnson and Sieburth, 1982). Together with prokaryotes (Giovannoni and Stingl, 2005), it is now well established that picoeukaryotes are fundamental components of marine ecosystems in terms of biomass, activity and diversity (Massana, 2011). Nevertheless, it is clear that picoeukaryotes have specific singularities that might condition their ecological role as compared with prokaryotes.

In this review we will focus on free-living marine microbes of comparable size, the picoplankton, but that belong to different life's domains: the prokaryotes and the eukaryotes. Although particle-associated microbes in the plankton normally form biofilms with its own features, we do not consider those types here. We will first mention briefly the main characteristics of prokaryotic and eukaryotic cell organization and life cycles. Then, we will present the similarities that both types of cells have in terms of ecological roles. Finally, we will discuss three aspects where cell organization has a direct influence on the ecological outcome: the positioning in food webs, the influence of sex in structuring natural populations, and the relevance of dormancy stages on extant diversity and biogeography.

Brief outline of cell organization and life cycles

Life as we see it today is the result of evolutionary processes taking place in an ecological context, underlying the intimate connection between ecology and evolution (Pelletier *et al.*, 2009). The origin of life can be traced about 3.8 billion years ago, in the form of a prokaryote cell. It is assumed that these cells initially used abiotically synthesized organic matter by fermentation, until the appearance of electron transport systems allowed a better use of chemical energy (by respiration) and light

(by photosynthesis). Prokaryotes have kept a simple cell organization, with an uncompartmented cytoplasm without membrane-bound organelles, a primitive cytoskeleton (Shih and Rothfield, 2006), and a rigid cell wall that often functions as an external skeleton. They are osmotrophs, so they incorporate substrates through cell membranes generally by active transport. Since there is a maximal molecular size that can be transported through membranes, they often exhibit extracellular digestion of macromolecules and the uptake of the smaller resulting compounds.

Cell division in prokaryotes is entirely asexual, generally through binary fission. The circular DNA molecule first replicates, each copy attaches to a different region of the membrane, and the cell divides into two genetically identical daughter cells. There are mechanisms of genetic transfer between cells unrelated to reproduction (such as conjugation, transformation and transduction) that, when involving homologous recombination among closely related lineages, could lead to a type of sexual speciation (Fraser *et al.*, 2007). Genetic exchanges also occur among individuals from distant lineages, resulting in horizontal gene transfer, which has transformed our view of prokaryote diversity and evolution (Doolittle and Papke, 2006). Prokaryote genomes are typically composed of a core set of vertically transmitted genes and a flexible set of horizontally transmitted genes, often related to ecological adaptations and located in genomic islands (Dobrindt *et al.*, 2004). A recent study of the genomics islands of 70 marine bacteria reveals that they may account for 12% of the genome size (Fernández-Gómez *et al.*, 2012).

A plausible explanation for the origin of the eukaryotic cell, around 2 billions years ago, is the evolution of an anaerobic wall-less bacteria to a primitive eukaryote (de Duve, 2007). At some point, this primitive phagotroph engulfed a proteobacteria that instead of being digested evolved to mitochondria (Margulis, 1981), the powerhouse of eukaryotes. The endosymbiosis with cyanobacteria in the archaeplastida lineage derived in primary chloroplasts, which then spread to other lineages through secondary endosymbiosis. As a consequence, a modest fraction of genes in the eukaryotic nucleus have been imported from endosymbionts, in the process named Endosymbiotic Gene Transfer (Timmis *et al.*, 2004). In contrast with prokaryotes, eukaryotes have a highly compartmentalized cytoplasm containing membrane-bound organelles, and a nucleus containing the genetic material organized in linear chromosomes. Furthermore, they have an elaborate cytoskeleton of microtubules and filaments that provide internal structure and a defined cell shape, the flagellar apparatus for movement, and the ability to build up complex morphological structures. Most importantly, the cytoskeleton is involved in phagocytosis, driving invaginations of the cell membrane to form

digestive vacuoles. So, eukaryotic cells have the unique ability of engulfing other organisms. Assuming that evolutionary ancestors had a larger size, picoeukaryotes represent the successful miniaturization of the eukaryote cell by keeping the minimal components necessary for an independent life (Massana, 2011).

Unicellular eukaryotes might reproduce asexually yielding two identical daughter cells, with a more complex mechanism than in prokaryotes of chromosome duplication and separation, the mitosis. In addition, they might also exhibit sexual reproduction, characterized by two steps: meiosis, which is the formation of haploid gametes from a diploid cell (during which chromosomes recombine resulting in non-identical gametes), and syngamy, which is the fusion of two gametes to form a new diploid cell. Sexuality promotes variability within a population, since all daughter cells are genetically different from each other and from the parents, and at the same time can serve as an evolutionary cohesive force that shapes species and constrains species divergence (Achtman and Wagner, 2008). The combination, timing and peculiarities of the asexual and sexual events in each eukaryotic species forms the life cycle, which can be very simple or extremely intricate. While sexual reproduction is known in larger protists such as ciliates, diatoms, dinoflagellates or radiolaria, its existence in smaller protists is uncertain, being only inferred from genomic analyses (Worden *et al.*, 2009).

Similarities in prokaryotic and picoeukaryotic marine ecology

The first obvious similarity between prokaryotes and picoeukaryotes is their small size. Certainly picoeukaryotes are slightly larger than prokaryotes (typical cell diameters of 2.0 and 0.5 μm respectively), but they are similarly sized when considering the whole spectrum of living beings, including planktonic microbes (from 0.2 to 200 μm). Body size is the most powerful descriptor of individual metabolic rates (Peters, 1983), and these may control ecological processes according to the metabolic theory of ecology (Brown *et al.*, 2004). Smaller organisms have lower absolute metabolic rates than larger organisms, but higher mass specific rates. This translates to faster growth rates in smaller organisms and higher energy needs relative to biomass than larger organisms. Other implications of body size are that small organisms are generally more abundant than larger organisms and that they contain less reserves for starvation (Peters, 1983), a fact often compensated by their capacity to switch to a low-power demand mode (Lennon and Jones, 2011). Typically, size–metabolism relationships follow a power formula with an exponent of 3/4, although this allometric scaling law could be broken at the two main transitions of life, prokaryotes-to-unicellular eukaryotes, and unicellular-to-multicellular eukaryotes (DeLong *et al.*, 2010). Using the 3/4 exponent and the above cell sizes, a prokaryote would have a growth rate only three times higher than a picoeukaryote. Measured rates with cultured strains show that the fastest bacteria can double every 20 min, whereas the fastest protist needs 2–3 h (Prescott *et al.*, 1999). These fast rates are seldom realized in marine systems, where community-doubling times for prokaryotes and picoeukaryotes are in the same range of several days (Kirchman, 2008), although growth rates for individual populations may differ significantly (Ferrera *et al.*, 2011). So, from both theoretical grounds and empirical inferences, prokaryotes and picoeukaryotes have comparable metabolic rates.

Another remarkable similarity among prokaryotes and picoeukaryotes is their widespread distribution. These minute cells populate all marine habitats, including the whole water column and diverse types of particles and sediments, where they typically account for the majority of organisms. Each habitat is occupied by different species that have specific adaptations, with prokaryotes exhibiting a wider environmental range. For instance, a typical surface sample has, per millilitre seawater, 5×10^5 heterotrophic prokaryotes, 5×10^4 cyanobacteria, 2000 phototrophic and 500 heterotrophic picoeukaryotes (each of these four groups contribute 10–40% of the picoplankton biomass). As compared with other size classes, the picoplankton constitutes a substantial share of the total biomass and is often dominant in oligotrophic systems (Fogg, 1995). So, both prokaryotes and picoeukaryotes are major contributors to ecosystem processes like primary production and respiration. They exemplify how minute individual activities result in global biogeochemical impacts given widespread distributions and huge abundances.

The variability in picoplankton abundance in seawater is fairly constrained, forming a stable ocean's veil that contrasts with larger protists like diatoms or ciliates that exhibit orders of magnitude variation in their abundance during blooms or in different seasons (Smetacek, 2002). Moderate growth rates, together with constant numbers over short temporal scales, suggest that picoplankton production is well compensated by mortality. For prokaryotes, there is an extensive literature on mortality factors such as protozoan grazing (Pernthaler, 2005) or viral lysis (Weinbauer, 2004). Grazing incorporates microbes into food webs, whereas viral lysis forms the viral shunt that dissipates nutrients and energy (Wilhelm and Suttle, 1999). Moreover, viruses may control diversity following the 'killing the winner' hypothesis (Thingstad and Lignell, 1997). Picoeukaryotes seem to be controlled by similar mortality factors (Brussaard, 2004; Worden *et al.*, 2004). The tight connection between production and mortality

indicate that prokaryotes and picoeukaryotes collectively participate in highly efficient recycling systems.

Finally, prokaryotes and picoeukaryotes seem to have similar biogeographical patterns in the sea. Early microbiologists already noticed that microbial biogeography could be different from that of animals and plants, since the small body size and huge abundances of microbes could translate to unrestricted dispersal. This could be the case for marine picoplankters living in surface waters, which are the smallest microbes and live in a very well-connected habitat. Indeed, molecular surveys using the small subunit (SSU) rDNA gene have identified globally distributed marine prokaryotes and picoeukaryotes (Morris *et al.*, 2002; Massana *et al.*, 2006; Amaral-Zettler *et al.*, 2010), exhibiting a biogeography that seems more associated to contemporary environmental conditions than to historical events or neutral processes (Lindström and Langenheder, 2012). Thus, marine picoplankters may follow to a certain extent the long-standing tenet 'everything is everywhere, but the environment selects' (Baas Becking, 1934), which in current metacommunity theory is known as 'species sorting' (Holyoak *et al.*, 2005). This is the expected outcome at intermediate levels of dispersal, which prevents mass effects or dispersal limitation. In contrast, restricted distributions due to dispersal limitation could be expected in less connected habitats like lakes (Vyverman *et al.*, 2007) or the deep ocean (Agogué *et al.*, 2011). Larger protists may have lower dispersal ability and exhibit restricted distributions (Casteleyn *et al.*, 2008). The view of surface picoplankton species globally distributed needs further refinement using more variable genetic markers. For instance, using the hypervariable internal transcribed spacer (ITS) regions of the rDNA operon, locally distinct microdiversity has been detected (Martiny *et al.*, 2009), but also examples of similar ITS in widely separated oceanic regions have been reported (Rodríguez-Martínez *et al.*, 2012).

Metabolic versus structural complexity

The simple cell organization of prokaryotes contrasts with their extreme functional versatility, achieved by metabolic diversity. Prokaryotes have invented most metabolic pathways, such as the capacity to degrade organic matter by fermentation or aerobic/anaerobic respiration, synthetize organic matter by photoautotrophy or chemoautotrophy, and fix nitrogen. Many of these pathways are based on redox reactions that derive energy by transferring electrons from a reduced to an oxidized molecule through electron transport systems. Prokaryotes are central players in the global carbon cycle, both as primary producers and degraders of organic matter through respiration. Moreover, since almost all energetically possible combinations of electron donors and acceptors have been

detected in different lineages, prokaryotes exhibit unique metabolisms that translate to crucial roles in virtually all biogeochemical cycles (Arrigo, 2005). For example, the oxygenated atmosphere was established after oxygenic photosynthesis appeared in cyanobacteria, and the current anoxic habitats are often due to prokaryotic activity. Prokaryotes are solely responsible for critical steps in the nitrogen cycle and are also essential in the sulfur, phosphorus and iron cycles.

Despite this huge metabolic potential marine prokaryotes remain generally very small: heterotrophs are seldom larger than 1 μm, whereas most phototrophs are unicellular cyanobacteria below 2 μm. In addition, they remain osmotrophs, implying that substrates can only be incorporated through cell membranes using specific transport systems. As a consequence, most interactions between prokaryotes seem to be cooperative, by sharing extensively substrates and metabolites. This is illustrated by the nitrogen cycle, where two different prokaryote species are needed to oxidize ammonia to nitrate (Zehr and Ward, 2002). Other prokaryotic consortia cooperate to complete a specific step within a given biogeochemical cycle (Boetius *et al.*, 2000) or to bioremediate contaminants (Gertler *et al.*, 2009). Moreover, antagonistic relationships among prokaryotes can also be important, and these would be mediated by competition for the same resources, by growth-inhibiting substances like antibiotics, or by direct attack using particular predatory strategies (Martin, 2002).

Evolutionary innovations within eukaryotes have been based on their capacity to incorporate pre-existing components by endosymbiosis and on the potential given by the cytoskeleton to explore new shapes, larger sizes, motility, and phagocytosis. Contrasting with these structural and behavioural innovations, the metabolic repertoire of eukaryotic cells with respect to energy use is rather limited, and even the main processes of aerobic respiration (in mitochondria) and photosynthesis (in chloroplasts) have been imported from the bacterial world. Picoeukaryotes, which remain as simple cells, are either primary producers using light or organic matter consumers (and some, like in prokaryotes, can do both, being thus mixotrophs). While photosynthetic prokaryotes and picoeukaryotes play similar ecological roles and are considered together in many surveys (Li, 2002), this does not apply for their heterotrophic counterpart. Heterotrophic picoeukaryotes base their living mostly in phagocytosis and intracellular digestion of smaller organisms. Eukaryotic osmotrophy, so prevalent in the terrestrial fungal world, seems to play little role in the marine plankton (Richards *et al.*, 2012). By eating smaller organisms, typically prokaryotes, picoeukaryotes place themselves in a higher trophic level and form part of food webs. The more aggressive predatory interactions established by eukaryotes with other organisms often result in an evolutionary

arms race (Dawkins and Krebs, 1979). In addition, since osmotrophy and membrane transport seem more specific than predation, heterotrophic prokaryotes could be more specialized in their substrates than eukaryotic grazers.

Pico-sized species from different life's domains

The concept of species emerged from the need to organize living beings into discrete categories, and for a long time there has been a heated discussion on the nature of species and how they can be delimited (Coyne and Orr, 2004). The theory of Evolution provided a framework for understanding the emergence of diversity, but still a universal species concept has not been established. Part of the problem is that Evolution is an ongoing process, so species can be at different stages of formation. Moreover, speciation mechanisms are influenced by the life cycles in different organisms, and the fundamentally different modes of reproduction between eukaryotes and prokaryotes certainly prevents the application of a universal species concept.

The absence of sexual reproduction within prokaryotes provides a particularly complicated scenario, since each cell could establish an independent clonal lineage by reproducing asexually and factors constraining variability within populations are not clear. Moreover, horizontal gene transfer among prokaryotes blurs the traditional species view based in vertical-inheritance, and poses a problem for delimiting the species boundaries (Doolittle and Papke, 2006). Nevertheless, it is clear that there is a unifying evolutionary force among prokaryote cells, which can be classified into separate units by several independent criteria (Ochman *et al.*, 2005; Achtman and Wagner, 2008). Categories analogous to species exist and there are several theories to explain how they are formed and maintained. One theory points to ecological factors as the unifying force, with periodic selective sweeps purging variability within related lineages (Cohan, 2002). So, a prokaryote species would be an assemblage of clonal lineages containing non-adaptive variation and occupying the same ecological niche. A contrasting theory points to sexual factors, assuming homologous recombination being more frequent among closely related cells (Fraser *et al.*, 2007). Both theories explain the genome cohesion within a species, but differ in the sense that the first implies genome-wide selective sweeps whereas the second implies gene-adaptive sweeps (Shapiro *et al.*, 2012).

Sexual reproduction is an eukaryote attribute that led to the development of the Biological Species Concept (BSC): individuals are from the same species if they can reproduce sexually and have fertile offspring (Mayr, 1942). Sex allows maximizing genetic variability, generating populations better adapted to fluctuating environments or to antagonistic biological interactions. In addition, it also

works as a cohesive force that homogenizes the intraspecific genetic pool and constrains its variability (Achtman and Wagner, 2008); individuals from different species can freely follow divergent evolutionary paths. The applicability of the BSC to protists, and to picoeukaryotes in particular, is limited since it is uncertain the existence and frequency of sexual events besides the observed asexual divisions (Schlegel and Meisterfeld, 2003). Many of the smallest protists were considered to be exclusively asexual (Fenchel, 1987), but recent molecular data are challenging this view. Genome analysis of a marine picoalga has identified the complete set of genes putatively involved in meiosis (Worden *et al.*, 2009), suggesting sexual reproduction, although this has never been observed in this species. Analyses of ITS rDNA secondary structures of an uncultured and widespread picoeukaryote suggested sexual compatibility among cells from distant oceans (Rodríguez-Martínez *et al.*, 2012). Also, recombination signatures have been detected in hypervariable regions of *Ostreococcus* genomes, allowing calculating the rate of one sexual division per million divisions (Grimsley *et al.*, 2010). Considering that *Ostreococcus* might divide once a day, this implies one sexual event within a clonal lineage every 2700 years; at abundances of 1000 cells ml^{-1} this implies one sexual event per litre seawater each day. Nevertheless, it remains to be determined whether or not all picoeukaryote species have sex, at what frequency, and if that may control the genetic structure of marine populations.

The different evolutionary forces working on eukaryotic and prokaryotic species should leave an imprint on their natural populations. So, eukaryotic species would have their genetic diversity well delineated and homogenized by sexuality, whereas prokaryotic species would present a genetic continuum where the limits of species are less defined. Environmental molecular surveys of marine prokaryotes have detected clusters of tightly related sequences very similar but seldom identical (Acinas *et al.*, 2004). The structuring of diversity in microdiverse clusters is consistent with both cohesive forces (ecological or recombining) that are purging (to some extent) the variability within a given species but that also allow some non-adaptive variability within prokaryotic species. A similar study of the microdiversity of marine picoeukaryotes is needed to evaluate how constrained is their natural variability. It appears that they might not contain the same degree of microdiversity, at least at the SSU rRNA gene (Rodríguez-Martínez *et al.*, 2012), but this may depend on the lineage considered.

The rare biosphere in picoplankters

Ecologists have long known that natural communities are typically composed of few abundant species together with

many rare species (Magurran and Henderson, 2003), a fact that strongly influences the richness estimates from a community and may complicate community comparisons. High-throughput sequencing studies of bacterial diversity have revealed the same pattern, leading to the 'rare microbial biosphere' concept (Sogin *et al.*, 2006), proposed as a seed bank of less competitive and functionally redundant microbes that may provide an insurance to maintain biogeochemical processes in the face of ecosystem change (Caron and Countway, 2009). Species within the rare biosphere could exhibit one of three contrasting strategies. First, many could be taxa that are in a reversible state of low metabolic activity waiting for particular environmental conditions in order to grow. Indeed, prokaryotes can survive for months to years in starvation by minimizing size as a predation refuge, entering a state of low metabolic needs, or forming resting stages (Lennon and Jones, 2011). Examples of this strategy are taxa that seasonally shift from being rare to abundant (Campbell *et al.*, 2011) or taxa that develop in response to oil spills (Pedrós-Alió, 2012) or after other disturbances (Sjöstedt *et al.*, 2012). Second, part of the rare biosphere could be taxa that remain always rare (Galand *et al.*, 2009), despite some could be very active (Jones and Lennon, 2010) and even play a key ecosystem function (Pester *et al.*, 2010). Third, some rare taxa may have been imported from another habitat due to unrestricted dispersal (i.e. terrestrial microbes in the sea), so being on their way of extinction.

The rare biosphere has also been observed in molecular surveys of protist diversity (Caron and Countway, 2009; Stoeck *et al.*, 2010), and here we hypothesize that its extent could be comparatively smaller, given that survival mechanisms in protists may be less developed than within prokaryotes. Thus, even by reducing cell size, picoeukaryotes would never escape predation by small grazers. Moreover, most picoeukaryotes are naked, and the lack of a rigid cell wall probably limits their survival by starvation. It is known that many protists form resting stages, like spores, at some time of the life cycle, but this is not universal for all protists species, and has never been documented in picoeukaryotes. Furthermore, it has been shown that dormancy stages in lake ecosystems are more common in bacteria than in microbial eukaryotes (Jones and Lennon, 2010). Finally, if sex plays a significant role as a cohesive evolutionary force in picoeukaryotes, this would prevent clonal diversification and probably would also limit the importance of the rare biosphere. In addition, if sex is needed, taxa that are always rare would have troubles in finding a partner. Preliminary high-throughput sequencing data of both components in the same samples have revealed a higher operational taxonomic unit (OTU) number in bacteria than in protists (Brown *et al.*, 2009; McCliment *et al.*, 2012), in agreement with the view of the lower importance of the rare bio-

sphere within protists. Nevertheless, more studies are clearly needed where both prokaryote and eukaryote diversity are simultaneously determined using comparable molecular markers.

Concluding remarks

Despite protists are main contributors of biomass, activity and diversity in marine ecosystems (Caron *et al.*, 2009), they are often disregarded in microbial ecology and many studies refer only to prokaryotes when dealing with microbes. Besides prokaryotes, the smallest protists also participate in forming the ubiquitous planktonic ocean's veil. Both prokaryotes and picoeukaryotes share many properties derived from their small cell size, such as huge population abundances, high-specific activity levels and supposedly unrestricted dispersal in surface oceans. So, in some aspects, small pico-size translates into similar ecological roles and biogeographical patterns. In addition, ecological differences between prokaryotes and picoeukaryotes emerge due to their different cell organization. The main differences are the phagocytic ability of eukaryotes that enable the establishment of foods webs, the putative presence of sex in eukaryotes that may affect their evolutionary diversification, and the plausible lower survival potential of protists that can influence their distribution patterns, including a less dramatic rare biosphere. Picoeukaryotes and prokaryotes share many properties but also exhibit fundamental differences in ecological roles, functional versatility, and evolutionary pathways. These differences should be considered in future studies that aim at understanding the relationships between prokaryotes and picoeukaryotes within marine microbial communities.

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