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Phototrophic bacteria as potential probiotics for corals

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Coral-associated microorganisms provide crucial nutritional, protective, and developmental benefits, yet many functional traits remain unexplored. Phototrophic bacteria may enhance coral nutrition and reduce oxidative stress during bleaching via photosynthesis and antioxidant production. Despite this potential, their role in the holobiont's energy budget and heat stress resilience is understudied. This review explores the functional traits and potential of phototrophic bacteria to enhance coral health and resilience under environmental stress.

The key role of the coral microbiome

Coral bleaching represents a critical threat to coral reefs worldwide, largely driven by the increasing frequency and extended duration of marine heatwaves[1,2]. This bleaching process occurs due to the breakdown of the symbiotic relationship between the cnidarian host and its photosynthetic algae, *Symbiodiniaceae*[3,4.] This symbiosis is vital because it provides the coral hosts with photosynthetically fixed carbon, which fulfills up to 90% of their nutritional requirements, in exchange for inorganic waste, which is essential for algal photosynthesis[5].

During a bleaching event, likely triggered by competition for nutrients[3,6], a post-heat stress disorder takes place[7], and the holobiont needs to deal with a cascade of chain or parallel impacts. One of them is the excessive production of reactive oxygen species (ROS) which overwhelms the antioxidant system and is correlated with the expulsion of the *Symbiodinianceae*[4,8,9]. When corals experience severe bleaching, their chances of survival may depend on several key factors. These factors are complementary and, when combined, can enhance coral survival, including:: (i) the host's ability to acquire food from heterotrophic sources or use food reserves (e.g., lipids) present in the host tissue, if these reserves are sufficient to sustain the host's metabolic needs during the stress period[10], (ii) the successful recolonization of the algal symbionts in the host tissue once the environmental conditions return to optimal levels, in the cases where corals are still alive when that happens, and (iii) the ability to retain a microbiome that can mitigate some of the damages and offer additional nutritional support, which will be addressed in detail below.

In addition to their symbiotic relationship with algae, corals also form associations with diverse microbial communities that play crucial roles in coral biology (reviewed in refs. 11,12). The coral microbiome composition seems to vary according to the coral host[13,14], compartment (i.e., mucus, skeleton, phycosphere, and tissue)[15–17], and geographic location[18,19], and provide critical functions for the holobiont's biology, such as providing and recycling essential nutrients, mitigating toxic compounds, controlling pathogens, and releasing other important metabolites to maintain the holobiont homeostasis[20–22]. The diversity and composition of coral microbiomes are complex[23,24], as microbiomes might be flexible and quickly respond to environmental changes[25,26], or—comparatively—stable, while still favoring taxa that support the holobiont in withstanding stressors[27]. Consequently, microbiomes associated with corals and other marine hosts/environments have been heavily impacted by anthropogenic activities, which is correlated with biodiversity loss[28,29], turning marine microbiome stewardship (i.e., the use of different microbial therapies that can promote the beneficial restoration and rehabilitation of damaged microbiomes[12,28]) into an urgent topic[29,30].

As an important background for the microbiome stewardship approach[28], the coral probiotic hypothesis highlighted the ecological importance and functional roles of the coral microbiome several decades ago[31]. Early data also suggested the potential to manipulate the coral microbiome at different life stages[32,33]. This potential was later proposed to be harnessed and actively applied to enhance coral resilience to different impacts[22]. The definition of specific functional beneficial targets and a framework[22] as a microbial therapy to promote microbiome stewardship (i.e., the targeted management of the microbiome)[28] was followed by the proof of concept that the active rehabilitation of the microbiome of adult corals is possible and shown to mitigate the effects of pathogen infection and thermal bleaching[34]. A surge of other reports further expanded our knowledge of the potential power of coral probiotics to mitigate an array of impacts, such as oil spills, disease, and thermal stress [e.g.,[35–42]], and even prevent coral mortality[7], while demonstrating the feasibility for field applications[43].

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However, our understanding of microbial dominance and the potential of the microbiome to be beneficial for the coral host is currently limited to a few taxa, such as the specific probiotic bacteria studied in the papers mentioned above (e.g., *Pseudoaltermononas* spp., *Halomonas* spp., *Cobetia* spp., *Bacillus* sp.), some of them found within the coral tissue[42], or the prevalence of dominant and coral-tissue associated[44,45] such as *Endozoicomonas* spp[46]. Urgent knowledge in the field is required to reveal other potential approaches, tools and microbial candidates that can be applied for coral rehabilitation[28]. To fill these gaps, a more diverse array of microorganisms should be explored, including members of the coral dark matter (i.e., yet to be cultured, see refs. 47–49). Additionally, different approaches have been suggested to accelerate and improve the selection of additional putative beneficial functions and taxa[50–53], and enhance the selection of beneficial microbes and implement even more efficient or alternative microbial therapies[51,54,55], including the selection of new probiotic candidates and beneficial functions[28], such as the use of phototrophic bacteria.

Phototrophic bacteria are organisms that can use light as their energy source, and are integral components of the coral-associated microbiome in various habitats and bioregions (e.g. refs. 18,56–58,59). These bacteria contain chlorophyll (B-Chl) and abundant carotenoids (Fig. 1), which allow them to harness light through photosynthesis[60]. While their photosynthetic capabilities could theoretically play a similar role of the algal symbionts in supplementing the host's diet during nutrient-poor periods like bleaching[57,61–63], this hypothesis remains underexplored. Additionally, phototrophic bacteria produce carotenoids, a diverse class of pigments that play crucial roles as antioxidants and photoprotective agents. These pigments can mitigate oxidative stress by scavenging an array of free radicals, which could protect coral cells from damage[22,64,65,66]. Carotenoids may also specifically shield the host from reactive oxygen species (ROS) during heat stress, further enhancing coral resilience[20,21,66]. Although these functional traits have not yet been fully explored, they place phototrophic bacteria as promising candidates, alongside other taxa, for potentially enhancing coral thermal resilience under climate change. Despite the incomplete understanding of their functional roles within the coral holobiont, this article aims to explore the current knowledge on phototrophic bacteria and their potential contributions to reduce stress by providing additional energy supplies, acting as a barrier against potential light damage, and regulating ROS within the coral holobiont. We also present a framework in which phototrophic bacteria can be considered as putative probiotics, to be further explored in conservation initiatives to improve coral stress resilience.

Who are these "phototrophic bacteria"?

Phototrophic bacteria can be autotrophs or heterotrophs, and the two main mechanisms for autotrophy are retinalophototrophy and chlorophototrophy[67]. Retinalophototrophs use retinal-binding proteins called rhodopsins to convert light energy into chemical energy by generating ion gradients, such as protons, sodium, or chloride (e.g., *Halobacteria* spp. and *Pelagibacter ubique*). Chlorophototrophs use chlorophylls (Chls) and/or bacteriochlorophylls (B-Chls) to harness light energy and facilitate light-driven redox reactions, referred to as photochemistry, to fix carbon dioxide[68]. Notably, while all photosynthetic organisms are chlorophototrophs, some also use organic compounds and are thus classified as photoorganoheterotrophs, while some chlorophototrophs, primarily those that are anoxygenic, also possess the ability to produce retinal-binding proteins. Therefore, not all chlorophototrophs are photosynthetic and certain chlorophototrophs may also function as retinalophototrophs[67].

Phototrophs include cyanobacteria, sulfur/nonsulfur purple and green bacteria, and heliobacteria. Based on the structure of their photosynthetic machinery and capacity to release oxygen during photosynthesis, they are further divided into other two groups: anoxygenic and oxygenic groups.

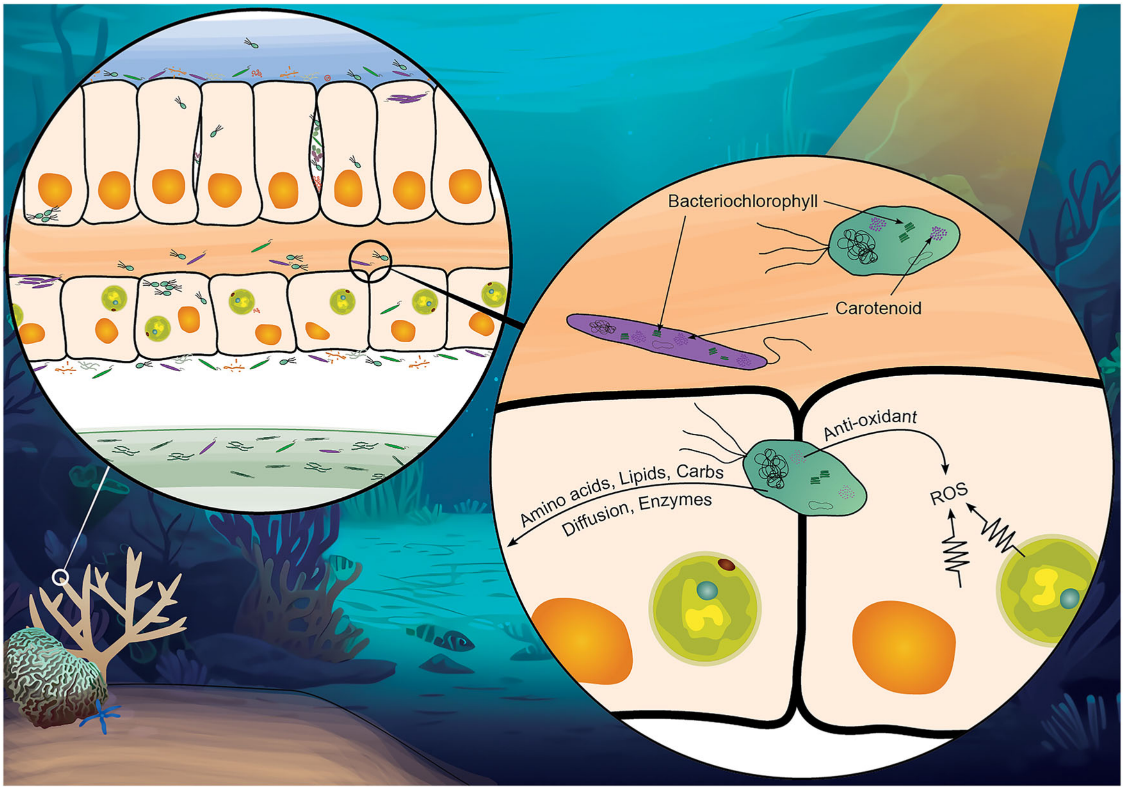

Fig. 1 | Schematic hypothetical illustration of phototrophic bacteria and their potential role in the coral holobiont. Phototrophic bacteria have been recovered from coral mucus and skeleton samples, although it also seems to be associated with coral tissue samples. Phototrohphic bacteria contain bacterial chlorophyll and carotenoids. These bacteria fix carbon, to produce organic carbon which can potentially support the host's diet during and after bleaching-induced starvation periods. However, their contribution to corals' energy budget and mechanisms of nutrient transfer remains unclear. Additionally, many phototrophic bacteria produce large amounts of carotenoids that could act as antioxidants, scavenging excess reactive oxygen species (ROS) during stressful conditions. These bacteria belong to different taxa and therefore may have varying potential capacities for carbon fixation and antioxidant production.

Cyanobacteria can have both photosystems I and II, similar to algae and plants, and can release oxygen during photosynthesis, being the only oxygenic chloroautotrophs[67]. Phototrophic bacteria possess functional photosynthetic systems with well-documented and recently explored carbon fixation pathways that include, but are not restricted to, the Calvin–Benson–Bassham cycle[69,70], although some species may lack functional photosynthetic capabilities[71,72]. Furthermore, most phototrophic bacteria (i.e., purple, green, and heliobacteria) have a single photosystem (either bacteriochlorophyll I or II) and are therefore unable to split water to release oxygen (i.e., anoxygenic). Alternatively, they use simple organic acids (nonsulfur bacteria) and/or hydrogen and sulfide (sulfur bacteria) as electron donors. As such, phototrophic bacteria, which are prevalent members of bacterioplankton communities, play a vital role in the global carbon, nitrogen, and sulfur cycles[73,74]. Phototrophy facilitated by bacteriochlorophyll (B-Chl) has been estimated to contribute around 5 to 10% of the energy generation in the upper layers of tropical oceans[75,76] (reviewed in ref. 77).

Phototrophic bacteria have been documented in a wide range of environments, including terrestrial, freshwater, and marine ecosystems[78,79]. In marine settings, these bacteria have been found in both shallow (e.g., green sulfur bacteria[80]) and deep-sea environments[81], as well as in samples collected across multiple locations, such as hydrothermal vents[82] and cold seeps[83]. They can exist as free-living organisms or in association with various hosts and microbes, including endolithic algae of the genus *Ostreobium*[84], diatoms[85], sponges[86], corals[18], oysters[87], starfish[88], rhizosphere of mangrove plants[89], and seagrass leaves[90]. Additionally, phototrophic bacteria have also been found in extreme habitats, such as hot springs with high temperatures, hypersaline lakes, and acidic lakes (see ref. 91). One of the reasons for their ecological success may be explained by their ability to utilize a broad spectrum of light wavelengths (350–1100 nm) to sustain their metabolic processes, due to structural variations in their chlorophylls and bacteriochlorophylls contents[92,93]. Notably, some of the green sulfur bacteria can utilize either blue light at mesophotic depths[94] or infrared light emitted near hydrothermal vents for photosynthesis[82,95].

As for their identity, phototrophic bacteria containing bacterial chlorophyll are classified into several phyla, including *Cyanobacteria*, *Proteobacteria*, *Chlorobi*, *Chloroflexi*, *Firmicutes*, *Acidobacteria*, and *Gemmatimonadetes*[96]. These groups are widespread in seawater and also associated with corals, residing in various compartments (i.e., tissue, skeleton, or mucus). However, their precise niches within the coral holobiont are still uncertain due to limited empirical data. Phototrophic bacteria, as a functional group, have been predominantly found within the coral skeleton among endolithic communities. They have also been documented, elbeit less frequently, in coral tissues and mucus layers, suggesting a more complex spatial distribution within the coral holobiont. For instance, assessments of diazotrophic diversity using the *nifH* gene suggest that while these diazotrophs are primarily abundant in the skeleton, they are also present in coral tissue and mucus[97]. Similarly, cyanobacteria seem to be found in the coral tissue[98], although their presence is less common compared to the skeleton[99] and mucus[100]. Whether these associations in tissue or mucus are species-specific or persistent, transient, or perhaps incidental remains an open question. Identifying the exact locations of these microbial groups within coral compartments is crucial, as it directly improves our understanding of their physiological roles and their potential for coral health benefits.

Cyanobacteria, in particular, are recognized by their symbiotic associations with corals, exhibiting nitrogen-fixing abilities and transferring photosynthetic assimilates or nitrogen to support the coral host diet[101–104]. They may use glycerol from the coral's symbiotic algae for metabolic needs, which could play a crucial role in nutrient cycling in tropical nutrient-poor environments[98]. Cyanobacteria also form symbiotic associations and colonize the entire skeletal structure in cold-water corals[105] that show a complete nitrogen cycle similar to those in tropical reefs[106]. Interestingly, some cyanobacteria (i.e., *Acaryochloris sp.*) can utilize the red-shifted chlorophyll-d as their main photosynthetic pigment, which may allow them to effectively utilize near-infrared light conditions[107]. This infers that certain cyanobacteria strains could play a key role on the coral holobiont physiology under different light conditions[108]. In addition, some cyanobacteria coevolved with their coral host, although this is species-specific, and their interactions are yet to be fully explored[109]. Despite these potentially beneficial interactions, it is important to emphasize that cyanobacteria, which are more resistant to increased light incidence and are becoming more abundant in degraded coral reefs[110,111], have also been found associated with coral disease and disease susceptibility[112,113].

Unlike cyanobacteria, other phototrophic phyla have received less attention despite their frequent association with corals across different compartments. For example, various taxa of the genus *Erythrobacter* (phylum Proteobacteria) also seems to be found and eventually isolated from both coral mucus[18] and tissue of several reef-building[114–116] and soft corals[88,117]. Furthermore, phototrophic bacteria play a significant role in the endolithic community of coral skeletons[57], as observed in the skeleton of *Isopora palifera* where *Chlorobi* sp. and *Prosthecochloris* sp. are dominant species[118]. Cai et al.[80], showed a potential symbiotic relationship between *Prosthecochloris korallensis* and its coral hosts, in which the bacteria potentially offer organic and nitrogenous nutrients and assist the host in sulfide detoxification. In return, the host could create an anaerobic environment suitable for the bacteria's survival, provide carbon dioxide and acetate for their growth, and offer hydrogen sulfide as an electron donor for photosynthesis[80]. Moreover, *Prosthecochloris* sp. associated with *I. palifera* coexists with sulfate-reducing bacteria, further indicating a potential synergistic relationship and functional role within the coral skeleton[119]. Several other photosynthetic microorganisms, such as *Chromera velia*[120] and *Vitrella brassicaformis* (both members opf the superphylum *Alveolata*) [121] are widespread in corals and phylogenetically close to photosynthetic members of the phylum Apicomplexan, which are also frequently found in coral samples[120,122]. It is important to highlight, though, that in many cases, the roles of these groups have not been elucidated[123]. In fact, some studies indicate that *Chromera* spp. may not be beneficial to *Acropora digitifera* larvae, implying they may act as parasites, commensals, or incidental associates[124]. In other words, despite the potential beneficial roles of some phototrophic bacteria, there is still much to discover about their specific functions, and the identification of sub-groups that are not consistently defined as beneficial. The underlying mechanisms of interactions between these microbial groups and the other members of the holobiont also need to be further explored, particularly photosynthesis and antioxidant traits, and whether and how these activities could potentially contribute to coral health.

Photosynthetic capacity of phototrophs and their contribution to holobiont nutrition

Bacteria can transfer beneficial molecules to their hosts across various biological systems. For instance, rhizobacteria fix atmospheric nitrogen for plants, enhancing their growth[125]. In the human gut, bacteria produce short-chain fatty acids that support intestinal health and metabolism[126]. In deep-sea environments, chemosynthetic bacteria may provide essential nutrients to their hosts, such as tube worms, through symbiotic relationships[127,128]. In coral hosts, phototrophic members of the coral-associated endolithic community (including algae, cyanobacteria, and various bacteria) may also play crucial roles in the primary productivity of coral reefs (reviewed in ref. 57,59,84), although the contribution of phototrophic bacteria to the coral holobiont's energy budget and the mechanisms involved are not yet understood.

Endolithic algae, such as members of the genus *Ostreobium*, have been documented to assimilate inorganic carbon and fix up to 40 μg C cm^{-2} during the day, transferring photoassimilates into the tissues of azooxanthellate corals, such as *Tubastrea micranthus*[129,130]. In zooxanthellate corals, the endolithic community can also transfer photosynthates to coral tissues during coral bleaching, providing an additional or alternative source of energy and nutrients in the absence of symbiotic dinoflagellates[61,62,129,131,132]. Additionally, endolithic communities participate in carbon and nitrogen assimilation processes in both healthy and bleached corals, resulting in the translocation of organic carbon and nitrogen to host tissue[84,130]. Diazotrophic cyanobacteria, for example, can contribute to coral nitrogen requirements via nitrogen fixation[130–132] and their abundance is associated with coral health[133]. Phototrophic bacteria might, therefore, similarly provide the host with photoassimilates through unexplored mechanisms. Cárdenas et al. [134] proposed a functional connection between endolithic microbiome composition, metabolic activity, and bleaching vulnerability, suggesting that the prevalence of endolithic photoautotrophs could facilitate the translocation of surplus nutrients to coral tissues.

For a long time, cyanobacteria and the green algae *Ostreobium* spp. were believed to be the only contributors to endolithic microbial communities due to their prevalence in coral skeletons[98]. However, more recent studies have revealed that a significant portion of the taxa in these communities are bacteria belonging to various groups, including both anaerobic (members of the phylum *Chloroflexi*) and aerobic (*Chlorobi spp.*) green sulfur bacteria, as well as members of the phyla *Actinobacteria* and *Firmicutes*[135]. Among these, green sulfur bacteria, such as *Prosthecochloris* spp., have been widely reported associated with the coral skeleton[118,136].

Among the groups mentioned above, members of the phylum *Chloroflexi* and *Chlorobi* spp. are predominantly found as part of the coral endolithic community[137], while they have also been reported in the coral tissue[138,139]. They are typically found in low abundance within corals, but their presence becomes more pronounced when corals inhabit fluctuating[140] or extreme[141] environmental conditions. These phototrophic bacteria may contribute significantly to the coral's nitrogen needs, potentially supplying 55–60% of the nitrogen required by their coral host[142]. Specifically, green sulfur bacteria, which are potential nitrogen fixers, may provide essential nitrogen and carbon sources to the coral holobiont[118]. Members of the genus *Prosthecochloris*, for example, possess functional genes related to nitrogen and sulfur metabolism and fixation, suggesting important roles in coral health[137]. These bacteria thrive exclusively in oxygen-depleted skeletal environments, where their metabolic activities influence nitrogen and sulfur cycling. This, in turn, impacts the broader microbial community and enhances coral health[137]. Phototrophic bacteria are could therefore contribute to the input of organic carbon and nitrogen to the coral host (Fig. 1), which plays a vital role in its physiology, particularly as corals typically inhabit oligotrophic waters where nutrient concentrations are low[143].

Antioxidant capacity

Corals are naturally exposed to temperature and light stress, which may trigger oxidative stress due to excessive production of reactive oxygen species (ROS) within the coral holobiont[4]. When ROS production exceeds the host capacity, this results in damage to the cellular machinery of both the host and symbionts, leading to dysbiosis and contributing to coral bleaching (reviewed in ref. 144). Therefore, corals use several mechanisms to neutralize excess ROS and to minimize damage. The coral microbiome has demonstrated its ability to scavenge ROS[145], for example, which could be due to production of ROS-reactive pigments such as carotenoids[146]. This can be achieved by either quenching chlorophyll triplet states, preventing the formation of singlet state oxygen molecules, or directly scavenging singlet oxygen[147]. Many bacterial taxa, including photobacteria, possess various pathways for carotenoid production that can dissipate the excess free radicals leaking from the photosynthetic processes of the algal symbionts. This suggests that phototrophic bacteria, which naturally contain large amounts of carotenoids, may play a protective role against oxidative damage and potentially enhance coral fitness, making them promising candidates for probiotics.

In fact, antioxidant capabilities to mitigate toxic compounds and oxidative stress have been proposed as critical traits for selecting beneficial microbial consortia (BMCs), through ROS scavenging mechanisms[22], or carotenoids production[20], both of which have been explored when selecting and monitoring BMCs[7,34,51]. ROS scavenging as a tool for selecting efficient BMCs was recently validated as beneficial for corals[145]. Further, the presence and activity of carotenoids and ROS scavenging genes have been documented in coral-associated microbes[7,42,51,64,117,148]. This suggests that some bacteria associated with corals have the potential and capacity to detoxify free radicals (e.g. ref. 50), which still needs to be further explored and validated. Diaz et al. [149], demonstrated the ability of corals and/or their microbiomes to regulate superoxide in their immediate environment. Similarly, *Flavobacteriaceae* strain (GF1) produced a robust antioxidant zeaxanthin that played a significant protective role for *Symbiodiniaceae* against thermal and light stress[150]. Further, microbial manipulation in *Symbiodiniaceae* cultures (using antibiotics) to enhance the prevalence of pigmented mutualistic bacteria has been proven effective in protecting algae from light stress by the production of carotenoids[151]. Even though they are still exploratory, these results suggest that photobacteria with inherent high levels of carotenoids could play crucial roles in neutralizing reactive oxygen species within the coral holobiont (Fig. 1).

In addition to carotenoids, the ability of the microbiome to control ROS may involve other mechanisms, some of which may or may not be found in phototrophic bacteria. For example, some bacteria have the capacity to produce antioxidant enzymes such as catalase, peroxidase, and superoxide dismutase to protect themselves from oxidative stress[152]. Coral-associated bacteria can also synthesize dimethylsulfoniopropionate (DMSP), a crucial chemical compound known for its antioxidant properties (and implication in other key processes), that helps improve coral physiology[153,154]. For example, members of the class *Alphaproteobacteria* produce DMSP[155], many of which are known to harbor dsyB gene (involved in the synthesis of DMSP) which is present in up to 50% of bacterial communities associated with some reef-building coral species[156]. Other bacteria are also known to synthesize vitamin B12[157], an important cofactor for the biosynthesis of the amino acid methionine, and is involved in various metabolic pathways, including the generation of antioxidants such as glutathione and DMSP[158]. The genes responsible for Vitamin B12 biosynthesis have been identified in coral-associated bacteria[159] and were proposed as beneficial microbes for corals[21,50]. The presence of similar mechanisms in phototrophic bacteria remains an area for future exploration.

Potential benefits of phototrophic bacteria as probiotics

Phototrophic bacteria have been demonstrated to be beneficial for agricultural crops lee and colleagues[160] demonstrated that the inoculation of purple non-sulfur bacteria (PNSB) on plants can enhance their growth through various mechanisms, including nutrient acquisition, phytohormone production, and induction of immune system responses. Moreover, PNSB can alleviate abiotic stress in plants through the production of endogenous 5-aminolevulinic acid and induce systemic resistance against pathogens under biotic stress[160]. In addition, PNSB can improve soil fertility by increasing nutrients (see ref. 161). Recently, the strain YH-07T of the genus *Erythrobacter* was identified as a promising plant growth-promoting bacterium for future agricultural applications as it can increase nutrient availability, antibiotic biosynthesis, siderophore production, root colonization, and tolerance to harsh environments[162]. These findings highlight the potential of phototrophic bacteria as a sustainable probiotic solution in agriculture that can enhance crop production and mitigate environmental stress.

Additionally, photobacteria have been extensively detected in sponge-associated bacterial communities and have the capacity to transfer carbon and nitrogen to the host, providing another example of their significant role in benthic holobiont organisms. Net primary productivity and stable isotope analyses revealed nutrient translocation of photosynthates, including glycerol and organic phosphate, from bacterial and algal symbionts to their sponge hosts[163]. This translocation significantly contributes to host metabolism and growth[164,165]. Phototrophic cyanobacteria can also contribute up to 80% of the carbon assimilation in sponges[166,167] enabling them to thrive in low-nutrient areas. In addition, sponge living in low light environment showed that photosynthetically fixed carbon produced by its symbiotic cyanobacteria provides up to 52% of sponge holobiont's respiratory demand and contributed by 7% to total daily carbon uptake when considering the total mixotrophic community[163]. Fixed carbon and nitrogen by phototrophic bacteria could be similarly transferred into coral hosts.

Several phototrophic bacteria members have also demonstrated the potential to enhance host health, although the underlying mechanisms remain unexplored. For instance, co-culture of members of the genus *Erythrobacter* with microalgae (*Marinichlorella kaistiae*) showed a threefold increase in microalgal growth rates and a 20% increase in electron transport rates, improving microalgal photosynthetic rates[168]. It is hypothesized that the tested *Erythrobacter* strain may provide *M. kaistiae* with inorganic carbon sources for photosynthesis, as well as vitamins or growth hormones[168]. Additionally, *Mameliella alba* (a phototrophic bacterium of the family *Roseobacteraceae*) consistently isolated from dinoflagellate cultures enhanced the dinoflagellate growth rates, suggesting the production of growth-promoting hormone[146,169]. However, it is important to note that these studies were conducted in vitro, not within the holobiont, where the dynamics may be more complex. Further research is required to elucidate how bacterial contributions may shift from beneficial to harmful, as well as how this dynamic will play out when corals and algae are exposed to stressful conditions. Furthermore, analyses of the genome and core metabolic pathways have revealed that the bacterium "Candidatus *Prosthecochloris korallensis*," which is associated with coral skeletons, has photoautotrophic capacities[80]. Specifically, a hypothetical mutualistic interaction between the coral host and this microbe, could involve "Ca. *P. korallensis*" providing organic and nitrogenous nutrients to the host, while benefiting from anaerobic conditions, carbon dioxide, acetate for growth, and hydrogen sulfide as an electron donor for photosynthesis provided by the host[80]. In addition, phototrophic bacteria can produce terpenoids which can be important for the coral host[170]. Altogether, these mechanisms could fulfill some of the metabolic needs of corals, although targeted studies investigating these specific interactions are needed.

Caveats, challenges, and opportunities

In contrast to the possible benefits described above, studies have suggested that some phototrophic microbes may also have a negative impact on coral health. Algae of the genus *Ostreobium* can penetrate both dead carbonate substrates and live corals which potentially increase the susceptibility of coral colonies to physical damage[99]. In fact, *Ostreobium* can dissolve up to 0.9 kg of $CaCO_3$ per m^2 of reef per year[171]. Further, phototrophic bacteria, such as some *Erythrobacter* spp. strains, have been suggested to be opportunistic pathogens in corals based on their genetic characteristics and abundance increase correlated with coral disease, such as the white plague[15,172,173]. *Erythrobacter* spp. strains have been demonstrated to increase the expression of genes related to pathogenicity, such as genes related to the production of membrane disrupting cytotoxins (TlyA and TlyC) and to siderophore scavengers when associated to corals in sugar-rich environments[174]. Further, it has been shown that *Erythrobacter* spp. carries genes that encode proteins responsible for the breakdown of multiple plant and algae cell-wall components, therefore, having characteristics of plants and algae pathogens or scavengers[175]. Lastly, bacteria of the phylum, *Cyanobacteria* can also negatively impact coral health by outcompeting corals for space on the reef substrate, leading to reduced coral growth and survival[176]. Additionally, some *Cyanobacteria* species can produce harmful toxins to corals, causing tissue damage and diseases[177,178]. This implies that not all phototrophic bacteria are beneficial, underscoring the need for caution in selecting target members (and applying the appropriate dosage), following careful risk assessment steps for the use of microbial therapies[28] to minimize potential risks. Furthermore, targeted research on the beneficial members, doses, regime of application and underlying mechanisms promoting coral health may advance and accelerate research in this field (Fig. 2).

The link between phototrophic bacterial abundance and their functions to the host also remains controversial. As such, it might be assumed that the overall low relative abundance of phototrophic bacteria in corals (e.g., *Erythrobacter* sp.[18]) indicates a limited contribution to the coral hosts' diet. We argue here that despite their low relative abundance, the absolute abundance in coral tissue can still be enough to play a vital role in corals (e.g. ref. 179). Low bacterial abundance does not necessarily predict their functional significance, and some of the least abundant microbes in lake water, for example, contribute significantly to nutrient uptake[180]. Similarly, low-abundance and core intracellular bacteria have been linked to nitrogen fixation, phytohormone production, and growth promotion in corals[181]. Importantly, most probiotic bacteria tested so far are found in low abundances in the coral microbiome and, still, their enrichment is associated with significant improvements in the holobiont health[7,34,42]. This warrants empirical research and could be a promising avenue for future research (Fig. 2). Understanding the functional roles of phototrophic bacteria, even at low abundances, could inform strategies to improve coral health, particularly in stressed environments.

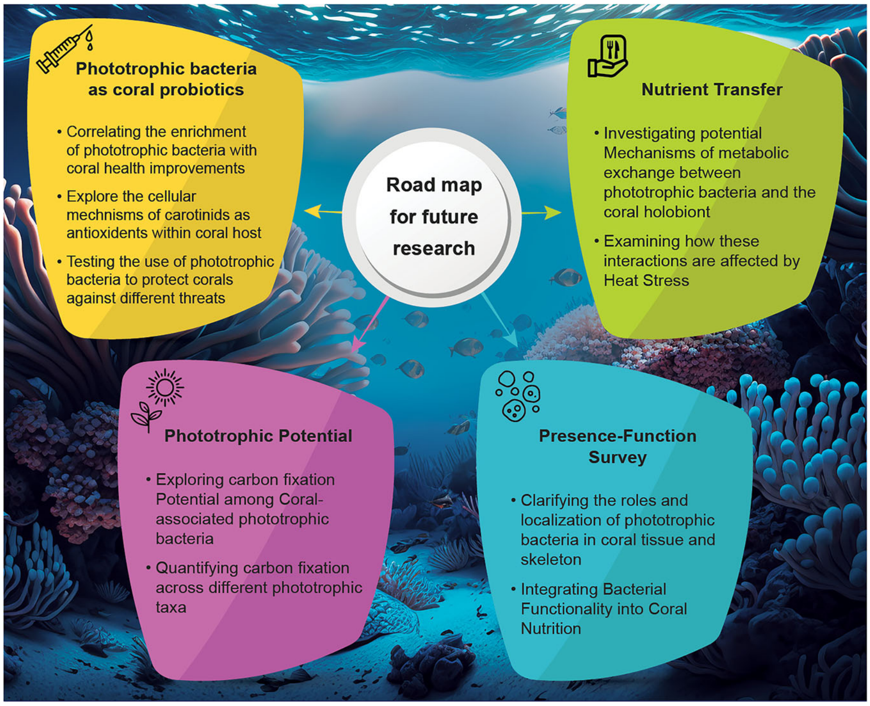

Fig. 2 | Roadmap highlighting key research topics to improve our understanding of the role of phototrophic bacteria in coral health. This roadmap emphasizes four main research priorities: (1) determining the potential use of phototrophic bacteria as probiotics for corals and underlying mechanisms, (2) exploring the potential of various phototrophic taxa and quantifying their capacity for carbon fixation, (3) investigating nutrient transfer mechanisms to determine whether photoassimilates are transported from bacteria to corals, and (4) identify locations and understanding the role of phototrophic bacteria within the coral holobiont and their contribution to the coral's energy budget. Addressing these research priorities is crucial for enhancing our understanding of the interactions between phototrophic bacteria and corals.

Another area of uncertainty is whether hosts intentionally increase the abundance of phototrophic (or any other) bacteria during heat stress to benefit from their food resources or whether this is a stochastic response. Evidence suggests that endolithic algae, notably *Ostreobium spp.*, increase in abundance during bleaching and help supplement the coral diet[61]. Consequently, biomass, photosynthetic pigments, and the rates of photoassimilate translocation is higher in the skeletons of bleached corals compared to those of non-bleached corals[61,63] (reviewed in ref. 57,84). Increases in endolithic algae in the coral skeletons could be a result of bleaching, which increases light penetration into the skeleton and drives greater autotrophic nutrients acquisition and higher cell numbers (i.e., the loss of Symbiodiniaceae facilitates greater light penetration, leading to higher phototroph proliferation). This mechanism may be similarly applied to bacteria where certain taxa, including phototrophic bacteria, may increasein abundance (or become more active) due to their functional traits during stress. The correlation between microbial composition shifts and extended coral survival in suboptimal conditions is a well-documented pattern (e.g. refs. 65,182). This relationship is nonetheless complex and although some molecular mechanisms promoted by bacteria have been correlated with coral heat resistance[183] and survivorship[7], most of them are yet to be understood. For example, an increased abundance of *Erythrobacter* spp. has been observed following exposure to extreme thermal stress[184] or with rising sea surface temperatures across latitudinal gradients[18], but whether they actually provide functional benefits for corals or are just opportunists remains unknow. Additionally, it is not clear if such regulation is actively driven by the host or the surrounding environment and how it correlates with health improvements. Despite this, chemoautotrophic bacteria seem to be prevalent members of the microbiome associated with deep-see organisms (e.g., the coral *Callogorgia delta*, the sponge *Aphrocallistes beatrix* and a sea anemone *Ostiactis pearseae*[19,185,186,186], and might serve as the primary nutritional source to their hosts, through the translocation of nutrients (reviewed in ref. 128). Based on this observation, a similar nutrient translocation mechanism could be used for phototrophic bacteria in shallow-water corals, potentially enhancing coral resilience and nutrient acquisition in these environments, although this has yet to be explored.

The mechanisms underlying nutrient transfer between phototrophs and corals, as well as the influencing factors, also remain remain to be elucidated. Phototrophic bacteria may release photoassimilates such as amino acids, glycerol, and fatty acids to coral tissue, similar to algal symbionts[187]. These compounds may be transported through diffusion or facilitated by enzymes or transport proteins[188]. While members of the phylum *Cyanobacteria* can fix nitrogen and produce organic compounds[102,189], the details of nutrient assimilation by the host are still unknown. We propose that mechanisms analogous to those of algal symbionts and cyanobacteria may also apply to phototrophic bacteria. However, this hypothesis is speculative due to the lack of direct evidence testing these pathways. As such, it remains unclear whether phototrophic bacteria employ a similar approach as other symbionts to transfer photoassimilates to their host. Addressing this gap represents a critical opportunity for future research to uncover the potential mechanisms underlying nutrient exchange between phototrophs and coral hosts (Fig. 2).

Additionally, the variability in photosynthetic capabilities across different bacterial phylotypes[190,191], hinder our ability to identify which ones can contribute positively to coral health (Fig. 2). Polyphasic approaches combining improved culture-based techniques[48,49] that can culture different taxa of phototrophic bacteria, multi-omics, and experimental assessments of the effects of phototrophic bacteria on corals, are crucial to explore and correlate their presence, abundance, and function with holobiont health.

Finally, the primary goal of our review is to discuss the largely overlooked potential importance of phototrophic bacteria and their interactions with corals. By expanding the studies to understand their role, localization and mechanisms of interaction and action, we can expand our knowledge on the coral microbiome. Additionally, we can explore the possibility of testing their use as potential probiotics, although such use will also need to overcome other challenges. For example, the active enrichment of phototrophic bacteria in corals due to their application, or their ability to promote microbiome restructuring following such inoculation, should be among the first steps to be evaluated.

Conclusion

Phototrophic bacteria exhibit functional traits that could be beneficial and play a crucial role to enhance coral survival under stressful conditions. Their active phototrophic capacity suggests an underexplored potential contribution to coral nutrition or competition advantages against coral pathogens. Despite such potential, the extent of the contribution of phototrophic bacteria to the coral diet and overall health remains unclear, indicating a clear opportunity for studies incorporating experimental and isotopic analyses that can provide a more comprehensive understanding of their role. Furthermore, the significant production of anti-oxidant compounds (e.g., carotenoids) by phototrophic bacteria could also contribute to minimizing the concentration of excessive reactive oxygen species (ROS) within the coral holobiont during heat stress. These functional traits highlight the potential role of phototrophic bacteria as coral probiotics and encourage further studies targeting the specific contributions of phototrophic bacteria to the health of the coral holobiont and their underlying mechanisms.

Data availability

No datasets were generated or analyzed during the current study.

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Author contributions

E.O.O. and R.S.P. developed the review outline, while E.O.O. drafted the initial MS version, and all other authors contributed to writing, editing, and approving the final manuscript.

Competing interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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