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Time series are critical to understand microbial plankton diversity and ecology

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How diverse are marine planktonic protist communities? How much seasonality do they exhibit? For very long time, these two old and challenging questions in the field of plankton ecology could be addressed only for large-size protist species, based on cell counting under the microscope. The recent application of molecular techniques, notably massive marker-gene amplicon sequencing or metabarcoding approaches, has allowed investigating with unprecedented level of resolution the small-sized (<20 µm) planktonic eukaryotes too. An amazing diversity of these tiny organisms has been unveiled but details about their temporal dynamics have remained much more elusive. In this issue of *Molecular Ecology*, Giner et al. (2018) introduce a new Recurrence Index (RI) to specifically look for seasonality in time-series metabarcoding data. They inspected the temporal dynamics of all operational taxonomic units (OTUs) in a rich sequence dataset of pico- and nano-planktonic eukaryotes in samples collected monthly during 10 years. Although most OTUs did not show seasonality, some abundant ones did, which explains why some averaging methods can find seasonality at the less-detailed level of whole planktonic communities. Not surprisingly, the very complex small-sized eukaryotic plankton communities are composed of organisms with miscellaneous temporal dynamics.

'As there are good and bad wine and fruit years, so there are rich and barren plankton years' (Haeckel, 1891). With these eloquent words, Ernst Haeckel exemplified more than one century ago the critical role that time series must play in the study of plankton, which cannot be fully understood just on the basis of punctual observations, as they may lead to wrong conclusions if done in moments when, for whichever reason, plankton does not behave normally. Indeed, *'to obtain a complete and more certain survey of the temporary variations of plankton composition requires an unbroken series of observations, carried on at one and the same place at least for the space of a full year—still better for several successive years—to obtain from the yearly and monthly oscillations a*

general average'. This idea is behind the remarkable proliferation of marine stations across the world during the XIXth and early XXth centuries. For decades, naturalists were observing marine plankton, describing new species, their interactions, and the functioning of the complex plankton ecosystem. This continuous surveillance also allowed discovering periodical rhythms in the abundance of particular species, leading to the elaboration of the concept of "periodic plankton" (Hensen, 1890). Because of the obvious easiness of observation and identification, early work largely concentrated on planktonic animals. By contrast, the study of microbial planktonic populations was more challenging but, after some decades of scrutiny, periodicity begun to be described, especially for some conspicuous species (see Fig. 1 for some examples), with strong emphasis on phytoplanktonic species because of their importance as primary producers in the global C cycle (e.g., diatoms: Pratt, 1959).

Knowledge remained for a long time much more partial for the difficult-to-observe, smallest planktonic size fractions (pico- and nano-plankton, 0.2-3 μm and 3-20 μm , respectively), mostly composed of prokaryotes but also of a variety of tiny eukaryotic cells. Among those eukaryotes, some important algal species, such as the globally distributed *Micromonas pusilla* (Butcher, 1952), were described, though most diversity was considered to correspond to heterotrophic, likely bacterivorous, species. These organisms were recognized to play a significant role in the function of the plankton trophic chain by fuelling the "microbial loop" (Azam et al., 1983). However, the precise taxonomic identity of these tiny eukaryotic predators remained for the most part unknown and were collectively classified as "eukaryotic nanoflagellates" and treated as a sort of black box in ecological studies (Fenchel, 1982). Only in the early 2000's, thanks to 18S rRNA gene PCR amplification and sequencing from environmental DNA, it started to become possible to fully appreciate the actual wealth of diversity that this black box hid (Díez, Pedrós-Alió, & Massana, 2001; López-García, Rodríguez-Valera, Pedrós-Alió, & Moreira, 2001; Moon-van der Staay, De Wachter, & Vaultot, 2001). Metabarcoding, initially based on time-consuming Sanger sequencing and now on high-throughput techniques, revealed an extensive diversity of small-sized eukaryotes in marine plankton, largely dominated by heterotrophic -including parasitic- species (de Vargas et al., 2015;

Moreira & López-García, 2002). Not surprisingly, the relatively simple morphologies of these small eukaryotes concealed a vast cryptic phylogenetic diversity that has been intensively studied in recent years through several large-scale plankton sampling and metabarcoding efforts (e.g., de Vargas et al., 2015; Pernice et al., 2016). However, these efforts, despite their wide geographical scope, lack the temporal dimension indispensable to really understand plankton community composition, dynamics, biogeography, and ecology, something that only the examination of time series can achieve.

Analysis of time series of small-sized plankton samples using molecular techniques, such as terminal restriction fragment length polymorphism and metabarcoding, had been applied for several years to study prokaryotic communities and, more rarely, eukaryotic ones. These studies have revealed seasonal rhythmicity of the marine and freshwater eukaryotic communities, notably by measuring pairwise Bray–Curtis similarity values between communities sampled at different time intervals (e.g., Kim et al., 2014; Simon et al., 2015). However, this averaging approach misses the fine-grain information contained in the temporal dynamics of each individual species or OTU. Analyzing that information is challenging because the structure of the planktonic eukaryotic communities is very complex, as they contain hundreds or thousands of different OTUs and most of these OTUs appear at first glimpse to exhibit a rather sporadic temporal behavior. Giner et al. (2018) have developed a new Recurrence Index (RI) to specifically address this question on a rich dataset of plankton samples collected monthly over 10 years at the Blanes Bay Microbial Observatory (Mediterranean Sea) and submitted to 18S rRNA gene metabarcoding analysis. For both eukaryotes and prokaryotes, a recurrent observation in previous marine plankton metabarcoding analyses is that diversity patterns are most often dominated by rare OTUs occurring at very low frequencies and in single or very few samples (Pedrós-Alió, 2006; Sogin et al., 2006). By applying their new RI index, Giner et al. corroborated this expectation as they found that only 13% and 19% of the pico- and nano-eukaryotic OTUs, respectively, showed seasonality. However, these OTUs represented a large proportion of the sequence reads

(39% and 37%, respectively), indicating that they are quantitatively important members of the small-size eukaryotic plankton community. The high abundance of these OTUs probably drives the seasonality pattern at the global eukaryotic community level inferred from the Bray–Curtis similarity analyses.

Among the OTUs with the highest RI values, there are several Mamiellophyceae green algae. Planktonic microalgae have traditionally been considered seasonal organisms that tend to bloom during spring and summer as a response to favorable conditions (e.g., increased daylight availability and warmer waters). Some heterotrophic eukaryotes also appear among the high-RI OTUs, in particular MALV-III marine alveolates. For these organisms, seasonality appears to be a conserved class-level trait since the most abundant OTUs of these groups have high RI. By contrast, non-seasonality can be the general trait of most OTUs in other taxonomic groups, both photosynthetic (e.g., Chlorodendrophyceae) and heterotrophic (e.g., cercozoa) ones. Similarly, the proportion of seasonal and non-seasonal OTUs varies in other groups. Thus, seasonality seems to be a trait that differs among classes and even among OTUs within classes. This result stresses that eukaryotic taxonomic groups must not be regarded as homogeneous assemblages but, in most cases, as bins of species with idiosyncratic temporal dynamics, most likely owing to their specific niche adaptations.

A general assumption to explain plankton seasonality is that algal growth, driven by seasonal changes in physicochemical parameters (light, temperature, nutrient availability) drives in turn the abundance of heterotrophic species (e.g., predators and parasites) that depend on them for growth. However, seasonality has also been observed for deep-sea protists, probably much less influenced by those changes in the phytoplanktonic species (Dolan, Ciobanu, Marro, & Coppola, 2017). Likewise, for most eukaryotic heterotrophs, it remains to be elucidated whether they rely directly on the co-occurring algae or whether they rely on other types of prey, notably bacteria. This open question raises an important point concerning time series: sampling frequency. Aquatic microbial communities are highly dynamic and many microorganisms can exhibit fast

population size fluctuations (Mangot et al., 2013). Thus, given the complexity of plankton communities both in terms of structure and temporal oscillation of the composing species, it seems clear that even a monthly sampling strategy most likely misses part of such rapid plankton dynamics and still does not allow to fully infer the fine temporal interplay between autotrophic and heterotrophic plankton populations. The next challenge in this field will be to apply similar techniques as Giner et al. to datasets coming from times series with higher sampling frequencies to look both into eukaryotic and prokaryotic OTU temporal dynamics.

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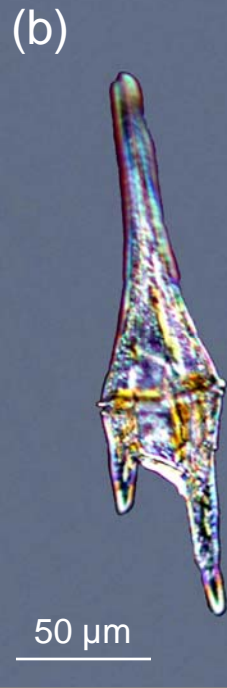
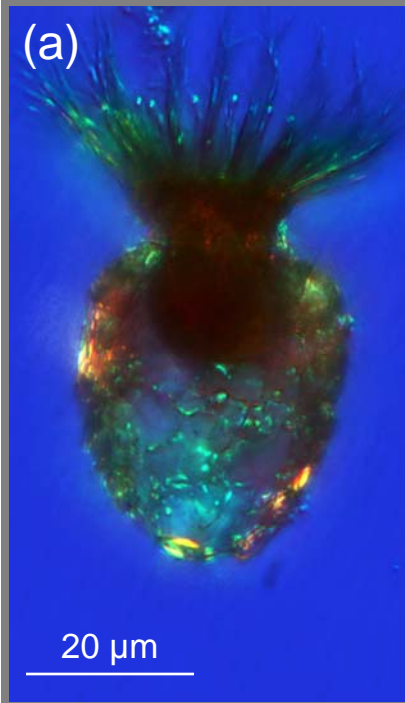
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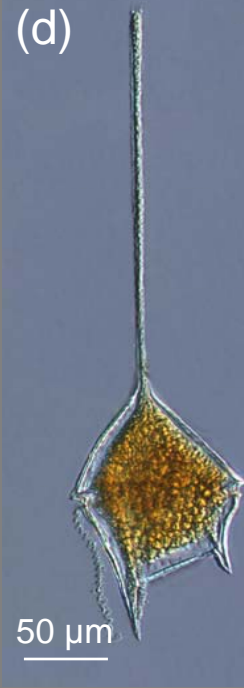
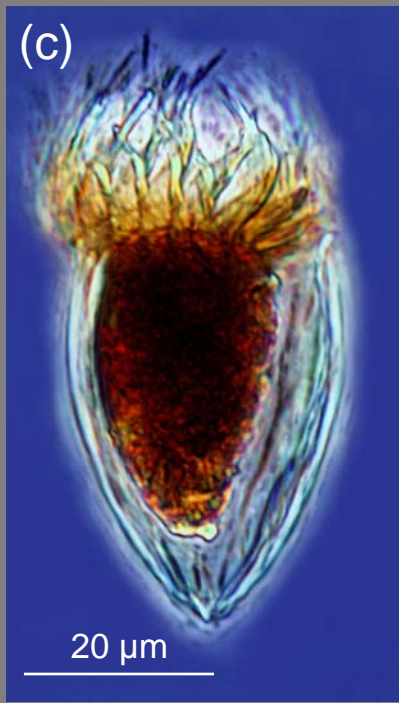
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Figure legend

FIGURE 1 Large protists with seasonal dynamics: the tintinnid ciliate *Stenosomella nivalis* (a) and the dinoflagellate *Ceratium furca* (b) have abundance peaks during winter, whereas their counterparts *Protorhabdonella curta* (c) and *Ceratium pentagonum* (d) increase their abundance during summer (photographs by John Dolan).



Winter



Summer