Drivers That Structure Biodiversity in the Plankton

Tatiana A. Rynearson and Susanne Menden-Deuer

Plankton Biodiversity

Plankton (Fig. 1) made Earth habitable by initially oxygenating the atmosphere some 2–3 billion years ago (Canfield 2005; Crowe et al. 2013). Currently, plankton generate as much oxygen and organic matter as all terrestrial plants combined (Field et al. 1998), fueling fisheries production, driving gas exchange between the atmosphere and oceans, and serving as key agents in global climate cycles (Falkowski et al. 2008). Plankton are the base of the marine food web and thus support virtually all protein derived from the ocean. These microbes represent sentinels of climate change and may harbor solutions to providing renewable energy sources.

A quantitative understanding of the abundance, distribution, and diversity of plankton is essential for estimating their biogeochemical impact, particularly under a changing environment. Yet none of these basic metrics are well known. Even the number of extant planktonic species is unknown, although current estimates yield staggering numbers. A recent global survey of eukaryotic plankton species estimated 150,000 extant species (de Vargas et al. 2015) and it has been estimated that the number of prokaryotic species reaches into the millions (Ward 2002). The "paradox of the plankton," coined by Hutchinson (1961), describes the conundrum that the observed high biodiversity of planktonic organisms is not reconcilable with the competitive exclusion principle (i.e. winner takes all) (Hardin 1960). The basic argument has been that the surface ocean is a well-mixed, homogeneous environment that only permits the strongest competitor for a specific resource to persist, ultimately leading to only few coexisting species and a low level of biodiversity in the plankton. Thus, the paradox lies in the fact that many planktonic species coexist where few should remain.

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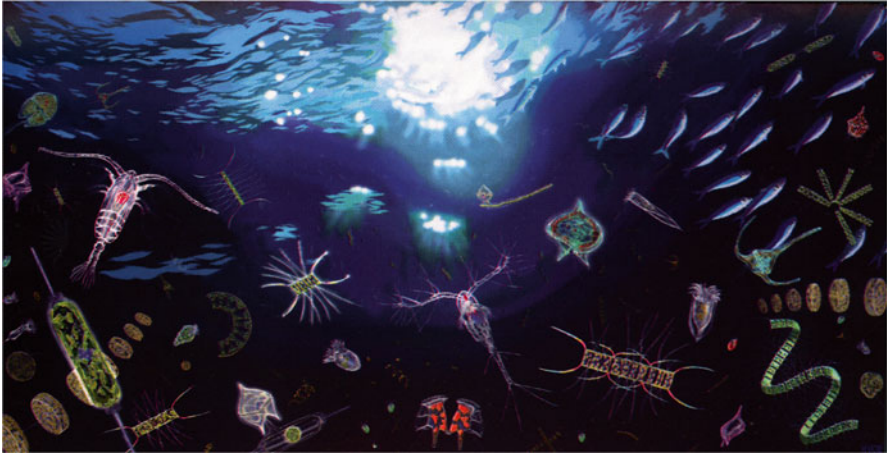e-mail: rynearson@uri.edu; smenden@uri.edu

Fig. 1 Plankton make life on Earth habitable. They are genetically, morphologically, physiologically, and behaviorally diverse and stunningly beautiful. Illustration by Dean Jacobson, by permission of the artist

Alternate Hypotheses That Explain the Paradox of the Plankton

Naturally, the paradox has found numerous explanations over time, including the role of resource competition (Tilman 1994), emergence of chaotic oscillations in species abundances (Huisman and Weissing 1999), chaotic fluid motion (Károlyi et al. 2000), spatial structure and localized competition (Levin 1992; Kerr et al. 2002), competition and predation as structuring factors (Record et al. 2013; Cropp and Norbury 2012) as well as large-scale spatial factors such as latitudinal and seasonal gradients (Barton et al. 2010). Gause (1934) made early observations of the competitive exclusion principle, suggesting that as long as environmental conditions were variable, then biodiversity could be enhanced, e.g. by offering a spatial refuge in his predator–prey experiments through the addition of a sediment base in his test tube cultures. Most likely, all these factors contribute to some degree to the overall high biodiversity in the plankton.

Most studies that have aimed to explain the paradox of the plankton rely on some external, environmental factor that provides a disturbance to the assumed homogeneous environment. Consequently, the disturbance (e.g. fluid mixing or selective predation) results in enhancement of biodiversity by providing an opportunity for hanger-on species to emerge. And indeed spatial heterogeneity and temporal disturbances are easy to invoke as key drivers of biodiversity. Unlike the assumption of homogeneity, the ocean is a complex and heterogeneous environment, characterized by steep gradients in physical, chemical, and biological properties over a continuum from microscopic to global scales. An organism's location relative to these gradients is critical for its survival. For example, because light decays exponentially with

depth, light-dependent photosynthetic organisms can be exposed to vastly different solar irradiances, depending on their depth in the water column, from high irradiance that can be harmful to insufficient amounts that prohibit survival. In fact, environmental heterogeneity is thought to be an important factor structuring planktonic communities (Levin 1976, 1992). However, are external drivers the sole factors that can be invoked to maintain planktonic biodiversity? Are there inherent characteristics of the organisms themselves that lead to the maintenance of multiple species in the water column?

One explanation of the paradox of the plankton that is based on inherent, species-specific characteristics rather than external, environmental factors draws on the resource competition theory developed by Tilman (1994). This theory was applied by Huisman and Weissing (1999) who showed that in model simulations, non-equilibrium conditions permitted coexistence of more species than the number of limiting resources in those conditions. The validity of these model predictions has subsequently been demonstrated through long-term observations of laboratory cultures of mixed plankton species that included a multi-trophic food web and was void of external disturbances (Benincà et al 2008). The work by Huisman and Weissing (1999) and Benincà et al (2008) clearly demonstrate that coexistence of multiple plankton species is possible in the absence of external disturbances. One limitation of both model and empirical evidence is that the number of species supported is still vastly smaller than the high levels of species diversity observed in the ocean (Ward 2002; de Vargas et al. 2015).

An Organismal Perspective on the Paradox of the Plankton: A Biodiversity Explosion from Within?

A crucial element that is missing from explanations of the paradox of the plankton is a focus on individual organisms. This element takes into account the fact that organisms compete and are selected upon as individuals, not as species. In addition to the immense biodiversity of plankton, the vast time and space scales of ocean ecology require an integrative view, and necessitate assessing the outcomes of ecological interactions—resource uptake, predation, and reproduction—at the population level. However, virtually all processes that affect the abundance, distribution, or production rates of a species occur at the individual level, including feeding, motility, resource uptake, reproduction, and mortality.

Shifting the level of investigation from that of a species to that of an individual brings opportunities and challenges. Putting the individual at the center shifts the time and space scales over which ecological interactions affect the survival of the species and refocuses them on the level of cellular interactions with the abiotic and biotic environment (Fig. 2). In this individual-centric perspective, cellular interactions that occur on time scales of seconds to hours and over spatial scales of microns to centimeters become the drivers of the ecosystem functions ultimately of interest, such as abundance, distribution, and production. Predicting biological function
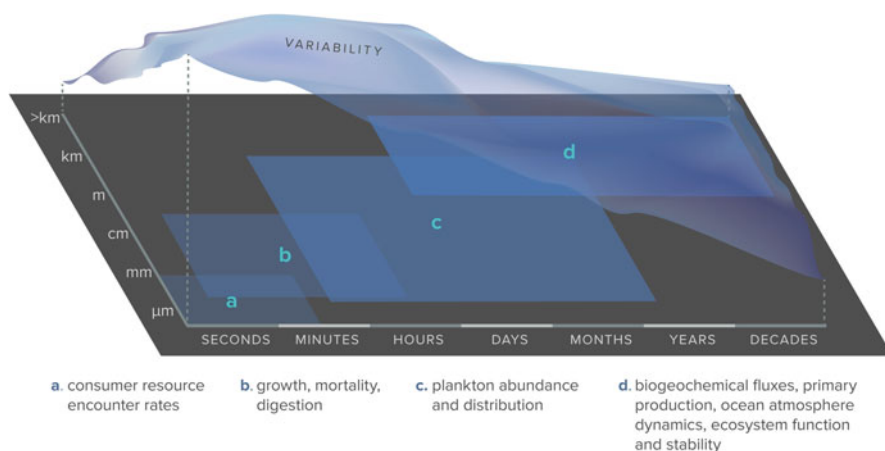
Fig. 2 Modified version of a Stommel diagram, showing the linkages of biological processes in the ocean over ecologically relevant time and space scales. Overlain is the degree of associated variability. It is noteworthy that large-scale processes emerge from underlying, often poorly characterized smaller-scale processes. Integrating small-scale processes to characterize biogeochemically important, large-scale events (e.g. the annual cycle of phytoplankton) constitutes a key challenge for oceanographers. Illustration by Josh Wood

within a system that changes on scales from micrometers and seconds to kilometers and years defies available approaches. While it is intellectually and analytically challenging to link a myriad of micro-scale processes to their large-scale ramifications, taking such a scale-integrative approach would also provide the opportunity to identify the underlying mechanisms driving processes (e.g. Kiørboe 2008) and ultimately provide a predictive understanding across spatio-temporal scales.

Linking Individual Level Behaviors with Plankton Ecology

To incorporate the importance of cell–cell interactions into both plankton ecology and investigations of the mechanisms underlying the high biodiversity of planktonic species, we recently developed a mathematical theory that suggests a unifying explanation and the causal mechanism for the staggering species diversity of plankton (Menden-Deuer and Rowlett 2014). This approach was motivated by laboratory and field observations of high, inherent, intra-specific variability in the genetics, physiology, and behaviors of plankton. To examine the importance of these observed characteristics, we created a new theoretical model and tested this model with high-resolution simulations across a robust parameter space. The results showed both theoretically, in the form of a mathematical theorem, and numerically, in the form of competition simulations across a robust parameter space, that (1) incorporation of individual variability supports arbitrarily high biodiversity among plankton, (2) elimination of behavioral or physiological heterogeneity produces results consistent with the competitive exclusion principle, and that (3) spatial structure can delay extinction of

species with invariant physiological or behavioral characteristics but extinction is inevitable. Using the modeling approach described in Menden-Deuer and Rowlett (2014) we explored the importance of intra-specific variation, including in competition experiments with superior and inferior competitors. In agreement with the findings in Menden-Deuer and Rowlett (2014), our results consistently show that intra-specific variability is sufficient to explain high species diversity in planktonic organisms, independent of specific external factors, providing a mechanistic underpinning for previously advanced explanations of the paradox of the plankton (Fig. 3).

Pervasive Intra-specific Variability in the Genetic Diversity, Physiological Capacity, and Behavioral Repertoire of Plankton

If our theoretical considerations are correct, intra-specific variability is highly adaptive for plankton, and indeed variation is commonly observed in a range of physiological, demographic, and morphological traits among and within phylogenetically distinct plankton species. Anywhere researchers have looked, they have found intra-specific variability, including in global, inter- and intra-specific patterns of temperature regulation (Thomas et al. 2012; Boyd et al 2013), responses to elevated pCO_2 concentrations (Schaum et al. 2013), tolerance of environmental conditions (Brand 1984), elemental composition (Moal et al. 1987), and growth rates (Rynearson and Armbrust 2004). A comprehensive study of intra-specific variability in one phytoplankton species showed distinguishing characteristics among strains in terms of cell size, maximum growth and photosynthesis rates, tolerance of low salinities, resource use, and toxicity (Fredrickson et al. 2011). Linked empirical and theoretical analyses have shown that intra-specific variability in motility can enhance species dispersal, with downstream ramification for organism distributions and ecological function (Menden-Deuer 2010). Molecular analyses have shown that physiological variability is associated with genetically distinct strains (Rynearson and Armbrust 2000, 2004). Blooms of the otherwise slow growing dinoflagellate species *Akashiwo sanguinea* have been tracked by satellites over vast spatial (100 s of kms along the US West Coast) and temporal (months to years) scales (Du et al. 2011; White et al. 2014). Laboratory examination of multiple *A. sanguinea* strains revealed that a high degree of intra-specific variability in the temperature tolerance, movement behaviors, and growth rates of *A. sanguinea* appears to be an important factor in broadening the species' niche, suggesting that intra-specific variability supports persistent blooms of this dinoflagellate species (Menden-Deuer and Montalbano 2015).

The ecological function of intra-specific variability had been determined only in very few cases, partly because intra-specific variability in the physiology and behavior of planktonic organisms has, for the most part, only recently been recognized and quantified. Thus we suggest that pervasive intra-specific genetic, behavioral, and physiological variability provides a fundamental organizing principle in the ecology of unicellular, self-replicating organisms.
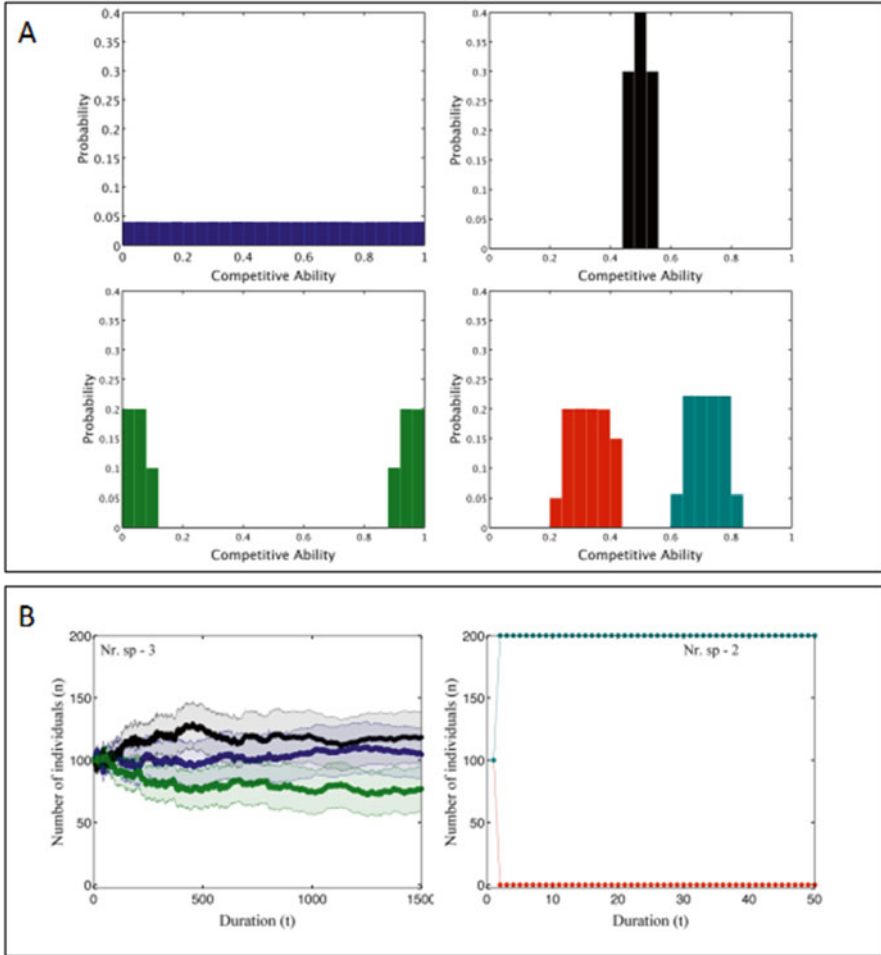
Fig. 3 Modeling approaches provide insights into the role of intra-specific variation in maintaining inter-specific diversity in the plankton. Panel (**a**) shows three different probability distributions of competitive ability, each with an average competitive ability of 0.5 and, bottom right, two probability distributions representing unequal competitive abilities (average competitive abilities of 0.3 (red) and 0.7 (green)). Panel (**b**) shows abundance over time of species representing the outcomes of a species competition model simulation (after Menden-Deuer and Rowlett 2014) including three competing species with on average identical but differently shaped probability distributions (*left figure*) and two competing species (*right figure*) with grossly different competitive abilities. Color of species abundance in panel (**b**) matches underlying probability distribution of competitive abilities from panel (**a**). Incorporation of intra-specific variability permits persistent species coexistence (panel (**b**), *left figure*), whereas competitive exclusion is accurately reproduced only when species are grossly different in their competitive ability (panel (**b**), *right figure*). Note rapid extinction indicated by difference in simulation durations in panel (**b**)

The mechanisms that maintain intra-specific variability are not well understood but may be related to the complexity of cellular morphology (Gray et al. 2010; Huisman et al. 2001). Moreover, specific traits and their variability are not easily eliminated within a microbial population (e.g. "the plankton cloud" sensu Smetacek 2012) due to the vast number of independent clones. Some species even retain possibly maladaptive traits, reflecting ancient, rather than current environmental conditions (Hutchins et al. 2013). Plasticity, or the ability for a single strain to vary its physiology, has been identified as a key characteristic for adapting to changing or novel conditions, can be observed in the phytoplankton (e.g. Schaum et al. 2013), and is associated with elevated success in range expansion of invasive species (Lee et al. 2003).

Evolution: Generating and Structuring Diversity over the Long Term

Thus far, we have discussed the structuring function of intra-specific variability in *maintaining* planktonic species diversity. Here, we focus on the processes that *generate* diversity and how those factors play into the structure and function of planktonic ecosystems. De novo mutation is the primary generator of diversity and has been observed in cultured phytoplankton (Collins and Bell 2004; Lakeman and Cattolico 2007; Collins 2011). There is growing evidence for the role of horizontal gene flow in transferring chunks of exogenous DNA into planktonic cells, even in eukaryotic plankton, where bacterial DNA has been found embedded in diatom genomes (Bowler et al. 2008).

Novel mutations and newly incorporated exogenous DNA are then acted on by natural selection. Depending on the type of selection pressure, evolution may maintain, reduce, or even eliminate that diversity. In fact, most mutation is deleterious (e.g. Sanjuan et al. 2004). Planktonic microbes may be able to avoid the negative impacts of deleterious mutation through enormous population and census sizes. For example, a spring bloom of the diatom *Ditylum brightwellii* likely contained some 2400 genetically different clonal lineages (Rynearson and Armbrust 2005). That same bloom had cell numbers of >10,000 cells L^{-1}, highlighting that the blooming population also had a very large census size. In addition to maintaining diversity (as discussed above), the large number of clonal lineages provides enormous diversity for selection to act upon.

Organism life cycles also influence diversity. For example, sexual reproduction events release new diversity into populations. Other components of plankton life cycles may be equally important although their import has, for the most part, not been quantified. For example, resting spores are essentially an archive of extant diversity for future selection to act upon (Härnström et al. 2011; Rynearson et al. 2013). Of course, asexual reproduction, the most common means of replication in the plankton, provides successful cells with the opportunity to generate many copies

of themselves (except see references above showing that asexual reproduction has less than perfect fidelity). Some phytoplankton, such as coccolithophorids alter their ploidy, changing from diploid to haploid with life stage (Green et al. 1996). By having a range of reproductive modes on hand, it is likely that planktonic species can influence how selection acts on their gene pool.

Opportunities for Progress

Intra-specific Variability and Its Ramifications for Plankton Ecology Need to Be Quantified

Just as an experiment lacking within-treatment replication is difficult to interpret in terms of among-treatment differences, attempts to characterize among-species differences are limited if no information is available regarding within-species variation. The observation of high, intra-specific variability in physiology, behavior, and genetics of planktonic species suggests that approaches that try to distinguish species, or even genera or classes based on single characteristics (e.g. dinoflagellates are slow growers) need to first quantify the degree of within-species variability and determine if variation among strains of one species is sufficiently small to permit distinction among species and higher taxonomic levels. Otherwise, multiple traits will be necessary to place species in multi-niche space.

One aspect of within-species variation that has only recently been identified is the existence of genetically distinct populations. There is robust evidence showing that the gene pools of dinoflagellates (Richlen et al. 2012), diatoms (Rynearson and Armbrust 2004; Rynearson et al. 2006; Casteleyn et al. 2010), and coccolithophores (Iglesias-Rodriguez et al. 2006; Gäbler-Schwarz et al. 2015) can be subdivided into genetically distinct populations, despite the enormous potential for both continuous dispersal of individuals and mixing between populations. There is some evidence that these populations are physiologically distinct, allowing populations to diverge and perhaps adapt to local conditions (Rynearson and Armbrust 2004). This is supported by data from the diatom *Skeletonema marinoi* showing that a genetically unique population persisted in one fjord for at least 100 years (Härnström et al. 2011). These observations suggest that the potential to adapt to changing conditions is present in marine phytoplankton, though the relative importance of adaptation by local populations versus replacement by immigrant types has yet to be established and is an important avenue of research.

At the same time, further development of mathematical theory and exploration using model simulations will provide opportunities to formulate testable hypotheses on the role of intra-specific variability in the maintenance of biodiversity. Our own simulations (Menden-Deuer and Rowlett 2014), for example, can be enhanced from current assumptions of general "competitive abilities" on which strains and species are compared by incorporating biological realism and complexity.

Plankton Ecology, Now and in the Future

An important application of enhanced understanding of intra-specific variability is the prediction of plankton responses to environmental conditions. Such predictive capacity is urgently needed in order to better understand how planktonic communities will respond to increases in temperature, pCO_2 and other variables and conditions related to climate change (e.g. Hoegh-Guldberg and Bruno 2010). Currently, our ability to conduct appropriate measurements of plankton ecology in the context of climate change is stifled by the fact that climate change is forcing environmental change that is gradual but sustained (e.g. rates of ocean acidification and temperature change). One approach toward understanding the response of plankton to these changes is to use elegant but time-consuming, long-term studies using experimental evolution (reviewed in Collins et al. 2014) which have shown that at least for some climate change variables, such as changing pCO_2, phytoplankton may evolve by adapting to decreasing pH.

Experimental evolution experiments are typically done with single clones, pointing to a second limitation plankton ecologists currently face: our inability to conduct incubation measurements with *mixed* plankton assemblages that have been acclimated to target conditions (e.g. temperature). Acclimation of mixed plankton communities to target treatments poses a particular challenge because the issues of examining long-term responses on a single species (most often a single clone) are multiplied by the varied growth requirements of multiple species and interactions among species. Identification of appropriate acclimation procedures is thus far an unsolved challenge. It is unclear how a mixed assemblage of diverse species can be acclimated to target conditions. Each species likely requires a different acclimation rate and type (e.g. gradient vs. step functions), which may vary depending on the process (e.g. enzymatic activity vs. growth). Acclimation is challenging and in itself may induce biases. For example, for mono-specific phytoplankton laboratory cultures, Brand et al. (1981) found that in order to achieve constancy of a single metric (growth rate), the required acclimation period was 1–3 weeks, depending on species. Thus, acclimation of diverse plankton communities to a target condition would require a prolonged incubation, while at the same time maintaining initial biotic and abiotic conditions, including species composition and nutrient concentrations to ensure applicability of results. Nevertheless, such challenges need to be solved, so that physiological and community responses to changing temperatures and other climate variables can be examined experimentally, leaving behind the current practice of keeping acclimation undefined or inadequate in most studies.

Ultimately, the inclusion of an organismal focus that incorporates fundamental individual-level variation should provide deep insights into the factors driving marine biodiversity, strengthen the theoretical underpinnings of ecology, and enhance our understanding of the population dynamics of microbes. Identification of structuring mechanisms is not only scientifically fascinating but also has significant implications for how we understand the function of planktonic ecosystems, and our ability to predict how these ecosystems may respond to changing climate conditions.

Tatiana A. Rynearson and Susanne Menden-Deuer

Since the New York Times featured our wedding announcement, there is little information that is publicly inaccessible about our relationship. Thankfully, the intricate details of our intersecting science interests were of minor interest to the NYT fact checker, so a few things are left to be told. We both had our first immersion in oceanography on a long cruise to the southern ocean polar frontal zone as part of the Southern Ocean JGOFS effort, led by mentor Professor V. Smetacek. During the cruise, a look through the microscope at the phytoplankton community composition gave a more accurate account of location and water mass than most other metrics measured on the cruise. This left us both with a lasting impression of the importance of an organismal perspective and a deep desire to understand the factors driving these distributions. As any good couple, we subsequently took vastly different approaches to pursue our scientific interests. One of us uses molecular tools to investigate the evolution, speciation, and biogeochemical function of phytoplankton and feeding ecology of zooplankton, while the other has focused on linking microscopic predator-prey behaviors with their population-level ramifications of plankton production, food web structure, and patchiness. With the help of supportive mentors, we have been fortunate to spend long stretches of our career in the same place, first at the Alfred Wegener Institute as technician and M.Sc. student, then as graduate students at the University of Washington, and finally as faculty members at the Graduate School of Oceanography, University of Rhode Island. Although we do not try to work together formally, sometimes it is unavoidable and we have coauthored a few papers. Nonetheless, our most productive and joyful collaboration matured in December 2013 when our daughter was born.

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