The ISME Journal (2020) 14:1065–1073
https://doi.org/10.1038/s41396-020-0603-9

REVIEW ARTICLE

Mixotrophy in marine picocyanobacteria: use of organic compounds by *Prochlorococcus* and *Synechococcus*

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Received: 2 October 2019 / Revised: 28 January 2020 / Accepted: 28 January 2020 / Published online: 7 February 2020

Abstract

Marine picocyanobacteria of the *Prochlorococcus* and *Synechococcus* genera have been longtime considered as autotrophic organisms. However, compelling evidence published over the last 15 years shows that these organisms can use different organic compounds containing key elements to survive in oligotrophic oceans, such as N (amino acids, amino sugars), S (dimethylsulfoniopropionate, DMSP), or P (ATP). Furthermore, marine picocyanobacteria can also take up glucose and use it as a source of carbon and energy, despite the fact that this compound is devoid of limiting elements and can also be synthesized by using standard metabolic pathways. This review will outline the main findings suggesting mixotrophy in the marine picocyanobacteria *Prochlorococcus* and *Synechococcus*, and its ecological relevance for these important primary producers.

Introduction

Cyanobacteria are the only known prokaryotes able to perform oxygenic photosynthesis, which allowed them to play a crucial role in the formation of atmospheric oxygen around 2.3 billion years ago [1]. The marine cyanobacteria *Prochlorococcus* [2] and *Synechococcus* [3] are the most abundant photosynthetic organisms on Earth and contribute about 25% of primary production in the oceans [4]. Therefore, they play a significant role in the global carbon cycle, having a substantial implication in the maintenance of the biosphere [5–9]. As a consequence, they are considered as model organisms in marine ecology, used in a large series of studies (over 2200 papers published since their discovery) and providing a huge amount of genomic and metagenomic datasets [10].

Mixotrophy in cyanobacteria

The term mixotrophy was first used by Pfeffer in 1897 referring plants with low-chlorophyll content that need to complement their nutritional needs by the uptake of organic substances [11]. It has traditionally been defined as alternative forms of carbon acquisition but can also comprise the acquisition of molecules containing nitrogen, phosphorus, trace elements (as Fe), vitamins, and high-energy compounds such as ATP [12]. This term soon expanded to refer to the combination of different nutritional pathways in a single organism. The word photoheterotroph refers to a prokaryotic organism that uses light to enhance uptake of organic molecules [13, 14].

In cyanobacteria, mixotrophy was early described by Rippka [15]. In 1967, it was reported that four blue-green algae (cyanobacteria) could assimilate acetate in a light dependent reaction [16]. Years later, it was shown that half of the strains tested that far were capable of heterotrophic growth [17].

Marine cyanobacteria are oxygenic prokaryotes that use CO_2 as a carbon source owing to the presence of a

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Supplementary information The online version of this article (https://doi.org/10.1038/s41396-020-0603-9) contains supplementary material, which is available to authorized users.

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chlorophyll-based light harvesting complex and thus, these organisms have been traditionally considered photoautotrophs [18]. However, the concept of marine cyanobacteria being purely photoautotrophic is currently seriously questioned. Early genomic data from *Prochlorococcus* and *Synechococcus* strains, such as the presence of genes encoding amino acid, oligopeptide, and sugar transporters [19–21], suggested that at least certain strains are not pure photoautotrophs. This has a great ecological importance since mixotrophic bacteria could dominate broader aquatic environments due to their capability to use additional resources compared to both photoautotrophic and organoheterotrophic bacteria [22].

Cells have a limited surface area, and mixotrophs must partition it to accommodate transport sites for both inorganic and organic resources. The mixotrophy strategy requires an investment in both photosynthetic and heterotrophic cellular machinery, and the profit must outweigh these costs to be energetically advantageous. These costs may lower the efficient use of resources by the mixotroph, and it can result in a reduced growth rate when compared with specialist organisms [23]. However, the fact that mixotrophs successfully coexist with specialists under different conditions indicates that the benefits of mixotrophy in nature can compensate the anticipated high costs of preserving two nutritional systems [24].

Hypothetically, mixotrophs require duplication of energy investment since they need not only photosynthetic but uptake cellular machinery. However, laboratory experiments suggest that they may be more ecologically successful when light energy is plentiful but nutrient resources are limited [25], as it is the case of oligotrophic oceanic gyres. The strong pressure of natural selection to eliminate redundant or not essential genes [26] makes improbable for planktonic prokaryotes to maintain genes non vital for cell survival. Therefore, the conservation of genes for the active uptake of some organic molecules by marine cyanobacteria must be energetically beneficial [27].

Amino acids

Amino acids are a source of carbon and nitrogen for marine picocyanobacteria. *Prochlorococcus* and *Synechococcus* are responsible for a large fraction of the oceanic amino acid incorporation [28–35]. Amino acid uptake by marine picoplankton was early attributed to photosynthetic microorganisms, since chlorophyll *a*-containing picoplankton from different oceanic areas along with cultures of some representative marine *Synechococcus* strains (WH7803, WH8101), showed light-stimulated incorporation of amino acids [31]. The use of on board flow cytometry cell sorters allowed the identification of marine cyanobacteria as the group of microorganisms incorporating amino acids in both oligotrophic and mesotrophic areas of the oceans [33]. These results were in good agreement with the *Prochlorococcus* genome sequences, which showed the presence of genes encoding for amino acids transporters [21]. There is an important level of diversity in the presence of genes encoding transporters of organic compounds in different picocyanobacterial strains (Fig. 1, Supplementary Table 1). For instance, amino acid ABC transporters membrane protein of two different families (PAAT family (TC 3.A.1.3.-) and HAAT family (TC 3.A.1.4.-) are present in the genomes of marine and freshwater cyanobacteria, but the HAAT family is only present in the LL IV clade (Fig. 1, Supplementary Table 1).

The assumed nature of *Prochlorococcus* and *Synechococcus* as strict phototrophic organisms led to firstly consider amino acids as a nitrogen source, instead of an evidence of mixotrophy in marine cyanobacteria. The ecological significance of amino acid uptake seems to be different for the predominant cyanobacterial genera in the ocean: while *Prochlorococcus* is responsible for 33% of the bacterial methionine turnover in oligotrophic regions (where this organism represents around 95% of all cyanobacteria), the methionine consumption in mesotrophic regions attributed to *Synechococcus* (which dominates those waters, accounting for 97% of all cyanobacteria), is of only 3% of bacterial methionine turnover [33]. Table 1 shows the uptake rates for different organic compounds, determined in *Prochlorococcus* and *Synechococcus* in the field or in laboratory experiments. Comparison with uptake rates of inorganic N compounds determined in the field [36] shows that the values compiled in Table 1 are in similar ranges of magnitude (amol/cell day). Interestingly, the uptake rates for specific compounds can be higher in *Synechococcus* (i.e., dimethylsulfoniopropionate (DMSP) [32]) or in *Prochlorococcus* (i.e., amino acids [33]).

Prochlorococcus and *Synechococcus* can be responsible for up to 10% of total amino acid uptake in some areas where they represent 10% of prokaryotes [30]. Hence, in oceanic regions with a high abundance of these picocyanobacteria, amino acid uptake is potentially large. Light-stimulated amino acid assimilation reported in those areas might be attributed to both genera of cyanobacteria, although light-stimulated amino acid uptake has been described for areas where their abundances are low [28, 30, 37–40]. The study of the mechanism of light enhancement of uptake systems in marine cyanobacteria will allow to clarify whether it is a specific effect or derived from growth.

DMSP

DMSP is a tertiary sulfonium compound that is a significant source of carbon and sulfur to the microbial community

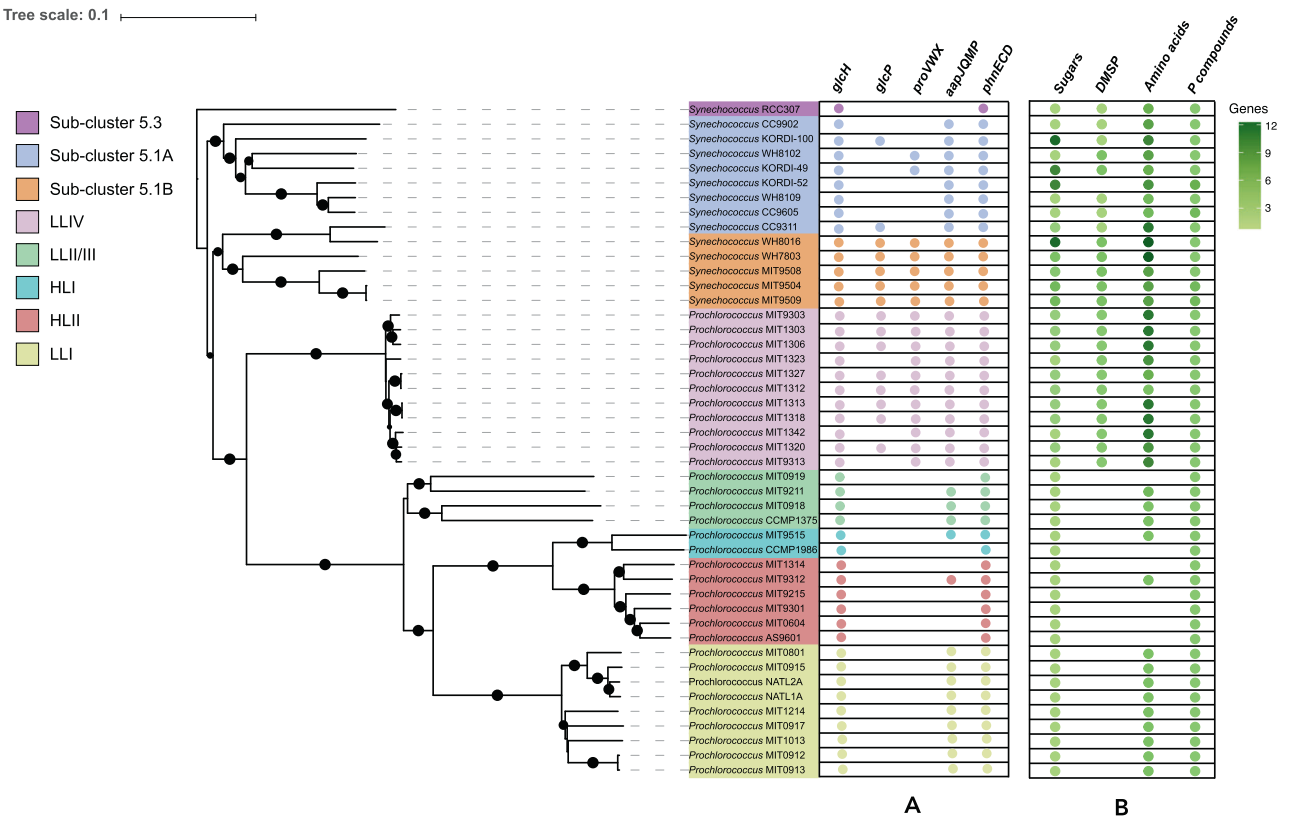

Fig. 1 Phylogenetic species tree representing the diverse capabilities of selected *Prochlorococcus* and *Synechococcus* strains to take up different organic compounds. Neighbor joining phylogenetic tree was based on the collection of *Prochlorococcus* and *Synechococcus* sequences of the genomes used by [10]. Bootstrap values (100 replicates) above 80% are indicated on the branches by size-scaled black dots at nodes. The sequences corresponding to *Synechococcus* sp. RCC307 acted as outgroup in this tree. A, table showing the presence/absence of genes encoding sugars (*glcH* and *glcP*), amino acids (*aapJQMP*), DMSP (*proVWX*), and phosphonate transporters (*phnECD*). Filled circles represent the presence of the indicated genes. B, table showing the number of genes involved in sugars (*glcH*, *glcP, CUT1, malK*), DMSP (*proVWX*), amino acids (*aapJQMP*), and P compounds uptake (*phnECD*). The green circles represent the number of genes for each category in the corresponding strain, according to the scale shown on the side. Presence of genes is described in Supplementary Table 1.

[41, 42], acting as a link between primary production and chemoheterotrophic bacteria [43]. DMSP is produced by phytoplanktonic organisms, likely with osmoregulatory and antioxidant functions [42, 44].

DMSP synthesized by phytoplankton taxa can be used by the cyanobacteria *Synechococcus* and *Prochlorococcus* [45, 46], which were found to be major consumers of this organic-sulfur compound. Both genera are responsible for about 20% of DMSP assimilation by prokaryotes, a similar proportion to that of other abundant bacterial groups in the sea [45, 46]. Light affects DMSP assimilation by marine *Synechococcus*, being the proportion of DMSP assimilated greater when incubated in the light than in the dark [45].

Although concentrations of sulfate are typically 10^7-fold greater than those of DMSP in the ocean, marine *Synechococcus* strains show a high uptake of DMSP [45], indicating that *Synechococcus* would prefer DMSP over sulfate because it is energetically more efficient the incorporation of reduced sulfur from DMSP directly than the assimilation of the more oxidized sulfur from sulfate [41]. This preference of reduced compounds over the corresponding oxidized ones had previously been observed for nitrogen assimilation in picocyanobacteria, since *Prochlorococcus* strains prefer ammonium to nitrate and nitrite, to the extent that some of them are not able to metabolize nitrate and lack the gene encoding nitrate reductase [47, 48]. Moreover, genes encoding for membrane transporter for DMSP and glycine betaine are found in the genome of four strains of *Prochlorococcus*, all of them members of the low-light clade of this cyanobacteria (Fig. 1, Supplementary Table 1 [21, 49]).

ATP and phosphonates

The importance of the metabolization of dissolved organic phosphorus has been increasingly highlighted for the last years [50–57]. Moreover, light-stimulated uptake of

Table 1 Specific uptake rates of organic compounds by *Prochlorococcus* and *Synechococcus* determined under selected experimental conditions, in the field and in the laboratory.

	Prochlorococcus		*Synechococcus*	
	Field	Laboratory	Field	Laboratory
Amino acid	1.442 ± 0.814 (amol/cell day)[a]	2.88 ± 0.24 (amol/cell day)[b]	1.258 ± 0.538 (amol/cell day)[a]	
DMSP	0.0596 (amol/cell day)[c]		0.21 (amol/cell day)[c]	
ATP	0.672 (amol/cell day)[d]	480 (amol/cell day)[e]	0.672 (amol/cell day)[d]	
Glucose	0.1152 (amol/cell day)[d] 0.0624 (amol/cell day)[f]	256.23 ± 29.45 (amol/cell day)[g] 16.15 ± 1.37 (pmol/min mg prot)[h]	0.144 (amol/cell day)[d]	1.21 ± 0.18 (pmol/min mg prot)[h]

[a]Determination provided by the authors [82].

[b]Calculated on the basis of the reported data [81].

[c]Determination provided by the authors [32].

[d]Calculated on the basis of the reported data. Determined in the Pacific Ocean [27].

[e]In P-limited cultures; calculated on the basis of the reported data [88].

[f]Determined in the Atlantic Ocean [64].

[g][63].

[h]Units could not be converted to amol/cell day, but are included nevertheless since they are the only reported glucose uptake rates in the laboratory determined for both *Prochlorococcus* and *Synechococcus* in the same study [14].

phosphorus-containing compounds might offer a competitive advantage of phototrophic microorganisms over chemotrophic ones, although phytoplankton are able to sustain a relatively high phosphorus transport in the dark, which must be beneficial since the uptake of this compounds into the cell is an energy-costly process [52].

Dissolved organic phosphorus compounds in oligotrophic oceanic areas include phosphate esters as the largest class of phosphorus-containing compounds, followed by phosphonates [58]. Both SAR11 alphaproteobacterial clade and the *Prochlorococcus* genera have shown light-stimulated uptake of ATP [38, 50, 52]. However, other bacterioplankton did not demonstrate this light-stimulated response [38].

Phosphonates are reduced organophosphorus compounds with a highly stable carbon–phosphorus bond, which can be found at relatively high concentrations in the oceans [58]. Phosphorus availability appears as a major selective pressure that has shaped the genome content and adaptations shown by abundant bacterial populations [59]. Therefore, the presence of pathways for the transport and hydrolysis of bioavailable organic phosphorus sources in seawater (phosphonates and phosphate esters) are in agreement with their decisive role in bacteria to cope with inorganic phosphorus scarcity in the ocean [55, 56, 60].

Sugars

Although initial studies on *Prochlorococcus* PCC 9511 strain showed no indication for sugar employment as energy source [61], *psbA* expression decreased upon glucose addition in cultures subjected to darkness [62], suggesting that *Prochlorococcus* could use glucose as an alternative energy source under light limitation. Later, glucose uptake has been demonstrated in *Prochlorococcus* and *Synechococcus* strains using both laboratory cultures and natural populations [14, 54, 63, 64]. Furthermore, higher abundance of *Prochlorococcus* upon addition of glucose and mannitol was observed in oligotrophic areas of South Pacific [65].

Experiments performed in laboratory cultures revealed a substantial diversity in the rate of glucose uptake within *Prochlorococcus* strains [63]. Glucose transport in *Prochlorococcus* and *Synechococcus* displays multiphasic kinetic with high affinity *Ks* matching the glucose concentration estimated for the oligotrophic Atlantic Ocean, in the nanomolar range (Fig. 2) [14, 64]. However, comparison of uptake efficiency (calculated by dividing the uptake rate by the K_s constant [64]) demonstrated *Prochlorococcus* to be 7 times more efficient than *Synechococcus* despite of the K_s value to be 6 times lower than that described for *Prochlorococcus* [14]. The glucose uptake rates observed in the field are very low (Table 1), *Prochlorococcus* contributing to ca. 5% of the total microbial glucose uptake [54, 64] and there is the caveat that uptake determinations are close to detection limits. This notwithstanding, glucose uptake has been observed in the laboratory [14, 63] and in the field at different locations [54, 64], by different teams. More precise uptake determination methods will allow to assess in the future the actual contribution of glucose to C metabolism in picocyanobacterial populations in the ocean.

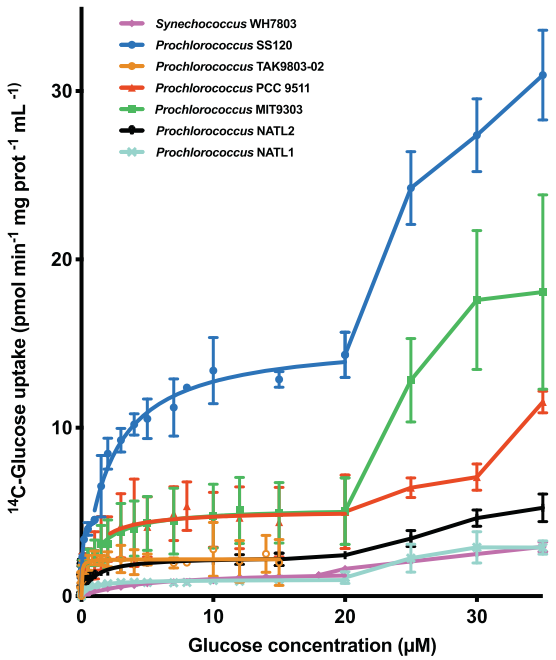

Fig. 2 Glucose uptake kinetics in *Prochlorococcus* sp. strains SS120, TAK9803-2, PCC 9511, MIT9303, NATL2, and NATL1 and *Synechococcus* sp. strain WH7803. The chart shows ^{14}C-glucose concentration versus its uptake. Data are replotted from [64] and [14].

Genome analysis of *Prochlorococcus* strains nominated a gene annotated as *melB* (melibiose transporter, later nominated *glcH*), as a putative candidate for glucose transporter [63]. The ectopic expression of this gene demonstrated that the protein encoded by *glcH* confers the capacity of glucose uptake to *Synechococcus* sp. strain PCC 7942, a strain naturally unable to transport glucose. Furthermore, transport in this mutant replicates the same multiphasic kinetics shown by *Prochlorococcus* cells. Sugar competition experiments, performed in this mutant, where other sugar was added together with glucose, allowed to establish that GlcH is highly specific for glucose [64]. Characterization by inhibitors suggests glucose transport to be dependent on ATP production and therefore to be active [14].

Several studies have dealt with the effect of glucose availability on transport rate, gene expression, and protein abundances. The gene encoding the high affinity transporter, *glcH*, is expressed in the absence of added glucose and increases, upon glucose addition, in *Prochlorococcus* and *Synechococcus* [63, 66]. The diversity of the response of *glcH* expression to the availability of glucose or to darkness is remarkable, reflecting the different habitats where the strains proliferate: higher response is shown for low-light adapted strains as SS120 [66].

Two pathways have been designated in cyanobacteria for glucose assimilation [14, 63, 67]: the pentose phosphate and the Entner–Doudoroff pathways. Relative quantification of gene expression suggested pentose phosphate to be involved in glucose metabolization in *Prochlorococcus*, since the expression of the genes *zwf* (encoding for glucose 6P dehydrogenase), *gnd* (encoding for glucose 6P gluconate dehydrogenase), and *tal* (encoding for transaldolase) increased upon glucose addition [14, 63]. Quantitative proteomics also revealed increases in protein abundance of enzymes related to pentose phosphate and Entner–Doudoroff pathways [14] although these changes were not dramatic. These studies do not allow to clarify which is the primary pathway allowing metabolization of glucose in *Prochlorococcus*.

It was early demonstrated that glucose uptake is essentially detained in cyanobacteria, both in the dark and by the addition of DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea), an inhibitor of photosystem II [68]. Preincubation in the dark for 24 h promotes a decrease in glucose uptake of ca. 40% in *Prochlorococcus* sp. strain SS120 [63]. Furthermore, addition of DCMU and DBMIB (2,5-dibromo-6-isopropyl-3-methyl-1,4-benzoquinone, another inhibitor of the photosynthetic electron transport) also decreases glucose uptake using the same strain [14]. In addition, DCMU reduces glucose uptake in natural picocyanobacterial populations [54]. All these results suggest that light availability is an important factor affecting glucose utilization. Darkness promotes a decrease in the expression of *glcH* with a high diversity of responses depending on the *Prochlorococcus* and *Synechococcus* strain [66]. These results may suggest a higher regulatory capacity of glucose uptake in low-light adapted cyanobacterial strains.

Genomic and metagenomic analysis of mixotrophic metabolism in marine picocyanobacteria

First metagenomic analysis in the photic zone, which found mixotrophy lifestyle, showed the presence of genes associated with the uptake of amino acids and amino sugars in microbial communities including *Prochlorococcus* [69]. In contrast, deep water samples (from depths of 200 m and below) were not enriched in this kind of genes. Later, genes involved in amino acids, sugars, and peptides uptake and also in the degradation pathways of these compounds were identified in 67 strains of the genera *Prochlorococcus* and *Synechococcus* [70]. The authors examined the Tara Oceans marine metagenomic survey [71, 72], finding a universal mixotrophy capacity for marine picocyanobacteria (Fig. 1), which was more dominant in deeper waters [70]. This is consistent with the higher concentrations of nutrients in these waters [73].

All *Prochlorococcus* clades possess the high affinity glucose transporter *glcH* gene, suggesting that this gene is important for *Prochlorococcus* and it has been subjected to selective evolution [14]. This importance is reinforced by the widespread distribution of *glcH* in the ocean [70] and the large

diversity in glucose uptake kinetics within *Prochlorococcus* strains [14]. This transporter was consistently found in all picocyanobacterial reference genomes in a gene cluster with a glycogen debranching enzyme (E.C. 3.2.1.-), which suggests both genes function would be providing glucose to the cell.

All *Prochlorococcus* clades have a single glucose transporter gene (*glcH*), except clade LL IV where the presence of *glcP*, a specific glucose permease found in free-living and symbiotic cyanobacteria [74], has also been reported and normally located proximate to the sugar porin *oprB* [70]. By contrast, some *Synechococcus* also possess more than one gene coding for sugar transporters [70].

Pangenomic analysis identified multiple sugar metabolism genes in *Prochlorococcus* strains that were absent in previously published metagenomic analyses [75]. Methodological differences could explain the low detection of some genes by metagenomic analysis since pangenomic gene clusters are formed based on homology between amino acid sequences, while metagenomic analyses are done at the DNA sequence level [75]. Using pangenomic analysis, these authors revealed a small set of core genes linked to sugar metabolism that mostly occurred in hypervariable genomic island of the *Prochlorococcus* populations suggesting potential benefits to *Prochlorococcus* populations [75].

Potential role for vesicles in mixotrophy

Many bacterial species release extracellular vesicles, which have roles in various processes, including quorum sensing, virulence, and horizontal gene transfer [76]. Bacterial vesicles have been observed in marine ecosystems, produced by *Prochlorococcus* and *Synechococcus* [77]. In coastal and open water seawater samples, these vesicles range from 70 to 100 nm in size and contain lipids, proteins, and nucleic acids from different bacteria taxes, not only *Prochlorococcus* or *Synechococcus* [77].

Based on the number of vesicles found in *Prochlorococcus* cultures, it is estimated that wild *Prochlorococcus* cells release 10^{27}–10^{28} vesicles [77] into the oceans every day, a very significant amount of organic compounds, suggesting important implications for carbon cycling in marine systems [77, 78].

For marine cyanobacteria living in oligotrophic areas, the secretion of vesicles may seem a waste of resources. However, potential beneficial functions have been suggested for these vesicles, such as promoting the growth of "helper" bacteria, reducing viral attacks or even as gene transfer vehicles [77–79]. The hypothesis that *Prochlorococcus* and *Synechococcus* vesicles can be used for nutrient transfer suggests an important impact on the marine carbon flux.

Furthermore, the presence of proteins and nucleic acids within vesicles would imply a potential role as N and P sources as well. The fact that other bacteria appear to depend on theses vesicles content (for lost metabolic functions or nutrients as organic carbon) to persist in their environments is consistent with the coevolutionary dynamics expected under the Black Queen hypothesis [80].

Ecological relevance

Utilization of organic compounds by marine picocyanobacteria forces to reconsider their role in the oceanic metabolic fluxes. But the question is: where does the value of these molecules come from? Why does the assimilation of organic molecules represent a worthy investment? Possible answers to this question will be explored in this section.

Provision of limiting elements in oligotrophic environments

The first studies showing organic molecules uptake by marine picocyanobacteria were focused on amino acids [28, 30, 33–35, 39, 81, 82] and later, DMSP [32, 45, 46] and ATP [52, 54] uptake was also demonstrated. These molecules contained chemical elements, as N or P, which are found at low concentrations in the oligotrophic environments where *Prochlorococcus* and some *Synechococcus* clades are most abundant. Therefore, the uptake of those elements containing molecules was initially considered as a way of obtaining essential resources. Furthermore, early studies proposed that a high efficiency in amino acids uptake might be one of the reasons underlying the dominance of *Prochlorococcus* in the oceans [33].

Energy savings

The cost of glucose uptake by marine picocyanobacteria has not been calculated on the basis of experimental data, but it is carried out by a transporter similar to the *melB*-encoded melibiose-sodium symporter [83]. If we assume a similar molecular mechanism for both homologous transporters, it would mean that the uptake of three glucose molecules consumes 1 ATP when taken up from the environment; by contrast, biosynthesis of one glucose molecule consumes the equivalent of 18 ATP [64]. This simple comparison shows that when organic compounds are available in the environment, it makes ecological sense to take them up, regardless of whether they contain limiting elements or not.

Removal of resources that might be used by competitors

A third hypothesis to be considered is that picocyanobacteria take up organic compounds as a way to deplete

resources, which might be used by coexisting competitors (be it mixotrophic or heterotrophic) [84]. This strategy would be especially useful in oligotrophic habitats, allowing picocyanobacteria to become dominant players in these areas. If this hypothesis holds true, then the advantage offered by mixotrophy to marine picocyanobacteria would come from displacing potential competitors.

Coevolved mutualism

This hypothesis proposes that *Prochlorococcus* metabolic rate (and also its organic carbon excretion rate) have increased over the course of the evolution [9]. As a consequence, there is a depletion of nutrients in the ocean surface, resulting in an increase in total biomass at the ecosystem level, and promoting the coevolution of cells in that ecosystem. Furthermore, this model proposes that the metabolic codependencies of *Prochlorococcus* and SAR11 are similar to those of chloroplasts and mitochondria in vegetal cells, by interchanging glycolate or pyruvate (from *Prochlorococcus* to SAR11) and malate (from SAR11 to *Prochlorococcus*). Addition of glucose and pyruvate (but not of glucose alone) has also been shown to extend the survival of *Prochlorococcus* under darkness [85], highlighting the role of external organic compounds on the physiology of marine picocyanobacteria.

Coevolved mutualism is in sharp contrast with previous ideas regarding the adaptive strategies of *Prochlorococcus* to oligotrophic environments, including small cell size, a small, streamlined genome, and a high surface/volume ratio. This involved that nutrients were scavenged by *Prochlorococcus*, but rarely released to the environment. The discovery of vesicles produced by *Prochlorococcus* and *Synechococcus* was shocking in this regard [77, 86], since it contradicted those previous ideas: the vesicles released contained a wide range of organic compounds. Release of organic carbon might be related to making iron bioavailable, and this would indirectly push the oceans from an anoxic, iron-free rich state to an oxygenated state with organic carbon molecules binding iron [5].

Conclusion

The discovery of organic compounds utilization by *Prochlorococcus* and *Synechococcus* has profound implications for the understanding of marine microbial ecology. The substrate specificity, kinetics, and regulation of most transporters annotated in marine picocyanobacterial genomes remain an open question, requiring molecular analysis for confirmation; in this regard, the development of a genetic system in *Prochlorococcus* [87] will be an invaluable tool. The pathways for assimilation of the different compounds, and their relative contribution to the nutrition of the cells, should also be analyzed in detail to understand the impact of mixotrophy on the growth of marine cyanobacterial populations. Further quantitative studies in the field determining the uptake rates for different compounds at different oceanic regions are needed to assess the consequences of marine cyanobacterial mixotrophy for global biogeochemical cycles. This, in turn, will help us to understand how global warming might affect the nutritional balance of these populations in the future.

Acknowledgements Work of the authors on mixotrophy in marine picocyanobacteria has been funded by Gobierno de España (grants BFU2009/08008/BMC, BFU2013-44767-P, and BFU2016-76227-P, Ministerio de Ciencia, Innovación y Universidades, cofunded by European Regional Development Fund), Junta de Andalucía (Excellence projects P07-CVI-3055 and P12-BIO-2141, Consejería de Conocimiento, Investigación y Universidad, cofunded by European Regional Development Fund), and Universidad de Córdoba (Programa Propio de Investigación). We are indebted to Dr. Pedro Candau (Instituto de Bioquímica Vegetal y Fotosíntesis, Sevilla, Spain), Dr. Ignacio Luque (Instituto de Bioquímica Vegetal y Fotosíntesis, Sevilla, Spain) and Prof. Mikhail Zubkov (Scottish Association for Marine Science, United Kingdom) and their teams, since their collaboration was essential in our studies on glucose uptake in marine picocyanobacteria. We thank Prof. Josep M. Gasol and his team (Institut de Ciències del Mar-CMIMA, CSIC, Barcelona, Spain) and Prof. Mikhail Zubkov (Scottish Association for Marine Science, United Kingdom) for providing DMSP and amino acid uptake rates by *Prochlorococcus* and *Synechococcus* in the field, respectively.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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