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Mahasweta Saha, Simon M Dittami, Cheong Xin Chan, Jean-baptiste Raina, Willem Stock, Fatemeh Ghaderiardakani, Ann Mary Valathuparambil Baby John, Shauna Corr, Guy Schleyer, Jonathan Todd, et al.

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Viewpoint

Progress and future directions for seaweed holobiont research

Summary

In the marine environment, seaweeds (i.e. marine macroalgae) provide a wide range of ecological services and economic benefits. Like land plants, seaweeds do not provide these services in isolation, rather they rely on their associated microbial communities, which together with the host form the seaweed holobiont. However, there is a poor understanding of the mechanisms shaping these complex seaweed–microbe interactions, and of the evolutionary processes underlying these interactions. Here, we identify the current research challenges and opportunities in the field of seaweed holobiont biology. We argue that identifying the key microbial partners, knowing how they are recruited, and understanding their specific function and their relevance across all seaweed life history stages are among the knowledge gaps that are particularly important to address, especially in the context of the environmental challenges threatening seaweeds. We further discuss future approaches to study seaweed holobionts, and how we can apply the holobiont concept to natural or engineered seaweed ecosystems.

Introduction

Seaweeds – including red, green, and brown macroalgae – are photosynthetic multicellular organisms that grow in various habitats, from intertidal zones to deep waters, and are essential for the functioning of marine ecosystems. They produce oxygen and organic matter that support the marine food web, and also provide habitat, shelter, and food for a diverse range of marine animals, including finfish, shellfish, crustaceans, and invertebrates (e.g. Cotas *et al.*, 2023). Seaweeds also enhance coastal protection by reducing wave energy and erosion (Gao *et al.*, 2021). They can modulate biogeochemical cycles by absorbing nutrients and carbon dioxide from the water column and releasing them back into the atmosphere or sediment (Gao *et al.*, 2021). Seaweeds can also ameliorate ocean acidification and hypoxia by buffering pH and oxygen levels (Xiao *et al.*, 2021). As with land plants, seaweeds do not function in isolation but are host to a wide range of microorganisms (Egan *et al.*, 2013; Cavalcanti *et al.*, 2018). These include both epi- and endosymbiotic prokaryotes and eukaryotes, which together with the seaweed host make up an assemblage referred to as a holobiont.

Although the holobiont concept is broadly accepted among biologists, the interpretation of what constitutes a holobiont is continually evolving and can vary greatly between research disciplines (Skillings, 2016). Until now, most seaweed studies defined the holobiont as the sum of all the living components (microbes and host) and their interactions that make up one ecological functional unit (Egan *et al.*, 2013). This simple definition has proven useful for uncovering the key roles diverse microbial symbionts play in the health (e.g. Saha & Weinberger, 2019; Li *et al.*, 2022a) and functioning of seaweeds (e.g. Wichard, 2015; Dittami *et al.*, 2016), but is limited because it does not discriminate between core and transient symbionts, nor does it differentiate ecological interactions from those that have an evolutionary dependence.

While a more refined definition of the seaweed holobiont is required, the diversity of seaweeds and the diverse ecological niches they inhabit, combined with their complex life histories (Lee, 2018; see Box 1) make this a challenging task. Evidence to date suggests seaweed holobionts are predominantly ecological units, but few studies have explicitly assessed co-evolution between seaweeds and their microbial symbionts (Hollants *et al.*, 2013b). Baseline data on temporal and spatial differences in the microbiome, across an alga's thallus over its lifetime and under different environmental conditions, will contribute to our understanding of seaweed holobionts, but obtaining these data will require a substantial collaborative effort. Accurately defining the seaweed holobiont therefore presents both challenges and opportunities. Here, we highlight the progress made so far in our understanding of the seaweed holobiont and identify areas of research that require urgent attention. We further argue that understanding seaweeds as holobionts has the potential to contribute towards sustainable seaweed aquaculture and the development of innovative technologies to mitigate the impacts of anthropogenic stressors on natural ecosystems.

Uncovering the microbial partners of the seaweed holobiont

Seaweeds are colonised by a diverse group of microbes, including bacteria, eukaryotes, archaea, and viruses. Associations range from nonspecific epibioses, where thalli of seaweeds provide a surface for the colonisation of biofilm-forming microbes, to more intimate relationships, where the algal host and associated microbes (either as epibionts or endosymbionts) are dependent on each other (Wahl *et al.*, 2012). The symbiotic relationships between seaweeds and their microbial partners have garnered significant attention, with research shedding light on the intricate dynamics and functional significance of these associations (Hollants *et al.*, 2013a; Egan *et al.*, 2013; Singh & Reddy, 2014; Wichard, 2015; Saha &

Box 1 Diversity of macroalgal life cycles

Three different life cycles are generally distinguished in seaweeds, based on the ploidy levels of the life stages and their morphologies (Coelho *et al.*, 2007; Bogaert *et al.*, 2013; Cock *et al.*, 2014). A diplontic life cycle, where gametes fuse immediately to create a new diploid cell, like is the case for most animals (e.g. *Mus musculus*), is found for certain green and brown algae, such as *Fucus spiralis* and *Sargassum*. Conversely, if meiosis follows syngamy, the zygote is the only diploid cell. This haplontic cycle is common in microalgae, but rare in seaweeds. Many brown, green, and red seaweeds have a diplohaplontic life cycle, with mitotic divisions occurring in the haploid and diploid stages. Land plants also have a diplohaplontic life cycle, whereby the initial haploid cell (spore) divides a few times (vascular plants, such as *Arabidopsis thaliana*), or even develops into the most familiar form of the life cycle (mosses). Haploid and diploid stages of seaweeds sometimes appear similar (isomorphic, like in the sea lettuce, i.e. *Ulva*) but can also be extremely different (heteromorphous) as is the case in kelps (e.g. *Saccharina latissima*). Both haploid and diploid stages in these cycles can reproduce asexually. A 'third generation' (extra diploid stage) is often observed in red seaweeds (e.g. *Gracilaria* sp.): the carposporophyte which grows from the fertilised egg cell and releases diploid spores (carpospores) that become diploid tetrasporophytes. The role of the microbiome in the complex life cycles of seaweeds is likely important but currently underexplored.

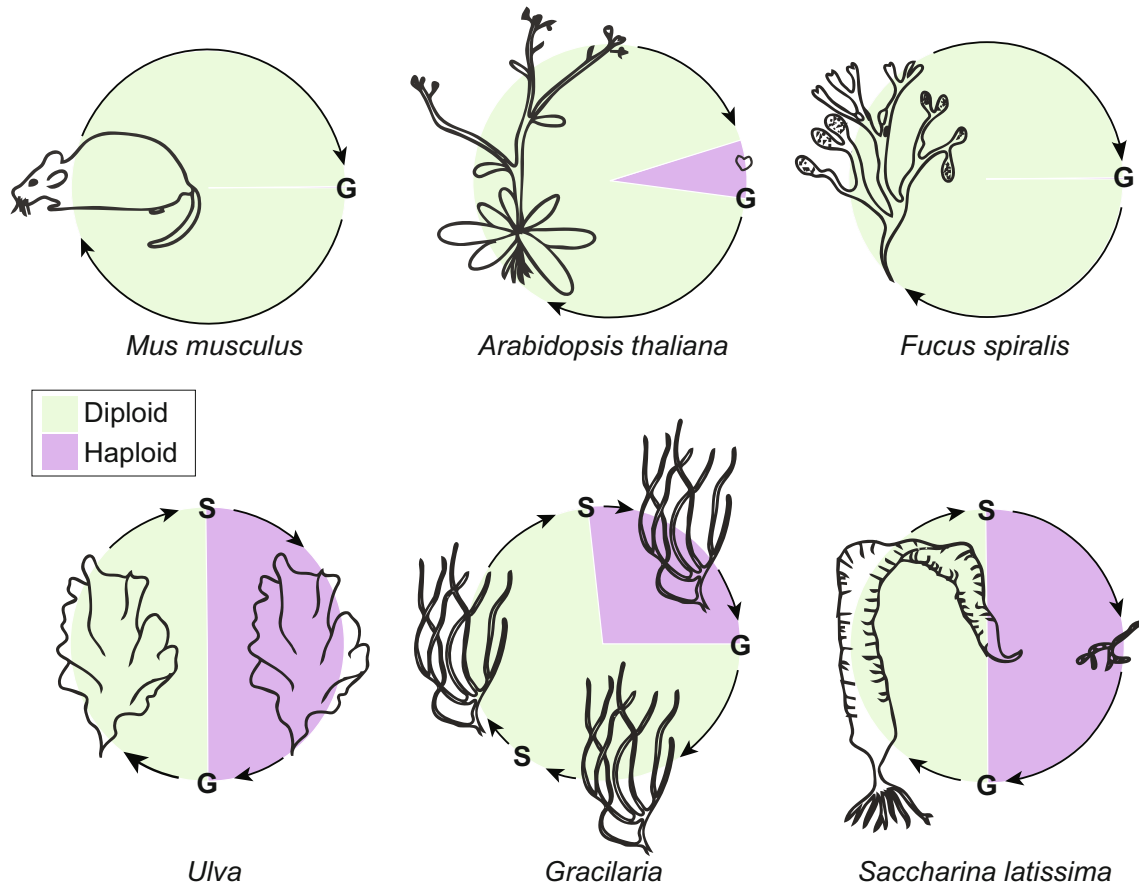


Fig. B1 Examples representing the diversity of diplontic and diplohaplontic (isomorphic or heteromorphous) life cycles. The diploid phase in the life cycle is highlighted in green, and the haploid phase in purple. The occurrence of gametes and spores in the life cycle is indicated by a 'G' and 'S', respectively.

Weinberger, 2019; see also the [Determining the function of individual members of the seaweed holobiont](#) section).

Bacteria have received the most attention and are considered the key microbial symbionts of seaweeds (Egan *et al.*, 2013). The current consensus is that bacterial communities vary considerably depending on host-, geographic-, and environmental factors, and along the thallus and over different life history stages (e.g. Roth-Schulze *et al.*, 2018; Lemay *et al.*, 2021; Wood *et al.*, 2022; van der Loos *et al.*, 2023a; Syukur *et al.*, 2024). These observations suggest that while similarities exist at high taxonomy levels (e.g. phylum or order), not all seaweeds harbour a common

set of core bacterial species or even genera. However, most of our understanding of these communities is based on individual datasets, the majority of which have low spatial and/or temporal resolution, making the identification of 'core' or even 'common' bacterial partners of seaweeds a challenge. Nevertheless, with the increasing availability of microbiome data and improvements to data analyses (Saha *et al.*, 2020; Wood *et al.*, 2022; Lu *et al.*, 2023; van der Loos *et al.*, 2023b; Khan *et al.*, 2024), opportunities to re-examine these paradigms are arising. Indeed, common seaweed symbiont genera are starting to emerge, such as those belonging to the genus *Granulosiccoccus* commonly observed in brown and green

macroalgal microbiomes (Califano *et al.*, 2020; Capistrant-Fossa *et al.*, 2021; Burgunter-Delamare *et al.*, 2022; Weigel *et al.*, 2022), and members of the Planctomycetes belonging to *Blastopirellula* and the uncultured lineage OM190, shared by some brown, red and green macroalgal microbiomes (Bengtsson & Øvreås, 2010; Kim *et al.*, 2016; Wiegand *et al.*, 2021). In other cases, bacterial taxa including *Alteromonas*, *Phaeobacter*, and *Hyphomonas* are repeatedly observed across all major seaweed groups (Friedrich, 2012). In addition, specific host–bacterial associations are likely to occur, for example between siphonous green algae and the intracellular endosymbionts, *Candidatus Endobryopsis*, that are proposed to fulfil important defensive roles in their hosts (Hollants *et al.*, 2013c; Zan *et al.*, 2019). In another example, genera of the marine *Flavobacteriaceae* induce the morphogenesis of *Ulva* and *Monostruma* in different ways depending on the recipient (Matsuo *et al.*, 2005; Spoerner *et al.*, 2012; Alsufyani *et al.*, 2020). It remains to be determined whether these commonly observed taxa play similar or complementary ecological functions that are important for the holobiont, or if they are simply adapted to the seaweed surface (e.g. as algal polysaccharides degraders).

Eukaryotic symbionts are also prevalent in and on seaweed tissues. Notable examples of endophytic eukaryotes are species of *Ulvella*, commonly associated with a range of red and brown seaweeds (Rinkel *et al.*, 2012; Nielsen *et al.*, 2013). While some species are host-generalists and relatively easy to isolate in culture (e.g. *U. viridis*), others are host specialists (e.g. *U. operculata* appears to be confined to the red alga *Chondrus crispus*) and are more difficult to isolate. However, the diversity and distribution of eukaryotes have rarely been investigated in microbiome studies until very recently (Bjørnbækmo *et al.*, 2023), and most of our knowledge of these symbionts is based on their potential to cause harm, including endophytes (e.g. gall-forming oomycetes, such as *Eurychasma dicksonii* (Gachon *et al.*, 2009)). Yet, the symbiotic association between the Fucales *Ascophyllum nodosum*, *Pelvetia canaliculata* and the fungal endosymbiont *Mycophycias ascophylli* (formerly *Mycosphaerella ascophylli*) was described over a century ago (Cotton, 1907). The symbiont *M. ascophylli* has been suggested to impact the host development, fitness, and protection against desiccation (Garbary & London, 1995). Other eukaryotic symbionts can have positive impacts on seaweed development, for example endophytic fungi (including members of the genera *Lulworthia*, *Halorosellinia*, and *Phaeosphaeria*) residing within macroalgal tissues, can positively influence the algal life cycle (Bjørnbækmo *et al.*, 2023), growth, defence mechanisms, and the production of bioactive compounds (Vallet *et al.*, 2018). A recent study on kelp (*Laminaria digitata* and *Saccharina latissima*) could not identify a common core of fungal taxa in either the endophyte or the epiphyte community (Tourneroche *et al.*, 2020), suggesting these kelp holobionts consist of a complex and variable fungal communities. Furthermore, eukaryotic symbionts can indirectly affect seaweeds by shaping their bacterial microbiome both via antagonistic interactions with bacterial partners mediated by antibiotics and/or by attracting their own symbionts, creating a ‘microbiome within microbiome’ situation (Kessler *et al.*, 2018; Saha & Weinberger, 2019).

Similarly, to the eukaryote component of the seaweed holobiont, very little is known about the archaeal or viral members. To date,

archaea are rarely considered in macroalgal research, even though some groups, such as the ammonia-oxidising archaea, are found on red and brown macroalgae and on seagrass (Trias *et al.*, 2012; Berlinghof *et al.*, 2024), where they may compete for ammonium with bacterial ammonia oxidisers as well as with the host. To date, metabarcoding studies have mostly focussed on the bacterial component of the seaweed microbiome, even if generic primers also exist for archaea (Parada *et al.*, 2016). The presence and activity of archaea should be further explored as they are known to be widespread in coastal marine environments (DeLong, 1992). Viral partners have also been largely unexplored. Beyond viral pathogens that infect economically important seaweeds (Gachon *et al.*, 2010) and/or modulate population dynamics (McKeown *et al.*, 2017), only a handful of reports have described the viral communities of seaweeds, including those that infect microbial members of the holobiont (Beattie *et al.*, 2018; Chiba *et al.*, 2020; van der Loos *et al.*, 2023a).

Further research is needed to assess the diversity and distribution of seaweed symbionts, especially for the nonbacterial organisms. Future studies should attempt to discriminate transient microbial members from those that interact (directly or indirectly) with the host and those that are essential to holobiont functions. However, this cannot be done without a clearer understanding of the exact location (e.g. Ramírez-Puebla *et al.*, 2022) and functional role of individual players within the seaweed holobiont.

Determining the function of individual members of the seaweed holobiont

Despite evidence highlighting the importance of microorganisms for normal seaweed growth and development dating back over 50 years (Pedersén, 1968), our understanding of the mechanisms and discrete functions of individual members of the seaweed holobiont remains limited. Even if the importance of function rather than taxonomy has long been highlighted in seaweed holobiont research (Burke *et al.*, 2011; Florez *et al.*, 2017), our understanding of microbial functions is predominantly based on a few well-characterised bacterial associations. One of the best-studied systems is the green algal genus *Ulva* (Wichard, 2023), in which certain bacterial symbionts produce zoospore settlement and/or morphogenic cues required for macroalgal development. Another green seaweed, *Bryopsis*, benefits from grazer-deterrent toxins produced by *Flavobacterium* living within its cytosol (Zan *et al.*, 2019). Several macroalgae, among which the invasive alga *Caulerpa taxifolia*, benefit from associated nitrogen-fixing bacteria that provide organic nitrogen to nutrient-depleted sediments, thereby stimulating the turnover of organic matter and aiding the proliferation of algal growth (Chisholm & Moulin, 2003; Tilstra *et al.*, 2017). Specific bacteria protect the red alga *Delisea* from diseases (Li *et al.*, 2022a) and strains of the brown seaweed *Ectocarpus siliculosus* tolerate reduced salinity much better in the presence of certain bacterial associates (Dittami *et al.*, 2016). While these examples illustrate the wide diversity of seaweed–bacterium interactions (Fig. 1), the extent to which these functional interactions apply to seaweeds at large is unknown. Even for these

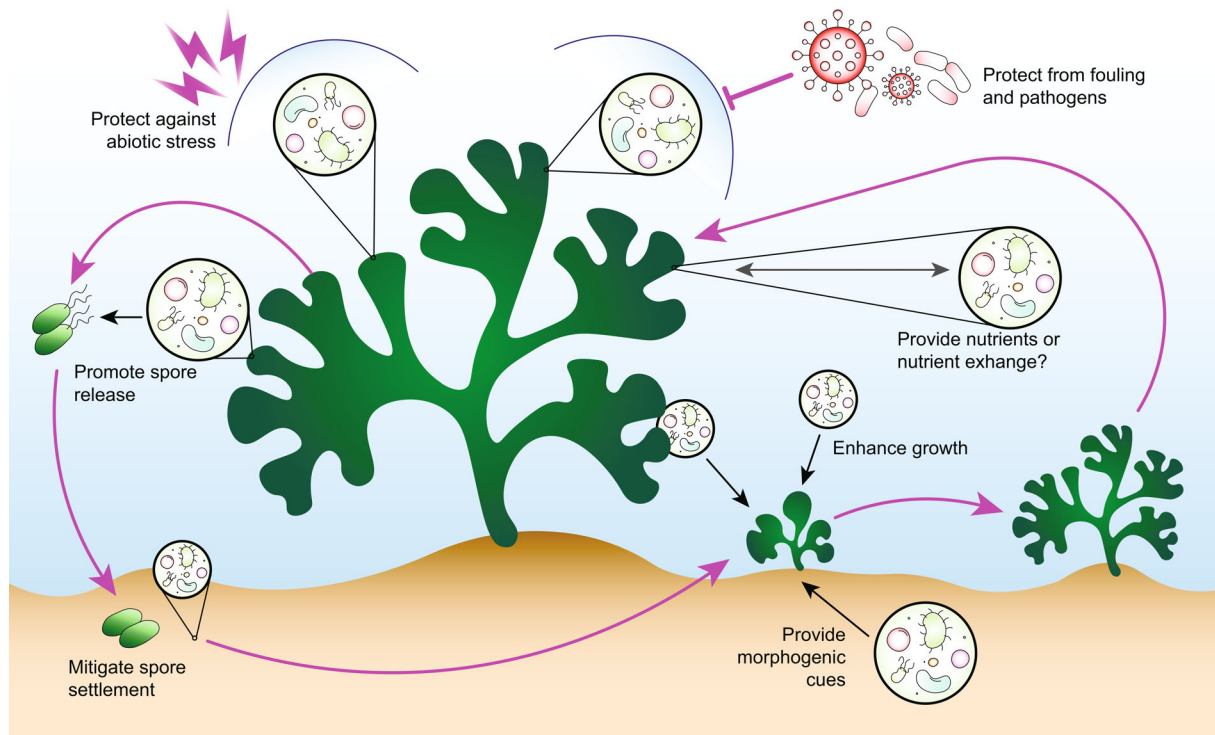


Fig. 1 Conceptual diagram showing multiple functions provided by microbial partners in the seaweed holobiont along its life cycle (represented by the purple arrows), from reproductive stage (spore release and settlement), morphogenesis and growth to physiological adaptive responses upon biotic (protection from pathogens and fouling) and abiotic stress. The black arrows indicate nutrient, metabolite, or cue fluxes between microbial partners and the algal host.

examples, yet-to-be-discovered interactions and metabolite exchanges with other microbes are likely.

One of the central challenges in the coming years will be to expand our knowledge of the functional contribution of microorganisms to the full breadth of seaweed species. Given the broad phylogenetic diversity of seaweeds and their associated microorganisms, we expect that this expansion will go together with the discovery of new intimate interactions between seaweeds and their associated microbiomes. In that context, the establishment of additional experimental microbial-seaweed models in yet unexplored branches of the algal phylogenetic diversity (Fig. 2) and the specific development and integration of cutting-edge techniques (see the [Near-future approaches to study seaweed holobionts](#) section) will be key steps to further identify and validate essential functional interactions.

Investigating the source of microbial partners and how relationships are maintained

Although it has long been theorised that beneficial symbionts should be directly transmitted from parents to offsprings (vertical transmission; Boucher *et al.*, 1982), this view is rapidly evolving. Indeed, environmentally (horizontally) acquired symbionts are also common in many marine and terrestrial hosts, and both transmission modes can be linked to stable mutualistic interactions (Fisher *et al.*, 2017). While vertical transmission has been studied extensively in terrestrial systems, a recent meta-analysis suggests that horizontal symbioses are more common in aquatic

systems (Russell, 2019). Horizontally acquired symbionts are likely to have the capacity to swim and respond to chemotactic cues and signals (Raina *et al.*, 2019), especially as chemical gradients develop more easily in aquatic environments (Stocker, 2012).

Symbiont acquisition and maintenance have been poorly studied in seaweeds, which often feature complex life cycles (Box 1). Most of our understanding is based on observational studies that suggest epiphytic microbial (predominantly bacterial) diversity is host- and tissue-specific (Aires *et al.*, 2016, 2023; Ihua *et al.*, 2020). The complex chemical exudates released by seaweeds into their surroundings are thought to select for specific microbiota (Wetzel & Penhale, 1979; Schmidt & Saha, 2021; Valler *et al.*, 2021), an observation also true for microalgae (Shibl *et al.*, 2020; Roager *et al.*, 2023). Since the communication between individual components of the holobiont is driven by infochemicals (Wichard & Beemelmanns, 2018; Saha *et al.*, 2019; Schmidt & Saha, 2021), these molecules may be important for initial recruitment and homeostasis. However, except for a few discrete examples (e.g. dimethylsulfoniopropionate (DMSP) and glycerol in *Ulva mutabilis* (Kessler *et al.*, 2018), or DMSP and fucoxanthin in *Fucus vesiculosus* (Saha *et al.*, 2011, 2012), the signalling molecules involved in seaweed holobionts remain unknown).

Horizontal transmission may not be the only mechanism for symbiont acquisition in seaweeds, as some seaweed symbionts are unlikely to respond to chemical gradients in seawater (e.g. nonflagellated members of the Bacteroidota). Given the taxonomic

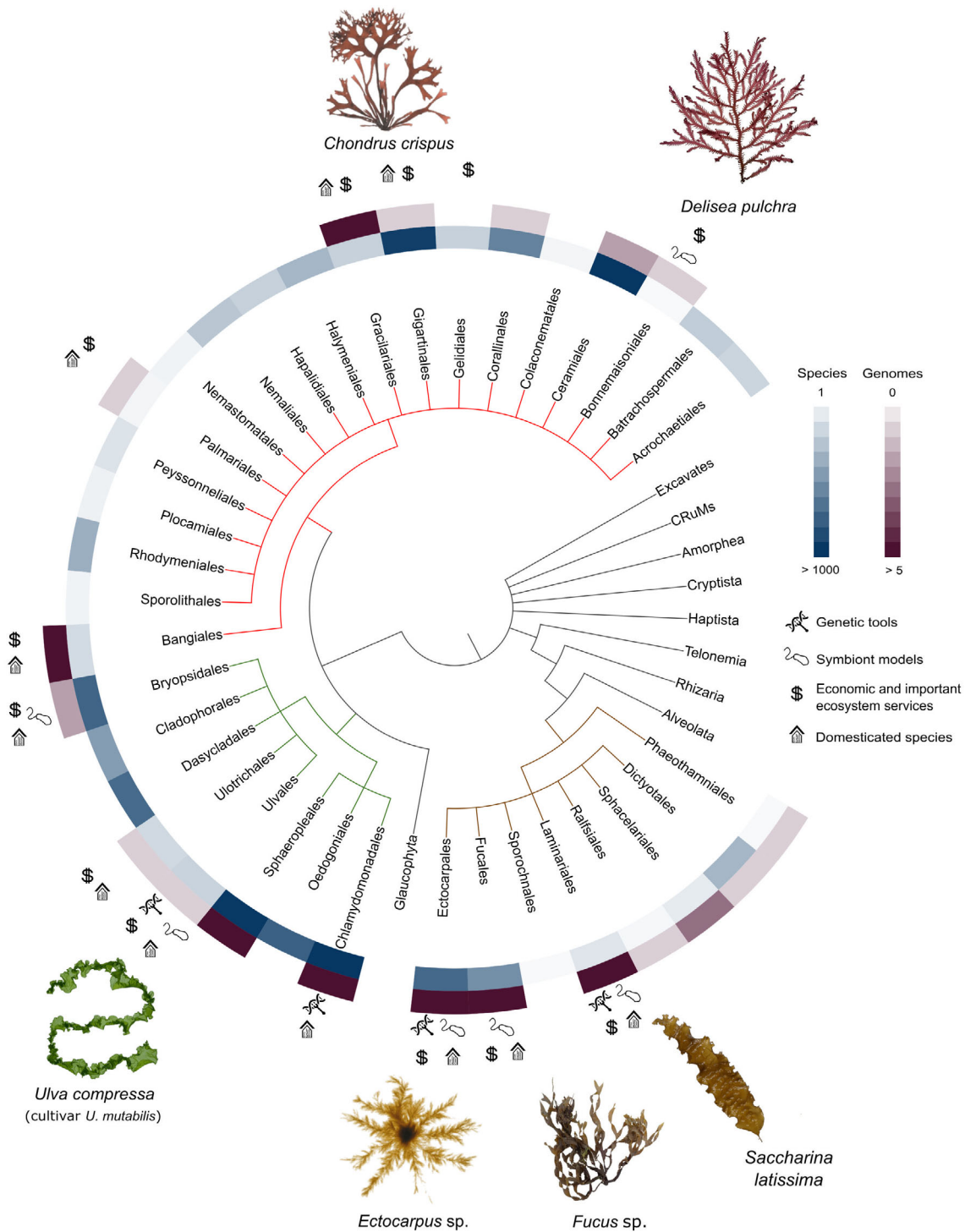


Fig. 2 Taxonomy tree representing the diversity of marine multicellular orders in Rhodophyta (red branches), Chlorophyta (green branches), and Heterokontophyta (brown branches) and showing associated resources (number of sequenced genomes, genetic tools, and availability of symbiotic models), cultivated and economically and ecologically important species (Cai *et al.*, 2021). Only orders with > 30 described species in AlgaeBase are displayed (search on 20 February 2024; Guiry & Guiry, 2023). The number of available genomes was taken from Borg *et al.* (2023) for red algae and GenBank for green and brown algae (search on 20 February 2024). For brown algae, we also counted the genomes available in Phaeoexplorer (<https://phaeoexplorer.sb-roscoff.fr/home/>). Photo credits of some emblematic macroalgal models: *Chondrus crispus* © Jonas Collen/Station Biologique de Roscoff (SBR); *Ectocarpus siliculosus* © Delphine Scornet/SBR; *Saccharina latissima* © Sylvie Rousvoal/SBR; *Delisea pulchra* © Suhelen Egan; *Ulva compressa* © Ulrich & Wichard (2024); *Fucus* © Aschwin Engelen.

and ecological breath of seaweeds and their symbionts, both horizontal and vertical transmissions must occur. Indeed, a recent study suggests seaweeds use diverse symbiont transmission strategies with varying degrees of parental inheritance (Syukur *et al.*, 2024). Characterising the molecular and ecological mechanisms underpinning seaweed–bacteria interactions will therefore go hand in hand with the understanding of when and where microbial symbionts may be recruited (Lambert *et al.*, 2017; Raina *et al.*, 2022; Clerc *et al.*, 2023). For this purpose, the use of high-resolution mass spectrometry-based techniques, combined with target metabolite localisation (Parrot *et al.*, 2019) and the development of dedicated behavioural assays targeting the responding symbionts (Raina *et al.*, 2022) on algal holobiont models, is needed to isolate and identify signalling molecules mediating seaweed–microbe interactions. In addition, more studies are required that draw on the theory and experimental approaches developed during the long history of seaweed–community ecology, including manipulative experiments that follow succession dynamics of microbial symbionts, ideally across all life cycle stages and multiple generations.

Near-future approaches to study seaweed holobionts

Earlier approaches for studying seaweed holobionts largely focused on the identification of microbial taxa associated with the host, mostly using cultivation-based approaches and 16S rRNA gene and ITS amplicon sequencing. To enhance the reproducibility of the results, these studies were commonly conducted using seaweed species grown under controlled conditions (e.g. stressed vs control, or different life history stages). These approaches provide insights into the associated microbial communities and how certain growth conditions may shape them. However, methodological challenges remain and can be broadly grouped into three categories: (a) complexity (in determining causality, i.e., which component of a holobiont is related to a specific function?); (b) translatability (i.e. is knowledge gained from experiments under laboratory conditions relevant to the environment?); and (c) generalisability (i.e. can knowledge gained from a single seaweed holobiont be applied to other conspecifics, geographic locations, or other related species?).

New tools and techniques in holobiont culturing, genetics, chemistry, biology, and data science, combined with multi-omics approaches, manipulative experiments, and the expansion of suitable model systems will undoubtedly allow us to better understand seaweed holobionts. For example, recent advances in metagenomics have enabled the reconstruction of high-quality genomes from seaweed bacterial symbionts (Weigel *et al.*, 2022; Lu *et al.*, 2023) allowing coupling of functional potential with phylogenetic inference. Similarly, genome editing tools (e.g. CRISPR–Cas9) have been developed lately for microbial communities (Rubin *et al.*, 2022) and model seaweed hosts (Fig. 2) and will be important for understanding the mechanisms of seaweed–microbe interactions. Metabolomics is an emerging approach enabling the qualitative, quantitative, and spatial analysis of metabolites in a sample at a given time (Johnson *et al.*, 2016; Parrot *et al.*, 2019). However, as for other -omic methods, annotation of metabolomes from nonmodel organisms remains a substantial challenge. Recently, combining metabolomic approaches with the use of MS/MS-based molecular

networks has led to the annotation of specific metabolites of the *Taonia atomaria* surface metabolome, such as sesquiterpenes at the apical region or DMSP at the basal parts. These differences in surface chemistry have been correlated to the variations of the surface microbiota along the same thallus (Paix *et al.*, 2020). As the metabolome can originate from both the seaweed and its associated microbiota, this technique can provide important information on the putative molecular interactions within the holobiont. Some holo-metabolomes have already been studied, including that of *Fucus* (Rickert *et al.*, 2016; Parrot *et al.*, 2019), *Taonia atomaria* (Othmani *et al.*, 2016; Paix *et al.*, 2019, 2020, 2021), and several species of *Ulva* (Fort *et al.*, 2019; Vallet *et al.*, 2021; Ghaderiadekani *et al.*, 2022). The coupling of meta-omics and environmental data using modelling of interaction networks (e.g. Paix *et al.*, 2021) will provide new functional understanding of seaweed holobionts. These rapid technological and computational advances provide a higher resolution that will undoubtedly improve our understanding of seaweed holobionts. However, without carefully designed and controlled manipulative experiments, outputs from these advanced methodologies will be limited in their ability to establish causality. To date most seaweed manipulative studies have focused on altering environmental conditions and assessing broad-scale changes to the host microbiota under laboratory conditions (e.g. Qiu *et al.*, 2019; Morrissey *et al.*, 2021; Gonzalez *et al.*, 2024; see the [Seaweed holobionts under environmental stress](#) section), with fewer studies directly manipulating microbial community members (but see Saha & Weinberger, 2019; Nappi *et al.*, 2023; Delva *et al.*, 2023; Deutsch *et al.*, 2023; Ma *et al.*, 2023). Future research efforts will need to focus on directly assessing causality in the field and determining the extent to which observations made in laboratory or mesocosm settings can be translated to the natural environment. Encouragingly, field manipulation of seaweed microbiota has recently been achieved for both subtidal (Longford *et al.*, 2019) and intertidal seaweeds (McGrath *et al.*, 2024).

Once causality is established, the next challenge will be to develop suitable genetic tools that can be applied to bacterial symbionts and the eukaryotic partners of seaweeds (e.g. endophytic algae, fungi, and oomycetes) to study specific gene functions via the construction of gene knockout or overexpression mutants. Such mechanistic studies will be important to understand the underlying relationships between specific microorganisms and their seaweed hosts. In this context, seaweed model organisms, such as *Ectocarpus*, *Chondrus*, and *Ulva* (Fig. 2), will continue to play crucial roles in advancing our understanding of development, physiology, and various other aspects of seaweed biology (Fig. 1, Wichard *et al.*, 2015; Coelho & Cock, 2020; Borg *et al.*, 2023).

Seaweed holobionts under environmental stress

Global climate change poses a severe challenge to the seaweed holobiont. Water temperature is the main driver determining geographic differentiation of co-occurring microorganisms, and abrupt regime shifts may therefore occur due to increased ocean warming (Capistrant-Fossa *et al.*, 2021; Martin *et al.*, 2021). Coastal rocky shores, where most seaweeds reside, are exposed to local urbanisation pressures, such as increased pollution and habitat

destruction. Whereas excess nutrients due to urban run-off can result in green and golden seaweed tides (Smetacek & Zingone, 2013), nutrients along with pollutants can alter the algal microbiome, reduce biodiversity, and limit the availability of suitable habitats for other seaweeds (Paix *et al.*, 2021; Mancuso *et al.*, 2023).

These stressors can disturb beneficial symbiotic relationships by altering the microbial community to include higher proportions of bacteria with pathogenic potential, inducing algal physiological responses with a direct impact on symbiosis, and/or diminishing the chemical defence of the seaweed host (Case *et al.*, 2011; Qiu *et al.*, 2019; Ghaderiardakani *et al.*, 2020, 2022). Epibacterial communities can thus dramatically shift as pathogens invade, during which the beneficial bacteria decline, with a marked increase in microbes that confer functions of algal degradation and pathogenicity (Campbell *et al.*, 2011; Fernandes *et al.*, 2012; Zozaya-Valdés *et al.*, 2017; Liu *et al.*, 2020; Kopprio *et al.*, 2021). These disruptions can lead to the occurrence of various diseases (Longford *et al.*, 2019; Egan *et al.*, 2020; Ling *et al.*, 2022; Li *et al.*, 2022a) evidenced in both wild (e.g. *Delisea pulchra* and *Ecklonia radiata*) and farmed (e.g. *Saccharina japonica* and *Ulva rigida*) populations (Campbell *et al.*, 2011; Marzinelli *et al.*, 2015; Kumar *et al.*, 2016; Qiu *et al.*, 2019; Califano *et al.*, 2020; Murúa *et al.*, 2023).

In seaweeds, positive physiological responses and microbiome stability of rhodoliths exposed to high pCO₂ conditions have been observed (Cavalcanti *et al.*, 2018), indicating the potential role of microorganisms in host resilience to ocean acidification induced by climate change. Ocean warming can result in negative impacts on seaweed health and is often correlated with significant changes to the host microbiota (Düsedau *et al.*, 2023); however, unlike other environmental stressors, recent studies suggest that microbially mediated protection from heat stress is unlikely (Delva *et al.*, 2023; Gonzalez *et al.*, 2024). Some seaweeds are highly responsive to additional nutrient loading, bioaccumulating metals (Gubelit *et al.*, 2016) and have the capacity to reduce the environmental concentration of polluting endocrine disruptors (Hardegen *et al.*, 2023). In other cases, the interaction between seaweeds and their microbiota is likely key to metal detoxification and nutrient cycling (Morrissey *et al.*, 2021). Environmental stress may also impact the beneficial traits provided by bacterial symbionts, for example the provision of essential algal growth and morphogenesis-promoting factors (AGMPFs; Ghaderiardakani *et al.*, 2020, 2022). A study of algal longitudinal growth revealed that certain alga–bacterium interactions that promote algal growth were temperature sensitive. Although some bacteria can produce these growth factors in response to stress, others cannot (Hmani *et al.*, 2024) and may switch from beneficial to detrimental behaviour (Seyedsayamdost *et al.*, 2011). Taken together, these observations suggest that while the microbiome has the potential to aid in the adaptation of seaweeds to future environmental conditions (Ghaderiardakani *et al.*, 2020), the extent of the benefit is likely specific to context and host.

While single-stressor studies are important, it is crucial to consider the combined (additive, synergistic, and/or antagonistic) effects of multiple environmental drivers on seaweed holobionts. For instance, nutrient enrichment significantly influences the

taxonomic and functional structure of the *Caulerpa* microbiome, but the lowest recovery of bacterial communities, that is return to the original state (before disruption), is observed when the holobiont is exposed to combined nutrient and temperature stress, relative to controls (Morrissey *et al.*, 2021). As microbiota and host dynamics are intimately connected to environmental parameters, arguably the biggest challenge for the field is establishing causality. Only through carefully designed manipulation experiments, under controlled laboratory or mesocosm conditions followed by appropriate field studies (see the [Near-future approaches to study seaweed holobionts](#) section), can we understand the extent to which the microbial partners of the seaweed holobiont buffer environmental stress. Here, transplant experiments can also provide valuable insights into the importance of native microbiota for environmental adaptation. For example, Campbell *et al.* (2015) found the microbiota of transplanted individuals of *Phyllospora comosa* were not habitat specific but were strongly influenced by local conditions in which they were transplanted and to a lesser extent their genotype. Similar observations have been made for seagrass, where transplanting resulted in a high microbiota turnover, a feature suggested to provide a mechanism by which the host can rapidly adapt to changing conditions (Adamczyk *et al.*, 2022). A detailed understanding of how seaweeds and their microbiomes respond to environmental change will lead to better mitigation strategies to protect seaweeds under future environmental and engineered scenarios. While Anthropocene impacts on holobionts have until now focused predominantly on negative outcomes (i.e. disease), microbial symbionts may also provide a mechanism for holobiont stress adaptation and environmental resilience (Li *et al.*, 2022b; Allsup *et al.*, 2023; Voolstra *et al.*, 2024).

Manipulation of seaweed microbiomes

Microbiome manipulation to enhance growth, protect against disease, and buffer organisms from environmental stress is gaining interest across a range of engineered and natural systems (Gouda *et al.*, 2018; El-Saadony *et al.*, 2021; Peixoto *et al.*, 2022; Sorbara & Pamer, 2022; Voolstra *et al.*, 2024). Recently, seaweed beneficial microorganisms (SBMs; Li *et al.*, 2023) that mitigate bleaching disease occurrence under laboratory conditions have been identified (Saha & Weinberger, 2019; Li *et al.*, 2022a; Ma *et al.*, 2023). Osborne *et al.* (2023) also found key bacterial taxa correlated with increased biomass of mature sporophytes of cultivated *Macrocystis pyrifera* (Osborne *et al.*, 2023). In addition, AGMPFs detected in land-based integrated multitrophic aquaculture facilities are thought to directly benefit *Ulva* production (Ghaderiardakani *et al.*, 2019, 2020). In these experiments and long-term cultivation in the laboratory, a stable microbiome is naturally formed that contains beneficial bacteria at a higher proportion than in the open water (Califano *et al.*, 2020; Ghaderiardakani *et al.*, 2022; Nguyen *et al.*, 2023; van der Loos *et al.*, 2023a). These studies support the idea that seaweed diseases, development, and productivity can be controlled by microbiome manipulation with SBMs or their products.

Unlike probiotics that serve as feed supplements for animals, or plant growth-promoting bacteria (PGPM) as soil supplements, an

effective application of SBM will require the development of new approaches. One possibility is to directly apply the biologically active agent(s). For example, AGMPF-producing bacteria can already be replaced by specific compounds, such as thallusin. Complete chemical synthesis of thallusin is possible (Dhiman *et al.*, 2022) and *in situ* methods for its detection have been developed (Ulrich *et al.*, 2022), paving the way for thallusin to be used in commercial-scale *Ulva* production. A second option is to apply SBMs in seaweed hatcheries, such that the benefits last during the entire cultivation or out-planting period, as has been reported in the PGPMS with strong rhizosphere colonisation properties (Amaya-Gómez *et al.*, 2020; Allsup *et al.*, 2023). However, the realisation of large-scale microbiome manipulation of seaweeds will require a better understanding of the *in situ* stability of microbiomes, the interactions between introduced SBM and other holobiont members, and the environmental conditions that maintain SBM across the entire life history of individual seaweeds (Osborne *et al.*, 2023; Syukur *et al.*, 2024). This information will not only be key for the practical application of SBM but will also be important to ensure future *in situ* applications do not cause unintentional environmental consequences or pose a broader biosecurity risk.

While still in the early stages of development, microbiome manipulation and engineering are rapidly gaining momentum as novel biotechnological tools for aquaculture and marine restoration projects (Perry *et al.*, 2020; Peixoto *et al.*, 2022; Li *et al.*, 2023; Delgadillo-Ordoñez *et al.*, 2024). Therefore, in addition to filling the scientific knowledge gaps described above, early and frequent engagement with all stakeholders (e.g. scientists, environmental managers, and industry end users) will be necessary to ensure the effective, sustainable, and responsible application of SBM in future (Li *et al.*, 2023; Wichard, 2023).

Conclusion and future directions

A holistic approach to studying seaweed holobionts involves collaboration, standardisation, integration across scales, and a combination of exploratory and mechanistic studies using both systems biology and reductionist methodologies. Such a strategy is essential for advancing our understanding of these complex ecosystems.

To understand host-bacteria interactions, future omics-based studies should focus on functional, acclimation, and adaptation processes, and also consider microbial acquisition, their dynamics, and the different roles they may play during the life cycle. All these approaches are relevant for understanding the fitness of the seaweed holobiont in a changing environment and for economic purposes. Identifying candidate functional traits can be achieved with integrated omics approaches including transcriptomics, metabolomics, and proteomics. Following those exploratory studies, mechanistic studies may examine the biological pathways by which specific infochemicals (e.g. signal molecules) interact with specific receptors. Therefore, methodically well-developed seaweed model systems are advantageous and recommended. Genetic manipulation will allow us to disentangle the underlying chemically mediated interactions between the symbionts and their

environment. This decisive step will bring seaweed research in line with the advances in terrestrial systems for example the plant model *Arabidopsis* (Poupin *et al.*, 2023). Model organisms should be selected and prioritised based on their economic and ecological importance, and further complemented by underexplored phylogenetic groups (Fig. 2). To achieve these ambitious goals, collaborative efforts, standardised sampling, cultivation, and sharing of metadata will be essential prerequisites. Great examples of community-building initiatives that aim to follow standardised methodologies include the Earth Microbiome Project (<https://earthmicrobiome.org/>), Gordon and Betty Moore Foundation Symbiosis in Aquatic Systems Initiative (McKenna *et al.*, 2021), the Tara Oceans project (Sunagawa *et al.*, 2020), and EU-COST Action Networks (<https://www.cost.eu/>).

Importantly, ecologists and environmental engineers need to fully consider aspects of microbial functioning in seaweed-dominated ecosystems, and their cascading effects on ecosystem function, including nutrient cycling (Pita *et al.*, 2018). For example, *Fucus vesiculosus* secretes large amounts of fucoidan polysaccharides in the surrounding seawater, up to 0.3% of their biomass per day. Degradation of these seaweed polysaccharides requires complex enzymatic processing that is predominantly driven by microorganisms (Sichert *et al.*, 2020; Buck-Wiese *et al.*, 2023). Thus, as the fate of organic carbon in seaweed-dominated ecosystems is largely dependent on alga-microbe interactions, understanding how a changing climate, expanding seaweed aquaculture, and artificial microbiome manipulation of seaweeds impact broader ecosystem functions, including global carbon fluxes, needs further investigation.

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Competing interests

None declared.

Author contributions

MS, CL and SE planned and designed the paper. CXC created Fig. 1. CX, AMV, ECS and GS prepared Fig. 1. SMD and CL prepared Fig. 2. CXC, AHE and WS created Fig. B1. JB-R edited the references. MS, SD, CXC, JR, WS, FG, JT, UC, MMB, SP, DS, SC, ECS, AHE, GW, TW, JB, CL and SE contributed to the drafting and editing of the manuscript text.

ORCID

Mia M. Bengtsson  <https://orcid.org/0000-0002-2115-9139>
 Juliet Brodie  <https://orcid.org/0000-0001-7622-2564>
 Ulisse Cardini  <https://orcid.org/0000-0002-0816-6158>
 Cheong Xin Chan  <https://orcid.org/0000-0002-3729-8176>
 Shauna Corr  <https://orcid.org/0000-0002-3934-8296>
 Simon M. Dittami  <https://orcid.org/0000-0001-7987-7523>
 Suhelen Egan  <https://orcid.org/0000-0003-3286-4279>
 Aschwin H. Engelen  <https://orcid.org/0000-0002-9579-9606>
 Fatemeh Ghaderiardakani  <https://orcid.org/0000-0003-3497-8421>
 Catherine Leblanc  <https://orcid.org/0000-0001-7149-0332>
 Soizic Prado  <https://orcid.org/0000-0002-8071-9642>
 Jean-Baptiste Raina  <https://orcid.org/0000-0002-7508-0004>
 Mahasweta Saha  <https://orcid.org/0000-0001-9308-1054>
 Guy Schleyer  <https://orcid.org/0000-0001-9756-9356>
 Derek Skillings  <https://orcid.org/0000-0002-1295-1669>
 Eva C. Sonnenschein  <https://orcid.org/0000-0001-6959-5100>
 Willem Stock  <https://orcid.org/0000-0001-7648-6404>
 Jonathan Todd  <https://orcid.org/0000-0003-0777-9312>
 Ann Mary Valathuparambil Baby John  <https://orcid.org/0009-0009-2787-852X>
 Gaoge Wang  <https://orcid.org/0000-0001-7047-607X>
 Thomas Wichard  <https://orcid.org/0000-0003-0061-4160>

Mahasweta Saha^{1*} , **Simon M. Dittami²** ,
Cheong Xin Chan³ , **Jean-Baptiste Raina⁴** ,
Willem Stock⁵ , **Fatemeh Ghaderiardakani⁶** ,
Ann Mary Valathuparambil Baby John¹ , **Shauna Corr¹** ,
Guy Schleyer⁷ , **Jonathan Todd^{8,9}** , **Ulisse Cardini¹⁰** ,
Mia M. Bengtsson¹¹ , **Soizic Prado¹²** ,
Derek Skillings¹³ , **Eva C. Sonnenschein¹⁴** ,
Aschwin H. Engelen¹⁵ , **Gaoge Wang^{16,17,18}** ,
Thomas Wichard⁶ , **Juliet Brodie¹⁹** ,
Catherine Leblanc^{2*}  and **Suhelen Egan^{20*}** 

¹Plymouth Marine Laboratory, Marine Ecology and Biodiversity, Prospect Place, Plymouth, PL1 3DH, UK;
²CNRS, Integrative Biology of Marine Models Laboratory (LBI2M, UMR 8227), Station Biologique de Roscoff, Place Georges Teissier, Sorbonne Université, Roscoff, 29680, France;

- ³Australian Centre for Ecogenomics, School of Chemistry and Molecular Biosciences, The University of Queensland, Brisbane, Qld, 4072, Australia;
⁴Climate Change Cluster, Faculty of Science, University of Technology Sydney, Ultimo, NSW, 2007, Australia;
⁵Phycology Research Group, Ghent University, Krijgslaan 281 Sterre S8, Ghent, 9000, Belgium;
⁶Institute for Inorganic and Analytical Chemistry, Friedrich Schiller University Jena, Lessingstr. 8, Jena, 07743, Germany;
⁷Department of Biomolecular Chemistry, Leibniz Institute for Natural Product Research and Infection Biology (HKI), Beutenbergstr. 11a, Jena, 07745, Germany;
⁸School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich, NR4 7TJ, UK;
⁹Frontiers Science Center for Deep Ocean Multispheres and Earth System, and College of Marine Life Sciences, Ocean University of China, Qingdao, 266003, China;
¹⁰Department of Integrative Marine Ecology (EMI), Genoa Marine Centre, Stazione Zoologica Anton Dohrn – National Institute of Marine Biology, Ecology and Biotechnology, Genoa, 16126, Italy;
¹¹Institute of Microbiology, University of Greifswald, Felix-Hausdorff-Str. 8, Greifswald, 17489, Germany;
¹²National Museum of Natural History, Unit Molecules of Communication and Adaptation of Microorganisms (UMR 7245), Paris, France;
¹³Department of Philosophy, University of North Carolina Greensboro, Greensboro, NC 27402, USA;
¹⁴Department of Biosciences, Swansea University, Singleton Park, Swansea, SA2 8PP, UK;
¹⁵CCMar, Universidade do Algarve, Faro, 8005-139, Portugal;
¹⁶College of Marine Life Sciences, Ocean University of China, Qingdao, 266003, China;
¹⁷Institute of Evolution & Marine Biodiversity, Ocean University of China, Qingdao, 266003, China;
¹⁸MoE Key Laboratory of Evolution & Marine Biodiversity, Ocean University of China, Qingdao, 266003, China;
¹⁹Natural History Museum, Research, Cromwell Road, London, SW7 5BD, UK;
²⁰Centre for Marine Science and Innovation (CMSI), School of Biological, Earth and Environmental Sciences (BEES), UNSW Sydney, Sydney, NSW, 2052, Australia
 (*Authors for correspondence: email: sahamahasweta@gmail.com (MS); catherine.leblanc@sb-roscoff.fr (CL); s.egan@unsw.edu.au (SE))

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