Review

Marine Vallet*

Chemical ecology of plankton parasitism in algae

Abstract: Plankton parasites such as viruses, bacteria, fungi, and unicellular eukaryotes are associated symbionts colonizing algal groups in aquatic ecosystems. They occur within a network of microbe–microbe interactions in which they parasitize phytoplankton and seaweeds, i.e., primary producers generating organic carbon and forming the basis of marine food webs. These parasites use algae as a source of nutrients and reproduce at the expense of their host, causing infectious symptoms leading to disease and death. Plankton parasites can reduce the algal populations, and the infection of one specific species may, in turn, favor the development of another, influencing the seasonal succession of algal blooms in oceans, seas, and lakes. Many parasites have free-living stages that zooplankton graze upon, representing a significant trophic link in food webs. The biology and life cycle of plankton parasites are well investigated in marine and freshwater algal hosts. Still, the chemical signaling mediating these microbial interactions and the effect of co-occurring symbionts remain underexplored. This review focuses on the diversity of plankton parasites infecting algae, with a particular emphasis on unicellular eukaryotes. The ecological role of plankton parasites, the mechanisms regulating cellular infection and host resistance, and the interplay of alga-parasite interactions with coexisting microorganisms are discussed.

Keywords: plankton parasites; chemical signaling; algae; parasitism; microbial interactions

1 Introduction

Marine microorganisms can form intricate networks to access valuable resources such as light and nutrients, supporting the colonization of aquatic ecosystems (Lima-Mendez et al. 2015).

*Corresponding author: Marine Vallet, Research Group Plankton Community Interaction, Max Planck Institute for Chemical Ecology, Hans-Knoell Strasse 8, D-07745 Jena, Germany; and Bioorganic Analytics, Institute for Inorganic and Analytical Chemistry, Friedrich Schiller University, Lessingstrasse 8, D-07743 Jena, Germany, E-mail: mvallet@ice.mpg.de. https://orcid.org/0000-0002-6878-0459

Microbes are prevalent in most ocean biotic interactions, but studies of aquatic food webs rarely include eukaryotic parasites. In marine ecosystems, opportunistic parasitic microorganisms can live on the surface of the host cell, i.e., as ectoparasites, or invade the cell membrane to develop within the host as an endoparasite (Gleason et al. 2015). Plankton parasites can infect many hosts, including algae, copepods, and other grazers from the food chain (Bjorbækmo et al. 2020). These single-cell parasitic organisms, like viruses, are a polyphyletic group that contributes to the termination of algal blooms (Chambouvet et al. 2008). Many groups of microorganisms from the plankton will form a parasitic interaction with algae, including chytrids (Frenken et al. 2017; Gleason et al. 2015; Sime-Ngando 2012), marine fungi (Ilicic and Grossart 2022; Richards and Chambouvet 2016), and alveolates from the Perkinsea clade (Itoïz et al. 2022; Jephcott et al. 2016). The algal hosts comprise phytoplankton, i.e., unicellular photosynthetic eukaryotes and seaweeds, constituting the basis of the marine food web. Hence, these algal hosts greatly support carbon flow transfer to other trophic levels by rendering phytochemicals and other nutrients available to higher organisms, contributing to the carbon flow (Treves et al. 2022). Some phytoplankton species can form blooms by gathering millions of cells in one location, and effects on individuals can extend to the population and community levels. Plankton parasites may choose an algal host depending on the host abundance, species identity, and host susceptibility due to adaptive strategies and a long co-evolution history (Alacid et al. 2017). Metabolic production could also be one adaptive trait that determines the choice of host, with potentially an inclination towards species releasing chemoattracting cues (Friesen and Detwiler 2021).

In aquatic ecosystems, chemical interactions regulate many physiological processes and biological interactions, such as defense, mating, predation, and nutrient foraging (Hay 2009). Aquatic parasites can modify the host's chemical cues, with far-reaching consequences for the community dynamics and organisms at all trophic levels. For example, oxylipin-mediated signals released by hosts infected with plankton parasites might modify fish and herbivore behavior to increase parasite transmission in the population (Friesen and Detwiler 2021). Oxylipins are also used by the algal hosts to interact with the microbial community and defend against microorganisms and potentially against

plankton parasites (Pohnert and Boland 2002). Oxylipins and other chemicals might mediate the parasite invasion and regulation of host cell populations. The algal substances that serve a role in defense against predators, parasites, and pathogenic microbes include small, readily diffusible organic molecules that activate cellular metabolic pathways (Deng et al. 2022b). As the algal hosts produce various metabolites, they can attract, supply, and maintain a cohort of microorganisms within a microscale area called the phycosphere (Bell and Mitchell 1972; Seymour et al. 2017). This area comprises a viscous boundary layer of algal exudates in which chemicals are exchanged during interspecific interactions with microorganisms (Raina et al. 2019; Seymour et al. 2017). Phytoplankton can also release lytic substances into the phycosphere to defend against plankton parasites (Long et al. 2021). These cues are released in minute trace amounts, but can be detected and identified thanks to the increased sensitivity and resolution of modern mass spectrometers (Feng 2023; Stettin et al. 2020).

Furthermore, parasitic organisms can live in association with multiple algal species by invading the host cell, feeding on it, and reproducing to form free-living flagellate cells, i.e., zoospores, that can swim to infect the population (Deng et al. 2022b; Gleason et al. 2015). The complexity of these life cycles means that, at a single time-point, the algal population comprises healthy cells and individuals infected by different parasites. Single-cell omics can thus enable the study of these different cell phenotypes and the identification of metabolites associated with the different infection stages and host species (Baumeister et al. 2020; Vallet et al. 2023).

Despite their substantial role in facilitating energy transfer and promoting species succession by altering microbial competition (Valois and Poulin 2015), the chemical ecology of plankton parasites is mainly unknown. Further, the role and identity of metabolites structuring the microbial community, and their effect on plankton parasites, remains uncharted. Studying the chemically mediated interactions between algae and parasites would deepen our understanding of marine food webs, their structure, and their resilience to environmental changes. Identifying metabolites involved in host cell invasion, host population regulation, and defense against parasites may also unveil the evolutionary mechanisms of plankton parasitism.

2 Alga-parasite interactions in aquatic ecosystems

The term 'plankton parasites' comprises diverse organisms that belong to different taxonomic groups and have unusual lifestyles, alternating from the zoospore stage to a cellular association with an algal host. This section covers the biological diversity, unique lifestyle, and ecological roles of plankton parasites in aquatic ecosystems, focusing on single-cell eukaryotes. Molecular mechanisms that enable cellular invasion are reported, as well as the process supporting parasite reproduction transitioning from the host-associated form to the free-living zoospore.

2.1 What are the plankton parasites?

The classic definition of a parasite is an organism that lives on or within another organism and obtains nutrients at the expense of this host (Poulin 2007). Plankton parasites may be prone to rapid evolution, having short generation times. Their short generation times further imply the potential to generate large population sizes in short time periods, increasing the chances of sexual reproduction and dissemination in the host cells (Kochin et al. 2010). Throughout evolutionary history, plankton have been using cell-to-cell associations during one or more life cycle stages to increase survival and avoid the harsh environmental conditions of nutrient-depleted open waters (Picoche 2022). Phytoplankton and seaweeds utilize photosynthesis to sustain their nutritional needs, rendering them suitable hosts for plankton parasites. Opportunistic microorganisms, such as single-cell eukaryotes (namely protists), can infect algae and feed on their metabolites for growth and reproduction during their life cycle stages, impacting their host's fitness, metabolism, and associated microbiome (Figure 1). Other microorganisms, such as bacteria and viruses, can also cause infectious diseases and parasitize algae, and are equally important marine pathogens in oceans (Gachon et al. 2010). Parasitic bacteria may inhabit the algal membranes of dinoflagellates such as *Alexandrium tamarense* and can induce cell wall degradation using β-glucosidase and chitinase (Wang et al. 2010). The most studied pathogens of algae are viruses, which usually have a narrow host range and can control their host populations by infecting the most abundant species (Brussaard 2004).

Among the groups of protists reported as parasites of algae is the clade of Alveolata, which contains the perkinsids, a sister group to dinoflagellates, that can infect algae, bivalves, fishes, and amphibians (Itoïz et al. 2022). Another dinoflagellate group from the Syndiniales, also referred to as marine alveolates, comprises many obligate parasites of phytoplankton. Syndiniales parasites can significantly reduce carbon flux via host cell lysis by increasing the sinking rate of infected hosts or zoospores on particles (Anderson et al. 2023). According to genome sequencing analysis, Syndiniales parasites are critical players in ocean
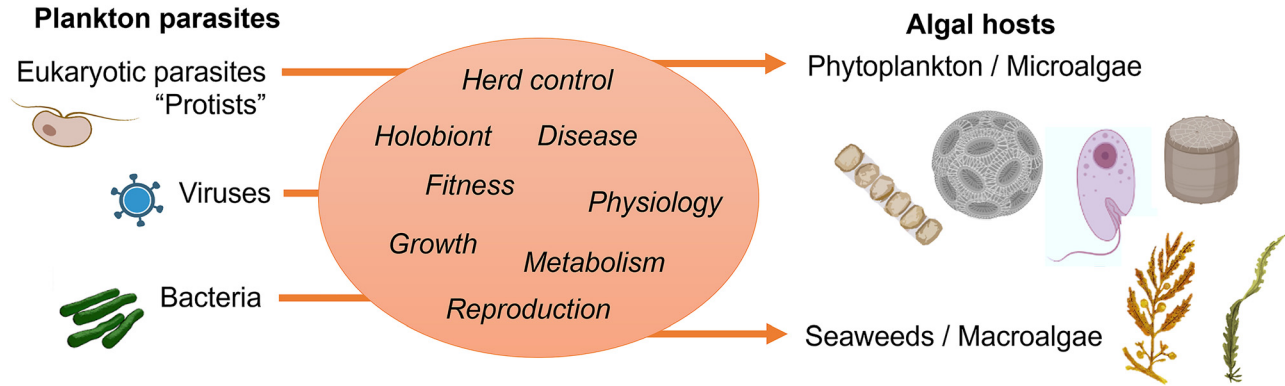
Figure 1: Plankton parasites and their diverse effects on their algal hosts. Parasites can influence their host's growth, fitness, metabolism, and reproduction, leading to symptoms of disease in seaweeds and bloom termination of microalgae due to the death of the population. The herd control of algae maintained by plankton parasites also has a positive outcome, supporting a population equilibrium in aquatic ecosystems.

surface waters, including sea-ice environments (Clarke et al. 2019). Syndinian and perkinsid parasites can infect toxic, harmful dinoflagellates, thus accelerating their bloom termination and the succession of algal species (Chambouvet et al. 2008; Jephcott et al. 2016).

The Oomycetes, a stramenopile group once classed as Fungi, are plankton parasites responsible for top-down control of phytoplankton hosts such as diatoms (Hanic et al. 2009). Several oomycete species are obligate biotrophic pathogens, but other members can also use host-jumping to evolve followed by radiation, specialization, and speciation (Thines 2019). These processes are well studied in the terrestrial environment for parasites of plants, but not yet for plankton parasites of algae. Several marine oomycete parasites have been established in cultures as laboratory models, including the specialist *Lagenisma coscinodisci* that infects the diatom genus *Coscinodiscus* (Buaya et al. 2019), and the generalist *Ectrogella* sp. that targets diatoms such as the pennate diatom *Licmophora* (Garvetto et al. 2020). Remarkably, marine oomycetes are stramenopiles, a heterotrophic sister group of brown algae and diatoms, which are the targeted hosts of these parasites (Thines et al. 2015). These oomycetes possess cellulosic cell walls, contrasting with Fungi and their chitinaceous cell walls (Scholz et al. 2014). Stramenopile parasites have reduced, smaller genomes than their host, possibly due to the simplification and reduction of the genomes during evolution (Wolf and Koonin 2013). Consequently, these parasites might hijack the host biosynthetic machinery to produce metabolites during infection and cellular invasion.

Oomycetes infect macroalgal species and planktonic diatoms and could shift from one host to another (Scholz et al. 2014). This infection strategy is shared by many generalist parasites of algae, such as the perkinsid *Parvilucifera* that can target multiple dinoflagellate species and therefore can thrive and survive if one host disappears (Garcés et al. 2013a). Generalist plankton parasites usually prefer the most susceptible host available, given that reproductive success depends on their ability to infect a host, and use chemical cues to detect the host's presence (Garcés et al. 2013b). Parasitic organisms from aquatic environments can also be specialists for single algal species, emerging from long co-evolutionary histories (Anderson and May 1981). Many plankton parasites of phytoplankton can be specialists or generalists, and some are parasitoids, i.e., living at their host's expense and inducing the death of infected cells (Mills 2009).

The kingdom of Fungi also encompasses unicellular eukaryotes that infect algae. By definition, marine fungi include any fungus repeatedly recovered from marine habitats that can (i) grow and reproduce in marine environments, (ii) form symbiotic relationships with other organisms during their life cycle, or (iii) adapt and evolve at the genetic level or is metabolically active in a marine environment (Rédou et al. 2016). The kingdom of Fungi (Opisthonkonta) includes the chytrids that can infect diatoms in both freshwater (Ibelings et al. 2004) and marine (Gutiérrez et al. 2016) environments. One established model of chytrids is *Dinomyces arenysensis*, which was isolated from a toxic bloom of *Alexandrium minutum* (Lepelletier et al. 2014a). The chytrid *Dinomyces* can infect a wide range of dinoflagellates, with a preference for *Alexandrium* species under culture conditions (Lepelletier et al. 2014a). Strikingly, chytrids are found in terrestrial soils, where they can live without a host as free-flagellate zoospores thriving on a film of surface water (Shearer et al. 2007). Due to their wide distribution across climatic regions, including freshwater and marine ecotypes, and their potential as generalist opportunistic pathogens, chytrids have been a topic of rising interest in recent years (Frenken et al. 2017). Their biology and ecology have been reviewed by Ilicic and Grossart (2022) and Rasconi et al. (2014). The predominant ecological

role of chytrids and other fungus-like organisms infecting algae might be their contribution to carbon cycling and food web dynamics by channeling carbon flow to the food chain in freshwater ecosystems (Klawonn et al. 2021).

Osmotrophic and saprotrophic eukaryotes can also be counted among the plankton parasites, and they usually acquire their nutrients through the direct uptake of dissolved organic substrates (Richards and Talbot 2018). The Labyrinthulomycetes, which include labyrinthulids and thraustochytrids, are another stramenopile group that parasitizes algae and uses osmotrophy as a nutrition mode. They are commonly found in marine snow (Bochdansky et al. 2017) and sediments (Rodríguez-Martínez et al. 2020). Thraustochytrids are also detected during decaying blooms of coccolithophores (e.g. *Emiliana huxleyi*) and might contribute to the termination of the bloom (Vincent et al. 2021). These organisms are considered parasitic due to extracellular digestion via lysotrophy (also chemoheterotrophy), which involves the secretion of enzymes into the environment to break down larger substrates such as polymers (e.g., cellulose, lignin) into their building blocks (e.g., sugars, fatty acids, amino acids), that will serve for nutrition (Richards et al. 2006).

The Oomycetes, Hypochytriomycetes, and Labyrinthulomycetes all use osmotrophy in one or more life stages and prey on coastal planktonic diatoms, hence contributing to total long-term organic carbon sequestration (Armbrust 2009). Diatoms such as *Fragilariopsis* and the domoic acid toxin producer *Pseudo-nitzschia* are Tychoplankton, as they can alternate between benthic and pelagic waters (Cahoon 2016). Due to this versatile lifestyle, these algae could be responsible for transferring plankton parasites from one environment to another. At the same time, the symbionts can use a hitchhiking or piggybacking strategy to colonize new host cells. Indeed, pathogens can become a new parasite species for algae by host jumping, leading to species diversification (Thines 2019). Remarkably, diverse protists and fungi from the same taxonomic clades as plankton parasites of algae were found in marine invertebrates (Holt et al. 2022), raising the question of whether the same organisms are infecting a wide array of hosts. This process has been shown for the genus *Labyrinthula*, which can infect various seagrass species and is associated with other algae and phytoplankton (Bower et al. 1998).

2.2 Ecological roles of plankton parasites of algae

Plankton parasites are abundant in aquatic ecosystems and impact host populations by modifying the interspecific competition between hosts and other species (Van Donk 1989). Plankton parasites adapted and co-evolved with their hosts in terms of metabolite production and use, as well as gene expression and catalytic function due to their long-term presence and adaptation to marine habitats (Alacid et al. 2017; Blanquart et al. 2016).

Parasites are considered integral components of co-evolved microbial communities and can be assessed to determine the health and functioning of aquatic ecosystems (Drew et al. 2021). Parasite diversity is connected to the health of aquatic communities, and itself plays a direct role in shaping and modulating algal populations (Deng et al. 2022b). Remarkably, plankton parasites can selectively prey on weaker individuals, as shown by the widespread aquatic thraustochytrids exploiting the diatom genus *Chaetoceros* (Laundon et al. 2021). The preferential infection of unhealthy algal cells promotes the overall health of the host population without impacting its density, a phenomenon typically associated with animal predators and their prey. Parasite-alga interactions are thus not always detrimental to the host population, and these dynamics were coined as healthy herd selection. Hence, host and parasite abundances are not always in phase, with a lag between the host and parasite cell densities akin to the temporal dynamics of predator-prey interactions.

Field studies showed that parasites are usually present in their host from 5 to 18 % by cell number in the algal population, and high competitive pressure exists between infective free-living zoospores of different species (Alacid et al. 2017). Hence, plankton parasites in oceans are presumably involved in more diverse and complex microbial interactions than expected (Bjorbækmo et al. 2020). Strikingly, parasitic infections of phytoplankton can also modify the microbiome surrounding the host cells in laboratory cultures, which may favor opportunistic organisms that prey upon algae (Klawonn et al. 2021). The changes in host-microbiome composition might also potentially disrupt co-evolved relationships between hosts and their symbionts, leading to disease emergence (Llewellyn et al. 2017).

Plankton parasites might have more ecological roles beyond the top-down control of the algal population and a number of examples has been reported for freshwater environments. The transfer of inaccessible organic matter from large, inedible hosts, such as the freshwater diatom *Asterionella*, to zooplankton is enabled through predation on the zoospores, a process framed as the "mycoloop", which has been shown for chytrids infecting freshwater diatoms (Kagami et al. 2014). Furthermore, the fungal shunt, i.e., photosynthetic carbon being diverted from the microbial loop to fungal parasites, promotes zooplankton-mediated remineralization (Klawonn et al. 2021). In laboratory studies, freshwater plankton parasites possess a significant capacity to structure the plankton community by increasing the trophic chain length and channeling

the carbon flow (Klawonn et al. 2021). Freshwater parasitic fungi could hence shunt 20 % of the total diatom-derived photosynthetic carbon as they themselves are being grazed by copepods, leading to an increase in carbon transfer to higher trophic levels and the bypass of the microbial loop (Klawonn et al. 2021). Parasite-infected algal cells and free-living flagellated parasitic zoospores contain a high amount of polyunsaturated fatty acids (PUFAs) and sterols, which represent a nutrient-rich food source for grazers and zooplankton (Gerphagnon et al. 2019). Further studies should focus on whether similar processes, i.e., the fungal shunt and the "mycoloop", also occur in the oceans.

2.3 Life cycles, infection stage, and cellular invasion

The shared property among plankton parasites of algae is their ability to produce small, free-living zoospores to ensure dispersal in the water column during their life cycles (Cachon and Cachon 1987). The zoospores might require chemical cues to find new hosts, and swimming might be directed by chemoattraction, i.e., an active movement in response to a chemical gradient. Generally, symbiotic relationships rely on nutrient acquisition from recruited microbial partners, and the active migration towards, and colonization is often driven by chemotaxis (Raina et al. 2019). Chemotaxis governs the movement of marine microbes, particularly prokaryotes, towards phytoplankton-derived compounds, as demonstrated in field assay experiments (Raina et al. 2022). Positive correlations were found between marine bacteria and compounds such as the sugar alcohol erythritol and aminopiperidin-2-one, which were investigated in laboratory-based chemotaxis assays. More than half of the tested compounds induced a positive chemotactic response and are commonly used by marine bacteria to support their growth. For alga-bacterium interactions, bacterial chemotaxis has been investigated in laboratory-controlled models (Sonnenschein et al. 2012). The role of dimethylsulfoniopropionate (DMSP) as a general, broad, and relatively non-specific chemical cue of the marine microbial food web has been found in phytoplankton and bacteria (Seymour et al. 2010). However, in the case of eukaryotic marine parasites of algae, few studies have been conducted to identify the chemoattractant released by susceptible hosts. In cultures of the dinoflagellate *Alexandrium minutum*, DMSP is hydrolyzed into dimethylsulfide (DMS), which led to the maturation of the parasite *Parvilucifera*, enabling the transition from the immature to the mature sporont that releases free-living zoospores (Garcés et al. 2013b). Genes of signaling pathways involving proteases and transporters were overexpressed, suggesting that the free-

living parasitic zoospores can perceive and sense chemical cues (Farhat et al. 2018).

The chemo-attractive properties of metabolites were investigated by exogenous addition to cultures of plankton parasites. For instance, the ectoparasite dinophyte *Paulsenella* sp. is attracted to glucose and mannose, common sugars released by the centric diatom *Streptotheca thamesis*, and the attraction was lower in the dark period (Schnepf and Drebes 1986). Several studies have focused on the chemo-attracting cues sensed by aquatic chytrid parasites. For instance, free-living flagellated chytrids were found to be attracted by whole-cell extracts of stressed hosts and a combination of carbohydrates in solution (Scholz et al. 2017). Furthermore, the marine chytrid species *Rhizophydium* is positively attracted to amino acids and carbohydrates, both being photosynthetic by-products (Muehlstein et al. 1988). Investigating the volatiles released by infected and non-infected hosts revealed different metabolic profiles, with a decrease in anti-fungal beta-ionone in chytrid-infected cells (Yoneya et al. 2021). Hosts might release diverse organic compounds that can serve as food and habitat-finding cues for grazers, defense against herbivores, and microbial interactions during the algal bloom (Saha and Fink 2022).

While parasite chemotaxis has been as yet insufficiently investigated in marine and freshwater environments due to the challenges in laboratory cultivation, the chemical exchange that facilitates and influences parasite infection in plants is well-researched. Plant exudates, i.e., volatiles, sugars, and amino acids, can accelerate the germination of terrestrial oomycetes. Zoospores of terrestrial oomycetes can be attracted to specific compounds released by plants, such as prunetin, daizein, and genistein (Judelson and Ah-Fong 2018). These isoflavones possess multifunctional roles and can influence encystment and germ tube orientation (Morris et al. 1998). Exogenous addition of sesquiterpenes, such as abscisic acid, attracts the zoospores of the parasitic oomycete *Plasmopara viticola*, which infects many plants (Kiefer et al. 2002). Abscisic acid is a known plant signaling molecule mediating seed dormancy, growth, and adaptation to environmental stresses (Hauser et al. 2011). In microalgae, this compound and several other phytohormones have been detected in a broad spectrum of microalgal lineages, including diatoms (Lu and Xu 2015), but it is not yet established how or whether they relate to plankton parasites. Notably though, adding phytohormones to microalgal cultures induces lipid production and promotes cell growth, which might play a role in the interactions with parasites (Yang et al. 2023). In plants, the chemotaxis of the oomycete parasites involves G-proteins (Judelson and Ah-Fong 2018). A G-protein coupled receptor was identified in unicellular marine eukaryotes, including 81 diatom and 24 dinoflagellate groups (Mojib and Kubanek

2020). Another study revealed that four diatoms share genes related to G protein-coupled receptors (Port et al. 2013). This evidence suggests that analogous receptor proteins and signaling pathways might be involved in the attraction and attachment of marine oomycetes and other parasites of algae. Furthermore, a repertoire of extracellular proteins is encoded within genomes of parasitic alveolates, suggesting a connection with cell wall degradation (Templeton and Pain 2016).

Pathogen-associated molecular patterns (PAMPs) are small molecular motifs conserved in pathogenic microbes (Mogensen Trine 2009). Many molecules can serve as PAMPs, including glycans and glycoconjugates. Multiple receptors, such as toll-like and pattern-recognition receptors, have been investigated in plants and animals but not yet in plankton parasites. However, to date, no studies have demonstrated whether marine plankton parasites of algae employ these molecular patterns. The latest whole-genome sequencing efforts might however reveal whether these receptors are present in plankton parasites and symbionts (Faktorová et al. 2020).

In terrestrial plants, pathogenic effectors can induce the modulation of immune responses (Dodds and Rathjen 2010). PAMPs are recognized by receptor proteins, also called pattern recognition receptors, that, once stimulated, lead to PAMP-triggered immunity. In seaweeds, such as the brown alga *Macrocystis pyrifera*, a local, inducible, autophagic mechanism serves in the defense against the marine oomycete *Anisolpidium ectocarpii* (Murúa et al. 2020). Phytoplankton hosts, i.e., unicellular photosynthetic eukaryotes, might not have evolved such elaborate molecular mechanisms to modulate immunity but might counteract cell invasion using other basal processes, such as programmed cell death and autophagy. These processes determine cell fate and can be triggered by various abiotic and biotic factors (Bidle 2016). Autophagy is also the hallmark of other pathogenic infections in the coccolithophore *E. huxleyi*, such as during the lytic phase induced by coccolithoviruses (Schatz et al. 2014). The coccolithoviruses manipulate their host lipid metabolism and alter glycosphingolipid production, regulating cell fate via programmed cell death (Vardi et al. 2012). Algal resistance might thus be modulated via the control of the programmed cell death machinery required for successful viral replication. It is unknown whether these processes are involved in the infection caused by eukaryotic parasites.

Due to the diversity of morphology and physiology of the algal species, distinct strategies of cellular invasion depending on the targeted host are expected. For instance, diatom hosts possess frustules, i.e., an external, siliceous part of the cell wall, which parasites encounter during cell invasion. Algicidal bacteria can attack diatoms by attaching and releasing enzymes to degrade this diatom matrix (Furusawa et al. 2003).

Coincidentally, co-existing eukaryotic parasites might use this bacterial action to invade and infect the algal cells alongside.

2.4 Parasite reproduction and dissemination

Plankton parasites share a similar pattern of reproduction and dissemination, alternating from a free-living phase (zoospore) and an intracellular parasitic phase (trophont and sporont) (Cachon and Cachon 1987). Generalist plankton parasites can also have a more complex life cycle that involves two or more hosts used for reproduction (Alacid et al. 2016).

Plankton parasites are characterized by these distinct infection stages, which involve specific metabolic pathways associated with growth and reproduction. Transcriptomics analysis of infective stages during *Amoebophrya* infection in the dinoflagellate host *Alexandrium* highlighted the diversification of transcribed metabolic pathways (Lu et al. 2014). Genes related to oxidative pathways, cell division, and proliferation were expressed during the maturation of the parasite-infected host cells. At the initial host encounter and penetration stage, the parasitic syndinian *Amoebophrya* induces genes related to cytoskeleton organization and signal transduction, including genes coding for G protein and guanine nucleotide-binding proteins (Lu et al. 2014).

In *Amoebophrya* parasitism, the host chloroplast and mitochondria remain fully functional after the cell invasion, stressing the importance of photosynthesis for parasite reproduction (Kayal et al. 2020). This occurrence contrasts with many plankton parasites, such as *Parvilucifera*, that kill their host before digesting them, which prevents cells from evolving resistance mechanisms in the course of the infection. By keeping the host cell alive with physiological functions, parasites such as *Amoebophrya* enable parasite reproduction quickly and efficiently. Moreover, *Amoebophrya*-infected cells remain motile, unlike *Parvilucifera* parasites that induce loss of motility in dinoflagellates at the initial cell invasion stage (Decelle et al. 2022). This phenomenon would serve the parasite by enabling dissemination to new environments while being protected inside its host. These features might have evolved multiple time in the Alveolates, as Perkinsids and Syndinians exhibit extracellular proteins to enable cell invasion (Templeton and Pain 2016). The metabolism of *Amoebophrya* parasites is sustained by the continuous carbon production of the host, a metabolic process shared by more distantly related apicomplexan parasites such as *Toxoplasma* and *Plasmodium* that infect human cells (Decelle et al. 2022). Strikingly, *Colpodella*, a predatory alveolate and close cousin to human parasites from Apicomplexa clade, as well as the intracellular fish-parasite *Perkinsus*, have developed apical

complexes and secretion systems that are indeed used during cellular infection (Brugerolle 2002).

Plankton parasites of algae employ a low-cost energy scavenging and harvesting strategy by altering the host's metabolism. The marine oomycete *Lagenisma coscinodisci* can hijack the algal metabolism by overexpressing two beta-carboline alkaloids (Figure 2), which are responsible for diatom cell division arrestment and conversely speed up the infection rate in the population (Vallet et al. 2019). This finding is also an example of plankton parasites counteracting the host defense by inhibiting host cell division and using the host machinery. However, the beta-carbolines constitute a group of alkaloids with antioxidant properties (Moura et al. 2007), and they may play a more diverse role in *Lagenisma* infection by mitigating the effect of oxidative stress induced by cell invasion and metabolic reshuffling.

Another example of a host metabolite serving in the reproduction of plankton parasites is the volatile compound DMS (Figure 2). This chemical cue mediates the transition from the trophont to the mature reproduction stage in the intracellular phase, i.e., the sporont. DMS was added exogenously to laboratory cultures of the dinoflagellate *Alexandrium minutum* infected with the alveolate parasite *Parvilucifera sinerae*, and induced the activation and maturation into the sporont (Garcés et al. 2013b). DMS effectively caused the release of the free-living zoospores, which could infect new surrounding host cells (Figure 2). Whether this compound has a broad-spectrum induction activity in other algal hosts has not yet been investigated.

Parasitic and pathogen infections in algae are often characterized by programmed cell death and the induction of reactive oxygen species, for example, during the viral infection of the coccolithophore *Emiliana huxleyi* (Vardi et al. 2012). On the one hand, plankton parasites of algae have sex and use meiosis to conduct genetic intermixing and evolve. These processes also occur after the cellular invasion and maturation of the trophont into the sporont (Jephcott et al.

2016). On the other hand, alga-parasite and alga-predator interactions are subjected to the Red Queen dynamics, defined as a long-term co-evolutionary motion in which species must constantly adapt, evolve, and proliferate to survive (Råberg et al. 2014; Van Valen 2014). Hence, sex is maintained as it creates novel genotypes with a selective advantage. This hypothesis was investigated in the predator-prey system of rotifer-alga *Brachionus-Chlamydomonas*. Sex rates were high in changing environmental conditions, increasing selection pressure on these organisms (Felpeto et al. 2013). In more constant conditions, predators evolved rapidly to lower sex levels, indicating that selection pressure can shift a phenotypic trait. High potential for Red Queen dynamics has been demonstrated in plankton parasites when challenging clones of the dinoflagellate *A. minutum* with *P. sinerae* (Råberg et al. 2014). These winnerless coevolution dynamics characterize parasitic chytrids (Kyle et al. 2015) and marine viruses (Avrani et al. 2012) in aquatic environments. More insights into the molecular mechanisms involved in plankton parasite reproduction are expected from recent whole-genome and transcriptome sequencing and analysis (Faktorová et al. 2020).

2.5 Effect of abiotic factors on alga-parasite interactions

Plankton parasites are influential in aquatic ecosystems as they facilitate energy flows through the food web and control the population of algal species (Deng et al. 2022b; Park et al. 2021). The changes in environmental factors, such as significant modification of light, temperature, salinity, and nutrient levels, can conceivably impact the algal hosts and their associated microbiota (Menaa et al. 2020). For instance, increased sea surface temperature might lead to modulation of parasitism in aquatic ecosystems (Wood et al. 2023). A study using 1000-L indoor mesocosm showed that a +4 °C warming treatment accelerated parasitic infections and the bloom
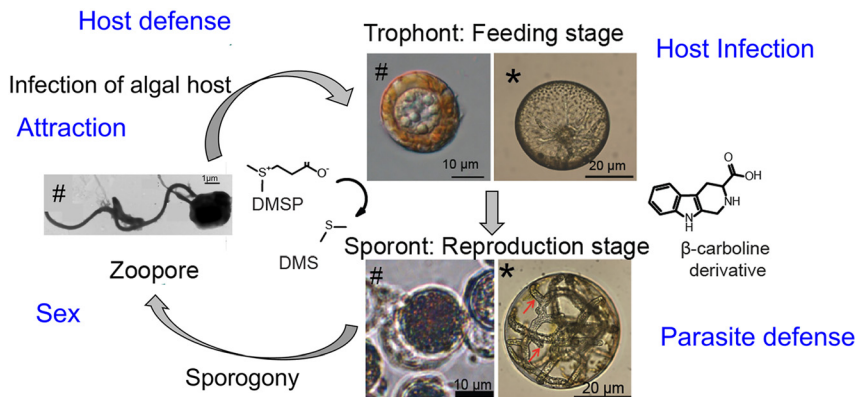

Figure 2: Life stages of the plankton parasitoids *Parvilucifera rostrata* (#) and *Lagenisma coscinodisci* (*) that infect the dinoflagellate *Alexandrium minutum* and the diatom *Coscinodiscus granii*, respectively. Biological functions involved in alga-parasite interactions (in blue) and the two metabolites DMS and β-carboline contributing to the infection processes are highlighted. Images reproduced from Lepelletier et al. (2014b) and Vallet et al. (2019), with permission.

termination of the diatom *Synedra* (Frenken et al. 2016). Conversely, in a laboratory-based infection assay conducted with the perkinsid *Parvilucifera* targeting two bloom-forming dinoflagellates, the toxin-producer *Alexandrium minutum* and non-toxic *Heterocapsa triquetra*, the parasite favored one or the other host species depending on the incubation temperature (Schmitt et al. 2022). Remarkably, higher infection rates of *A. minutum* were recorded at higher temperatures, while a lower temperature decreased the overall infection rates in both algal hosts. This is also because *Parvilucifera*, similar to *Amoebophrya*, forms a resting stage in its host to survive the winter months (Chambouvet et al. 2011; Lepelletier et al. 2014a). Hence, plankton parasites and their algal hosts will employ different adaptation responses to a temperature variation, and some species will be negatively impacted while others will thrive.

Other abiotic factors, such as salinity, can affect host susceptibility and parasite infectivity. For instance, *Parvilucifera* parasites thrive at lower salinity, promoting sporangial germination and higher infection rates (Figueroa et al. 2008). Concurrently, higher salinity correlates with losing fungal diversity in coastal waters (Rojas-Jimenez et al. 2019). Meanwhile, the algal hosts cope with a salinity increase by accumulating lipids to strengthen their membranes and enhance the production of osmoprotectant metabolites such as zwitterions (Fenizia et al. 2020, 2021). The change of these abiotic factors, such as temperature and salinity, might cause generalist plankton parasites to attempt a jump from one host to another. Environmental refugees were also proposed for plankton parasites, enabling the parasite or the host to subsist under global change (Gsell et al. 2023). Due to the tolerance range and sensitivity of many species to environmental factors, the outcome of alga-parasite interactions can be affected by abiotic changes. Non-specific generalist parasites can flourish in new hosts, while specialist parasites relying on one host species may face a higher risk of extinction. Hence, the persistence of plankton parasites in aquatic ecosystems will be determined also by the susceptibility of the algal hosts and their ability to defend themselves, and the resilience of the free-living forms of parasites that infect new cells (Sures et al. 2023).

3 Strategies of algal host defense against parasites

Aquatic ecosystems are characterized by complex multi-species interactions that result from a long evolutionary history. Algal hosts, both at individual and species levels, have developed adaptation traits to defend against their co-evolving parasites (Rigaud et al. 2010). No known defense mechanism in phytoplankton is similar to the immune system of multicellular algae and other higher organisms. Hence, algae have evolved different strategies, including change of behavior, modulation of cell phenotype, or induction of sexual reproduction to increase the acquisition of new genetic traits via meiosis (Van Donk et al. 2011).

Algae can increase their growth rate to produce a higher population count, representing an escape strategy of host cells to evade infected areas (Horas et al. 2018). Modification of swimming rate or direction of movement to escape contaminated zones might be used by dinoflagellates and other flagellated hosts. Indeed, high-speed video recordings could reveal how individual algal cells change direction while swimming and show the 'run-and-tumble' motion of the flagella, as in the species *Chlamydomonas reinhardtii* (Polin et al. 2009), or the silicate-directed movement of nutrient-starved diatoms in *Seminavis robusta* (Bondoc et al. 2019). Remarkably, when testing the effect of small-scale turbulence the infection of dinoflagellates by *Parvilucifera*, parasite prevalence was lower, and host cell abundance was reduced (Llaveria et al. 2010). This finding indicates that the surrounding environment also plays a role in the parasite foraging of their hosts.

Dinoflagellates are also characterized by a transitional lifestyle between active, swimming flagellate cells and a non-motile, dormant cyst that can persist for several years in sediments (Bravo and Figueroa 2014). The production of resistant cysts might represent a joint host defense strategy (Toth et al. 2004). The shift into resistant, resting cysts was also observed for the marine dinoflagellate *Alexandrium ostenfeldii* during exposure to filtrates of *Parvilucifera*-infected cultures (Toth et al. 2004). In the dinoflagellate host *Fragilidium duplocampanaeforme*, the induction of resistant cysts required direct contact with *Parvilucifera* zoospores (Lee and Park 2017). Therefore, it is unclear whether a specific waterborne chemical cue, or another mechanism is responsible for the induction of resistant cysts in dinoflagellates. However, experimental evidence with the dinoflagellate *Scrippsiella* showed that physical contact is required to trigger encystment, suggesting a relatively non-specific response of the algal hosts (Uchida 2001).

The physiological status and morphology of the algal host cells can play a substantial role in their susceptibility to plankton parasites, as shown in cultures of the diatom *Chaetoceros* subjected to chytrid parasites (Laundon et al. 2021). Furthermore, the formation of the coccoid non-motile stage was induced during the infection of the dinoflagellate *Symbiodinium natans* by the alveolate parasite *Parvilucifera corolla*, indicating that the alga might avoid or minimize infection by transitioning to another life cycle phase (Rodríguez and Figueroa 2020).

Plasticity is a common feature in unicellular planktonic algae, characterized by changes in cell size and composition (Raven 1986). The morphological plasticity can be induced by chemical cues released by grazing copepods, i.e., copepodamides (Selander et al. 2019). Additionally, these lipid cues induce toxin production in the diatom *Pseudo-nitzschia seriata* and the dinoflagellate *Alexandrium minutum* (Selander et al. 2015), but their effect on plankton parasites is not yet known. Another example of the morphological switch from a susceptible to a resistant subpopulation of cells concerns the bloom-forming coccolithophore *E. huxleyi*. Throughout the infection and direct contact with the lytic coccolithovirus (EhV), about 30 % of resistant cells appeared within the population and were characterized by a lack of flagella and thin scales (Frada et al. 2017). These non-motile cells exhibited a lower growth rate and overall fitness.

In non-motile algal hosts, such as some diatom species, regulation of the buoyancy, which can induce the sinking of cells and the production of mucilage to impede swimming parasites, has also been suggested as a defense strategy against plankton parasites (Van Den Wyngaert et al. 2022; Van Donk et al. 2011). Furthermore, diatoms possess silicified cell walls, which support the activity of extracellular carbonic anhydrase enzymes to acquire inorganic carbon (Jensen et al. 2019). Despite the expected physical restriction, plankton parasites successfully attack and infect the vegetative stage of diatoms with their silicified walls (Drebes 1966). However, infected cells might significantly increase their density, raising the chance of removing them from the population by sinking.

In diatoms, sexual reproduction can enable the appearance of resistant traits against parasites. Indeed, laboratory cultures of *Coscinodiscus wailesii* became resistant against *Lagenisma coscinodisci* after one meiotic event (Buaya et al. 2019). Host genetic diversity is an essential factor in the resilience against infections, and it allows the host to co-evolve with their parasites (Hiillos et al. 2023). The coccolithophore *E. huxleyi* uses its haploid phase as an escape mechanism against giant phycodnaviruses (Frada et al. 2008). Exposing the susceptible diploid algal stage induced the resistant haploid phase. Hence, the genes of dominant diploid clones are transmitted to the next generation in a virus-free environment. This strategy was also observed in the bloom-forming dinoflagellate *Alexandrium minutum*, which could shift its sexual recombination rate in response to the perkinsid parasite *Parvilucifera sinerae* (Figueroa et al. 2010). In field studies, host resistance differed depending on the algal species, suggesting that independent mechanisms might mediate the resistance against different parasite species (Blanquart et al. 2016). These processes might occur more often than expected, as co-infections of two or more parasites within one host are common.

Another proposition of algal resistance in phytoplankton involves regulating the programmed cell death machine during viral infection. Indeed, the analysis of genomic contents related to the susceptibility of algae to coccolithoviruses yielded one Bax inhibitor-1-like protein, which might serve as a cell death regulator by inhibiting Bax-induced cell death (Kegel et al. 2013). Notably, specific metabolic biomarkers for algal resistance to viral infection have been identified in a group of glycosphingolipids termed resistance-specific glycosphingolipids (Schleyer et al. 2023). These lipids contain an uncommon trihydroxylated long-chain base 18:0, which might hinder viral adsorption to the cells by impeding membrane fusion during the virus' entry. Remarkably, the course of viral infection of *E. huxleyi* cultures was also characterized by the formation of abundant, less infected aggregates of cells, which might trap newly produced virions, export them to the photic zone, and prevent dissemination in the bloom (Vincent et al. 2021). These findings suggest that distinct mechanisms of algal defense exist, and several defense strategies could protect the host population from the parasite attack of one clade versus another.

Algal host defense against marine parasites remains a new exploratory research field, with little knowledge on the molecular basis of cell resistance, especially against eukaryotic plankton parasites. Considering the high number of algal metabolites reported for their antibiotic, antiparasitic, and anti-fungal properties (Bhowmick et al. 2020; Zhang et al. 2023), we can expect that some of these substances might serve in the defense against plankton parasites.

In diatom hosts, oxylipins are involved in the chemical defense against grazers and algal sexual reproduction (Pohnert and Boland 2002). Oxylipins, oxygenated metabolites of fatty acids, are formed from polyunsaturated fatty acids (PUFAs) and have essential roles in cellular physiology, stress, and immune responses in eukaryotes (Gabbs et al. 2015). These compounds are involved in several ecological and biological functions, including deterrence against grazers, regulation of cell population, and mediating carbon recycling (Ruocco et al. 2020). In plants, pathogen-induced patatin-like lipid acyl hydrolase can contribute to host resistance against obligate parasites by inducing oxylipin biosynthetic genes and promoting cell death (Camera et al. 2009). Fatty acid precursors of specific oxylipins might affect and promote cell resistance against pathogens. Generally, oxylipins are versatile as they regulate plant immunity and control lifestyle and quorum-sensing (QS) signaling in bacteria and fungi (Beccaccioli et al. 2022). Hence, investigating oxylipins in alga-parasite interactions, particularly in the infection with intracellular parasitoids, represents a strenuous task as both the host and

the symbiont might produce and use the same molecules for distinct purposes. As oxylipins possess many repellent effects against various aquatic organisms (Friesen and Detwiler 2021), they may play a more substantial role in the defense against plankton parasites of algae.

In dinoflagellate hosts, lytic substances are usually involved in the allelopathic interactions with other competing species and cause damage to cell integrity and disturbance of photosynthetic activities (Poulin et al. 2018; Tillmann et al. 2007). Allelopathy refers to any metabolite exuded by one organism that affects the growth of another (Granéli and Hansen 2006). Remarkably, a similar strategy is employed by different resistant dinoflagellate species to target eukaryotic plankton parasites such as *Amoebophrya* sp. (Long et al. 2021). Lysis of the cell membranes of the free-living parasite forms in lab-cultures was induced by adding *Alexandrium minutum* filtrates and by non-contact dual cultivation with resistant hosts, indicating that a waterborne chemical cue is involved in the host defense. *Scrippsiella donghaienis* did not cause parasite lysis, but filtrates decreased infectivity, i.e., parasite entry and reproduction in the host cells were impeded when filtrates from resistant hosts were added. This study highlights the diversity of algal defense strategies, which most likely involve different lytic metabolites used by algal species against plankton parasites. This result most likely derives from the long co-evolutionary history shared by algae and parasites, with a co-existence that repeatedly shaped the metabolism of each organism over time.

4 Plankton parasites of algae in interactions with other microbes

The algal holobiont comprises the eukaryotic photosynthetic host and various microbial species within and around the algal cell, including plankton parasites (Simon et al. 2019). This holobiont exists for algal hosts living in marine and freshwater environments; similarities are observed between these ecosystems. Chemical cues and signals play a significant role in the interactions within and across algal holobionts, influencing processes like chemical defenses, nutrient acquisition, and biofilm formation (Dittami et al. 2021). The interaction between the algal host and eukaryotic parasites can expand to involve other microorganisms, such as bacteria, viruses, and competing eukaryotic parasites, translating into a complex multipartite interaction. Additionally, grazers at the higher trophic levels can disrupt the host-parasite dynamics by feeding on cells and interfering with parasite reproduction (Frenken et al. 2020). Different interactions can coexist during the various phases of algal blooms, such as the interplay of bacteria-algae associations in nutrient exchanges, signaling defense against plankton parasites, competition between susceptible and resistant algae, and predation by grazers (Figure 3). The success of parasite invasion might be influenced by the core microbiome of the host, depending on whether the existing bacteria and fungi can provide a metabolic defense against the invader, especially for seaweed hosts (van der Loos et al. 2019). However, there is limited research
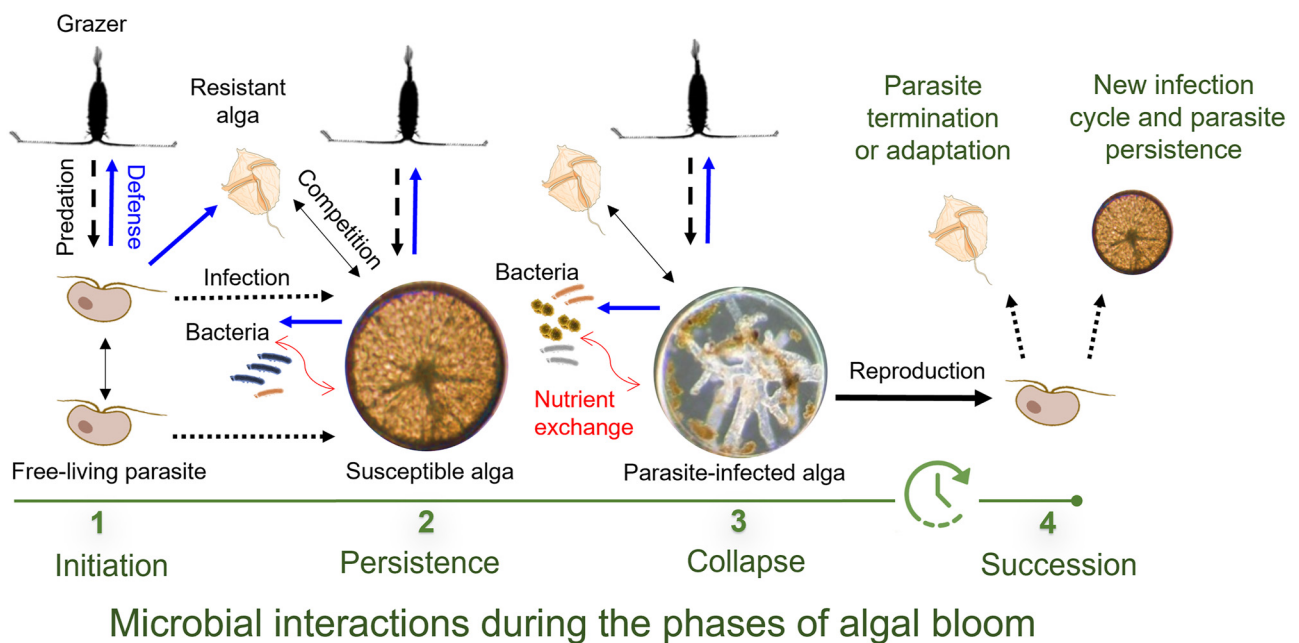

Figure 3: Types of interaction between algal hosts, plankton parasites, and other associated microorganisms during the phases of algal blooms, from initiation, persistence, collapse, and succession.

on the role of the holobiont in alga-parasite interactions. This section focuses on the effect of third-party microorganisms on alga-parasite interactions.

4.1 Interaction with larger predators

Grazers can preferentially prey on infected phytoplankton cells, hence sustaining the growth of the predators during an algal bloom (Evans and Wilson 2008; Rasconi et al. 2014). Conversely, another study showed that viral infection could also deter grazing by copepods (Vermont et al. 2016). These contrasting findings indicate the complexity of grazers' interactions with algae and their parasites. DMS, produced by the algal hosts, is a key player in the global sulfur cycle and performs multiple functions in marine microbial interactions (Mahajan et al. 2015; Yoch 2002). Remarkably, DMS has a role in parasitic infection and can serve as a chemoattractant for diverse protist grazers that prey on phytoplankton hosts (Shemi et al. 2021). Plankton parasites and grazers compete and sometimes target the same algal species, thus acting as a critical top-down control of the host populations in aquatic ecosystems (Lima-Mendez et al. 2015).

The predation on infected cells has been shown for several algal host species and their plankton parasites. For instance, grazers can interfere with host-parasite interactions by feeding on infected cells, as demonstrated during the bloom of *Planktothrix rubescens* parasitized by chytrids (Frenken et al. 2020). Ingestion of parasite-infected algae is not restricted to the diet of copepods, as *Parvilucifera*-infected cells of the bloom-forming dinoflagellate *Akashiwo sanguinea* were rapidly ingested by the algal predator *Luciella masanensis* (Park et al. 2021). In this laboratory-based assay, the parasitoid presence led to its co-occurrence with both prey and predator, suggesting that parasites play a role as a mediator in planktonic predator-prey interactions. Furthermore, in cultures, grazers ingested the infective zoospores, which can lead to an 80 % decrease in parasite infection of *Akashiwo sanguinea* (Johansson and Coats 2002). These findings did not fully translate into alga-virus interactions, as the predator *Oxyrrhis marina* did not ingest more virus-infected cells than healthy ones (Goode et al. 2019). In diatom hosts, chytrid-infected cells of the host *Asterionella formosa* were not grazed by the copepods. Still, the survival rate of the predator increased following a diet of infected cells, suggesting that the predators were feeding on the free-living parasitic zoospores instead (Kagami et al. 2011). Grazers could also function as a transmission vector for parasites of algae, as shown for coccolithoviruses (Frada et al. 2014).

4.2 Interactions with bacteria

Marine bacteria, including the most abundant clade, SAR11, are significant third-party microorganisms in alga-parasite interactions, as they are ubiquitous in oceans and found in association with all known algal hosts targeted by plankton parasites (Giovannoni 2017). In particular, many pathogenic bacteria are naturally more abundant during the decline phase of the diatom blooms (Branscombe et al. 2024). A unique bacterial consortium is usually present in the near surroundings of the algae, a process termed microbial gardening. For instance, the green macroalga *Ulva* enriches its environment with metabolites that attract and stimulate the growth of microorganisms necessary for algal morphogenesis (Wichard et al. 2015). These bacteria associated with phytoplankton and seaweeds can encounter plankton parasites in their free-living or host-associated form. Questions arise about whether algae possess a core bacterial microbiome that can be detected regardless of geographical location, environmental conditions, and physiological status (Dittami et al. 2021). The study of bacterial microbial communities associated with the brown alga *Saccharina latissima* demonstrated a high species variability (Tourneroche et al. 2020).

Further, the microorganisms were organized and partitioned according to the algal tissues. This observation was also made for green macroalgae, where the host releases DMSP, recruiting specific bacteria associated with the rhizoid and supporting the algal morphogenesis (Kessler et al. 2018). In turn, some thallus-specific bacteria release the osmoprotectant ectoine that protects the host during salinity stress (Vallet et al. 2021).

In multicellular algae living with epiphytic and endophytic microorganisms, bacterial symbionts might serve to protect against plankton parasites by producing bioactive molecules, and this might be a similar host strategy to that of mosquitoes harboring *Wolbachia* bacterial symbionts that protect against Dengue virus (Hoffmann et al. 2011). In amphibians, defensive bacteria associated with the skin can reduce their host susceptibility against chytrids (Bletz et al. 2013). These examples in terrestrial organisms suggest that bacterial symbionts can contribute to the host's defense against parasites, which will also vary according to the environmental conditions (Hopkins et al. 2017).

Marine bacteria can produce and release compounds used by the algal host (Amin et al. 2012, 2015), potentially affecting plankton parasites. Indeed, marine bacteria are well known for QS signaling, which enables the production of specific signaling molecules based on the cell population density and regulates functions such as virulence, niche colonization, biofilm formation, and toxin production (Atkinson and Williams 2009).

Hence, marine bacteria and their chemical signaling might have a cryptic but significant role in algal hosts that are parasitized by plankton parasites.

Bacterial QS signaling is also involved in the induction of virulence factors in pathogen-host associations (Zhou et al. 2016), for instance increasing the mortality of the alga *Emiliania huxleyi* (Harvey et al. 2016). Conversely, another study revealed that the bacterial QS compound 2-heptyl-4-quinolone protects the alga *E. huxleyi* from viral attacks (Pollara et al. 2021). Algal cells could get infected with viral entry, but replication and release were inhibited. Further studies should focus on testing the role of QS molecules in the infectivity of plankton parasites to provide insights into their potential influence on alga-parasite interactions.

Remarkably, marine bacteria have evolved lifestyle strategies that enable them to shift from mutualistic to pathogenic towards their algal hosts, which is sustained by the production of bioactive metabolites that serve the new role. The most outstanding example is an α-proteobacterium from the Roseobacter clade, *Phaeobacter gallaeciensis*, which promotes the growth of its algal host *E. huxleyi* by secreting auxins (Seyedsayamdost et al. 2011) at first. In response to the senescent host releasing *p*-coumaric acid, this bacterium switches to a pathogenic lifestyle by producing roseobacticides, which lyse *E. huxleyi* at a concentration of 2.2 μM. Another α-proteobacterium, *Sulfitobacter*, becomes a pathogen of *E. huxleyi* in the presence of algal DMSP (Barak-Gavish et al. 2023). *Sulfitobacter* can compete with pathogenic *Phaeobacter* species and protect *E. huxleyi* in laboratory cultures (Beiralas et al. 2023). These observed contrasting effects on algae might explain the diverse and complex multi-species plankton interactions (Deng et al. 2022a).

Other marine bacteria, such as *Kordia algicida,* are primary pathogens of algae, causing a rapid decline of algal populations due to the excretion of specific proteases that lyse algal membranes (Paul and Pohnert 2011). They also coexist with plankton parasites, as they arise together with eukaryotic plankton parasites at the collapse of algal blooms (Deng et al. 2022b).

During indoor enclosure experiments, algicidal bacteria were found to induce the bloom termination of the diatom *Chaetoceros socialis*, leading to the rise of an algal competitor, *Phaeocystis*, which is resistant to the bacterial lytic activity (Bigalke et al. 2019). This occurrence might hinder plankton parasites that target *Chaetoceros*, i.e., thraustochytrids, whose existence would also be threatened by these co-occurring natural bacteria. Considering that thraustochytrids can infect *Chaetoceros* senescent cells (Laundon et al. 2021), the actual effect of algicidal bacteria on eukaryotic plankton parasites can be questioned. Indeed, as these bacteria target and co-exist

with the same algal host that plankton parasites prey on, further studies using tripartite interactions are needed to reveal their potential role in parasitic infection and host defense.

Furthermore, during parasitic infection on phytoplankton cells, bacterial colonization is significantly promoted in fungal-infected cells in comparison to non-infected cells in the cultured model diatom *Synedra* infected by *Zygophlyctis* (Klawonn et al. 2023). In this laboratory-based study, fungal infections also reduced the formation of aggregations of algal cells and consequently modified the bacterial microbiome's abundance in the surrounding cells (Klawonn et al. 2023). In four freshwater algal species infected by the parasite *Amoeboaphelidium protococcarum* cultivated in photobioreactor systems, the overall bacterial diversity increased, with species-specific differences being observed over time (Höger et al. 2021). In another laboratory-based assay, the infection by the chytrid *Rhizophydiales* could also modify the bacterial species composition surrounding its diatom host *Asterionella* (Klawonn et al. 2021). The shift in the bacterial community composition upon viral infection was also detected in large-scale mesocosm experiments, followed by an increase in the extracellular release of acidic polysaccharides that contributed to the ocean carbon sink (Vincent et al. 2023). These examples indicate that bacteria interact with plankton parasites, and their presence is modulated during parasitic infection of algae.

4.3 Interactions with other unicellular eukaryotes

Chemical interactions between plankton eukaryotic parasites and other protists most likely occur in oceans. Still, as they are often short-lived, however, plankton parasites might not appear in large-scale field surveys recorded at specific locations and times. The species composition of the plankton communities can be derived from whole microbiome analysis studying microbial interactions in laboratory-based co-culture assays (Bjorbækmo et al. 2020). However, few studies have yet surveyed the role of single-cell eukaryotes on alga-parasite exchanges – future exploration using multipartite interactions in laboratory-based experiments is needed. Competitive and interdependent interactions might emerge within the algal population as novel species of plankton parasites are continuously being discovered (Buaya et al. 2021; Garvetto et al. 2019; Reñé et al. 2021; Van den Wyngaert et al. 2017). Since taxonomically different parasites can target and infect the same clade of algal hosts, we can expect highly competitive interactions between the co-existing microbes, with different chemical cues used for host foraging and cell attachment. During cross-infection studies, the perkinsid parasite

Parvilucifera corolla could infect the chlorophyte *Pyramimonas* without developing its complete life cycle by producing zoospores (Rodríguez-Martínez et al. 2020). The authors hypothesized that parasites might attempt to infect co-existing algae belonging to a completely distinct clade, leading to a parasite population sink, i.e., enabling parasite speciation and radiation to other, less frequent hosts. Hence, host specificity allows parasite speciation, which might be influenced by environmental and geographic factors (Brunner and Eizaguirre 2016).

Plankton parasites may alter the outcome of host-species interactions, such as competition, mutualism, and predation. In a meta-analysis based on phylogenetic studies, parasites adversely affected host-species interactions in aquatic habitats but conversely provided beneficial effects for terrestrial hosts (Hasik et al. 2023). These findings consolidate that an organism can be a parasite in one environment while shifting to a mutualistic or commensal lifestyle in another as it encounters other host species. Microsporidia from the kingdom of Fungi are common endoparasites infecting *Daphnia*, small aquatic crustaceans that prey on microalgae (Valois and Poulin 2015). When grazing predators were infected, they exhibited reduced fecundity under scarce resources and without the presence of virulent parasitic individuals. However, when more virulent parasites were present in the host, the infected grazer was more fecund (Rogalski et al. 2021). Another member of the fungal kingdom, *Aspergillus pseudoglaucus*, was isolated from a microalgal culture and cultivated in the presence of the dinoflagellate *Prorocentrum lima* (Berry et al. 2023). While in close physical contact with the fungus, the dinoflagellate released higher concentrations of toxins, including okadaic acid and dinophysistoxin 1, which might suggest a potential role in the algal defense. Remarkably, the alkaloid saxitoxin produced by the dinoflagellate genus *Alexandrium* was detected in higher amounts in *Amoebophrya*-infected cultures than in healthy cells but was not found in the free-living zoospore stage of the parasite (Kim and Park 2016). The function of toxins produced by bloom-forming harmful algae in the infection process has yet to be revealed. Future studies could explore the influence of third-party microbes on parasite infectivity during different bloom phases and whether they are beneficial or detrimental to the infection success of algae.

5 Conclusion and perspectives

Aquatic environments foster a high chemical connectivity and signaling between algae, plankton parasites, and other microorganisms. Evidence suggests that plankton parasites infecting algae are key players that balance aquatic food webs and contribute to carbon fixation. Parasite-infection of algae can increase grazer feeding and be of interest in aquaculture as the infection increases lipid content in cells. Plankton parasites are substantial drivers that shape, control, and regulate algal populations in aquatic ecosystems. Their positive effect as herd control is becoming more evident and reveals that parasites are a crucial pillar for the health and balance of aquatic ecosystems. Future research on the chemical signaling mediating alga-parasite interactions will highlight the mechanisms supporting cellular infection and host defense. Studying alga-parasite interactions at the community level and in field studies will further reveal the biological complexity of microbial interactions in plankton and the system's resilience to global change.

References

Alacid, E., Park, M.G., Turon, M., Petrou, K., and Garcés, E. (2016). A Game of Russian roulette for a generalist dinoflagellate parasitoid: host susceptibility is the key to success. *Front. Microbiol.* 7: 769.

Alacid, E., Reñé, A., Camp, J., and Garcés, E. (2017). In situ occurrence, prevalence and dynamics of *Parvilucifera* parasitoids during recurrent blooms of the toxic dinoflagellate *Alexandrium minutum*. Front. Microbiol. 8, https://doi.org/10.3389/fmicb.2017.01624.

Amin, S.A., Hmelo, L.R., van Tol, H.M., Durham, B.P., Carlson, L.T., Heal, K.R., Morales, R.L., Berthiaume, C.T., Parker, M.S., Djunaedi, B., et al. (2015). Interaction and signalling between a cosmopolitan phytoplankton and associated bacteria. *Nature* 522: 98–101.

Amin, S.A., Parker, M.S., and Armbrust, E.V. (2012). Interactions between diatoms and bacteria. *Microbiol. Mol. Biol. Rev.* 76: 667–684.

Anderson, R.M. and May, R.M. (1981). The population dynamics of microparasites and their invertebrate hosts. *Philos. Trans. Roy. Soc. London B Biol. Sci.* 291: 451–524.

Anderson, S.R., Blanco-Bercial, L., Carlson, C.A., and Harvey, E.L. (2023). Syndiniales parasites drive species networks and are a biomarker for carbon export in the oligotrophic ocean. bioRxiv, https://doi.org/10.1101/2023.06.29.547083.

Armbrust, E.V. (2009). The life of diatoms in the world's oceans. *Nature* 459: 185–192.

Atkinson, S. and Williams, P. (2009). Quorum sensing and social networking in the microbial world. *J. R. Soc. Interface* 6: 959–978.

Avrani, S., Schwartz, D.A., and Lindell, D. (2012). Virus-host swinging party in the oceans. *Mobile Genet. Elem.* 2: 88–95.

Barak-Gavish, N., Dassa, B., Kuhlisch, C., Nussbaum, I., Brandis, A., Rosenberg, G., Avraham, R., and Vardi, A. (2023). Bacterial lifestyle switch in response to algal metabolites. Elife 12, https://doi.org/10.7554/elife.84400.

Baumeister, T.U.H., Vallet, M., Kaftan, F., Guillou, L., Svatoš, A., and Pohnert, G. (2020). Identification to species level of live single microalgal cells from plankton samples with matrix-free laser/desorption ionization mass spectrometry. *Metabolomics* 16: 28.

Beccaccioli, M., Pucci, N., Salustri, M., Scortichini, M., Zaccaria, M., Momeni, B., Loreti, S., Reverberi, M., and Scala, V. (2022). Fungal and bacterial oxylipins are signals for intra- and inter-cellular communication within plant disease. Front. Plant Sci. 13, https://doi.org/10.3389/fpls.2022.823233.

Beiralas, R., Ozer, N., and Segev, E. (2023). Abundant *Sulfitobacter* marine bacteria protect *Emiliania huxleyi* algae from pathogenic bacteria. *ISME Commun.* 3: 100.

Bell, W. and Mitchell, R. (1972). Chemotactic and growth responses of marine bacteria to algal extracellular products. *Biol. Bull.* 143: 265–277.

Berry, O., Briand, E., Bagot, A., Chaigné, M., Meslet-Cladière, L., Wang, J., Grovel, O., Jansen, J.J., Ruiz, N., du Pont, T.R., et al. (2023). Deciphering interactions between the marine dinoflagellate *Prorocentrum lima* and the fungus *Aspergillus pseudoglaucus*. *Environ. Microbiol.* 25: 250–267.

Bhowmick, S., Mazumdar, A., Moulick, A., and Adam, V. (2020). Algal metabolites: an inevitable substitute for antibiotics. *Biotechnol. Adv.* 43: 107571.

Bidle, Kay D. (2016). Programmed cell death in unicellular phytoplankton. *Curr. Biol.* 26: 594–607.

Bigalke, A., Meyer, N., Papanikolopoulou Lydia, A., Wiltshire Karen, H., and Pohnert, G. (2019). The algicidal bacterium *Kordia algicida* shapes a natural plankton community. *Appl. Environ. Microbiol.* 85: 027799–18.

Bjorbækmo, M.F.M., Evenstad, A., Røsæg, L.L., Krabberød, A.K., and Logares, R. (2020). The planktonic protist interactome: where do we stand after a century of research? *ISME J.* 14: 544–559.

Blanquart, F., Valero, M., Alves-de-Souza, C., Dia, A., Lepelletier, F., Bigeard, E., Jeanthon, C., Destombe, C., and Guillou, L. (2016). Evidence for parasite-mediated selection during short-lasting toxic algal blooms. *Proc. Roy. Soc. B Biol. Sci.* 283: 20161870.

Bletz, M.C., Loudon, A.H., Becker, M.H., Bell, S.C., Woodhams, D.C., Minbiole, K.P.C., and Harris, R.N. (2013). Mitigating amphibian chytridiomycosis with bioaugmentation: characteristics of effective probiotics and strategies for their selection and use. *Ecol. Lett.* 16: 807–820.

Bochdansky, A.B., Clouse, M.A., and Herndl, G.J. (2017). Eukaryotic microbes, principally fungi and labyrinthulomycetes, dominate biomass on bathypelagic marine snow. *ISME J.* 11: 362–373.

Bondoc, K.G.V., Lembke, C., Lang, S.N., Germerodt, S., Schuster, S., Vyverman, W., and Pohnert, G. (2019). Decision-making of the benthic diatom *Seminavis robusta* searching for inorganic nutrients and pheromones. *ISME J.* 13: 537–546.

Bower, S.M., Blackbourn, J., and Meyer, G.R. (1998). Distribution, prevalence, and pathogenicity of the protozoan *Perkinsus qugwadi* in Japanese scallops, *Patinopecten yessoensis*, cultured in British Columbia, Canada. *Can. J. Zool.* 76: 954–959.

Branscombe, L., Harrison, E.L., Daniel, C.Z.Y., Keys, M., Widdicombe, C., Wilson, W.H., Cunliffe, M., and Helliwell, K. (2024). Cryptic bacterial pathogens of diatoms peak during senescence of a winter diatom bloom. *New Phytol.* 241: 1292–1307.

Bravo, I. and Figueroa, R.I. (2014). Towards an ecological understanding of dinoflagellate cyst functions. *Microorganisms* 2: 11–32.

Brugerolle, G. (2002). *Colpodella vorax*: ultrastructure, predation, life-cycle, mitosis, and phylogenetic relationships. *Eur. J. Protistol.* 38: 113–125.

Brunner, F.S. and Eizaguirre, C. (2016). Can environmental change affect host/parasite-mediated speciation? *Zoology* 119: 384–394.

Brussaard, C.P.D. (2004). Viral control of phytoplankton populations – a review. *J. Eukaryot. Microbiol.* 51: 125–138.

Buaya, A., Kraberg, A., and Thines, M. (2019). Dual culture of the oomycete *Lagenisma coscinodisci* Drebes and *Coscinodiscus* diatoms as a model for plankton/parasite interactions. *Helgol. Mar. Res.* 73: 2.

Buaya, A.T., Scholz, B., and Thines, M. (2021). A new marine species of *Miracula* (Oomycota) parasitic to *Minidiscus* sp. in Iceland. *Mycobiology* 49: 355–362.

Cachon, J. and Cachon, M. (1987). Parasitic dinoflagellates. In: Taylor, F.J.R. (Ed.). *The biology of dinoflagellates*. Blackwell Scientific Publications, Oxford, pp. 571–610.

Cahoon, L. (2016). Tychoplankton. In: *Encyclopedia of estuaries*. Springer, Netherlands, Dordrecht, p. 721.

Camera, S.L., Balagué, C., Göbel, C., Geoffroy, P., Legrand, M., Feussner, I., Roby, D., and Heitz, T. (2009). The *Arabidopsis* Patatin-Like Protein 2 (PLP2) plays an essential role in cell death execution and differentially affects biosynthesis of oxylipins and resistance to pathogens. *Mol. Plant-Microbe Interact.* 22: 469–481.

Chambouvet, A., Morin, P., Marie, D., and Guillou, L. (2008). Control of toxic marine dinoflagellate blooms by serial parasitic killers. *Science* 322: 1254–1257.

Chambouvet, A., Alves-de-Souza, C., Cueff, V., Marie, D., Karpov, S., and Guillou, L. (2011). Interplay between the parasite *Amoebophrya* sp. (Alveolata) and the cyst formation of the red tide dinoflagellate *Scrippsiella trochoidea*. *Protist* 162: 637–649.

Clarke, L.J., Bestley, S., Bissett, A., and Deagle, B.E. (2019). A globally distributed Syndiniales parasite dominates the Southern Ocean micro-eukaryote community near the sea-ice edge. *ISME J.* 13: 734–737.

Decelle, J., Kayal, E., Bigeard, E., Gallet, B., Bougoure, J., Clode, P., Schieber, N., Templin, R., Hehenberger, E., Prensier, G., et al. (2022). Intracellular development and impact of a marine eukaryotic parasite on its zombified microalgal host. *ISME J.* 16: 2348–2359.

Deng, Y., Mauri, M., Vallet, M., Staudinger, M., Allen, R.J., and Pohnert, G. (2022a). Dynamic diatom-bacteria consortia in synthetic plankton communities. *Appl. Environ. Microbiol.* 88: e01619–e01622.

Deng, Y., Vallet, M., and Pohnert, G. (2022b). Temporal and spatial signaling mediating the balance of the plankton microbiome. *Ann. Rev. Mar. Sci* 14: 239–260.

Dittami, S.M., Arboleda, E., Auguet, J.C., Bigalke, A., Briand, E., Cárdenas, P., Cardini, U., Decelle, J., Engelen, A.H., Eveillard, D., et al. (2021). A community perspective on the concept of marine holobionts: current status, challenges, and future directions. *PeerJ* 9: e10911.

Dodds, P.N. and Rathjen, J.P. (2010). Plant immunity: towards an integrated view of plant–pathogen interactions. *Nat. Rev. Genet.* 11: 539–548.

Drebes, G. (1966). Ein parasitischer Phycomycet (*Lagenidiales*) in *Coscinodiscus*. *Helgolander wissenschaftliche Meeresuntersuchungen* 13: 426–435.

Drew, G.C., Stevens, E.J., and King, K.C. (2021). Microbial evolution and transitions along the parasite–mutualist continuum. *Nat. Rev. Microbiol.* 19: 623–638.

Evans, C. and Wilson, W.H. (2008). Preferential grazing of *Oxyrrhis marina* on virus-infected *Emiliania huxleyi*. *Limnol. Oceanogr.* 53: 2035–2040.

Faktorová, D., Nisbet, R.E.R., Fernández Robledo, J.A., Casacuberta, E., Sudek, L., Allen, A.E., Ares, M., Aresté, C., Balestreri, C., Barbrook, A.C., et al. (2020). Genetic tool development in marine protists: emerging model organisms for experimental cell biology. *Nat. Methods* 17: 481–494.

Farhat, S., Florent, I., Noel, B., Kayal, E., Da Silva, C., Bigeard, E., Alberti, A., Labadie, K., Corre, E., Aury, J.-M., et al (2018). Comparative time-scale gene expression analysis highlights the infection processes of two *Amoebophrya* strains. Front. Microbiol. 9, https://doi.org/10.3389/fmicb.2018.02251.

Felpeto, A.B., Hairston, J., and Nelson, G. (2013). Indirect bottom-up control of consumer-resource dynamics: resource-driven algal quality alters grazer numerical response. *Limnol. Oceanogr.* 58: 827–838.

Feng, Y.-L. (2023). Chromatography high-resolution mass spectrometry in food and environmental chemistry. In: Picó, Y., and Campo, J. (Eds.), *Mass spectrometry in food and environmental chemistry*. Springer International Publishing, Cham, pp. 149–185.

Fenizia, S., Thume, K., Wirgenings, M., and Pohnert, G. (2020). Ectoine from bacterial and algal origin Is a compatible solute in microalgae. *Mar. Drugs* 18: 42.

Fenizia, S., Weissflog, J., and Pohnert, G. (2021). Cysteinolic acid is a widely distributed compatible solute of marine microalgae. *Mar. Drugs* 19: 683.

Figueroa, R.I., Garcés, E., Massana, R., and Camp, J. (2008). Description, host-specificity, and strain selectivity of the dinoflagellate parasite *Parvilucifera sinerae* sp. nov. (Perkinsozoa). *Protist* 159: 563–578.

Figueroa, R.I., Garcés, E., and Camp, J. (2010). Reproductive plasticity and local adaptation in the host–parasite system formed by the toxic *Alexandrium minutum* and the dinoflagellate parasite *Parvilucifera sinerae*. *Harmful Algae* 10: 56–63.

Frada, M., Probert, I., Allen, M.J., Wilson, W.H., and de Vargas, C. (2008). The Cheshire Cat escape strategy of the coccolithophore *Emiliania huxleyi* in response to viral infection. *Proc. Natl. Acad. Sci. U. S. A.* 105: 15944–15949.

Frada, M.J., Rosenwasser, S., Ben-Dor, S., Shemi, A., Sabanay, H., and Vardi, A. (2017). Morphological switch to a resistant subpopulation in response to viral infection in the bloom-forming coccolithophore *Emiliania huxleyi*. *PLOS Pathog.* 13: e1006775.

Frada, M. J., Schatz, D., Farstey, V., Ossolinski, Justin E., Sabanay, H., Ben-Dor, S., Koren, I., and Vardi, A. (2014). Zooplankton may serve as transmission vectors for viruses infecting algal blooms in the ocean. *Curr. Biol.* 24: 2592–2597.

Frenken, T., Alacid, E., Berger, S.A., Bourne, E.C., Gerphagnon, M., Grossart, H.-P., Gsell, A.S., Ibelings, B.W., Kagami, M., Küpper, F.C., et al. (2017). Integrating chytrid fungal parasites into plankton ecology: research gaps and needs. *Environ. Microbiol.* 19: 3802–3822.

Frenken, T., Velthuis, M., de Senerpont Domis, L.N., Stephan, S., Aben, R., Kosten, S., van Donk, E., and Van de Waal, D.B. (2016). Warming accelerates termination of a phytoplankton spring bloom by fungal parasites. *Global Change Biol.* 22: 299–309.

Frenken, T., Miki, T., Kagami, M., Van de Waal, D.B., Van Donk, E., Rohrlack, T., and Gsell, A.S. (2020). The potential of zooplankton in constraining chytrid epidemics in phytoplankton hosts. *Ecology* 101: e02900.

Friesen, O.C. and Detwiler, J.T. (2021). Parasite-modified chemical communication: implications for aquatic community dynamics. Front. Ecol. Evol. 9, https://doi.org/10.3389/fevo.2021.634754.

Furusawa, G., Yoshikawa, T., Yasuda, A., and Sakata, T. (2003). Algicidal activity and gliding motility of *Saprospira* sp. SS98-5. *Can. J. Microbiol.* 49: 92–100.

Gabbs, M., Leng, S., Devassy, J.G., Monirujjaman, M., and Aukema, H.M. (2015). Advances in our understanding of oxylipins derived from dietary PUFAs. *Adv. Nutr.* 6: 513–540.

Gachon, C.M.M., Sime-Ngando, T., Strittmatter, M., Chambouvet, A., and Kim, G.H. (2010). Algal diseases: spotlight on a black box. *Trends Plant Sci.* 15: 633–640.

Garcés, E., Alacid, E., Bravo, I., Fraga, S., and Figueroa, R.I. (2013a). *Parvilucifera sinerae* (Alveolata, Myzozoa) is a generalist parasitoid of dinoflagellates. *Protist* 164: 245–260.

Garcés, E., Alacid, E., Reñé, A., Petrou, K., and Simó, R. (2013b). Host-released dimethylsulphide activates the dinoflagellate parasitoid *Parvilucifera sinerae*. *ISME J.* 7: 1065–1068.

Garvetto, A., Badis, Y., Perrineau, M.-M., Rad-Menéndez, C., Bresnan, E., and Gachon, C.M.M. (2019). Chytrid infecting the bloom-forming marine diatom *Skeletonema* sp.: morphology, phylogeny and distribution of a novel species within the Rhizophydiales. *Fungal Biol.* 123: 471–480.

Garvetto, A., Perrineau, M.-M., Dressler-Allame, M., Bresnan, E., and Gachon, C.M.M. (2020). "*Ectrogella*" parasitoids of the diatom *Licmophora* sp. are polyphyletic. *J. Eukaryot. Microbiol.* 67: 18–27.

Gerphagnon, M., Agha, R., Martin-Creuzburg, D., Bec, A., Perriere, F., Rad-Menéndez, C., Gachon, C.M., and Wolinska, J. (2019). Comparison of sterol and fatty acid profiles of chytrids and their hosts reveals trophic upgrading of nutritionally inadequate phytoplankton by fungal parasites. *Environ. Microbiol.* 21: 949–958.

Giovannoni, S.J. (2017). SAR11 Bacteria: the most abundant plankton in the oceans. *Ann. Rev. Mar. Sci* 9: 231–255.

Gleason, F.H., Jephcott, T.G., Küpper, F.C., Gerphagnon, M., Sime-Ngando, T., Karpov, S.A., Guillou, L., and van Ogtrop, F.F. (2015). Potential roles for recently discovered chytrid parasites in the dynamics of harmful algal blooms. *Fungal Biol. Rev.* 29: 20–33.

Goode, A.G., Fields, D.M., Archer, S.D., and Martínez Martínez, J. (2019). Physiological responses of *Oxyrrhis marina* to a diet of virally infected *Emiliania huxleyi*. *PeerJ* 7: e6722.

Granéli, E. and Hansen, P.J. (2006). Allelopathy in harmful algae: a mechanism to compete for resources? In: Granéli, E., and Turner, J.T. (Eds.), *Ecology of harmful algae*. Springer, Berlin, Heidelberg, pp. 189–201.

Gsell, A.S., Biere, A., de Boer, W., de Bruijn, I., Eichhorn, G., Frenken, T., Geisen, S., van der Jeugd, H., Mason-Jones, K., Meisner, A., et al. (2023). Environmental refuges from disease in host–parasite interactions under global change. *Ecology* 104: e4001.

Gutiérrez, M.H., Jara, A.M., and Pantoja, S. (2016). Fungal parasites infect marine diatoms in the upwelling ecosystem of the Humboldt current system off central Chile. *Environ. Microbiol.* 18: 1646–1653.

Hanic, L.A., Sekimoto, S., and Bates, S.S. (2009). Oomycete and chytrid infections of the marine diatom *Pseudo-nitzschia pungens* (Bacillariophyceae) from Prince Edward Island, Canada. *Botany* 87: 1096–1105.

Harvey, E.L., Deering, R.W., Rowley, D.C., El Gamal, A., Schorn, M., Moore, B.S., Johnson, M.D., Mincer, T.J., and Whalen, K.E. (2016). A bacterial quorum-sensing precursor induces mortality in the marine Coccolithophore *Emiliania huxleyi*. Front. Microbiol. 7, https://doi.org/10.3389/fmicb.2016.00059.

Hasik, A.Z., de Angeli Dutra, D., Doherty, J.-F., Duffy, M.A., Poulin, R., and Siepielski, A.M. (2023). Resetting our expectations for parasites and their effects on species interactions: a meta-analysis. *Ecol. Lett.* 26: 184–199.

Hauser, F., Waadt, R., and Schroeder, Julian I. (2011). Evolution of abscisic acid synthesis and signaling mechanisms. *Curr. Biol.* 21: 346–355.

Hay, M.E. (2009). Marine chemical ecology: chemical signals and cues structure marine populations, communities, and ecosystems. *Ann. Rev. Mar. Sci* 1: 193–212.

Hiillos, A.-L., Rony, I., Rueckert, S., and Knott, K.E. (2023). Coinfection patterns of two marine apicomplexans are not associated with genetic diversity of their polychaete host. *J. Eukaryot. Microbiol.* 70: e12932.

Hoffmann, A.A., Montgomery, B.L., Popovici, J., Iturbe-Ormaetxe, I., Johnson, P.H., Muzzi, F., Greenfield, M., Durkan, M., Leong, Y.S., Dong, Y., et al. (2011). Successful establishment of *Wolbachia* in *Aedes* populations to suppress dengue transmission. *Nature* 476: 454–457.

Höger, A.-L., Griehl, C., and Noll, M. (2021). Infection with intracellular parasite *Amoeboaphelidium protococcarum* induces shifts in associated bacterial communities in microalgae cultures. *J. Appl. Phycol.* 33: 2863–2873.

Holt, C.C., Boscaro, V., Van Steenkiste, N.W.L., Herranz, M., Mathur, V., Irwin, N.A.T., Buckholtz, G., Leander, B.S., and Keeling, P.J. (2022). Microscopic marine invertebrates are reservoirs for cryptic and diverse protists and fungi. *Microbiome* 10: 161.

Hopkins, S.R., Wojdak, J.M., and Belden, L.K. (2017). Defensive symbionts mediate host-parasite interactions at multiple scales. *Trends Parasitol.* 33: 53–64.

Horas, E.L., Theodosiou, L., and Becks, L. (2018). Why are algal viruses not always successful? Viruses 10, https://doi.org/10.3390/v10090474.

Ibelings, B.W., De Bruin, A., Kagami, M., Rijkeboer, M., Brehm, M., and Donk, E.V. (2004). Host parasite interactions between freshwater phytoplankton and chytrid fungi (Chytridiomycota). *J. Phycol.* 40: 437–453.

Ilicic, D. and Grossart, H.-P. (2022). Basal parasitic fungi in marine food webs: a mystery yet to unravel. *J. Fungi* 8: 114.

Itoïz, S., Metz, S., Derelle, E., Reñé, A., Garcés, E., Bass, D., Soudant, P., and Chambouvet, A. (2022). Emerging parasitic protists: the case of Perkinsea. Front. Microbiol. 12, https://doi.org/10.3389/fmicb.2021.735815.

Jensen, E.L., Clement, R., Kosta, A., Maberly, S.C., and Gontero, B. (2019). A new widespread subclass of carbonic anhydrase in marine phytoplankton. *ISME J.* 13: 2094–2106.

Jephcott, T.G., Alves-de-Souza, C., Gleason, F.H., van Ogtrop, F.F., Sime-Ngando, T., Karpov, S.A., and Guillou, L. (2016). Ecological impacts of parasitic chytrids, syndiniales and perkinsids on populations of marine photosynthetic dinoflagellates. *Fungal Ecol.* 19: 47–58.

Johansson, M. and Coats, D.W. (2002). Ciliate grazing on the parasite *Amoebophrya* sp. decreases infection of the red-tide dinoflagellate *Akashiwo sanguinea*. *Aquat. Microb. Ecol.* 28: 69–78.

Judelson, H.S. and Ah-Fong, A.M.V. (2018). Exchanges at the plant-oomycete interface that influence disease. *Plant Physiol.* 179: 1198–1211.

Kagami, M., Helmsing, N.R., and van Donk, E. (2011). Parasitic chytrids could promote copepod survival by mediating material transfer from inedible diatoms. *Hydrobiologia* 659: 49–54.

Kagami, M., Miki, T., and Takimoto, G. (2014). Mycoloop: chytrids in aquatic food webs. *Front. Microbiol.* 5: 166.

Kayal, E., Alves-de-Souza, C., Farhat, S., Velo-Suarez, L., Monjol, J., Szymczak, J., Bigeard, E., Marie, D., Noel, B., Porcel, B.M., et al (2020). Dinoflagellate host chloroplasts and mitochondria remain functional during *Amoebophrya* infection. Front. Microbiol. 11, https://doi.org/10.3389/fmicb.2020.600823.

Kegel, J.U., John, U., Valentin, K., and Frickenhaus, S. (2013). Genome variations associated with viral susceptibility and calcification in *Emiliania huxleyi*. *PLoS One* 8: e80684.

Kessler, R.W., Weiss, A., Kuegler, S., Hermes, C., and Wichard, T. (2018). Macroalgal–bacterial interactions: role of dimethylsulfoniopropionate in microbial gardening by *Ulva* (Chlorophyta). *Mol. Ecol.* 27: 1808–1819.

Kiefer, B., Riemann, M., Büche, C., Kassemeyer, H.-H., and Nick, P. (2002). The host guides morphogenesis and stomatal targeting in the grapevine pathogen *Plasmopara viticola*. *Planta* 215: 387–393.

Kim, S. and Park, M.G. (2016). Effect of the endoparasite *Amoebophrya* sp. on toxin content and composition in the paralytic shellfish poisoning dinoflagellate *Alexandrium fundyense* (Dinophyceae). *Harmful Algae* 51: 10–15.

Klawonn, I., Van den Wyngaert, S., Parada, A.E., Arandia-Gorostidi, N., Whitehouse, M.J., Grossart, H.-P., and Dekas, A.E. (2021). Characterizing the "fungal shunt": parasitic fungi on diatoms affect carbon flow and bacterial communities in aquatic microbial food webs. *Proc. Natl. Acad. Sci. U. S. A.* 118: e2102225118.

Klawonn, I., Van den Wyngaert, S., Iversen, M.H., Walles, T.J.W., Flintrop, C.M., Cisternas-Novoa, C., Nejstgaard, J.C., Kagami, M., and Grossart, H.-P. (2023). Fungal parasitism on diatoms alters formation and bio–physical properties of sinking aggregates. *Commun. Biol.* 6: 206.

Kochin, B.F., Bull, J.J., and Antia, R. (2010). Parasite evolution and life history theory. *PLOS Biol.* 8: e1000524.

Kyle, M., Haande, S., Ostermaier, V., and Rohrlack, T. (2015). The Red Queen race between parasitic chytrids and their host, *Planktothrix*: a test using a time series reconstructed from sediment DNA. *PLoS One* 10: e0118738.

Laundon, D., Mock, T., Wheeler, G., and Cunliffe, M. (2021). Healthy herds in the phytoplankton: the benefit of selective parasitism. *ISME J.* 15: 2163–2166.

Lee, B. and Park, M.G. (2017). Different life cycle strategies of the dinoflagellates *Fragilidium duplocampanaeforme* and its prey *Dinophysis acuminata* may explain their different susceptibilities to the infection by the parasite *Parvilucifera infectans*. *Harmful Algae* 65: 1–8.

Lepelletier, F., Karpov, S.A., Alacid, E., Le Panse, S., Bigeard, E., Garcés, E., Jeanthon, C., and Guillou, L. (2014a). *Dinomyces arenysensis* gen. et sp. nov. (Rhizophydiales, Dinomycetaceae fam. nov.), a chytrid infecting marine dinoflagellates. *Protist* 165: 230–244.

Lepelletier, F., Karpov, S.A., Le Panse, S., Bigeard, E., Skovgaard, A., Jeanthon, C., and Guillou, L. (2014b). *Parvilucifera rostrata* sp. nov. (Perkinsozoa), a novel parasitoid that infects planktonic dinoflagellates. *Protist* 165: 31–49.

Lima-Mendez, G., Faust, K., Henry, N., Decelle, J., Colin, S., Carcillo, F., Chaffron, S., Ignacio-Espinosa, J.C., Roux, S., Vincent, F., et al. (2015). Determinants of community structure in the global plankton interactome. *Science* 348: 1262073.

Llaveria, G., Garcés, E., Ross, O.N., Figueroa, R.I., Sampedro, N., and Berdalet, E. (2010). Small-scale turbulence can reduce parasite infectivity to dinoflagellates. *Mar. Ecol. Prog. Ser.* 412: 45–56.

Llewellyn, M.S., Leadbeater, S., Garcia, C., Sylvain, F.E., Custodio, M., Ang, K.P., Powell, F., Carvalho, G.R., Creer, S., Elliot, J., et al. (2017). Parasitism perturbs the mucosal microbiome of Atlantic Salmon. *Sci. Rep.* 7: 43465.

Long, M., Marie, D., Szymczak, J., Toullec, J., Bigeard, E., Sourisseau, M., Le Gac, M., Guillou, L., and Jauzein, C. (2021). Dinophyceae can use exudates as weapons against the parasite *Amoebophrya* sp. (Syndiniales). *ISME Commun.* 1: 34.

Lu, Y., Wohlrab, S., Glöckner, G., Guillou, L., and John, U. (2014). Genomic insights into processes driving the infection of *Alexandrium tamarense* by the parasitoid *Amoebophrya* sp. *Eukaryotic Cell* 13: 1439–1449.

Lu, Y. and Xu, J. (2015). Phytohormones in microalgae: a new opportunity for microalgal biotechnology? *Trends Plant Sci.* 20: 273–282.

Mahajan, A.S., Fadnavis, S., Thomas, M.A., Pozzoli, L., Gupta, S., Royer, S.-J., Saiz-Lopez, A., and Simó, R. (2015). Quantifying the impacts of an updated global dimethyl sulfide climatology on cloud microphysics and aerosol radiative forcing. *J. Geophys. Res. Atmos.* 120: 2524–2536.

Menaa, F., Wijesinghe, P.A.U.I., Thiripuranathar, G., Uzair, B., Iqbal, H., Khan, B.A., and Menaa, B. (2020). Ecological and industrial implications of dynamic seaweed-associated microbiota interactions. *Mar. Drugs* 18: 641.

Mills, N. (2009). Parasitoids. In: Resh, V.H., and Cardé, R.T. (Eds.), *Encyclopedia of insects*, 2nd ed. Academic Press, San Diego, pp. 748–751.

Mogensen Trine, H. (2009). Pathogen recognition and inflammatory signaling in innate immune defenses. *Clin. Microbiol. Rev.* 22: 240–273.

Mojib, N. and Kubanek, J. (2020). Comparative transcriptomics supports the presence of G protein-coupled receptor-based signaling in unicellular marine eukaryotes. *Limnol. Oceanogr.* 65: 762–774.

Morris, P.F., Bone, E., and Tyler, B.M. (1998). Chemotropic and contact responses of *Phytophthora sojae* hyphae to soybean isoflavonoids and artificial substrates. *Plant Physiol.* 117: 1171–1178.

Moura, D.J., Richter, M.F., Boeira, J.M., Pêgas Henriques, J.A., and Saffi, J. (2007). Antioxidant properties of β-carboline alkaloids are related to their antimutagenic and antigenotoxic activities. *Mutagenesis* 22: 293–302.

Muehlstein, L.K., Amon, J.P., and Leffler, D.L. (1988). Chemotaxis in the marine fungus *Rhizophydium littoreum*. *Appl. Environ. Microbiol.* 54: 1668–1672.

Murúa, P., Müller, D.G., Etemadi, M., van West, P., and Gachon, C.M.M. (2020). Host and pathogen autophagy are central to the inducible local defences and systemic response of the giant kelp *Macrocystis pyrifera* against the oomycete pathogen *Anisolpidium ectocarpii*. *New Phytol.* 226: 1445–1460.

Park, M.G., Kim, A., Jeon, B.S., and Kim, M. (2021). Parasite-mediated increase in prey edibility in the predator-prey interaction of marine planktonic protists. *Harmful Algae* 103: 101982.

Paul, C. and Pohnert, G. (2011). Interactions of the algicidal bacterium *Kordia algicida* with diatoms: regulated protease excretion for specific algal lysis. *PLoS One* 6: e21032.

Picoche, C. (2022). *Fine-scale modelling of the dynamics of phytoplankton communities. Modeling and simulation*, Unpublished thesis. University of Bordeaux.

Pohnert, G. and Boland, W. (2002). The oxylipin chemistry of attraction and defense in brown algae and diatoms. *Nat. Prod. Rep.* 19: 108–122.

Polin, M., Tuval, I., Drescher, K., Gollub, J.P., and Goldstein, R.E. (2009). *Chlamydomonas* swims with two-gears in a eukaryotic version of Run-and-Tumble Locomotion. *Science* 325: 487–490.

Pollara, S.B., Becker, J.W., Nunn, B.L., Boiteau, R., Repeta, D., Mudge, M.C., Downing, G., Chase, D., Harvey, E.L., and Whalen, K.E. (2021). Bacterial quorum-sensing signal arrests phytoplankton cell division and impacts virus-induced mortality. mSphere 6, https://doi.org/10.1128/msphere.00009-21.

Port, J.A., Parker, M.S., Kodner, R.B., Wallace, J.C., Armbrust, E.V., and Faustman, E.M. (2013). Identification of G protein-coupled receptor signaling pathway proteins in marine diatoms using comparative genomics. *BMC Genomics* 14: 503.

Poulin, R. (2007) Evolutionary ecology of parasites. In: *Evolutionary ecology of parasites*. Princeton University Press, Princeton.

Poulin, R.X., Hogan, S., Poulson-Ellestad, K.L., Brown, E., Fernández, F.M., and Kubanek, J. (2018). *Karenia brevis* allelopathy compromises the lipidome, membrane integrity, and photosynthesis of competitors. *Sci. Rep.* 8: 9572.

Råberg, L., Alacid, E., Garces, E., and Figueroa, R. (2014). The potential for arms race and Red Queen coevolution in a protist host-parasite system. *Ecol. Evol.* 4: 4775–4785.

Raina, J.-B., Fernandez, V., Lambert, B., Stocker, R., and Seymour, J.R. (2019). The role of microbial motility and chemotaxis in symbiosis. *Nat. Rev. Microbiol.* 17: 284–294.

Raina, J.-B., Lambert, B.S., Parks, D.H., Rinke, C., Siboni, N., Bramucci, A., Ostrowski, M., Signal, B., Lutz, A., Mendis, H., et al. (2022). Chemotaxis shapes the microscale organization of the ocean's microbiome. *Nature* 605: 132–138.

Rasconi, S., Grami, B., Niquil, N., Jobard, M., and Sime-Ngando, T. (2014). Parasitic chytrids sustain zooplankton growth during inedible algal bloom. Front. Microbiol. 5, https://doi.org/10.3389/fmicb.2014.00229.

Raven, J.A. (1986). Plasticity in algae. *Symp. Soc. Exp. Biol.* 40: 347–372.

Rédou, V., Vallet, M., Meslet-Cladière, L., Kumar, A., Pang, K.-L., Pouchus, Y.-F., Barbier, G., Grovel, O., Bertrand, S., and Prado, S. (2016) Marine fungi. In: *The marine microbiome: an untapped source of biodiversity and biotechnological potential*. Springer, Cham, pp. 99–153.

Reñé, A., Alacid, E., Gallisai, R., Chambouvet, A., Fernández-Valero, A.D., and Garcés, E. (2021). New Perkinsea parasitoids of dinoflagellates distantly related to Parviluciferaceae members. Front. Microbiol. 12, https://doi.org/10.3389/fmicb.2021.701196.

Richards, T.A. and Chambouvet, A. (2016). A role for fungi as parasites in the black box of marine trophic interactions. *Environ. Microbiol. Rep.* 8: 429–430.

Richards, T.A. and Talbot, N.J. (2018). Osmotrophy. *Curr. Biol.* 28: 1179–1180.

Richards, T.A., Dacks, J.B., Jenkinson, J.M., Thornton, C.R., and Talbot, N.J. (2006). Evolution of filamentous plant pathogens: gene exchange across eukaryotic kingdoms. *Curr. Biol.* 16: 1857–1864.

Rigaud, T., Perrot-Minnot, M.J., and Brown, M.J. (2010). Parasite and host assemblages: embracing the reality will improve our knowledge of parasite transmission and virulence. *Proc. Roy. Soc. Biol. Sci.* 277: 3693–3702.

Rodríguez, F. and Figueroa, R.I. (2020). Confirmation of the wide host range of *Parvilucifera corolla* (Alveolata, Perkinsozoa). *Eur. J. Protistol.* 74: 125690.

Rodríguez-Martínez, R., Leonard, G., Milner, D.S., Sudek, S., Conway, M., Moore, K., Hudson, T., Mahé, F., Keeling, P.J., Santoro, A.E., et al. (2020). Controlled sampling of ribosomally active protistan diversity in sediment-surface layers identifies putative players in the marine carbon sink. *ISME J.* 14: 984–998.

Rogalski, M.A., Merrill, T.S., Gowler, C.D., Cáceres, C.E., and Duffy, M.A. (2021). Context-dependent host-symbiont interactions: shifts along the parasitism-mutualism continuum. *Am. Nat.* 198: 563–575.

Rojas-Jimenez, K., Rieck, A., Wurzbacher, C., Jürgens, K., Labrenz, M., and Grossart, H.-P. (2019). A salinity threshold separating fungal communities in the Baltic Sea. Front. Microbiol. 10, https://doi.org/10.3389/fmicb.2019.00680.

Ruocco, N., Albarano, L., Esposito, R., Zupo, V., Costantini, M., and Ianora, A. (2020). Multiple roles of diatom-derived oxylipins within marine environments and their potential biotechnological applications. *Mar. Drugs* 18: 342.

Saha, M. and Fink, P. (2022). Algal volatiles – the overlooked chemical language of aquatic primary producers. *Biol. Rev.* 97: 2162–2173.

Schatz, D., Shemi, A., Rosenwasser, S., Sabanay, H., Wolf, S.G., Ben-Dor, S., and Vardi, A. (2014). Hijacking of an autophagy-like process is critical for the life cycle of a DNA virus infecting oceanic algal blooms. *New Phytol.* 204: 854–863.

Schleyer, G., Kuhlisch, C., Ziv, C., Ben-Dor, S., Malitsky, S., Schatz, D., and Vardi, A. (2023). Lipid biomarkers for algal resistance to viral infection in the ocean. *Proc. Natl. Acad. Sci. U. S. A.* 120: e2217121120.

Schmitt, M., Telusma, A., Bigeard, E., Guillou, L., and Alves-de-Souza, C. (2022). Temperature affects the biological control of dinoflagellates by the generalist parasitoid *Parvilucifera rostrata*. *Microorganisms* 10: 385.

Schnepf, E. and Drebes, G. (1986). Chemotaxis and appetence of *Paulsenella* sp. (Dinophyta), an ectoparasite of the marine diatom *Streptotheca thamesis Shrubsole*. *Planta* 167: 337–343.

Scholz, B., Küpper, F.C., Vyverman, W., and Karsten, U. (2014). Eukaryotic pathogens (Chytridiomycota and Oomycota) infecting marine microphytobenthic diatoms – a methodological comparison. *J. Phycol.* 50: 1009–1019.

Scholz, B., Küpper, F.C., Vyverman, W., Ólafsson, H.G., and Karsten, U. (2017). Chytridiomycosis of marine diatoms – the role of stress physiology and resistance in parasite-host recognition and accumulation of defense molecules. *Mar. Drugs* 15: 26.

Selander, E., Kubanek, J., Hamberg, M., Andersson, M.X., Cervin, G., and Pavia, H. (2015). Predator lipids induce paralytic shellfish toxins in bloom-forming algae. *Proc. Natl. Acad. Sci. U. S. A.* 112: 6395–6400.

Selander, E., Berglund, E.C., Engström, P., Berggren, F., Eklund, J., Harðardóttir, S., Lundholm, N., Grebner, W., and Andersson, M.X. (2019). Copepods drive large-scale trait-mediated effects in marine plankton. *Sci. Adv.* 5: eaat5096.

Seyedsayamdost, M.R., Case, R.J., Kolter, R., and Clardy, J. (2011). The Jekyll-and-Hyde chemistry of *Phaeobacter gallaeciensis*. *Nat. Chem.* 3: 331–335.

Seymour, J.R., Simó, R., Ahmed, T., and Stocker, R. (2010). Chemoattraction to dimethylsulfoniopropionate throughout the marine microbial food web. *Science* 329: 342–345.

Seymour, J.R., Amin, S.A., Raina, J.-B., and Stocker, R. (2017). Zooming in on the phycosphere: the ecological interface for phytoplankton–bacteria relationships. *Nat. Microbiol.* 2: 17065.

Shearer, C.A., Descals, E., Kohlmeyer, B., Kohlmeyer, J., Marvanová, L., Padgett, D., Porter, D., Raja, H.A., Schmit, J.P., Thorton, H.A., et al. (2007). Fungal biodiversity in aquatic habitats. *Biodivers. Conserv.* 16: 49–67.

Shemi, A., Alcolombri, U., Schatz, D., Farstey, V., Vincent, F., Rotkopf, R., Ben-Dor, S., Frada, M.J., Tawfik, D.S., and Vardi, A. (2021). Dimethyl sulfide mediates microbial predator–prey interactions between zooplankton and algae in the ocean. *Nat. Microbiol.* 6: 1357–1366.

Sime-Ngando, T. (2012). Phytoplankton chytridiomycosis: fungal parasites of phytoplankton and their imprints on the food web dynamics. Front. Microbiol. 3, https://doi.org/10.3389/fmicb.2012.00361.

Simon, J.-C., Marchesi, J.R., Mougel, C., and Selosse, M.-A. (2019). Host-microbiota interactions: from holobiont theory to analysis. *Microbiome* 7: 5.

Sonnenschein, E.C., Syit, D.A., Grossart, H.P., and Ullrich, M.S. (2012). Chemotaxis of *Marinobacter adhaerens* and its impact on attachment to the diatom *Thalassiosira weissflogii*. *Appl. Environ. Microbiol.* 78: 6900–6907.

Stettin, D., Poulin, R.X., and Pohnert, G. (2020). Metabolomics benefits from Orbitrap GC–MS – comparison of low- and high-resolution GC–MS. *Metabolites* 10: 143.

Sures, B., Nachev, M., Schwelm, J., Grabner, D., and Selbach, C. (2023). Environmental parasitology: stressor effects on aquatic parasites. *Trends Parasitol.* 39: 461–474.

Templeton, T.J. and Pain, A. (2016). Diversity of extracellular proteins during the transition from the 'proto-apicomplexan' alveolates to the apicomplexan obligate parasites. *Parasitology* 143: 1–17.

Thines, M. (2019). An evolutionary framework for host shifts – jumping ships for survival. *New Phytol.* 224: 605–617.

Thines, M., Nam, B., Nigrelli, L., Beakes, G., and Kraberg, A. (2015). The diatom parasite *Lagenisma coscinodisci* (Lagenismatales, Oomycota) is an early diverging lineage of the Saprolegniomycetes. *Mycol. Prog.* 14: 75.

Tillmann, U., John, U., and Cembella, A. (2007). On the allelochemical potency of the marine dinoflagellate *Alexandrium ostenfeldii* against heterotrophic and autotrophic protists. *J. Plankton Res.* 29: 527–543.

Toth, G.B., Norén, F., Selander, E., and Pavia, H. (2004). Marine dinoflagellates show induced life-history shifts to escape parasite infection in response to water–borne signals. *Proc. Roy. Soc. London Ser. B Biol. Sci.* 271: 733–738.

Tourneroche, A., Lami, R., Burgaud, G., Domart-Coulon, I., Li, W., Gachon, C., Gèze, M., Boeuf, D., and Prado, S. (2020). The bacterial and fungal microbiota of *Saccharina latissima* (Laminariales, Phaeophyceae). Front. Mar. Sci. 7, https://doi.org/10.3389/fmars.2020.587566.

Treves, H., Küken, A., Arrivault, S., Ishihara, H., Hoppe, I., Erban, A., Höhne, M., Moraes, T.A., Kopka, J., Szymanski, J., et al. (2022). Carbon flux through photosynthesis and central carbon metabolism show distinct patterns between algae, C3 and C4 plants. *Nat. Plants* 8: 78–91.

Uchida, T. (2001). The role of cell contact in the life cycle of some dinoflagellate species. *J. Plankton Res.* 23: 889–891.

Vallet, M., Baumeister, T.U.H., Kaftan, F., Grabe, V., Buaya, A., Thines, M., Svatoš, A., and Pohnert, G. (2019). The oomycete *Lagenisma coscinodisci* hijacks host alkaloid synthesis during infection of a marine diatom. *Nat. Commun.* 10: 4938.

Vallet, M., Kaftan, F., Grabe, V., Ghaderiardakani, F., Fenizia, S., Svatoš, A., Pohnert, G., and Wichard, T. (2021). A new glance at the chemosphere of macroalgal–bacterial interactions: in situ profiling of metabolites in symbiosis by mass spectrometry. *Beilstein J. Org. Chem.* 17: 1313–1322.

Vallet, M., Kaftan, F., Buaya, A., Thines, M., Guillou, L., Svatoš, A., and Pohnert, G. (2023). Single-cell metabolome profiling for phenotyping parasitic diseases in phytoplankton. Front. Anal. Sci. 2, https://doi.org/10.3389/frans.2022.1051955.

Valois, A.E. and Poulin, R. (2015). Global drivers of parasitism in freshwater plankton communities. *Limnol. Oceanogr.* 60: 1707–1718.

Van den Wyngaert, S., Seto, K., Rojas-Jimenez, K., Kagami, M., and Grossart, H.P. (2017). A new parasitic chytrid, *Staurastromyces oculus* (Rhizophydiales, Staurastromycetaceae fam. nov.), infecting the freshwater desmid *Staurastrum* sp. *Protist* 168: 392–407.

Van Den Wyngaert, S., Kainz, M.J., and Ptacnik, R. (2022). Mucilage protects the planktonic desmid *Staurodesmus* sp. against parasite attack by a chytrid fungus. *J. Plankton Res.* 45: 3–14.

van der Loos, L.M., Eriksson, B.K., and Falcão Salles, J. (2019). The macroalgal holobiont in a changing sea. *Trends Microbiol.* 27: 635–650.

Van Donk, E. (1989). The role of fungal parasites in phytoplankton succession. In: Plankton ecology: succession in plankton communities. Springer, Berlin, Heidelberg, pp. 171–194.

Van Donk, E., Ianora, A., and Vos, M. (2011). Induced defences in marine and freshwater phytoplankton: a review. *Hydrobiologia* 668: 3–19.

Van Valen, L. (2014). A new evolutionary law (1973). In: Felisa, A., and Smith, J.L.G.A.J.H.B. (Eds.), *Foundations of macroecology: classic papers with commentaries*. University of Chicago Press, Chicago, pp. 284–314.

Vardi, A., Haramaty, L., Van Mooy, B.A.S., Fredricks, H.F., Kimmance, S.A., Larsen, A., and Bidle, K.D. (2012). Host–virus dynamics and subcellular controls of cell fate in a natural coccolithophore population. *Proc. Natl. Acad. Sci. U. S. A.* 109: 19327–19332.

Vermont, A., Martínez Martínez, J., Waller, J., Gilg, I., Leavitt, A., Floge, S., Archer, S., Wilson, W., and Fields, D. (2016). Virus infection of *Emiliania huxleyi* deters grazing by the copepod *Acartia tonsa*. *J. Plankton Res.* 38: 1194–1205.

Vincent, F., Sheyn, U., Porat, Z., Schatz, D., and Vardi, A. (2021). Visualizing active viral infection reveals diverse cell fates in synchronized algal bloom demise. *Proc. Natl. Acad. Sci. U. S. A.* 118: e2021586118.

Vincent, F., Gralka, M., Schleyer, G., Schatz, D., Cabrera-Brufau, M., Kuhlisch, C., Sichert, A., Vidal-Melgosa, S., Mayers, K., Barak-Gavish, N., et al. (2023). Viral infection switches the balance between bacterial and eukaryotic recyclers of organic matter during coccolithophore blooms. *Nat. Commun.* 14: 510.

Wang, X., Li, Z., Su, J., Tian, Y., Ning, X., Hong, H., and Zheng, T. (2010). Lysis of a red-tide causing alga, *Alexandrium tamarense*, caused by bacteria from its phycosphere. *Biol. Control* 52: 123–130.

Wichard, T., Charrier, B., Mineur, F., Bothwell, J.H., Clerck, O.D., and Coates, J.C. (2015). The green seaweed *Ulva*: a model system to study morphogenesis. Front. Plant Sci. 6, https://doi.org/10.3389/fpls.2015.00072.

Wolf, Y.I. and Koonin, E.V. (2013). Genome reduction as the dominant mode of evolution. *BioEssays* 35: 829–837.

Wood, C.L., Welicky, R.L., Preisser, W.C., Leslie, K.L., Mastick, N., Greene, C., Maslenikov, K.P., Tornabene, L., Kinsella, J.M., and Essington, T.E. (2023). A reconstruction of parasite burden reveals one century of climate-associated parasite decline. *Proc. Natl. Acad. Sci. U. S. A.* 120: e2211903120.

Yang, Z.-Y., Huang, K.-X., Zhang, Y.-R., Yang, L., Zhou, J.-L., Yang, Q., and Gao, F. (2023). Efficient microalgal lipid production driven by salt stress and phytohormones synergistically. *Bioresour. Technol.* 367: 128270.

Yoch, D.C. (2002). Dimethylsulfoniopropionate: its sources, role in the marine food web, and biological degradation to dimethylsulfide. *Appl. Environ. Microbiol.* 68: 5804–5815.

Yoneya, K., Miki, T., Van den Wyngaert, S., Grossart, H.-P., and Kagami, M. (2021). Non-random patterns of chytrid infections on phytoplankton host cells: mathematical and chemical ecology approaches. *Aquat. Microb. Ecol.* 87: 1–15.

Zhang, M., Zhang, Q., Zhang, Q., Cui, X., and Zhu, L. (2023). Promising antiparasitic natural and synthetic products from marine invertebrates and microorganisms. *Mar. Drugs* 21: 84.

Zhou, J., Lyu, Y., Richlen, M.L., Anderson, D.M., and Cai, Z. (2016). Quorum sensing is a language of chemical signals and plays an ecological role in algal-bacterial Interactions. *Crit. Rev. Plant Sci.* 35: 81–105.

Bionote

Marine Vallet
Research Group Plankton Community Interaction, Max Planck Institute for Chemical Ecology, Hans-Knoell Strasse 8, D-07745 Jena, Germany
Bioorganic Analytics, Institute for Inorganic and Analytical Chemistry, Friedrich Schiller University, Lessingstrasse 8, D-07743 Jena, Germany
mvallet@ice.mpg.de
https://orcid.org/0000-0002-6878-0459

Marine Vallet studied Medical Sciences at the University of Paris Descartes. She then moved to Paris-Sorbonne University, where she pursued her doctoral studies in the group of Prof. Soizic Prado. In 2016, she joined Prof. Georg Pohnert's group at Max Planck Institute for Chemical Ecology in Jena, Germany as a postdoc working on algal ecology and single-cell metabolomics. In 2022, she started her research independent group on plankton microbiome at Friedrich Schiller University Jena.