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Algae–bacteria interactions that balance the planktonic microbiome

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Summary

Phytoplankton communities within the photic zones of the oceans and lakes are characterised by highly complex assemblages of unicellular microalgae and associated bacteria. The interconnected evolutionary history of algae and bacteria allowed the formation of a wide spectrum of associations defined by orchestrated nutrient exchange, mutual support with growth factors, quorum sensing mediation, and episodic killing of the partners to obtain more resources. In this review, we discuss how these cross-kingdom interactions shape plankton communities that undergo annual, seasonal switching between alternative states with balanced multispecies consortia. We illustrate how these microscopic interactions can have consequences that scale up to influence global element cycling.

I. Introduction

Plankton comprises all free-floating organisms in the open water, including microalgae that are the basis of marine and freshwater food webs. Over the last decades, our understanding of planktonic interactions has undergone fundamental changes. Up to the 1990s, the idea prevailed that the observed species richness in water is a result of fluctuating biotic and abiotic resources available to plankton. Locally and temporally varying growth conditions including nutrients, temperature and light set the stage for the transient dominance of selected phytoplankton species (algal blooms) in an ever-changing complex array of microbial community members (Sommer, 1989). Early observations of single metabolites from microalgae that act as regulators of the growth of competitors or as defence metabolites paved the way for the concept of chemically mediated plankton interactions (Gross, 2003). This concept predicts that interactions by means of production, storage and release of chemical mediators can influence the growth and prevalence of phytoplankton as well as their associated microorganisms (Pohnert, 2004). Selected compound classes were studied in detail, revealing that single metabolites can exhibit a multitude of cascading effects. For example, oxylipins produced by marine diatoms are used as an activated chemical defence of these algae against grazers, for antibacterial effects and even for the regulation of cell death within diatom blooms (chemical structures of metabolites discussed in this article are listed in Table 1; Ianora *et al.*, 2011). Given these complex roles of chemical mediators it is not surprising that signalling in water is not only reciprocal, as observed in predator–prey or competition situations, but that chemical signals shape and balance entire

Table 1 Example of signalling molecules and exchanged nutrients in aquatic microbial communities.

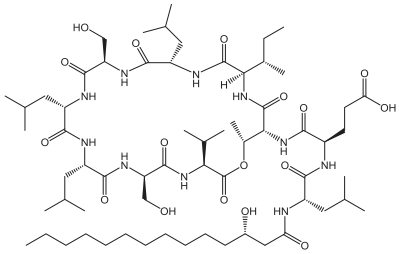
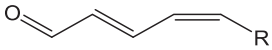
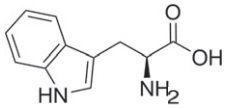
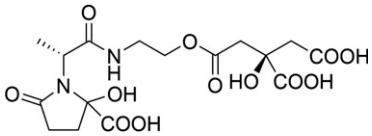
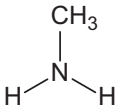
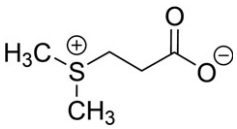
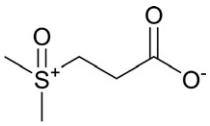
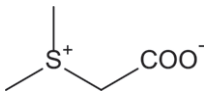
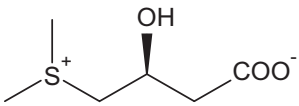
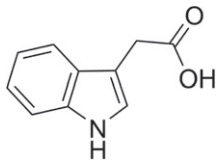
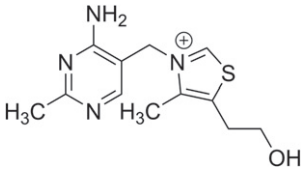
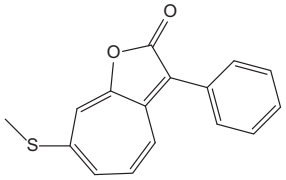
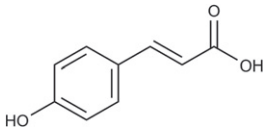
Molecules/Molecular class	Molecular structure	Function	References
Orfamide A		*Demobilisation and killing* This lipopeptide is produced by the bacterium *P. protegens* and induces deflagellation and disruption of Ca^{2+} homeostasis in the motile microalga *C. reinhardtii*	Aiyar *et al.* (2017)
Oxylipins		*Defence metabolites, antibiotics, and regulators* Oxylipins, here polyunsaturated aldehydes (R = alkyl, alkenyl) are metabolites derived from the oxidative transformation of polyunsaturated fatty acids. They have multiple functions in the environment	Ianora *et al.* (2011)
Amino acids	 **Tryptophan**	*Nutrients and signalling molecules* Tryptophan produced by microalgae serves as precursor for the biosynthesis of auxins in bacteria and promotes mutualism	Amin *et al.* (2015), Segev *et al.* (2016)
Vibrioferrin		*Binding and uptake of iron ions* The Fe complex with vibrioferrin can be photolysed, and releases Fe^{2+} that can be taken up by algae	Amin *et al.* (2009)
Methylamine	 **Methylamine**	*Nutrient and signalling molecule* Nitrogen-fixing bacteria and methylamine-degrading bacteria release ammonium, increasing nitrogen availability for microalgae	Amin *et al.* (2015), Suleiman *et al.* (2016)
DMSP		*Osmolyte, nutrient, regulator, signalling molecule* DMSP stimulates chemotaxis in certain marine bacteria, which can metabolise it as sulfur, carbon and energy source	Seymour *et al.* (2010), Amin *et al.* (2015), Johnson *et al.* (2016), Smriga *et al.* (2016)
DMSOP		*Osmolyte, nutrient (?)* DMSOP from algae is metabolised by bacteria to form oceanic dimethylsulfoxide	Thume *et al.* (2018)
S-containing osmolytes	 **Dimethylsulfonioacetate**  **Gonyol**	*Transfer reduced sulfur to bacteria* In addition to DMSP, an entire family of S-containing osmolytes contributes to S-shuttling between algae and bacteria	Gebser & Pohnert (2013), Durham *et al.* (2015)

Table 1 (Continued)

Molecules/Molecular class	Molecular structure	Function	References
Auxins	 **Indole-3-acetic acid (IAA)**	*Growth promotion molecules in plants and algae* IAA is produced by different bacteria and shows hormone effects: at low concentration promotes algal growth, at high concentration reduces growth and leads to cell death	Amin *et al.* (2015), Segev *et al.* (2016)
Vitamins	 **Thiamine**	*Nutrients and growth promoters* Certain microalgae cannot synthesise some vitamins *de novo*, so they use vitamins or their precursor produced by bacteria	Croft *et al.* (2005), Wienhausen *et al.* (2017)
Algicidal compounds	 **Roseobacticide B**	*Induce algal death or inhibit algal growth* *Phaeobacter* releases roseobacticides when *E. huxleyi* reaches senescence and promotes algal lysis. Other algicidal compounds inhibit algal growth	Seyedsayamdost *et al.* (2011)
Organic acids	 **p-coumaric acid**	*Signalling molecules* Some algae release organic acids, such as *p*-coumaric acid during senescence that can be recognised by bacteria, inducing pathogenic responses	Segev *et al.* (2016)

communities (Legrand *et al.*, 2003; Tillmann, 2004). This is manifested strikingly in associations of algae and bacteria that result in intricate cross-kingdom signalling networks. Tight species associations will lead to microbes with streamlined genomes that benefit from reduced reproduction costs, but face challenges due to the loss of metabolic functions that must be overcome by a symbiotic or parasitic lifestyle (Kazamia *et al.*, 2016).

A prerequisite for such association/exchange networks is the spatial assembly of interacting organisms. In 1972, Bell and Mitchell coined the term phycosphere (Box 1), defining a microscopic region rich in organic molecules that surrounded algal cells (Bell & Mitchell, 1972). This chemically enriched zone represents the key interface where tight interactions between algae and other organisms are controlled by exuded chemicals (Seymour *et al.*, 2017). These persistent zones allow for the formation of algae–bacteria associations and, in the context of the long and deeply interconnected evolutionary history of these two groups, intricate networks have evolved (Ramanan *et al.*, 2016). Here we illustrate the complex orchestration of microalgae–bacteria interactions that mediate resource (re)cycling, interkingdom signalling and community dynamics. We focus on the most recent progress in this area and

Box 1 Glossary of key terms

Algal bloom: The increase and dominance of one or more algal taxa within the plankton community.
Chemical mediators: Small molecules that play a role in regulating the composition and interaction of species in communities.
Heterotroph: An organism that must acquire organic carbon from an external source and sustain growth.
Marine food web: Description of the trophic linkages between all living organisms found in the marine environment.
Metabolome: The full complement of metabolites present in a cell, a tissue, an organism in a particular physiological and developmental state. Exometabolome refers to metabolites excreted by a cell or an organism.
Mutualism: Association between two organisms belonging to different species in which both benefit.
Phototroph: An organism capable of using the energy of light to carry out cellular metabolic processes.
Phycosphere: The region surrounding a (unicellular) alga in which gradients of exuded metabolites are maintained.
Quorum sensing: Density-dependent mechanism in which bacteria communicate and coordinate population behaviour and gene expression.

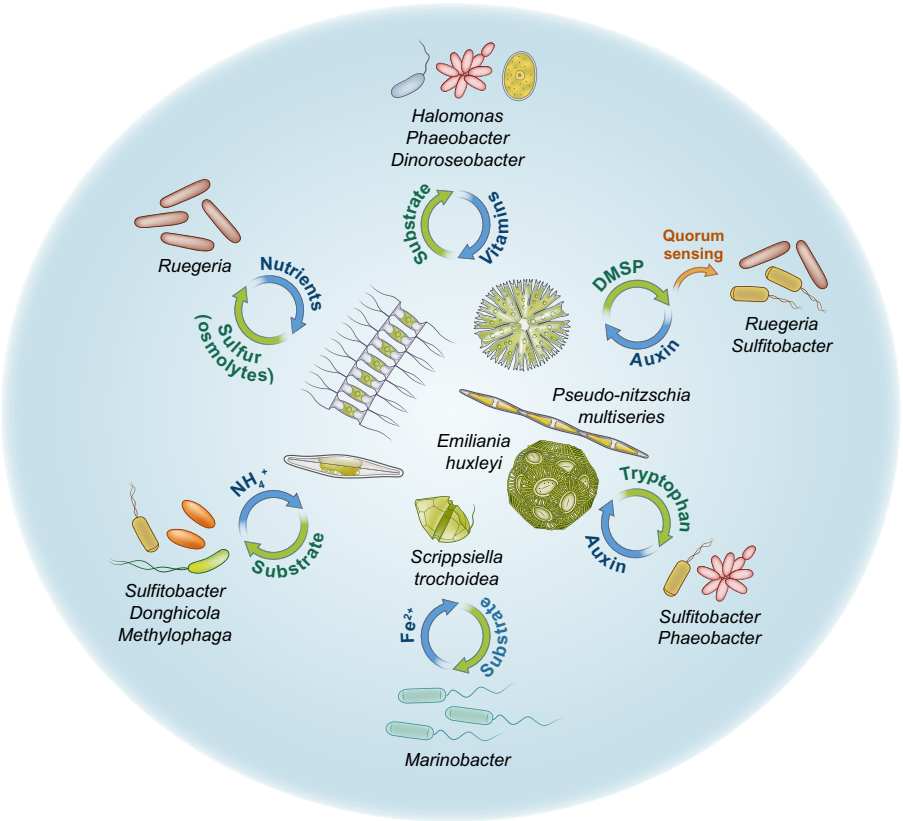


Fig. 1 Tight associations between microalgae and bacteria (mostly Proteobacteria, as highlighted in Amin *et al.*, 2012) have resulted in the evolution of a complex network of cross-kingdom interactions and a fine specialisation of different organisms. These interactions are mediated by diverse molecules and recognition mechanisms. Bacteria belonging to the *Roseobacter* clade (as *P. inhibens* and *Dinoroseobacter shibae*) and *Halomonas* species are able to exchange vitamins or vitamin precursors with algae that cannot synthesise them *de novo* (Croft *et al.*, 2005; Wienhausen *et al.*, 2017). *Phaeobacter inhibens* and *Sulfitobacter* can supply auxins, as well as ammonium, to diatoms and coccolithophores (*Pseudonitzschia multiseries*, *E. huxleyi*) in exchange for the amino acid tryptophan (Amin *et al.*, 2015; Segev *et al.*, 2016). *Ruegeria pomeroyi* is able to detect different sulfuric compounds released by microalgae and react both by realising auxins that sustain algal growth and quorum-sensing molecules that promotes bacterial proliferation (Johnson *et al.*, 2016; Durham *et al.*, 2017). The beneficial interaction between *Marinobacter* and the dinoflagellate *Scrippsiella trochoidea* is based on the exchange of Fe^{2+}, made bioavailable by the production of a light-labile siderophore (vibrioferrin) by the bacterium (Amin *et al.*, 2009). After complexation of Fe(III) with vibrioferrin, photolysis of the resultant complex leads to the release of Fe(II) that can be readily taken up by the algae. Chemical structures of nutrients and signalling compounds are summarised in Table 1.

refer the reader to seminal reviews that more broadly cover the field (Azam & Malfatti, 2007; Amin *et al.*, 2012; Seymour *et al.*, 2017).

II. Metabolic hotspots around the algal cells

Marine pelagic bacteria have evolved strategies to utilise resources released from living and decaying primary producing microalgae (Fig. 1). Prominent algicidal species are capable of controlling entire algal blooms by inducing algal lysis, and facilitating uptake of metabolites released during the process (reviewed in Meyer *et al.*, 2017). One example is the interaction between *Kordia algicida* and *Skeletonema costatum* (Paul & Pohnert, 2011): a protease produced by the bacterium causes the alga to lyse and the concomitant release of organic compounds sustains bacterial growth. Such interactions can go beyond random associations as it is strikingly shown by antagonistic bacteria that have evolved 'wolf pack' hunting strategies (Aiyar *et al.*, 2017). In this scenario, the bacteria (*Pseudomonas protegens*) accumulate around the initially motile freshwater algal cells of *Chlamydomonas reinhardtii* and immobilise the prey by deflagellation. This process, triggered by the lipopeptide orfamide A, leads also to the disruption of algal Ca^{2+} homeostasis (Aiyar *et al.*, 2017). The bacteria therefore shape their immediate environment and benefit from the resources released upon the following cell lysis. This dynamic tailoring of microenvironments, which is also observed in other examples mentioned below in this review, gives rise to temporal fluctuating chemical landscapes and local patchiness.

The phycosphere can be considered as a marketplace where cross-kingdom communications are mediated by the release and uptake of organic compounds (Wienhausen *et al.*, 2017). Gradients within this sphere guide chemoattraction of bacteria in microscale interactions (Sonnenschein *et al.*, 2012; Smriga *et al.*, 2016; Seymour & Raina, 2018). To date no spatially resolved chemical imaging of the phycosphere around a microalga is available, but Raman microscopy on macroalgal surfaces suggests that this zone extends several hundreds of micrometres into the water and a steep gradient with up to millimolar concentrations of chemical mediators directly above the algal surface can be observed (Grosser *et al.*, 2012). This chemical

landscape is a dynamic entity as revealed in time-lapse video recordings. Motile bacteria isolated from an enriched ocean community are attracted to phytoplankton cells and can form highly concentrated clusters around decaying cells that subsequently rapidly dissipate. The whole process lasts less than 10 min and movement pattern analysis suggests that the signal gradient extends to *c.* 2 mm around a lysed diatom (Smriga *et al.*, 2016).

More recently, the concept of chemical communication was extended beyond the mere diffusion limited exchange of metabolites. In an elegant study, Schatz *et al.* (2017) found that extracellular vesicles, produced by virus-infected microalgae *Emilinia huxleyi* enable cell–cell communication. Vesicles carry small RNAs that target sphingolipid metabolism and cell-cycle pathways. Their internalisation by *E. huxleyi* promotes a faster infection of the algal community. The mechanism of vesicle-mediated exchange might very well be relevant beyond this first example and further study might extend it to other microorganisms, as evidenced by bacteria that also produce extracellular vesicles to deliver different substances (DNA, antimicrobial peptides, quorum sensing molecules) (Schatz & Vardi, 2018). Despite the steep local chemical gradients and the temporally fluctuating composition of organic molecules in the oceans, the overall species composition in plankton is surprisingly balanced (see for example Teeling *et al.*, 2016 and other long-term surveys). Annually re-occurring patterns of prevalent groups indicate that a pronounced local shaping might be translated in cascading networks to interannual stable succession patterns in plankton communities. The elucidation of underlying organising principles will be a priority if ocean species dynamics are to be more fully understood.

III. Cross-kingdom exchange of resources

Element cycling is a long-standing topic in ocean sciences and exchange of carbon, sulfur, nitrogen and iron were recognised early as factors that determine species composition. With the idea of closely associated algae–bacteria interactions, our understanding of such element cycling expanded substantially. Especially with the advent of elaborate analytical techniques, the concept could be extended from simple 'element exchange' to the specific interaction by means of defined metabolites that is briefly highlighted in the following paragraph and in Table 1.

An untargeted exometabolome survey of two strains of the widely distributed *Roseobacter* clade revealed that bacteria supply vitamins, plant growth promotors, as well as amino acids that might serve as a nitrogen source to algae (Wienhausen *et al.*, 2017). In return, heterotrophic bacteria receive nutrients and can consume up to 82% of all algal-derived organic matter (Hornak *et al.*, 2017). The release of vitamins and vitamin precursors by bacteria is one of the most common and well studied means mediating algae–bacteria interactions (Croft *et al.*, 2005; Paerl *et al.*, 2017). Vitamin transfer supports algal growth and can be considered as bacterial farming of algae as suppliers of organic resources.

An intensively studied example of a metabolite that structures the marine environment is the omnipresent sulfur containing dimethylsulfoniopropionate (DMSP). This compound is produced by most phytoplankton species, but also certain bacteria contribute to the DMSP pool (Thume *et al.*, 2018). DMSP and its degradation products carry essential physiological functions as osmoregulators and antioxidants in the producing algae (Johnston *et al.*, 2016). Leaked DMSP is a chemoattractant, that guides bacteria and predators towards phytoplankton cells (Seymour *et al.*, 2010) and that stimulates the production of quorum-sensing molecules in bacteria (Johnson *et al.*, 2016). The metabolite therefore promotes mutualistic associations. Recently the concept of DMSP as an essential metabolite in sulfur cycling has been expanded by the description of the structurally related oxidised dimethylsulfoxonium propionate (DMSOP). This metabolite, that is formed by algae and bacteria can serve as precursor for oceanic dimethylsulfoxide (DMSO) and is expanding the oceanic sulfur cycle that is driven by the connected metabolism of algae and bacteria (Thume *et al.*, 2018). With the ongoing discovery of other widely distributed organic osmolytes containing reduced sulfur, including gonyol, dimethylsulfonioacetate and 2,3-dihydroxy-propane-1-sulfonate (DHPS), the field of algal–bacterial sulfur shuttling is now expanding (Gebser & Pohnert, 2013; Durham *et al.*, 2015). Initial studies investigating the coordinated regulation of these metabolites under osmotic stress already suggest a novel degree of complexity (Gebser & Pohnert, 2013).

By untangling interaction networks, it can be recognized that sulfur cycling is also connected to nitrogen cycling as evidenced by the interaction of *Phaeobacter inhibens* with a cosmopolitan microalga. *Phaeobacter inhibens* attaches to the cells of the coccolithophore *E. huxleyi* and exploits released DMSP as a source of carbon and sulfur (Segev *et al.*, 2016). After association, bacteria initially increase algal growth by releasing the growth promoting indole-3-acetic acid (IAA). IAA production is further increased by supply of the biosynthetic precursor tryptophan by *E. huxleyi*. During later stages of the interaction, a switch in bacterial strategy is observed, and the bacteria trigger algal cell death by activation of pathways of oxidative stress. Such a shift from mutualistic to pathogenic relationship seems to be more common as this was also observed in *Phaeobacter gallaeciensis–E. huxleyi* interactions (Seyedsayamdost *et al.*, 2011) with *Phaeobacter* initially producing auxins. When *E. huxleyi* reaches senescence and starts releasing *p*-coumaric acid the bacterium responds with the production of algicidal roseobacticides to kill the alga. Interestingly, IAA/tryptophan mediated interactions were also observed for the diatom *Pseudonitzschia multiseries* and associated *Sulfitobacter* (Amin *et al.*, 2015).

Ammonia is another key factor in microbial interactions in the aquatic environment. Most microalgae, including diatoms, cannot directly acquire nitrogen from N_2, but need inorganic forms such as nitrate or ammonium that are delivered by nitrogen-fixing bacteria and cyanobacteria (Foster *et al.*, 2011). In accordance, associations of algae with nitrogen-fixing bacteria or those that are able to transform other (in)organic nitrogen sources are observed. One of these compounds is methylamine, a typical degradation product of proteins that is abundant in surface waters. It is not accessible for the diatom *Phaeodactylum tricornutum* (Suleiman *et al.*, 2016) and to overcome this limitation, a mutualistic interaction with the methylamine-degrading α-proteobacterium *Donghicola* sp. is established. The

bacteria degrade methylamine to ammonia that is readily taken up by the algae. In return, the bacteria benefit from the diatom exudates and grow faster when compared with controls (Suleiman *et al.*, 2016).

These examples and other selected examples (Table 1; Fig. 1) demonstrate the complex mechanisms behind algae–bacteria interactions and their role in carbon and element cycling in the oceans. Transcriptomic data suggest, however, that many more, hitherto unrecognised, signalling pathways are present in algae–bacteria systems that will surely expand our understanding of orchestrated plankton dynamics in the future (Durham *et al.*, 2017; Krohn-Molt *et al.*, 2017).

IV. Interkingdom interactions shape population dynamics

The observed phytoplankton diversity and the specific metabolism of these diverse cells govern individual interactions. As a consequence, substrate utilisation and resistance to exuded antibiotics results in specialisation and most likely also diversification of the associated bacteria. Laboratory experiments demonstrated that bacterial colonisation strongly depends on the host and that bacterial communities change over time (Behringer *et al.*, 2018; Crenn *et al.*, 2018). Besides short-term associations, different diatoms establish long-term specific relationships with selected bacteria, creating a stable community unique for each species across strains. This situation suggests control of the associated microbiome based on chemical signalling (Behringer *et al.*, 2018). The involvement of chemical compounds in this process was further demonstrated by documenting community shifts in bacterioplankton after addition of organic matter derived from different phytoplankton species (Tada *et al.*, 2017). Laboratory findings were confirmed by monitoring species and functional diversity during spring phytoplankton blooms (Landa *et al.*, 2016). The observed succession of bacterial clades was indeed largely explained by specific substrate availability. Markedly, this succession pattern remained consistent despite considerable interannual variation between spring phytoplankton blooms (Teeling *et al.*, 2016). Similar concepts emerged from the study of naturally iron fertilised regions in the Southern Oceans, where the input of iron from island run-offs initiates phytoplankton blooms of variable compositions (Landa *et al.*, 2016). Heterotrophic bacteria rapidly respond to these blooms and process a substantial fraction of primary production with consequences for the entire pelagic ecosystem. Changes in algal primary production, therefore, create ecological niches for distinct bacterial populations. This control by substrate delivery leads to a succession of specialised bacteria that utilise different organic components and influence carbon recycling (Landa *et al.*, 2016; Teeling *et al.*, 2016). High resolution surveys have expanded the knowledge on this rapidly changing microbial landscape: by monitoring the fast expansion and decline of short-lived communities that display a high concentrations of cohesion (Martin-Platero *et al.*, 2018), these studies confirm the tight and highly adaptive interactions that connect microalgae and bacteria.

V. Conclusions

The phenomenon of fluctuating community compositions with defined annual species successions in plankton was recognised early and motivated a series of theoretical considerations to how the homeostasis of the system is maintained (Hutchinson, 1961). With the recognition of chemical factors mediating interactions, functional species associations, and recognition of the close link between phytoplankton and microbial communities we have made enormous progress in understanding marine species richness and plankton ecosystem functioning. However, we still lack fundamental knowledge on how the observed annually re-occurring balanced community patterns emerge, how they are stabilised, and how succession is triggered. Global surveys, such as the Tara Oceans expedition, that provide a comprehensive inventory of life in the oceans will facilitate further pattern recognition and correlations. However, the metabolic landscape must also be documented in time and space, providing an exciting challenge to link community dynamics directly with chemical mediators of interactions. The metabolic complexity of microbial systems, coupled with low concentrations of molecules in water, their hitherto poorly documented steep gradients within the phycosphere and open waters, and their rapid uptake pose interesting analytical problems that must be overcome to take the next step in understanding ocean functioning.

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